ECOLOGY AND INVASIVE POTENTIAL OF *PAULOWNIA TOMENTOSA* (SCROPHULARIACEAE) IN A HARDWOOD FOREST LANDSCAPE

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A. Christina W. Longbrake

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ECOLOGY AND INVASIVE POTENTIAL OF *PAULOWNIA TOMENTOSA* (SCROPHULARIACEAE) IN A HARDWOOD FOREST LANDSCAPE

BY

A. CHRISTINA W. LONGBRAKE

This dissertation has been approved

for the Department of Environmental and Plant Biology

and the College of Arts and Sciences by

Brian C. McCarthy

Associate Professor of Environmental and Plant Biology

Leslie A. Flemming

Dean, College of Arts and Sciences

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Director of Dissertation: Brian C. McCarthy

Introduction of non-native species is the oldest form of human-induced global change. From the exchange of agricultural crops and domestic animals, to the accidental introduction of weeds and microbes, non-native species have been incorporated into the floras and faunas of all continents and most oceanic islands. These organisms can have marked effects on ecosystems. I wanted to address the following facets of non-native species invasion: (1) What characteristics of ecosystems make them more susceptible to non-native species invasion? and (2) What characteristics of the invader allow invasion? To address these questions, I used a gradient of anthropogenic disturbance common in southeastern Ohio forests: intact secondary forest, forest edge, and aggrading clear cuts. *Paulownia tomentosa* is a tree native to Asia and thought to have been introduced to North America in the 1840's. The species has naturalized throughout Appalachia. I studied the growth, allocation, establishment, and seed persistence across habitats. I also became interested in the basic ecology of *P. tomentosa*, particularly the ability of the species to resprout and phenotypic plasticity in naturalized populations. The most important factors in determining the invasive potential of *P. tomentosa* were disturbance and herbivory. *Paulownia tomentosa* is an early successional species that can grow rapidly under high light conditions. Seed ecology suggests that the species can form a

persistent seed bank. However, light is required for germination and seeds responded positively to soil disturbance. Large gaps may be sufficient to allow seeds in the seed bank to germinate and grow to the canopy. However, the species is very susceptible to herbivory. Plants had to be protected from mammals in order to persist. Even though above- and below-ground competition affected plant growth and allocation, it did not affect the overall success of plants. *Paulownia tomentosa* can resprout at an early age and initially invests heavily in below-ground biomass. Naturalized populations showed some variability in traits, particularly in those associated with below-ground biomass and growth of roots. *Paulownia tomentosa* has potential to remain a part of the mixed mesophytic forests of North America since it can form a seed bank, disperse seeds to great distances, and grow quickly once established.

Approved

Associate Professor of Environmental and Plant Biology

This dissertation is dedicated to *mi madre* who, in giving up many

of her own dreams, helped make mine possible.

And the other matrons in my life who have passed away

only to guide and support us in new life someday.

Altagrácia Justina Castro Ulloa de Barrera

September 26, 1906 - November 18, 1999

Lillian May Williams - Wilson (Neé Rigsby)

July 19, 1909 - October 31, 2000

I can see clearly now the rain is gone,
I can see all obstacles in my way,
All of the dark clouds have passed me by,
It's gonna be a bright, bright, sun-shiny day.

- J. Ray

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Chapter 1 : Effects of forest management on plant invasion: a case study of *Paulownia tomentosa*

Introduction

Paulownia tomentosa, native to East Asia, was introduced into the eastern United States in 1844 (Hu, 1961). This species is known to establish after flooding disturbance in Virginia (Williams, 1993) and has become a pest species throughout much of the Great Smoky Mountains National Park (Langdon & Johnson, 1995). Naturalized populations flourish along highways and waterways and have persisted for at least twenty years (A. C. W. Longbrake, pers. obs.).

There are several hypotheses regarding the invasability of plant communities by non-native species (Fox & Fox, 1986; Rejmánek, 1989). They center on characteristics of plant communities that may make them resistant or susceptible to invasion, such as species richness or degree of disturbance. The Disturbance Hypothesis states that disturbed ecosystems will have a greater proportion of non-native species and will be more susceptible to invasion (Fox & Fox, 1986). There is evidence to support this hypothesis (Hobbs, 1989; Rejmánek, 1989; Hobbs & Huenneke, 1992) and some evidence against it (Pyle, 1995). Disturbance is a component of all communities at some scale (Sousa, 1984). Through succession in gaps, forests recover after disturbances (Pickett & White, 1985). However, it is becoming increasingly clear that human-caused disturbances are most often linked to non-native species invasion (Rejmánek, 1989).

Natural disturbances in the deciduous Appalachian forest range from small tree-fall gap disturbances to large wind throws and tornado damage. The forest is also affected by a multitude of human impacts, including clear cutting. Since the invasion of *P. tomentosa* has been associated with natural disturbance (Williams, 1993), we assume that it will be more successful in areas of greater anthropogenic disturbance.

Our experimental design is a disturbance gradient of anthropogenic origin common to Southeast Ohio. We chose to look at aggrading clear cuts (~7 yrs old), forest edges, and intact secondary forest. Clear cutting typically leads to higher stem density in aggrading stands (Gilliam *et al.*, 1995). Clear cutting increases bare ground, soil compaction and other factors that affect plant growth. For example, a study in Appalachian hardwood forests found 30 to 50% less soil moisture in the O1 and O2 soil horizons, but greater soil moisture in the A horizon (Swank & Vose, 1988). Light and the resulting changes in soil moisture are known to affect the establishment and persistence of plant species after an area is subjected to clear cutting (Meier *et al.,* 1995).

Traditionally, forest edges were believed to increase species richness, especially for wildlife species (Leopold, 1933). For this reason, land managers increased the amount of "edge" in a forest. However, research has not always supported this view (Harris, 1988). Studies of vegetation often show no change in plant species richness or diversity between recent clear-cuts and maturing secondary forests, even though there is a change in species composition that leads to greater β diversity for the region (Gilliam, et al., 1995; Goldblum &

Beatty, 1999). The forest edge environment can influence tree growth and recruitment (Chen, *et al.*, 1992). Moreover, forest edges have been shown to have a greater proportion of non-native species than forest interiors (Goldblum & Beatty, 1999).

A non-indigenous species must overcome many obstacles to become established and naturalized in a new ecosystem. Specific attributes of the invasive species may allow their establishment. Humans have assisted these plants in overcoming one obstacle: long distance dispersal. Many plants are now found on continents and oceanic islands far from where they evolved due to deliberate or accidental introduction by humans. Individual species characteristics, such as rapid growth, competitive ability, and seed viability are necessary for a newly introduced plant to naturalize in an ecosystem. It is thought that some obstacles to growth and reproduction of non-indigenous invaders may be removed in the new ecosystem. Many of the invader's native herbivores, parasites, and diseases may not be present in the new ecosystem. These advantages probably account for non-indigenous species being larger or more plentiful in invaded areas compared to where they are native (e.g., *Opuntia stricta* in Australia and South Africa, Hoffman *et al.*, 1998).

Another important trait for non-native species may be biomass allocation. Plant biomass allocation has an impact on growth rates and survival (Sipe & Bazzaz, 1995) and traits that may be important in allowing a species to invade, such as competitive ability (Aerts *et al.*, 1991). Plants can respond to their environment through phenotypic plasticity, a mechanism that may allow plants to

be successful in a range of environments (Sultan, 1987 & 1992). It has been suggested that early successional species have greater phenotypic plasticity than late successional species (Bazzaz, 1979) and further that this plasticity will tend to be morphological rather than physiological (Grime *et al.*, 1986).

Studies have begun to elucidate the ecological niche of *P. tomentosa* as an invasive species (see Chapters 2 and 3). Volunteer plants have recently been found in intact secondary forest in southeastern Ohio on newly created tip up mounds (B. C. McCarthy, pers. obs.). This is evidence that the species may be able to acclimate to a wide range of light availability. However, *P. tomentosa* is a sun-adapted plant that can grow rapidly in high light environments. Growth rates are extremely high compared to other tree species (see Chapters 2 and 3). *Paulownia tomentosa* has been shown to allocate resources as a typical sun plant when grown in low light in short term experiments (see Chapters 2 and 3). However, the effects of habitat, herbivory, and competition on the establishment of *P. tomentosa* are not known.

There are two main questions we wish to address with this paper: (1) What ecosystem properties make an ecosystem susceptible to *P. tomentosa* invasion? and (2) What characteristics of *P. tomentosa* assist it in invading these ecosystems? Specifically, we will assess the growth and survival of *P. tomentosa* seedlings across managed forest habitats, and elucidate the importance of community and species attributes in its invasive potential. *Paulownia tomentosa* is a good species for this study because Ohio is the Northern limit of its range at this time. This study may help to understand its

potential to expand its current range. Other interests in the species relate to its invasiveness and potential commercial value.

Methods

Paulownia tomentosa seeds were collected in fall of 1996 from a single tree in Athens, Ohio (39° 22' N, 82° 06' W). We chose to use a single tree as a seed source because variation in resource allocation is known to vary among seed sources (Chapter 3). Seeds were kept in cold, dry storage until used. Seeds were germinated in flats filled with potting mix (Sunshine Mix II, Sun Gro Horticulture Inc., Bellevue, WA) in a germination chamber (Percival Scientific, Boone, IA) with 12 hours of light and 12 hours of dark at 25C /15C, respectively, in March of 1997. After germinating, seedlings were transplanted into tall pots ($10 \times 10 \times 35.5$ cm, $L \times W \times H$) and allowed to acclimate in a greenhouse. Pots were transported to the field where seedlings were transplanted into experimental plots.

Field sites were located at the Waterloo Wildlife Experiment Station forest (39° 21'N, 82° 16'W). The forest is part of the mixed mesophytic forest with oak-hickory (*Quercus alba, Q. rubra, Q. velutina, Carya glabra, C. ovata*) in the mid and upper slopes with more mesic species (*Acer saccharum, Fagus grandifolia, Liriodendron tulipifera*) at the lower slope position (Braun, 1989). The Ohio Department of Natural Resources, Division of Wildlife currently maintains six clear cuts in the forest for game management. In the spring of 1997, at each of six clear cuts (replicate sites), we delineated three transects, at least 20 meters apart, perpendicular to the edge of the clear cut and forest, for a total of 18

transects. These transects were chosen so that they were all close to the midslope position and such that slope aspect was as consistent between plots as possible. On each transect, study plots were delineated in three habitats: clear cut, edge, and forest for a total of 54 plots. Plots in clear cuts were set up 25 m from the forest edge. Edge plots were placed in the edge of the forest, but within the forest canopy. Forest plots were placed 60 m from the edge of the clear cut in the intact forest (henceforth, forest). The area for each plot in the experiment was 2×2 m divided into four 1×1 m subplots.

In order to partition the effect of aboveground competition, half of the area (2 subplots) was randomly chosen to have all vegetation cut to ground level. In 27 plots in the first three replicate sites, half of the plants in each subplot were buried in their tall pots and half were transplanted directly into the soil. In this way, we were able to partition the effect of above- and belowground competition with *in situ* vegetation. In each subplot, eight seedlings were planted in a circle approximately equidistant from each other. Thus, a total of 32 plants were transplanted into each plot, for a total of 1728 experimental seedlings.

High rates of herbivory were observed on plants immediately after planting and some plants were replaced in the first week after planting. At the end of the growing season, at least half of all remaining plants in each circle were harvested for analysis.

To reduce future herbivory, cages were built over fall and winter of 1997-98. Cages were 1 x 2 m and consisted of 60 cm tall hardware cloth buried 15 cm to prevent access to burrowing animals. Wire mesh that was 1.2 m tall with 2.5

cm openings was added above the hardware cloth to prevent deer browsing. All wire was attached firmly to corner fence posts. A door was cut into the wire mesh to allow access and could be secured when not in use. At the time the cages were built, 10 pots were buried inside and outside cages. The pots were arranged in circles of 5 in each of the subplots. In this way, there would be minimal disturbance to plots in the spring when seedlings were transplanted. One of the replicate clear cuts had no survivorship of plants the first season and had a different composition of species than the other sites. This replicate was hereafter omitted from the study. Also, since there were no significant differences between the three transects at each site, only one set of cages was placed into each of five replicate sites. Thus, 15 cages were built along 5 transects in replicate clear cut sites as previously described. In all plots inside and outside cages, aboveground vegetation was clipped at the soil surface throughout the growing season.

Seeds were again germinated in trays in a germination chamber as before and were then acclimated to a greenhouse for three days. Seedlings were planted directly into subplots. Two circles of 10 plants inside cages and 2 circles of 10 plants outside of cages were planted. Five plants in each circle were in pots that had been buried previously. A total of 40 plants were transplanted into each habitat for a total of 120 plants at each of five replicate sites (600 seedlings total).

At the end of the season, half (one circle) of the plants were harvested in and outside cages. The next year, seeds were similarly germinated. Returning

to the same five replicate sites, subplots harvested the previous year were replanted (a total of 300 seedlings). At the end of the season in 1999, all plants, including any left from the 1997 and 1998 plantings were harvested. Thus, there are three years of data for 1-yr old plants, and one year of 2- and 3-yr old plants, respectively.

Plants were harvested and dried at 70C until a constant weight. Plant parts were individually weighed. Root biomass was partitioned into coarse and fine roots. Fine roots were defined as roots < 1 mm in diameter when dry. Allometric ratios calculated included leaf weight ratio (LWR), stem weight ratio (SWR), root weight ratio (RWR), fine root weight ratio, and coarse root weight ratio as a proportion of biomass invested in each plant part of all biomass of the plant. Relative growth rates were calculated as grams per gram biomass accumulated per year. Growth rates of whole plants (RGR_{total}) were partitioned between RGR_{above} and RGR_{below} only using above- or belowground biomass values. Leaf area ratio (LAR) was calculated as total leaf area divided by total plant dry weight. Specific leaf area (SLA) was calculated on a per plant basis in which total leaf area was divided by total leaf dry weight. Net assimilation rate (NAR) was calculated as a ratio of plant growth rate to leaf area ratio (Poorter & Van Der Werf, 1998).

Soil nitrogen was measured over spring, summer, and fall using ion exchange resins. Ion exchange resin bags measure long-term nitrate availability in soil (Binkley & Matson 1983; Binkley & Hart 1989; Hart & Firestone 1989). Resin bags contained 5 to 18 g wet weight of ion-exchange resin (Rexyn© 300

(H-OH), Fisher Scientific, Fair Lawn, NJ). Nitrate was extracted with 2M KCl solution and analyzed colorimetrically on a spectrophotometer (Spectronic 20D, Unicam, Rochester, NY) using Nitrate Reagent Powder Pillows (Nitra Ver, Hach, Loveland, CO). Soil samples were taken in July 2000. Soil samples were sieved through a 2 mm mesh, dried, and pH was measured (pH/Ion Analyzer 350, Corning Inc.) using a 2:1 water to soil mixture. Analyses on pH data were done using hydrogen ion concentrations. Light was measured at one of the sites in a clear cut plot, in an edge plot, and in an intact forest plot on September 9, 1998. Point sensors (Li-Cor) were connected to dataloggers (LI-1000, Li-Cor) and mean photon flux densities and soil and air temperatures were recorded every 5 minutes for a full day that was partly cloudy. On September 22, 1997, four leaf disks were taken from randomly chosen plants in each habitat and analyzed for chlorophyll content (Moran & Porath, 1980; Moran, 1982; Inskeep & Bloom, 1985). Leaf disks were taken from plants in cleared and undisturbed plots in each habitat.

Microsite data were analyzed using replicate sites as a random block in the General Linear Model Analysis of Variance (GLM ANOVA). Habitat and season were fixed effects in the models. Chlorophyll content of leaves was analyzed with a multivariate analysis of variance (MANOVA) followed by GLM ANOVAs for chlorophyll *a*, chlorophyll *b* and chlorophyll *a* to *b* ratio with habitat and aboveground competition as fixed factors. Bonferroni post hoc analyses were used to determine difference among the three habitats and seasons.

Survivorship data were analyzed for the 1997 cohort and other cohorts separately using a GLM ANOVA on percent survivors per replicate plot.

Data from the 1997 season were pooled from all replicate sites and analyzed using a GLM Analysis of Covariance (ANCOVA) with aboveground competition, belowground competition, and habitat as fixed categorical variables and biomass at the time of transplanting as a covariate. Biomass data were $\log_e$ transformed to meet assumptions of the model. Initial biomass was estimated using a regression model of height and diameter measurements taken at the time of planting and data from a destructive harvest of small plants and final harvest data. Allometric ratios were analyzed with a GLM ANCOVA with similar effects in the model, but with final plant biomass as a covariate.

Biomass data from the 3-yr experiment were $\log_e$ transformed to meet assumptions and analyzed using a GLM ANOVA with harvest year as a random effect, and age of seedling, habitat, and belowground competition as fixed categorical effects. Bonferroni's post-hoc analysis was used to determine whether differences between ages and habitats were significant. Plant heights were compared for plants surviving the 1998-1999 winter to those that did not survive using a Mann-Whitney U test for differences of the median, since height data were not normal or homoscedastic.

Results

Analysis of microsite variables among clear cut, edge, and forest sites revealed significant differences in light and soil characteristics in the three habitats (Table 1.1). Total light availability was different among all habitats (F =

217; $p < 0.001$; Table 1.1). Soil pH was not found to differ among sites ($F = 2.68$; $p = 0.13$; Table 1.1). Soil nitrate levels varied, as expected over the course of the year with the highest levels in the spring months, and lower levels in the summer ($F = 8.93$; $p < 0.001$; Table 1.1). Soil nitrate also varied across habitats with forest soils being greater in soil nitrogen than clear cut and edge soils ($F = 4.88$; $p < 0.05$; Table 1.1). Air and soil temperatures were greatest in the clear cut habitat and declined with decreasing light availability (Figure 1.1). Soil temperatures were more variable than air temperatures, and were probably affected by the variation in sun flecks in the forested habitats (Figure 1.1B).

Herbivory rates outside cages were high and variable among replicate sites in 1997 (Figure 1.2). Cages, however, effectively prevented mammal damage to seedlings. Rates of herbivory were extremely high in subsequent years (Table 1.2). Overwintering survival was high (~75%) with taller seedlings surviving the winter more often than smaller seedlings ($Z = 4.98$, $p < 0.001$). The 1999 summer was a drought year in which overall survivorship was reduced ($F = 20.1$, $p < 0.0001$; Table 1.2). Seedlings in clear cuts had greater percent survivorship ($70.5 \pm 5.9\%$) than the other locations (edge: $47.5 \pm 3.6\%$, forest: $48.5 \pm 6.3\%$) when protected from herbivory ($F = 4.44$, $p < 0.05$).

The 1997 harvest revealed that plant biomass differed significantly among habitats with plants grown in forest plots being smaller in all aspects than those in edge and clear cuts (Table 1.3). Above-ground competition reduced biomass of all plant parts except coarse root biomass and leaf area (Table 1.3). Below-ground competition affected root biomass, fine root biomass and total plant

biomass (Table 1.3). However, there were significant interactions that define the importance of above- and below-ground competition in the three habitats (Table 1.3). Above-ground biomass and leaf area were reduced primarily in the clear cut habitat (Figure 1.3). In contrast, belowground competition decreased root biomass and total biomass of plants growing in edge habitats (Figure 1.3). Further, leaf, stem, and total aboveground biomass were only reduced by above-ground competition in the presence of below-ground competition (Table 1.3).

Plants in edge and clear cut habitats generally had less investment in leaves and leaf area than those in forest habitats (Table 1.4). Belowground competition reduced investment in leaves, stems and coarse roots, but increased investment in total roots and fine roots (Table 1.4). Aboveground competition also reduced investment in leaves, but increased investment in roots, stems, and leaf area per unit of weight (Figure 1.4). Belowground competition decreased investment in leaves and increased investment in roots, particularly in the clear cut habitat (Figure 1.4). However, leaf ratios were not significantly affected by belowground competition (Figure 1.4, Table 1.4). In contrast, aboveground competition decreased leaf area ratio and specific leaf area in low light environments, including the clear cut habitat (Figure 1.4, Table 1.4).

The 3-yr study showed that all biomass variables exhibited a significant age and habitat effect, since biomass increased with increasing age and light availability (Table 1.5). Belowground competition significantly increased fine root biomass across habitats. However, there was a significant habitat by competition interaction effect for leaf, stem, aboveground biomass and leaf area because

there was always greater biomass with root competition in all habitats except the forest (Table 1.5).

The ANCOVA revealed that seedlings shifted investment patterns with age (Table 1.6). Older seedlings had lower leaf weight ratios, fine root weight ratios, specific leaf area, and relative growth rates (Figure 1.5). The effects of belowground competition were significant for all weight ratios although the effects varied across habitats (Table 1.5). Leaf weight ratio was lower without competition in the clear cuts, but greater in plants grown in the forest (Figure 1.5). The effect of belowground competition reduced fine root weight ratio across all habitats (Figure 1.5). Relative growth rate of belowground structures was significantly reduced with belowground competition, whereas other relative growth measures were not significantly affected (Table 1.6, Figure 1.5).

Chlorophyll *a*, chlorophyll *b*, and total chlorophyll were affected by the habitat in which plants were grown ($F = 98.96$, $p < 0.0001$; $F = 72.78$, $p < 0.0001$; $F = 92.28$, $p < 0.0001$, respectively). Plants growing in the forest edge had lowest chlorophyll *a* and *b* content (0.544 ± 0.058 mg $\cdot$ g^{-1}, 0.177 ± 0.022 mg $\cdot$ g^{-1}, respectively), followed by plants from the clear cut (0.976 ± 0.068 mg $\cdot$ g^{-1}, 0.360 ± 0.030 mg $\cdot$ g^{-1}) and then plants grown in intact forest (1.846 ± 0.074 mg $\cdot$ g^{-1}, 0.636 ± 0.027 mg $\cdot$ g^{-1}). The ratio of chlorophyll *a* to *b* did not vary significantly among habitats, but was always greater than 1 (2.91 ± 0.05). Leaf disk wet weights varied between habitats and in the presence of aboveground biomass and also had a significant habitat by competition interaction. This was due to the

light environment since the leaf disks from plants in the clear cut without aboveground vegetation were similar to the edge habitat (high light) and disks from plants in the clear cut with aboveground vegetation were similar to the forest habitat (low light).

Discussion

Forest management had significant effects on the growth and survival of *P. tomentosa*. The clear cut habitat had the greatest human disturbance and was most favorable for growth and survival of the species. However, the edge habitat was also conducive to survival and growth. Fragmentation of the forest ecosystem has changed abiotic and biotic components of the ecosystem (Saunders *et al.,* 1991), in this case, making parts of the ecosystem more susceptible to invasion.

The disturbance in the clear cuts, leading to greater light availability and shifting to an early successional habitat created better conditions for *P. tomentosa*. Other studies have found that early successional habitats have higher proportions of invaders (Rejmánek, 1989). *Paulownia tomentosa* plants grown in low light environments, such as intact forest plots, had slower growth rates and high specific leaf area and leaf area ratios. Thinner leaves and the increase in proportional investment to leaf area per unit of weight is a common response of a shade intolerant species (Givnish, 1988). In other ecosystems, areas of high nutrient availability are often areas with the greatest proportion of non-native plants (Hobbs & Atkins, 1991; Williams, 1991). In this deciduous forest, however, although there was more soil nitrogen in intact forest soils, this

was not sufficient to compensate for low light levels in this habitat. Higher nitrogen levels, however, may allow *P. tomentosa* to increase chlorophyll content of leaves in low light and maintain growth in these conditions.

This study showed very high losses of *P. tomentosa* seedlings to herbivory across the managed hardwood forest landscape. There was some insect damage noted on seedlings, although it did not seem result in mortality. In later years, however, small mammals were able to find plants more easily. All seedlings outside of cages were removed by vertebrate herbivory and activity by the last year of the experiment (Table 1.2). Only a portion of plants from the 1997 planting left in areas where the researchers did not frequent was left alone. Although the first plants to be lost to herbivory were in clear cut sites, animals were able to quickly find most plots in all three habitats. Herbivory in this ecosystem and the behavioral response of animals to human visitation was extremely important in the survival of the species.

Effect of competition with *in situ* vegetation varied across the managed forest landscape. The clear cut habitat was the only habitat to show effects of aboveground competition. Aboveground competition had effects on *P. tomentosa* similar to responses found at low light levels. Presence of vegetation around plants caused higher specific leaf area and leaf area ratios. In contrast, belowground competition affected plants growing in edge sites more than plants in other habitats. Longer term effects of belowground competition varied across habitats and with seedling age. Just as competition with *in situ* vegetation affects succession (Wilson & Shure, 1993), vegetation present in an ecosystem may

buffer and protect against invasion by a species. However, our data indicate that once *P. tomentosa* is established, competition will not hinder its invasive potential.

A study of southern Appalachian forests showed that soil nutrient levels and competition affect the species composition of early successional habitats (Wilson & Shure, 1993). In the case of *P. tomentosa*, light was the limiting resource and the effect of competition varied across habitats and lessened over time.

A study of forest edges and alien invasion of northern hardwood beech-maple forests found very few alien species in forest interiors (only 8 m from forest edge) and none were large enough to reproduce (Brothers & Spingarn, 1992). Likewise, for *P. tomentosa*, clear cuts were more favorable habitats, especially if cleared of aboveground vegetation. Belowground competition in the edge habitat may help to prevent its establishment there. It has been thought that the dense vegetation typically at forest edges may prevent invaders from gaining access to intact forest (Brothers & Spingarn, 1992).

Research in old growth forests in Indiana note that there are few non-native species along trails and in tree fall gaps, which they suggest is due to the low light environment of the intact forest (Brothers & Spingarn, 1992). This may also be true for *P. tomentosa*. We have observed an individual establish in intact forest on a tip up mound, but so far, this individual dies back to ground level every winter and cannot reach the forest canopy. This suggests that a large

disturbance, repeated disturbance, or a longer growing season may be necessary for *P. tomentosa* to establish within an intact forest matrix.

It has been argued that individual plant traits are unlikely to be predictive of their invasion potential in new habitats (Noble, 1989). This could be because of the extremely varied nature of successful plant invaders (Heywood, 1989), the various modes and history of their invasion (di Castri, 1989) and the variability and range of habitats that have been invaded by non-natives. The importance of individual plant traits will therefore be limited to the habitat being invaded. In the case of *P. tomentosa,* it is filling the niche of an early successional plant. It produces many small, wind-dispersed seeds, and has high relative growth rates typical of an early successional species (Huston & Smith, 1987). It is similar in many ways to *Cecropia*, a rain forest species. *Cecropia* also has small seeds, fast growth, is shade intolerant and grows fastest in high light, such as a large forest gap (Pompa & Bongers, 1988). We have shown *P. tomentosa* to have morphological and physiological plasticity in response to light, also typical of an early successional species (Bazzaz, 1979). The presence of two adult trees in a stand is sufficient to accumulate great numbers of *P. tomentosa* seed in the seed bank (Hyatt & Casper, 2000). Although we have used seeds from a single species, other work (see Chapter 3) suggests that although genetic variability is a factor in plasticity, it accounts for only a small portion of this variability.

There have been relatively few studies of woody invasive species in Appalachian forests. Exceptions have been *Lonicera maackii* and *Ailanthus altissima*, which also have high growth rates. In contrast to *P. tomentosa*, these

species are moderately shade tolerant and have been found to invade intact forests.

In areas where *P. tomentosa* may be a problem, proper management should include avoiding complete removal of the overstory. Large gaps and clear cuts will likely be susceptible to invasion by this species. However, *P. tomentosa* can resprout (Chapter 2) and has been shown to survive up to three years in intact forest once established. It is not known how long it can survive under a closed canopy. Its fast growth rates may allow it to establish after a second disturbance that opens up the forest canopy. Therefore the frequency, as well as the intensity of disturbance may be important to the establishment of *P. tomentosa*, and, therefore, to an ecosystem's resistance to invasion by this species.

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Table 1.1. Microsite characteristics (±SE) of three forest habitats studied. Light was measured for a whole day in June 1998 and the mean of light measures taken every five minutes was summed. Soil samples were taken at replicate sites and measured for pH. Resin bags were used to measure 3-month nitrate (NO_3^-) accumulation over spring, summer, and fall of 1999.

Habitat	Light† PAR $m^2 \cdot d^{-1}$	pH†	NO_3^- ($\mu g \cdot g^{-1}$)‡		
			Spring	Summer	Fall
Clear cut	46,566 a (±1,795)	5.19 a (± 0.27)	12.8 (± 2.2)	5.2 (± 2.0)	10.6 (± 3.2)
Edge	31,617 b (± 761)	4.31 a (± 0.29)	11.7 (± 1.8)	7.6 (± 2.0)	9.9 (± 1.7)
Forest	10,249 c (± 886)	4.72 a (± 0.38)	22.5 (± 2.7)	12.7 (± 3.0)	8.5 (± 1.0)

† - Significantly different means found with a post-hoc Bonferonni analysis are identified with different letters within the table column.
‡ - For results of the GLM ANOVA for soil nitrate, see text.

Table 1.2. Survivorship of plants over one growing season (except as noted†) transplanted throughout the course of the experiment (including 1997 study plants). Percent survivorship and number planted are given.

	Year of Transplanting				
Growing	**1997**	**1998**		**1999**	
Season		Cage	No Cage	Cage	No Cage
1997	24.9 ± 4.7% *n* = 54	------	------	------	------
1998	------	67.3 ± 4.3% *n* = 30	8.7 ± 3.4% *n* = 30	------	------
1999	15.2 ± 5.1%† *n* = 17	50.7 ± 6.8% *n* = 15	0% *n* = 15	36.7 ± 4.4% *n* = 15	4.7 ± 1.7% *n* = 15

† - this value represents survival over two winters and two growing seasons

Table 1.3. Analysis of covariance (ANCOVA) of plant biomass with initial biomass at time of planting as a covariate. Habitat (clear cut, edge, forest), belowground competition (BGC) if present or absent, aboveground competition (AGC), if present or absent, were entered as fixed effects in the model (*N* = 252). Significant effects and interactions are noted with asterisks. Only significant model interactions are shown.

Variable	Habitat (H)	BGC (B)	AGC (A)	H × B	A × B
Aboveground biomass	***	ns	***	***	**
Leaf biomass	**	ns	***	***	*
Stem biomass	***	ns	*	***	**
Root biomass	***	***	***	**	ns
Coarse root biomass	***	ns	***	**	ns
Fine root biomass	***	***	ns	ns	ns
Total biomass	***	*	***	***	ns
Leaf area	*	ns	ns	***	ns

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; Initial biomass was a significant covariate with all variables shown.

Table 1.4. Analysis of covariance (ANCOVA) of allometric measures with final plant biomass as a covariate. Habitat (clear cut, edge, forest), belowground competition (BGC) if present or absent, and aboveground competition (AGC), if present or absent, were entered as fixed effects (*N* = 252). Significant effects and interactions are noted with asterisks. Only significant model interactions are shown.

Variable	Habitat (H)	BGC (B)	AGC (A)	H × B	H × A
Leaf weight ratio‡	***	***	***	**	ns
Stem weight ratio	ns	*	*	ns	ns
Root weight ratio	***	***	*	***	ns
Coarse root weight ratio	**	***	ns	**	ns
Fine root weight ratio	ns	***	**	ns	ns
Leaf area ratio†	***	ns	**	***	*
Specific leaf area†	***	ns	***	ns	***
Relative growth rate	***	ns	*	ns	ns
Net assimilation rate	ns	*	ns	ns	ns

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

‡ - Biomass was a significant covariate with all variables shown, except leaf weight ratio

† - Variables were $\log_e$ transformed to meet assumptions of normality and homoscedasticity

Table 1.5. Analysis of variance (ANOVA) for biomass of plant parts over three years. The year of harvest was entered as a random effect (not shown). Seedling age, habitat (forest, clear cut, and edge), and belowground competition (BGC), whether present or absent, were entered into the model as fixed effects (*N* = 254). Only significant model interactions are shown.

Variable	Age	Habitat (H)	BGC (B)	Age × H	H × B
Above-ground†	***	***	ns	ns	*
Leaf biomass	***	***	ns	ns	**
Stem biomass	***	***	ns	ns	*
Below-ground†	***	***	ns	ns	ns
Coarse roots	***	***	ns	ns	ns
Fine roots	***	***	***	***	ns
Total biomass†	***	***	ns	ns	ns
Leaf area	***	***	ns	*	*

† - Year of harvest was found to be significant for these variables.

Table 1.6. Analysis of covariance (ANCOVA) with age, habitat, and belowground competition (BGC) as fixed effects, year of harvest as a random effect, and biomass as a covariate for plants harvested throughout the experiment (*N* = 254).

Variable	Effects						
	Age (A)	Habitat (H)	BGC (C)	A × H	A × C	H × C	A × H × C
Leaf weight ratio	***	ns	*	ns	ns	*	ns
Stem weight ratio†	***	***	*	**	*	ns	ns
Fine root weight ratio†	ns	ns	***	ns	ns	ns	ns
Coarse root weight ratio†	***	***	*	***	*	**	***
Root weight ratio	***	**	***	**	**	*	ns
Leaf area ratio†	***	***	ns	*	ns	ns	ns
Specific leaf area†	*	***	ns	***	ns	ns	ns
Net assimilation rate†	***	***	ns	ns	ns	ns	ns
RGR_{total}	***	***	ns	***	ns	*	*
RGR_{above}†	***	***	ns	***	ns	ns	*
RGR_{below}	***	*	*	**	ns	*	ns

* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$
† - Year of harvest was significant for this variable

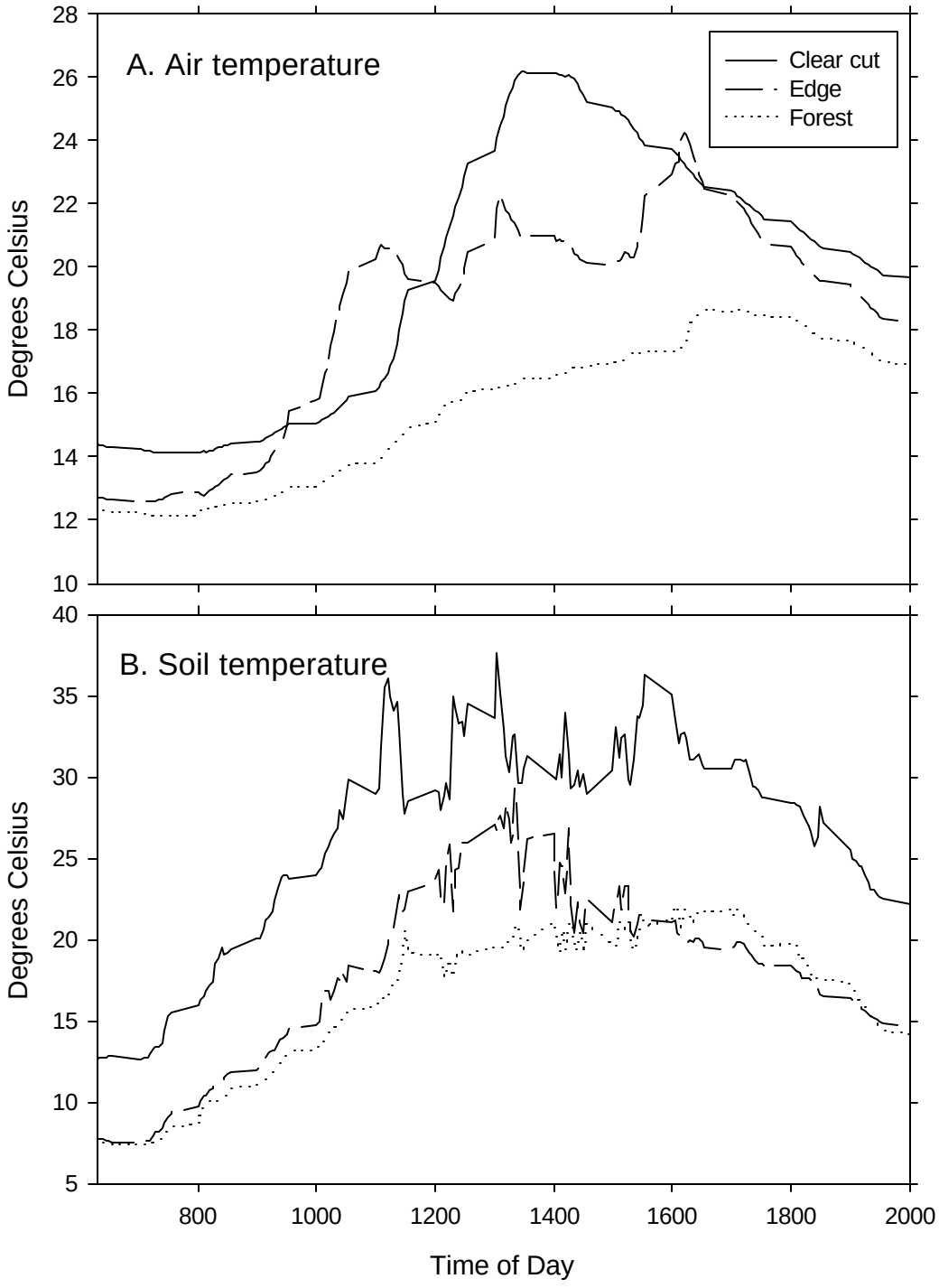

Figure 1.1. Air (A) and soil (B) temperatures taken over the course of a day at a replicate field site.

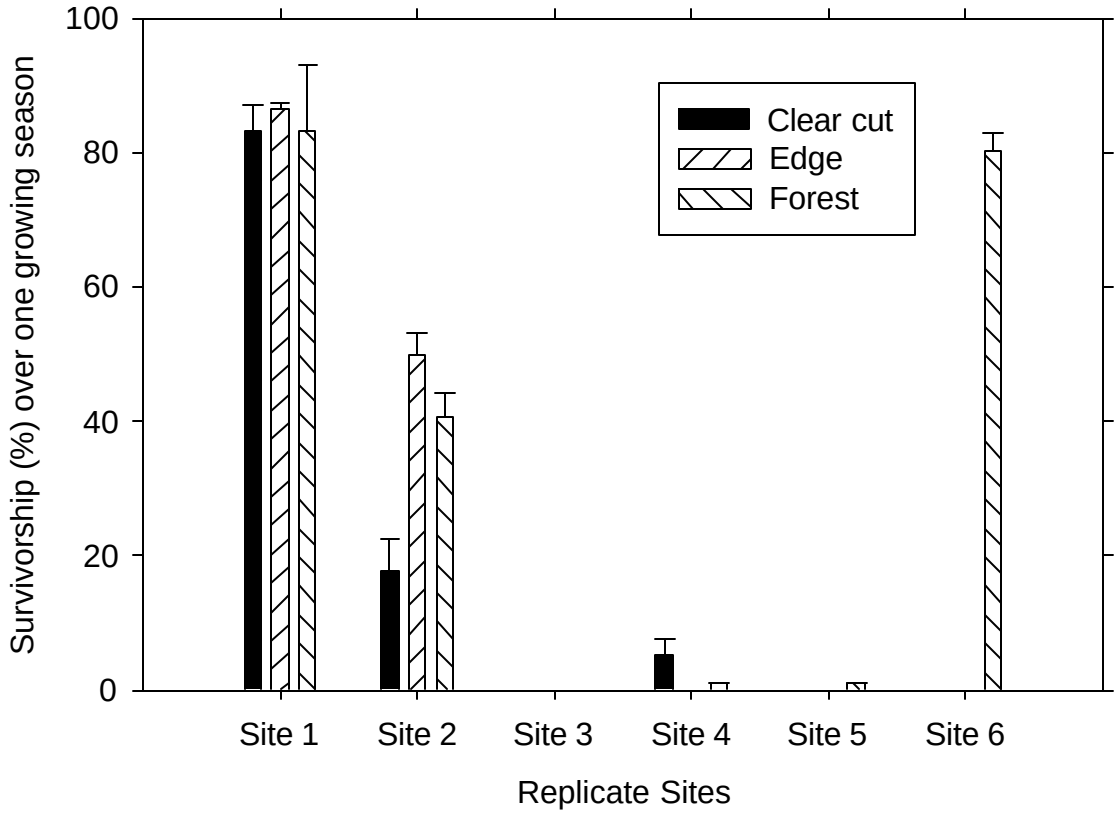

Figure 1.2. Survivorship of 1997 seedlings over the course of one growing season. Six replicate clear cut sites were used in which clear cut, edge, and forest plots were delineated.

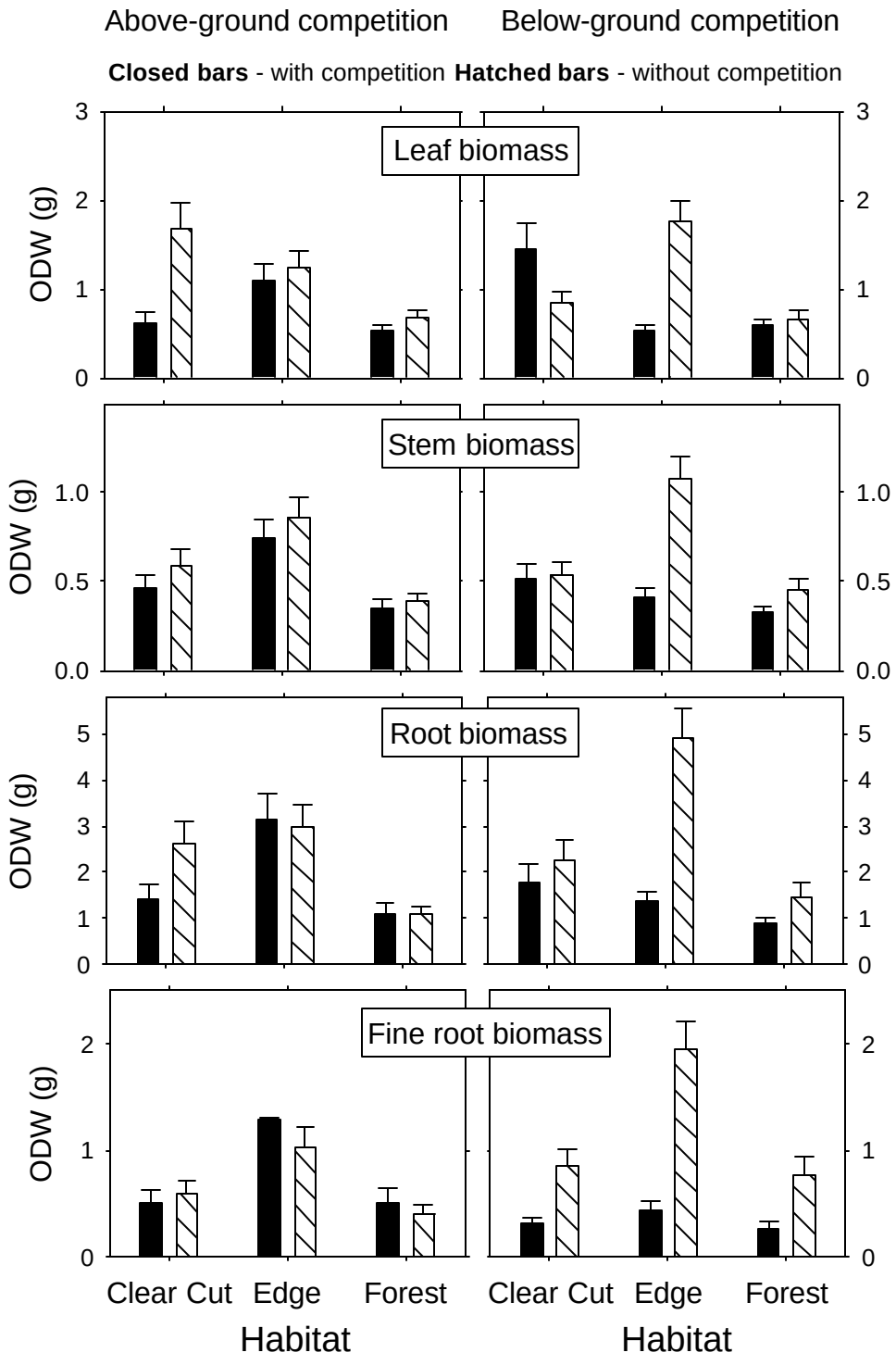

Figure 1.3. Oven dry weights (ODW) of 1997 seedlings at each habitat with and without above- or belowground biomass.

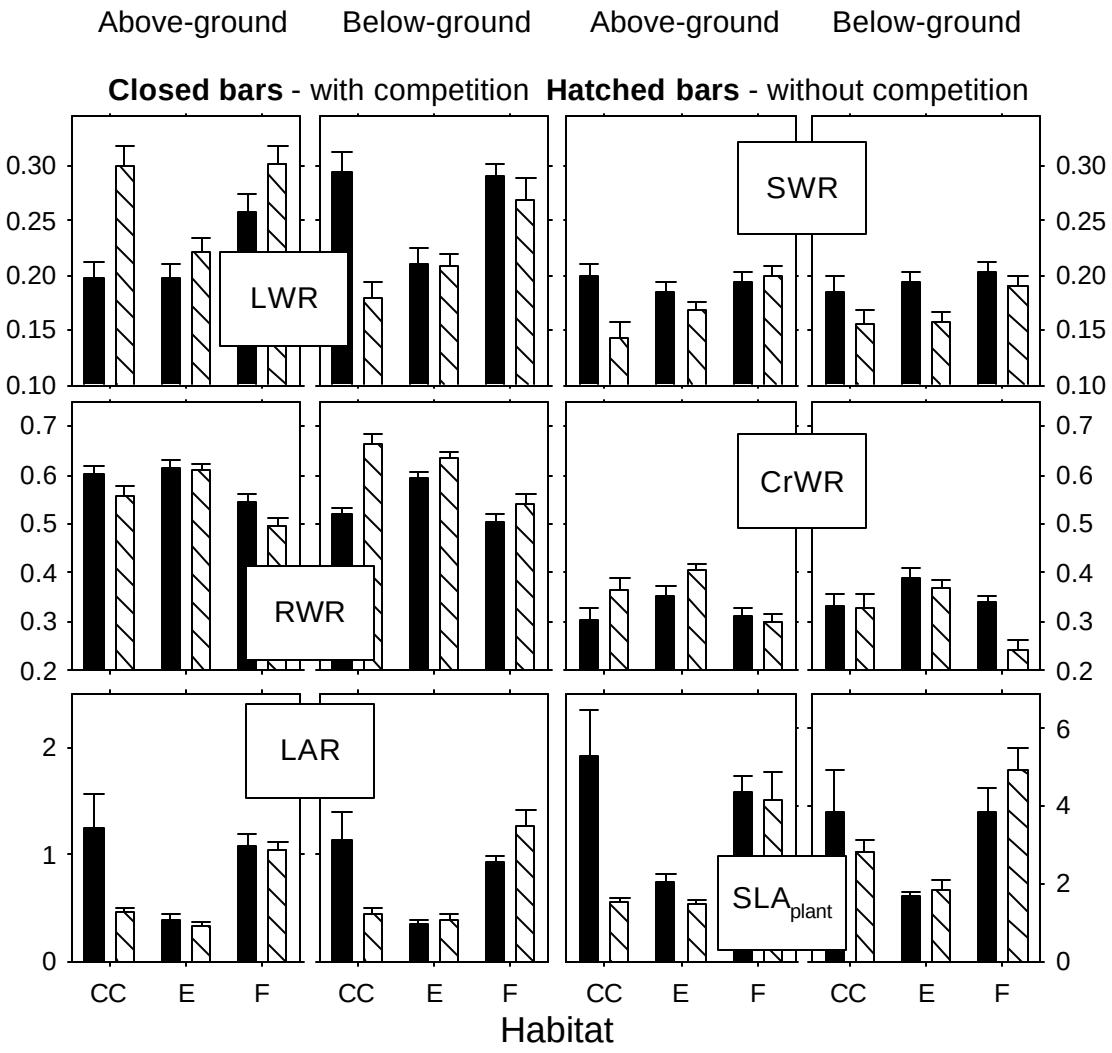

Figure 1.4. Allometric ratios of 1997 plants with and without competition. Open symbols are plants grown without competition and closed symbols are for plants grown with competition. Scales are the same across the figure, except for the bottom panels.

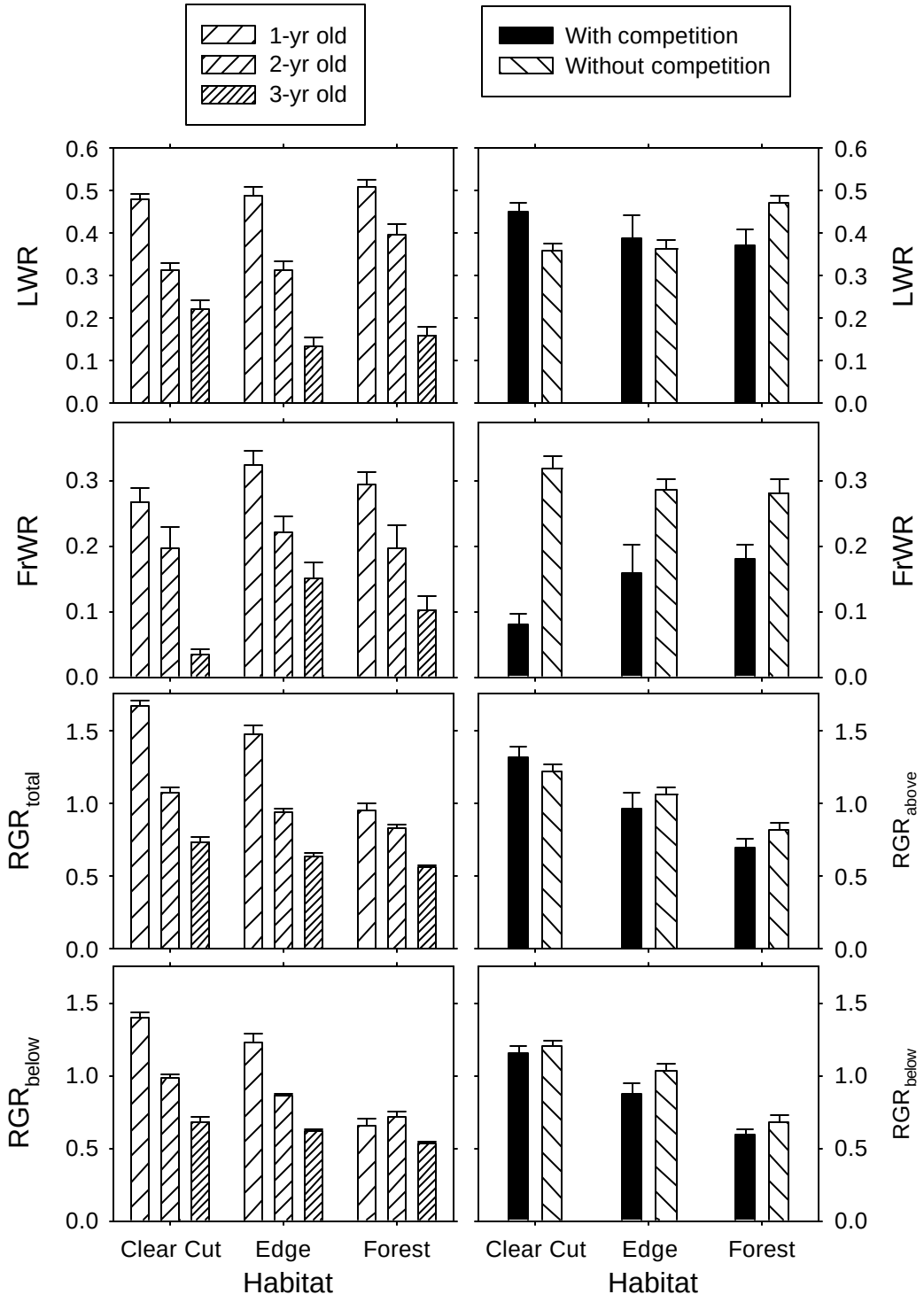

Figure 1.5. Weight ratios and relative growth rates for plants grown over three years in field sites. Left panels separate data by seedling age. Right panels separate data by plants with and without belowground competition.

Chapter 2 : Biomass allocation and resprouting ability of princess tree (*Paulownia tomentosa*) across a light gradient

Introduction

Paulownia tomentosa (Thunb.) Sieb. & Zucc. ex Steud. (Scrophulariaceae) is a tree, native to China, introduced into the eastern United States around the 1840s (Hu, 1961). It becomes established after disturbance (Williams, 1993), but volunteers have been found in intact secondary forest (A. Williams, pers. obs.). Since the species is not indigenous to North America and is quickly becoming an invasive pest, we wanted to assess patterns of biomass allocation in various light treatments comparable to intact deciduous forests, open fields, and forest edges. Further, given the palatability of the species to vertebrates (A. Williams, pers. obs.), we also wanted to examine the effect of herbivory on this invasive species.

Several characteristics of plants are thought to be important for invading species to survive and reproduce in new environments. Comparison of invasive and native species in Hawaii found that invasive, nonindigenous species had greater relative growth rates than natives (Pattison *et al.*, 1998). Phenotypic plasticity may be an important plant trait that allows a species to acclimate to varying environmental conditions, and thus, broaden the habitat a plant is able to invade. Due to the importance of herbivores in structuring vegetation (Darwin, 1859; Tansley and Adamson, 1925), Baker (1965) hypothesized that the ability to resprout is one characteristic that should be important to a successful invader.

Resprouting may allow an individual to persist after defoliation or disturbance (Barnes *et al.*, 1998). In fact, some shade tolerant tree species persist for decades in the forest understory, even after repeated dieback to the base of the stem (Merz and Boyce, 1956; Monk, 1981). Sprouting can be important in succession (Forcier, 1975; Bormann and Likens, 1979; Zammit and Westoby, 1987) and important in the regeneration of certain species (Held, 1983). So, the ability to resprout may be an adaptive trait that allows a long-lived species to persist and ultimately survive and reproduce.

Biomass allocation in response to low light could interact with a plant's ability to resprout following herbivory on aboveground structures. A plant that has initially made more investment in aboveground biomass due to low light levels may not have sufficient investment in biomass reserves belowground to resprout. Furthermore, the mechanism used by plants to adjust root to shoot ratio (R:S) after aboveground biomass removal is not well understood. It is not known if plants abort roots to adjust R:S or increase aboveground biomass growth (Bazzaz, 1997).

In general, plants maximize their ability to gain the most limiting resource by shifting biomass allocation (Chapin, 1991). Plants not adapted to low light often respond to shade by investing more biomass in aboveground structures with longer shoots and thinner leaves (Grime, 1979). Plants often respond holistically to a stress with many traits being correlated with each other (Schlichting, 1986). Plant characteristics such as specific leaf area have been correlated to photosynthesis, relative growth rate, and other traits (Poorter and

Remkes, 1990; Cornelissen *et al.*, 1996; Reich *et al.*, 1998). Furthermore, a plant under one stress may not be able to adjust to a different type of stress.

Our study had three objectives: (1) to explore biomass allocation and phenotypic plasticity of *Paulownia tomentosa* along a light gradient, (2) to assess the ability of *Paulownia tomentosa* to resprout after aboveground biomass removal, and (3) to interrelate biomass allocation and ability to resprout. We hypothesized that greater biomass allocation to aboveground biomass of plants grown in low light would interfere with the ability of those plants to resprout after clipping.

Methods

Seeds were collected from a single tree in Athens, Ohio (39°22' lat., 82°06' long.) and sown in trays of potting mix (Sunshine Mix II, Sun Gro Horticulture Inc., Bellevue, WA). They were then placed in a germination chamber (Percival Scientific, Boone, IA) set at 12 h light and 12 h dark at 25/15 C. After plants had reached about 2 cm tall (in ~1 wk) in the germination chamber, they were transplanted into tall pots ($10 \times 10 \times 35.5$ cm, $L \times W \times H$) and acclimated to a greenhouse for 3 d before being placed into experimental shade houses in a common garden.

Three light treatments were established: (1) full ambient sun (only the frame of a cage; henceforth full sun), (2) artificial edge (three layers of green/brown camouflage netting on the west half of the cage; henceforth edge), and (3) forest shade (three layers of camouflage netting covering entire cage; henceforth shade). Camouflage netting allowed small patches of half to a third of

full sun to reach the plants inside the cages since it created 1 to 3 cm gaps. It also created areas of shade which were covered by up to three layers of material.

Each shade house was replicated twice and 50 plants were placed into each house. Pots were placed into a wood and wire frame to keep them upright. The frames were surrounded by 2.5 cm wire mesh fencing to prevent nonexperimental herbivory by small mammals. All plants were watered daily for the first 2 wk and then weekly as needed. Plants that died within the first week were replaced; no plants were lost thereafter. Ten plants in each treatment were cut to ground level (experimentally browsed) at the end of weeks 4, 7, 8 and 9 after germination. At each clipping date, two whole plants from each treatment were harvested. All resprouts and two whole plants in each replicate shade treatment were harvested at the end of week 11. Harvested plants were oven dried at 70 C until constant weight. Plant parts were weighed separately to calculate resource partitioning to leaves, stems, coarse roots (dry roots > 1 mm diameter) and fine roots. The plants from the final harvest (week 11) were measured for leaf area using a LI-202 Leaf Area Meter (Li-Cor, Lincoln, NE). Presence of buds on clipped plant stems was the criterion for scoring plants as successfully resprouting.

Light measurements were taken for a full day in treatment shade houses at about 10 cm height and at ground level with vegetation <10 cm diameter clipped in clear-cut site, forest edge, and intact forest. One shade house of each treatment was randomly chosen to be measured for a full day on 25 July. The

intact forest and clear-cut measurements were taken on 9 September at Waterloo Wildlife Experimental Station in Athens County, OH. The intact forest was an upland oak-hickory forest. The edge site was on the western edge of the intact forest adjacent to the clear cut. Quantum sensors (Li-Cor) were connected to dataloggers (LI-1000, Li-Cor) and mean photon flux densities ($\mu mol \cdot m^{-2} \cdot s^{-1}$) were recorded every 10 min. Both days were clear and mostly sunny.

Light data taken throughout the day were compared among shade treatments using a general linear model analysis of variance (GLM ANOVA) with time as a nested blocking factor. A blocking factor was used to eliminate differences in light measurements due to time of day and thereby make more accurate comparisons (Sokal and Rohlf, 1995).

Biomass data of unclipped plant parts were analyzed using a GLM ANOVA with shade treatment and week entered into the model as fixed variables. Data from replicate shade houses were pooled. Data could not be tested for normality due to low sample size, but there was no *a priori* reason to assume data would not be normal and ANOVA is robust to deviations from normality (Scheffé, 1959). Homoscedasticity was tested using Hartley's F-max test (Hartley, 1950). Log_e transformations were used on all biomass measures to meet assumptions. Untransformed data are reported.

Since biomass measures were different across light treatments and ontogeny can affect allometry and relative growth rates (Venklaas and Poorter, 1998), an analysis of covariance (ANCOVA) was used with light treatment as a fixed effect and the log_e of total biomass as a covariate. Leaf weight ratio (LWR),

stem weight ratio (SWR), root weight ratio (RWR), fine root weight ratio (FrWR), coarse root weight ratio (CrWR) and relative growth rates were analyzed. In order to calculate RGR for plants over the course of the experiment, 20 seedlings were harvested before the plants were placed into shade treatments. The mean weight of these seedlings was used to calculate relative growth rate (RGR) for each plant harvested. RGR_{total}, RGR_{above} and RGR_{below} refer to the relative increase in total, aboveground and belowground biomass, respectively. LWR was calculated as the dry weight of leaves divided by the total dry weight of the plant. Likewise, RWR, SWR, FrWR and CrWR were calculated as the dry weight of root, stem, fine root and coarse root dry weight divided by the total dry weight of the plant, respectively.

The $\log_e$ of belowground biomass was regressed against the $\log_e$ of aboveground biomass using a Regression Model II Reduced Major Axis analysis in Excel (Regression Model II Reduced Major Axis add-in by M. Sawada, www.uottawa.ca/academic/arts/lpcweb/). This type of analysis is appropriate when both variables in the regression model have associated error (Sokal and Rohlf, 1995).

One-way GLM ANOVAs were used to analyze leaf area per plant, number of leaves per plant, specific leaf area (SLA), leaf area ratio (LAR), and leaf weight ratio for plants harvested in week 11. Homoscedascity was tested using Hartley's F-max test (Hartley, 1950). LAR was calculated as the total leaf area divided by the total plant weight. SLA was calculated in two ways: (1) on a whole plant basis (SLA_{plant}), in which total leaf area of the plant was divided by total dry

weight of leaves and (2) on a per leaf basis (SLA_{leaf}), in which individual leaves were measured for area, marked and, once oven dried, weighed individually. SLA_{leaf} used individual leaf areas divided by individual leaf dry weights. When possible, at least four leaves from each plant were measured individually. SLA_{leaf} data were tested for normality with the D'Agostino Omnibus test (D'Agostino *et al.*, 1990) and homoscedasticity with the Modified-Levene Equal-Variance test (N = 77; Conover, 1971). Data were $\log_e$ transformed prior to analysis to meet the equality of variance assumption. SLA_{plant} data were analyzed as described previously with an ANCOVA. Bonferroni post-hoc, pair-wise, comparison tests were used with ANOVA and ANCOVA analyses to determine significantly different ($P < 0.05$) means among treatment groups.

Correlation networks were prepared as per Schlichting (1986) to compare biomass allocation for treatments in the first weeks of harvest and later weeks. Correlation networks were also prepared for the final harvest date that included leaf area data. These networks connect plant traits with a line if there is a significant correlation between those traits. The more lines between plant traits, *i.e.* significant correlations, the higher the degree of integration of phenology in response to treatments applied in the experiment (Schlichting, 1986). The networks also serve to illustrate graphically the allometric relationship of biomass allocation of plants in the different light treatments. All significant results in this paper are reported at the $\alpha < 0.05$ level. However, significant correlations with $P < 0.10$ were also noted since the sample size was small (N = 4; all correlations were > 0.85).

Number of resprouts in each treatment was analyzed using a chi-square analysis (Dowdy and Wearden, 1991). Regression models with number of resprouts and belowground biomass or coarse root biomass were run to determine importance of these variables on the plants' ability to resprout. All statistical analyses were performed using NCSS (Hintze, 2000).

Results

Light data

There was a similar pattern of light availability between the oak-hickory forest and treatment counterparts (Fig. 2.1). Artificial edge and full sun treatments had similar light patterns until about 1400 when the light began to be reduced in the artificial edge treatment (Fig. 2.1a). The ANOVA showed light as a significant effect in the model ($F = 62.08$; $P < 0.001$) and, further, that all light treatments were significantly different from each other. Thus, a gradient of light availability in the treatments was achieved. We were not interested in precisely mimicking the forest counterparts, but rather in creating light environments within the range of possibilities. In fact, the artificial edge and full sun treatments have more light availability than their forest counterparts (Fig. 2.1).

Effect of shading on phenology

Unclipped plants in all treatments increased in aboveground biomass over time with the shade treatment having the least biomass and edge treatment having intermediate biomass (Table 2.1, Fig. 2.2b). The treatment by time interaction showed that the week 4 harvest biomass values for all treatments were closer to each other and then diverged in later weeks. Leaf biomass was

similar to aboveground biomass values since most of the aboveground biomass was in leaf biomass (Table 2.1, Fig. 2.2c). Total plant biomass, stem biomass and leaf biomass differed significantly between the shade treatment and the other two light treatments (partial shade and full sun were not significantly different) over time (Table 2.1). All variables also showed a significant light by time interaction with the exception of coarse root and stem biomass (Table 2.1).

Belowground biomass contributed a smaller proportion of total biomass than aboveground biomass (Figs. 2.2a, 2.2b, 2.2e). Belowground biomass was lower in the shade treatment than in the other light treatments ($F = 40.61$; $P < 0.001$). Artificial edge and full sun treatments did not differ significantly in allocation to belowground biomass.

Fine root biomass increased up to week 8, and then decreased, especially in the artificial edge and full sun treatments in week 11 (Fig. 2.2g). Coarse roots did not develop in plants until week 8 and, unlike fine roots, accumulated over time (Fig. 2.2f).

Effect of shading on plant allometry and growth

Root weight ratios (RWR) of plants in the shade treatment averaged significantly below those in the full sun and artificial edge treatments (Table 2.2). At the final harvest date, RWR of plants in all treatments were similar and low at ~0.3 (Fig. 2.2h). The last harvest corresponded to a marked increase in aboveground biomass (Fig. 2.2b). Although the ANCOVA for RWR and R:S (not shown) did not show a significant effect of the covariate, there was a linear relationship between the $\log_e$ of belowground biomass and $\log_e$ of aboveground

biomass that suggests a continual and constant rate of change between allocation to above and belowground structures despite light treatment (R^2 = 0.96; Fig. 2.3).

Leaf weight ratio of plants in the shade treatment tended to be greater than LWR for plants in the artificial edge and full sun treatments, but the results were not significant (Table 2.2). Stem weight ratio (SWR) showed effects of light and ontogeny with greater allocation to stems in the shade and artificial edge treatments and as plants got larger (Table 2.2). The proportion of biomass in fine roots (FrWR) was affected by light treatment and ontogeny, but coarse root weight ratio (CrWR) was affected only by ontogeny (Table 2.2).

RGR_{total}, RGR_{below}, and RGR_{above} showed effects of light treatment and an increase in RGR through ontogeny (Table 2.2). Plant in the shade treatment had slower growth rates than plants in the full sun and artificial edge treatments (Table 2.2).

Total leaf area per plant and leaf number per plant declined with declining light availability, although the full sun treatment was only significantly different than the shade treatment ($F = 6.84$, $p < 0.05$; $F = 4.62$, $p < 0.05$; Figure 2.4a,b). Leaf area ratio reveals greater investment in leaf area per unit leaf weight for plants in the shade treatment than in the other treatments ($F = 6.06$; $P < 0.05$; Fig. 2.4c). No differences in LWR were found among treatments in week 11 ($F = 0.33$; $P = 0.73$; Fig. 2.4d). Plants in the shade treatment had higher SLA_{plant} and SLA_{leaf} than those in full sun ($F = 10.31$, $P < 0.01$ and $F = 96.24$, $P < 0.001$

respectively; Figs. 2.4e, 2.4f). SLA_{plant} data were higher than SLA_{leaf} data for shade plants.

Data from the final harvest showed the most integration (*i.e.,* more significant correlations) in the artificial edge treatment (Fig. 2.5). Fine root biomass and belowground biomass were correlated with more traits in the shade and artificial edge treatments, which suggests that these traits are important and may help drive the response of plants not in high light conditions. Coarse root biomass was correlated with many traits across all treatments (Fig. 2.5). Correlation networks combining early harvests (weeks 4 and 6) and late harvests (weeks 8 and 11) showed that integration of all treatments increased over time, especially in the artificial edge and shade treatments (Fig. 2.6). Correlation networks for the shade and artificial edge treatments were similar in the early weeks, but in the last weeks of the experiment, plants grown in the artificial edge treatment showed more integration than shade treatment plants (Fig. 2.6). The greatest degree of integration was found in the full sun treatment (Fig. 2.6).

Resprouting ability

Resprouting of clipped plants was more prevalent in artificial edge and full sun treatments, especially in the last two weeks that the clipping treatment was applied (Table 2.3). The difference between expected and observed values originated from the shade treatment which had more resprouts than expected in week 4 and fewer than expected in week 7 and 8 (Table 2.3). Overall chi-square was significant ($\chi^2 = 18.366$; $P < 0.05$). Belowground biomass of clipped plants

surviving to the harvest date was always less than unclipped plants regardless of treatment (Table 2.4).

The regression model with belowground biomass as the independent variable, showed a significant positive relationship between the number of resprouts and belowground biomass at the time of clipping ($\beta = 0.155$; $R^2 = 0.796$). There was also a significant positive relationship between number of resprouts and coarse root biomass at the time of clipping, although this explained less of the variation in the data ($\beta = 0.025$; $R^2 = 0.569$).

Discussion

One of the objectives of this experiment was to assess the early biomass allocation and morphological characteristics of establishing *Paulownia tomentosa* seedlings in different light environments. Given herbivore preference, this is most likely the limiting stage of the life cycle of this invasive species. The effect of low light was to reduce RWR, increase SLA and LAR as predicted from Grime (1979). Clearly, *P. tomentosa* is a sun adapted plant. Although *P. tomentosa* can acclimate to a low light environment, it grows slower and produces thinner leaves in low light.

Clipped plants had higher mortality rates due to the change in allocation in low light as has been shown with the grass, *Bromus tectorum* (Pierson, *et al.*, 1990). Although survival of plants overall was low in the younger clipped plants, they did show an ability to resprout even at four weeks after germination. However, older seedlings and those grown in full sun were more likely to survive the clipping treatment and produce a new shoot.

Belowground biomass of clipped plants was not able to fully compensate for the loss of plant parts in the short time of the experiment. Root biomass did not return to unclipped levels, which demonstrates abortion of root biomass to adjust root to shoot ratio before an adjustment in aboveground biomass. Belowground biomass was an important factor explaining the number of plants that were able to resprout across all treatments.

The ability to resprout coupled with the notably high growth rate may permit *P. tomentosa* to become established in areas with heavy grazing pressure. After an herbivore attack, *P. tomentosa* may resprout and grow rapidly enough to reach a height and diameter where it would no longer be threatened by the same herbivore.

Besides the ability to resprout, *P. tomentosa* shows other plant traits that may be important in allowing it to establish in different ecosystems. Clearly, rapid relative growth rate is important for an invasive species. LWR, SLA, and LAR are components of RGR and have been shown to affect RGR (Poorter, 1989; Poorter and Remkes, 1990; Cornelissen *et al.*, 1996; Hunt and Cornelissen, 1997; Poorter and Van Der Werf, 1998). *Paulownia tomentosa* had higher RGR compared to all other woody species reviewed with the exception of a study of 5 *Eucalyptus* species (Poorter, 1989). Values of RGR were greater than those found for *Pinus* species (Norgren, 1996), which supports the trend that deciduous species have higher RGR than evergreen species (Cornelissen *et al.*, 1996). Studies in which light was varied consistently show an increase in

RGR with greater light availability (Latham, 1992; Walters *et al.*, 1993a; Walters and Reich, 1996; Veneklaas and Poorter, 1998).

Although RGR increased over time in all light treatments, it is likely that RGR of *P. tomentosa* will eventually decline over time since most woody species show reduced RGR through time (Walters *et al.*, 1993b). However, this experiment was not long enough to examine this longer trend. Leaf weight ratio of woody plants typically decreases over time (Walters *et al.*, 1993b), but this did not occur during the study. Other studies also showed no significant effect of light availability on LWR on plants grown in a range of light environments (Veneklaas and Poorter, 1998).

Specific leaf area (SLA) and leaf area ratio (LAR) are most often linked to RGR with LWR not related to RGR (Loach, 1970; Huxley, 1967). Low light has been shown to increase SLA and/or LAR in many other studies of woody species (Callaway, 1992; Messier, 1992; Walters *et al.*, 1993a; Veneklaas and Poorter, 1998). SLA and LAR values have been shown to be lower in trees than other woody growth forms (Cornelissen *et al.*, 1996), although *P. tomentosa* had higher growth rates than invasive *Lonicera* shrubs (Schierenbeck *et al.*, 1994).

A review of tropical tree seedlings and saplings showed that pioneer species are much more flexible in such characters as LAR, SLA, and RGR (Venklaas and Poorter, 1999) which fits with the results of this study of *P. tomentosa* seedlings. Also, a study of invasive and native Hawaiian woody seedlings found that invasive species always showed a response to lower light,

but not all native species responded to the light environment with higher SLA or LAR values (Pattison *et al.*, 1998).

Unlike LWR, RWR is sometimes altered with low light environment (Walters *et al.*, 1993a; Canham *et al.*, 1996). However, studies altering light and nutrients often find no effect of light on R:S, but a marked decrease in R:S with increased nutrients (Wang *et al.*, 1998; Latham, 1992). Species are known to differ in R:S; however, more variation was found among species than within a species (Monk, 1966). Like the results comparing native and invasive seedlings in Hawaii, some invasives showed decreased RWR with decreased light availability, but no native seedlings showed any response (Pattison *et al.*, 1998).

Studies comparing attributes of species have found positive correlations between RGR and LAR, RGR and SLA, and sometimes RGR and LWR (Poorter and Remkes, 1990; Garnier, 1992; Walters *et al.*, 1993b; Cornelissen *et al.*, 1996; Hunt and Cornelissen, 1997; Lusk *et al.*, 1997). These relationships do not hold within the phenotypic plasticity shown by *P. tomentosa*. RGR was highest when SLA and LAR were lowest.

Some authors suggest that plants have more integration of characteristics in stressful environments (Thomas *et al.*, 1971; Primack and Antonovics, 1981); however, we found the reverse. Full sun plants had the most integrated correlation networks, particularly early in ontogeny (Fig. 2.6). Artificial edge and shade plants showed more integration later in ontogeny than early in ontogeny, but they did not reach the same amount of integration as full sun plants (Fig. 2.6). Our observation is that plants for which correlation networks have been produced

have been annuals, which could respond much more rapidly to stress than a perennial species. The lack of a more integrated response may prevent *P. tomentosa* from establishing and reproducing in very low light conditions typical of a mature forest understory. Acclimation on the time scale of this experiment by a woody perennial, which is not likely to reproduce for 8+ years, may not be adaptive unless the plant can survive long enough to reproduce. On the other hand, an annual may be able to make rapid adjustments and quickly complete its life cycle, so an integrated response would be favored.

Paulownia tomentosa plants exposed to low light levels responded to the stress by adjusting allocation to biomass and leaf area. Although the plants had high growth rates, they were not able to compensate for the loss of plant parts. Nonetheless, resprouting ability of plants in the intermediate and high light levels was high compared to plants grown in low light. Other plants including woody species have shown compensatory growth after clipping (Cornelissen, 1993; Wilson, 1993; Shabel and Peart, 1994). This was not the case with young seedlings (<1 yr-old) of *P. tomentosa*, but cannot be ruled out as a response from older well-established individuals. As with other species that can resprout and persist in the understory, it is possible that once the plants accumulate enough belowground biomass, they may be able to resprout even in low light conditions and possibly show compensatory growth. Regardless, *P. tomentosa* has been shown to have many characteristics of an invasive species. *Paulownia tomentosa* can resprout at a young age and has fast growth rates.

Paulownia tomentosa exhibits traits typical of an early successional species. Its general response to light is that of a shade intolerant species. Characteristics, such as high plasticity and greatest growth rates in full sun support these conclusions. However, as an early successional species, *P. tomentosa* can be aggressive and successful, particularly in marginal habitats (A.C.W. Longbrake, pers. obs.). Our observations of naturalized stands throughout Appalachia suggest that it can remain the dominant tree species for 30 or more years. Its small, wind dispersed seeds also may allow it to find the open niches it needs to become established. Our data suggest that, although belowground biomass is important in resprout success, seedlings can resprout at an early age, even in low light. Very young seedlings invest heavily in belowground structures, so that the species may be able to become established even in areas of high herbivore density.

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Table 2.1. F-ratios for biomass variables of *Paulownia tomentosa* seedlings tested for effect of light treatment and week harvested

Response variable	Effect in Model		
	Shade treatment (df = 2)	Week of harvest (df = 4)‡	Shade × Week (df = 8)‡
Aboveground biomass	56.35***	241.42***	7.55***
Leaf biomass	59.45***	240.78***	7.79***
Stem biomass	45.75***	26.85***	1.21
Belowground biomass	43.89***	91.68***	3.91***
Coarse roots	8.49**	7.67**	0.59
Fine roots	42.16***	85.72***	4.12***
Total biomass	62.15***	195.72***	6.63***

‡ Degrees of freedom for coarse roots are 2 for Week of Harvest and 4 for Shade × Week, due to lack of coarse roots in first two harvests

* = P < 0.05, ** = P < 0.01, *** = P < 0.001

Table 2.2. Analysis of covariance with light treatment as a fixed factor and $\log_e$ biomass as a covariate for whole plants harvested throughout the experiment. Beta values are standardized regression coefficients. Lower table has means (±SE) in each treatment. Different letters denote significantly different means using a Bonferroni post-hoc, pair-wise, comparison test ($P < 0.05$)

	Light treatment (df = 2)		Biomass (df = 1)			Model (n = 61)	
Variable	F	P	Beta	F	P	R^2	P
LWR	3.06	ns	-0.029	0.05	ns	0.07	ns
SWR	6.35	**	0.738	53.14	***	0.46	***
RWR	4.34	*	-0.210	2.55	ns	0.09	*
FrWR	3.31	*	-0.406	10.00	**	0.14	**
CrWR	0.03	ns	0.669	39.42	***	0.41	***
RGR_{total}	8.08	***	0.476	23.20	***	0.49	***
RGR_{above}	6.30	**	0.540	30.85	***	0.51	***
RGR_{below}	8.85	***	0.376	12.84	***	0.42	***

Variable	Full sun	Artificial edge	Shade
LWR	0.46 (0.03) a	0.45 (0.03) a	0.55 (0.03) a
SWR	0.062 (0.010) a	0.073 (0.012) ab	0.075 (0.011) b
RWR	0.47 (0.03) a	0.48 (0.04) a	0.38 (0.03) b
FrWR	0.41 (0.04) a	0.42 (0.05) a	0.34 (0.03) b
CrWR	0.062 (0.014) a	0.058 (0.014) a	0.031 (0.015) a
RGR_{total}	0.95 (0.03) a	0.88 (0.04) a	0.73 (0.02) b
RGR_{above}	0.95 (0.02) a	0.88 (0.04) ab	0.76 (0.02) b
RGR_{below}	0.94 (0.03) a	0.88 (0.04) a	0.68 (0.03) b

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns - not significant; RGR is reported as $\log_e(g \cdot g^{-1}) \cdot wk^{-1}$

Table 2.3. Chi-square values and number of resprouts (in parentheses) are shown for each combination of light treatment and week harvested (df = 6)[1]

	Light treatment		
	Full sun	Artificial edge	Shade
Week 4	1.873 (0)	0.008 (2)	12.053 (2)
Week 7	0.292 (10)	0.021 (8)	1.139 (0)
Week 8	0.271 (15)	0.001 (13)	1.772 (0)
Week 9	0.184 (12)	0.013 (14)	0.739 (3)

[1]Chi-square was used to determine if there was an effect of clipping date (week) and light treatment on the number of *P. tomentosa* plants that resprouted. Significant chi-square for a three by four table at P = 0.05 is 12.59, thus we show an effect of light and week on the number of resprouts

Table 2.4. Means (±SE) of belowground biomass of *P. tomentosa* plants at final harvest of experiment by shade treatment and week (after germination) when plants were clipped (n = 2)

Shade treatment	Clipping treatment	Coarse root biomass	Total belowground biomass
Full sun	Not clipped	2.57 ± 0.68	4.25 ± 0.89
	Week 4	no survivors	no survivors
	Week 7	0.06 ± 0.016	0.42 ± 0.14
	Week 8	0.24 ± 0.056	0.69 ± 0.12
	Week 9	0.16 ± 0.030	0.72 ± 0.14
Artificial edge	Not clipped	1.35 ± 0.52	2.21 ± 0.62
	Week 4	none†	0.01 ± 0.001
	Week 7	0.05 ± 0.014	0.19 ± 0.029
	Week 8	0.08 ± 0.019	0.29 ± 0.051
	Week 9	0.25 ± 0.061	0.70 ± 0.15
Shade	Not clipped	0.34 ± 0.19	0.62 ± 0.25
	Week 4	none†	0.01 ± 0.003
	Week 7	no survivors	no survivors
	Week 8	no survivors	no survivors
	Week 9	0.05 ± 0.023	0.15 ± 0.069

† plants had only fine roots

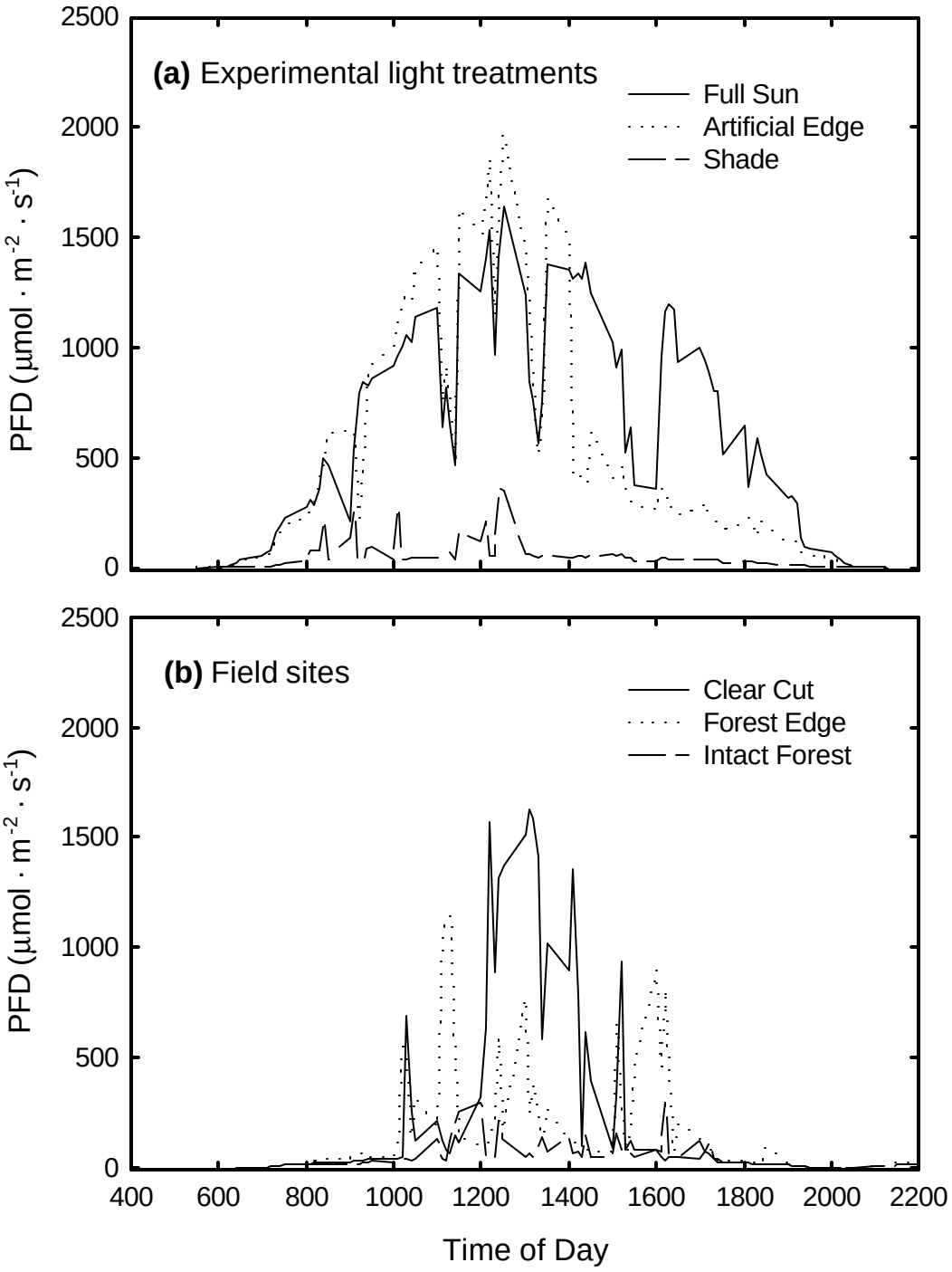

Figure 2.1. Photon flux density (PFD) from shade house treatments on July 25 (a) and at a site in Waterloo Wildlife Experimental Station on Sept. 9 in Athens Co., Ohio (b) every 10 minutes through the course of a day. Variations in patterns are due to differences in cloud cover on the two days

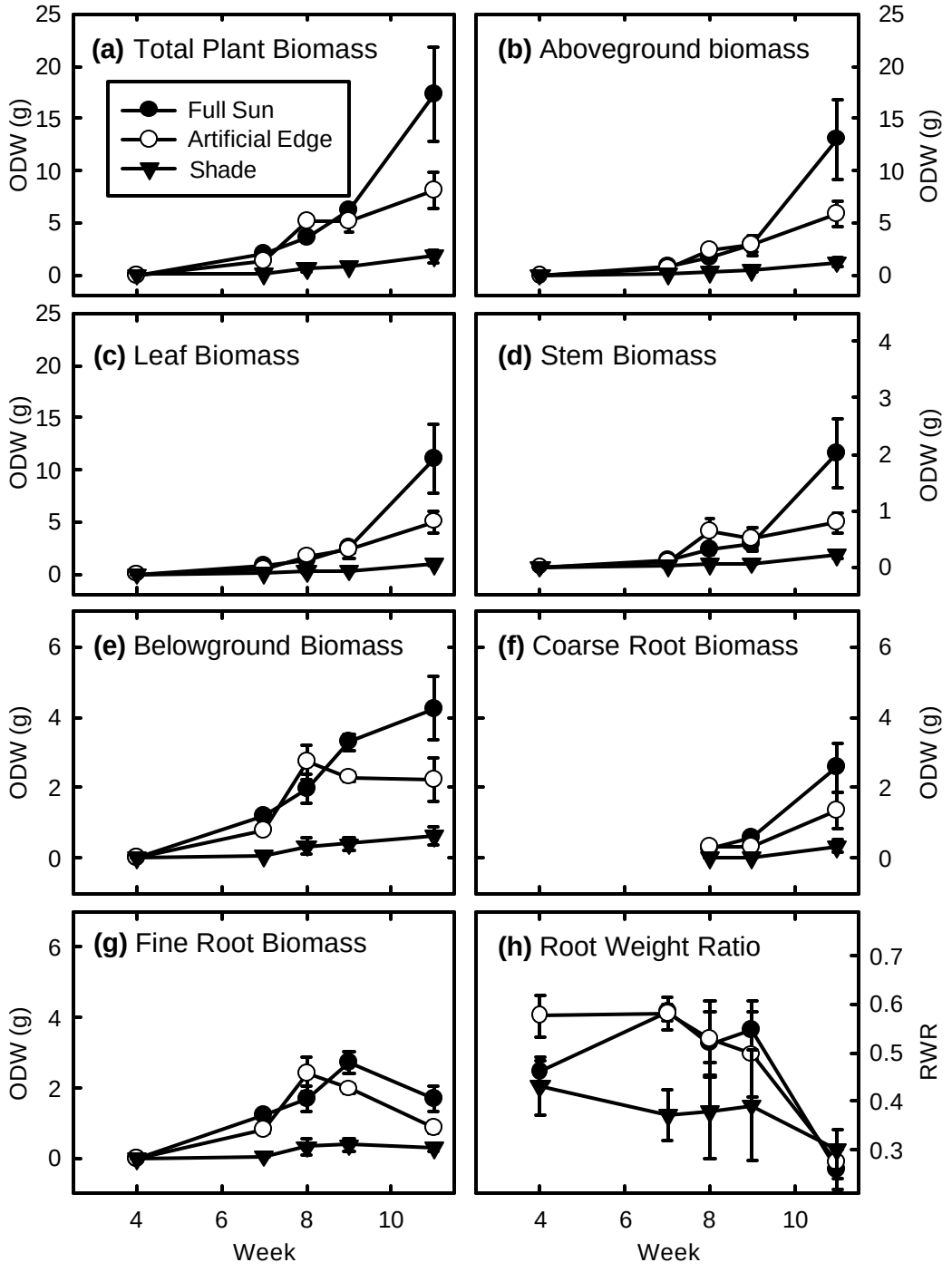

Figure 2.2. Means (±SE) of oven dry weights (ODW) of total plant biomass (a), aboveground biomass (b), leaf biomass (c), stem biomass (d), belowground biomass (e), coarse root biomass (f), fine root biomass (g) and root weight ratio (h) of unclipped plants over the course of the experiment in three light regimes

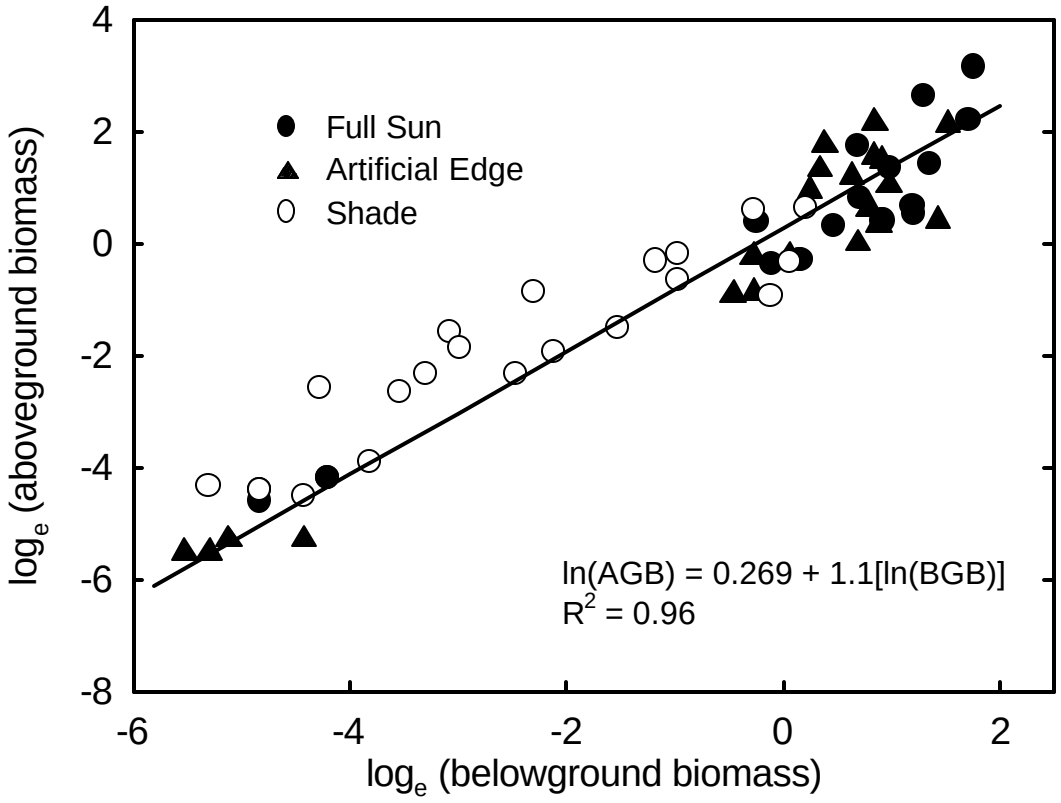

Figure 2.3. Log$_e$ transformed aboveground biomass and belowground biomass of unclipped plants. Regression coefficients were calculated using a Regression Model II Reduced Major Axis analysis. AGB = aboveground biomass, BGB = belowground biomass

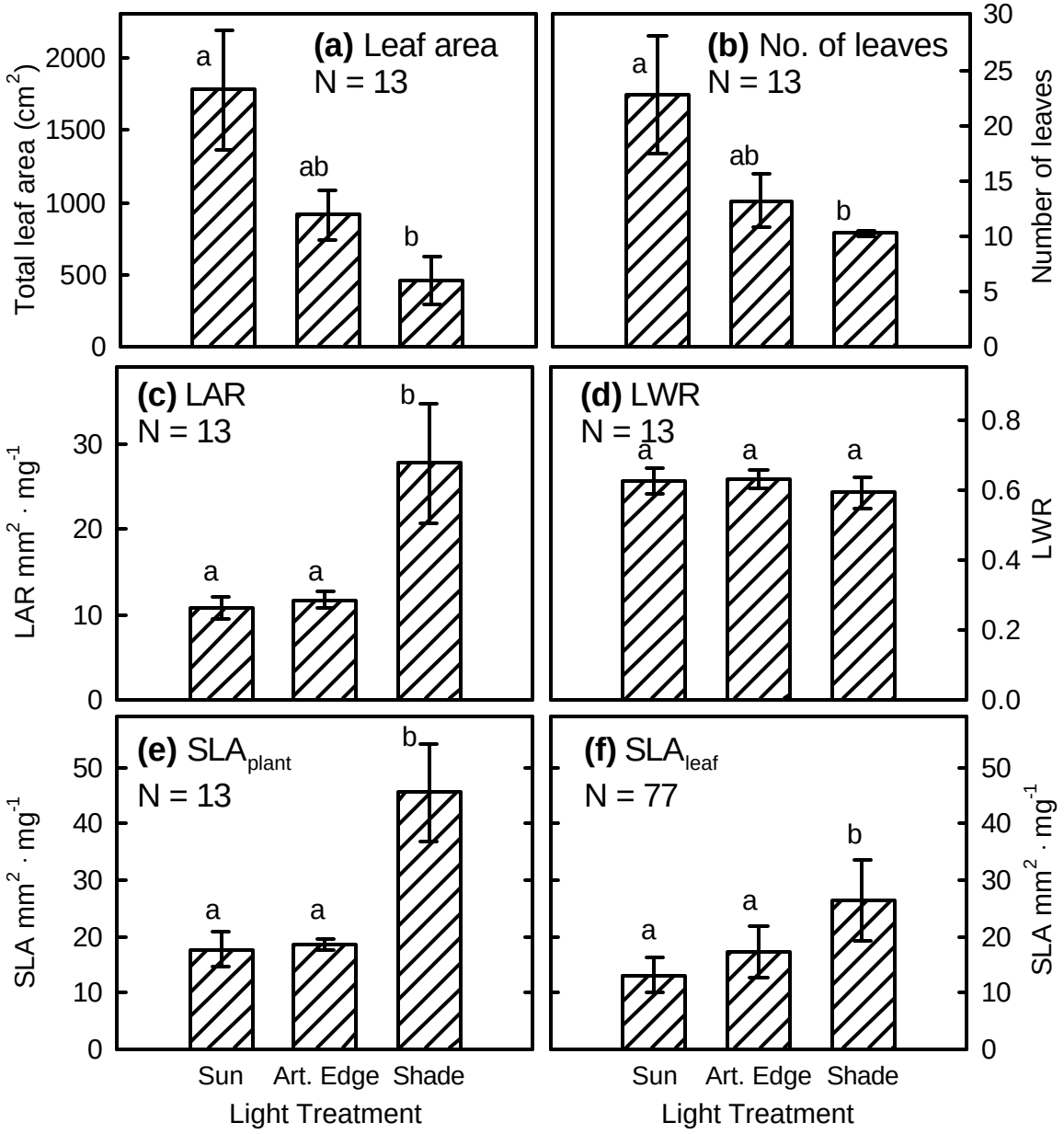

Figure 2.4. Means (±SE) of leaf attributes from unclipped plants harvested at the end of week 11 of the experiment from each light treatment: full ambient sun (sun), artificial edge (art. edge), and forest shade (shade) treatment. Total leaf area per plant (a). Number of leaves per plant (b). LAR = total leaf area / total plant dry weight (c). LWR = total leaf weight/total plant dry weight (d). SLA was calculated in two ways: on a whole plant basis (SLA_{plant}) (e) and on an individual leaf basis (SLA_{leaf}) (f). SLA = leaf area / leaf weight. Means with the same letter are not significantly ($P > 0.05$) different

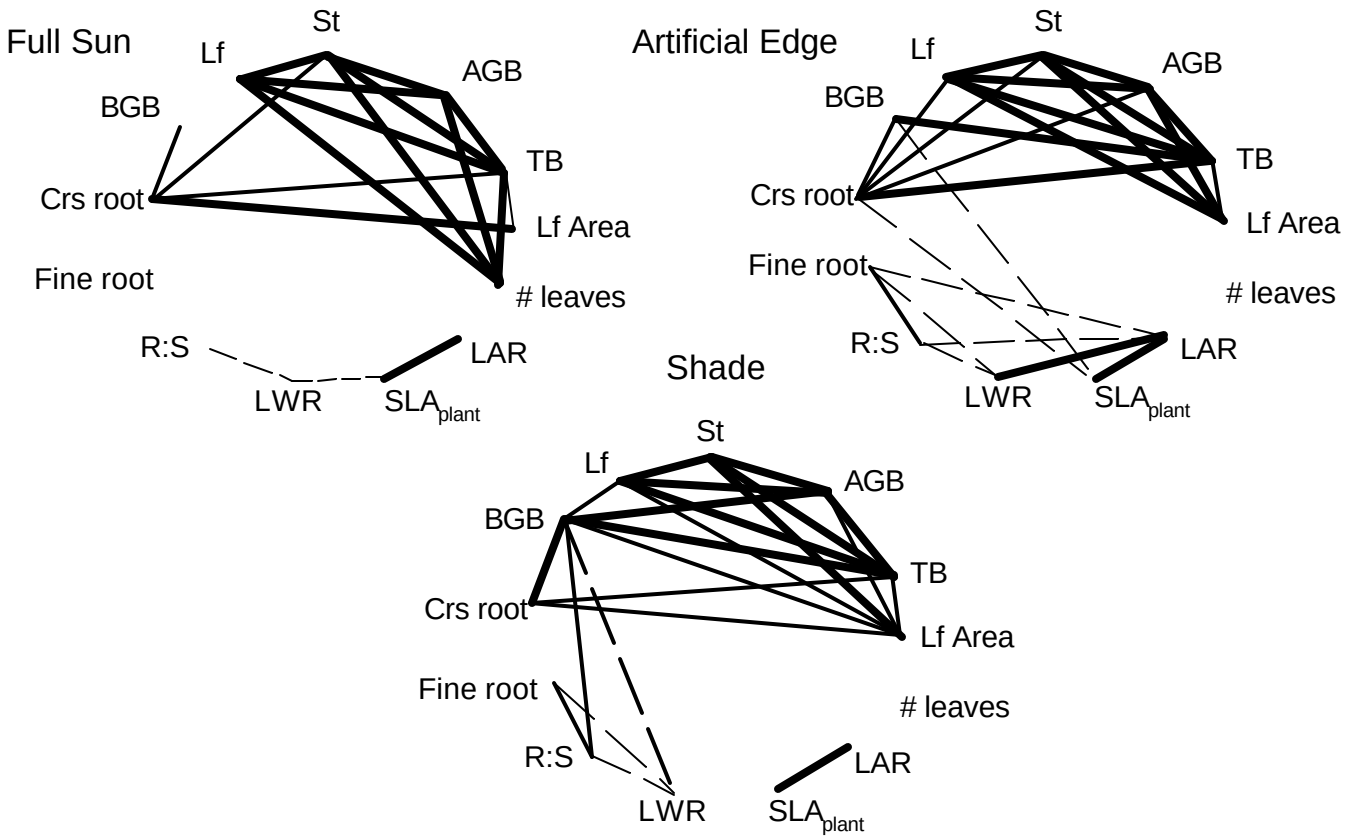

Figure 2.5. Correlation networks for unclipped plants harvested in week 11 in three light treatments. Lf = leaf biomass, St = stem biomass, AGB = aboveground biomass, TB = total biomass, Lf Area = plant leaf area, # leaves = number of leaves on plant, LAR = leaf area ratio, SLA_{plant} = plant specific leaf area, LWR = leaf weight ratio, R:S = root to shoot ratio, Fine root = Fine root biomass, Crs root = coarse root biomass, BGB = belowground biomass. Solid lines correspond to positive correlations. Dashed lines denote negative correlations. Thick lines denote significant correlations at $P < 0.05$ and thin lines correspond to significant correlations at $0.05 < P < 0.10$. All significant correlations had r-values > 0.85

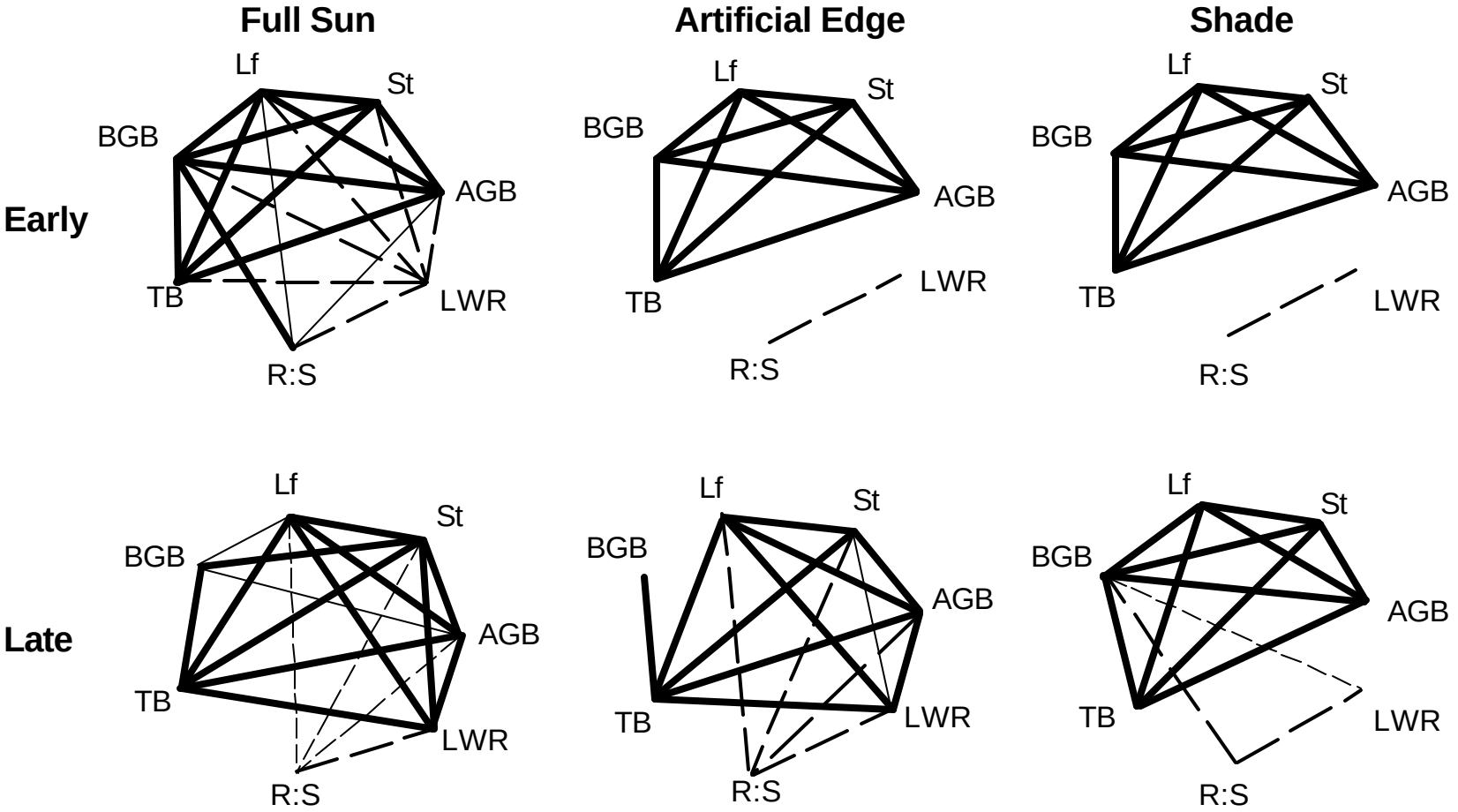

Figure 2.6. Correlation networks for plants in early part of experiment (weeks 4 and 7) and later part of the experiment (weeks 9 and 11) for each light treatment. See Fig. 2.5 legend for explanation of abbreviations

Chapter 3 : Phenotypic plasticity of *Paulownia tomentosa,* an invasive tree species of Eastern North America

Introduction

Paulownia tomentosa (Thunb.) Sieb. & Zucc. ex Steud. (Scrophulariaceae), known commonly as princess tree or empress tree, is native to east Asia and was introduced into the eastern United States in the 1840's (Hu, 1961). This tree is known to establish after disturbance in Virginia (Williams, 1993) and has become a pest species throughout much of the Great Smoky Mountains National Park (Langdon and Johnson, 1994). *Paulownia tomentosa* has become naturalized throughout much of the southeastern United States. Many populations grow along highways and rivers in SE Pennsylvania, Maryland, Delaware, West Virginia, Ohio, E Kentucky, Virginia, E Tennessee, and North Carolina (A. C. W. Longbrake, pers. obs.). Herbarium specimens have also been collected from Pennsylvania (near Pittsburgh), Missouri, Massachusetts, New Jersey, Arkansas, Alabama, and Georgia (Missouri Botanical Garden Herbarium Collection), as well as Washington, DC and Mississippi (Miami University Herbarium Collection). Early collections of *Paulownia tomentosa* were found in Washington DC in 1895 and the earliest collections in Ohio were in 1913 in Lawrence County along the Ohio River valley (Ohio State University Herbarium).

The ability to respond to the environment (phenotypic plasticity) is important for plants that encounter a changing environment through their life spans (Bradshaw, 1965). Early successional species, for example, are often

more plastic than later successional species (Bazazz, 1979). Plant traits may be constant in different environments (stability) or may change (plasticity). Different traits in the same organism may be plastic or stable, based on selection pressures for those traits. For example, number of seeds set is often plastic, while seed weight may be a stable trait. Furthermore, there may be changes in phenotypic plasticity throughout the life of an organism (Coleman, McConnaughay, and Ackerly, 1994).

Physiological and morphological characteristics of invasive plants may be important in allowing an invading species to survive and reproduce in new environments. Invasive, non-indigenous species in Hawaii had greater relative growth rates compared to natives (Pattison, Goldstein, and Ares, 1998). Further, plants can respond to their environment through phenotypic plasticity. Phenotypic plasticity may allow plants to be more successful in a wider variety of environments (Sultan, 1987 and 1992). Thus, phenotypic plasticity may be an important mechanism for non-indigenous plants to invade new areas (Williams, Mack, and Black, 1995; Weber and D'Antonio, 1999). The invasive fountaingrass (*Pennisetum setaceum*) was found to be more phenotypically plastic than other invasive plants and it had the greatest altitudinal gradient of invasive grasses in Hawaii (Williams, Mack, and Black, 1995).

A plant may exhibit phenotypic plasticity through its morphology or physiology. It has been suggested that the strategy of plants in nutrient-rich, stable environments may be in the form of increased morphological plasticity, whereas plants adapted to nutrient-poor or stressed environments may have

greater physiological plasticity (Grime, Crick, and Rincon, 1986). Greater physiological plasticity was found for *Metrosideros polymorpha*, a dominant Hawaiian tree growing in relatively nutrient-poor habitats along an altitudinal gradient (Cordell et al., 1998).

Because phenotypic plasticity imposes a cost on plant growth and/or reproduction (Scheiner, 1993), this mechanism is often thought to be adaptive. It has been suggested that a generalist species may use phenotypic plasticity as an adaptive trait to cope with a range of habitat variability (Bazazz, 1979). However, phenotypic plasticity may not always be adaptive (Taylor and Aarson, 1988; West-Eberhart, 1989). The specialization hypothesis suggests that species specialized to favorable environments will show greater phenotypic plasticity in a poor environment and this plasticity need not be adaptive (Lortie and Aarson, 1996).

Paulownia tomentosa is a sun-adapted plant able to grow fastest in high light environments suggesting its entry into forested ecosystems is facilitated by disturbance (Chapters 1 & 2). Even though *P. tomentosa* is commonly found in high light, marginal habitats (A.C.W. Longbrake, pers. obs.), volunteer plants are known to occur in intact primary and secondary forests in southeastern Ohio and New Jersey, associated with newly created tip-up mounds (B. C. McCarthy, pers. obs.). This is evidence that the species may be able to acclimate to a wide range of light availability. However, *P. tomentosa* is generally considered a shade intolerant species (Bonner, 1990).

Plants often respond holistically to a stress with many traits being correlated to each other (Schlichting, 1986). Plant traits such as specific leaf area, leaf area ratio, and leaf weight ratio are often positively correlated with relative growth rates in both herbaceous and woody species (Walters, Kruger, and Reich, 1993a, b; Cornelissen, Castro Díez, and Hunt, 1996; Hunt and Cornelissen, 1997; Lusk, Contreras, and Figueroa, 1997; Cornelissen, Castro Díez, and Carnelli, 1998; Poorter and Van Der Werf, 1998; Wang, Hawkins, and Letchford, 1998; Wright and Westoby, 1999). We wanted to see if these trends, found across many taxa, would be similar for the invasive tree, *P. tomentosa*. When traits are correlated, this may show evidence of constraints on phenotypic plasticity.

Naturalized populations of *P. tomentosa* are geographically widespread allowing us to compare phenotypic plasticity among populations when grown in a common garden. We will, therefore, compare the performance of plants from seeds from three disjunct populations of *P. tomentosa* from Ohio, West Virginia, and North Carolina in contrasting light environments. Objectives of this experiment were to (1) assess biomass allocation and physiological response of *P. tomentosa* to high and low light, (2) assess the plasticity within and across different naturalized populations of *P. tomentosa*, (3) explore the relationship between growth rates and allometric ratios, and (4) develop growth models for early ontogeny of *P. tomentosa* seedlings. *Paulownia tomentosa* is a good species for this study because it is invasive throughout much of its naturalized range and because of its potential commercial value.

Methods

Shade houses were set up in an experimental garden at Ohio University (39° 20’ 22” N, 82° 6’ 25” W; Athens Co.). The shade treatment was created by constructing shade boxes covered with untreated wood lattice and nylon screening material on the top, east, west, and south sides of the frame. The north side of the frame had only two layers of nylon screening to allow access into the shade house. The top of the frame had an extra layer of wood lattice offset so as to create smaller gaps between wood slats. The full sun treatment included only the frame of the shade house (without lattice or screening). Two replicates of each shade house were used. Fifty light measurements were taken every 10 cm at about 10 cm height in each light treatment using a point sensor (LI-190SA, Li-Cor, Lincoln, NE) to assess the light levels achieved using these treatments.

Mature capsules were collected in late fall from trees in three populations. The populations used were Athalia, Ohio (38° 30’ 03” N, 82° 18’ 51” W; Lawrence Co.), Charleston, West Virginia (38° 21’ 31” N, 81° 38’ 19” W; Kanawha Co.), and Pigeon River, North Carolina (35° 46’ 23” N, 83° 05’ 19” W; Haywood Co.). Seeds were collected from 4 trees in each population and kept separately in cold, dry storage until used. In June, seeds from each tree within each population germinated in flats placed in a germination chamber set for 12 h of light at 25°C and 12 h of dark at 15°C. Seeds germinated in about 10 days. Flats were then

placed into the shade houses to acclimate for 3 days before transplanting. Transplanted seedlings were about 1-2 cm tall.

Seedlings were transplanted into tall pots ($10 \times 10 \times 35.5$ cm, $L \times W \times H$) that were filled with 50% potting mix (Sunshine Mix II, Sun Gro Horticulture Inc., Bellevue, WA), 25% sand, and 25% local topsoil. Pots were kept upright in the field by using wood and wire frames. We also stapled wire mesh around the outside of the wooden frames to prevent small mammal herbivory on experimental plants.

Seedlings were watered daily the first two weeks after transplanting and weekly as needed thereafter. Seedlings that died in the first week were replaced. 120 seedlings were placed in each shade house in order to have five replicate plants for each harvest and treatment combination for a total of 480 plants in the experiment. Half of the seedlings were harvested 7 weeks after germination (July 27-30, 2000) and the other half 13 weeks after germination (Sept. 11-17, 2000). Roots of plants were carefully removed from the pots and washed. Leaves were analyzed for leaf area using Sigma Scan Pro 3.0 software (SPSS Inc., Chigaco, IL) and a video camera the day of harvest. Plant material was dried at 70°C until reading constant weight. Leaves, stems, coarse roots (roots with diameter of 1 mm or greater), and fine roots were weighed individually and recorded for each plant.

Allometric ratios measured included leaf weight ratio (LWR), stem weight ratio (SWR), coarse root weight ratio (CrWR), fine root weight ratio (FrWR), root weight ratio (RWR), root to shoot ratio (R:S), leaf area ratio (LAR), and specific

leaf area (SLA). All weight ratios were calculated as dry weight of plant organs divided by dry weight of the whole plant. Leaf area ratio is the leaf area divided by the total dry weight of the plant. Specific leaf area was measured in two ways: (1) on a whole plant basis (SLA_{plant}), in which total leaf area of the plant was divided by total dry weight of leaves, and (2) on a leaf basis (SLA_{leaf}), in which individual leaves were measured for leaf area, marked and, once oven dried, weighed individually. When possible, four leaves from each plant were measured for SLA_{leaf}.

Relative growth rates (RGR_{total}, RGR_{above}, and RGR_{below}) were calculated as relative growth per day for each plant using mean starting weights of 10 seedlings harvested at the time of out-planting. Net assimilation rate (NAR) was calculated for each seedling as a ratio of plant growth rate to leaf area ratio (Poorter and Van Der Werf, 1998).

On Aug. 9, measurements of photosynthesis rates were taken of nine randomly chosen seedlings in each light treatment. Seedlings chosen were temporarily removed from their light treatment and photosynthesis was measured in full sun and under a 30% shade cloth using a carbon dioxide leaf chamber analyzer (Analytical Development Co. Ltd., Type LCA3, Hobbarts, England). On Sept. 9, four leaf disks were taken from four randomly chosen plants in each population and treatment. Disks were analyzed for chlorophyll content using the DMF method (Moran and Porath, 1980; Moran, 1982; Inskeep and Bloom, 1985).

Light measurements of the shade treatment were compared to full sun values using a Wilcoxon Rank Sum analysis, since data were neither normal nor

homoscedastic. Plant biomass and leaf area data were analyzed using a General Linear Model Analysis of Variance (GLM ANOVA) with light as a fixed effect and population as a random effect. Tree was initially run as a nested factor within population, but the inclusion of this effect was not significant in the analyses, so it was consequently left out. These data were $\log_e$ transformed to meet assumptions of normality and homoscedasticity. Data from replicate shade houses were pooled after it was determined that there was no difference between replicates (blocks). Since plants in the second harvest were much larger than the first harvest plants, transformed data could not meet the assumption of homoscedasticity when analyzed together. The data were analyzed separately by harvest and *P* critical values for these analyses were Bonferroni-corrected to be $P < 0.025$ to keep overall experimental error equal to 0.05 (Sokal and Rohlf, 1995). A single degree of freedom planned comparison was conducted to compare the Ohio and West Virginia populations with the North Carolina population. We hypothesized that the sites with geographic proximity would be similar to each other and different than the southern population.

Since biomass measures were different across light treatments and ontogeny can affect allometry and relative growth rates (Venklaas and Poorter, 1998), an analysis of covariance (ANCOVA) was used with light as a fixed effect, population as a random effect, and the $\log_e$ of total plant biomass as the covariate. Again, first and second harvests were analyzed separately and a single degree of freedom planned comparison was conducted to compare

populations. *P* critical values were similarly adjusted to keep overall experiment error rate at $\alpha = 0.05$.

Allometric ratios and growth rates were regressed against each other using a Reduced Major Axis Model II Regression in Excel (add-in by M. Sawada, www.uottawa.ca/academic/arts/lpcweb/). This type of analysis is appropriate when both variables in the regression model have associated error (Sokal and Rohlf, 1995).

Chlorophyll content and photosynthesis rates were tested for normality with the Omnibus test (D'Agostino, Belanger, and D'Agostino, Jr., 1990) and homoscedasticity with the Modified Levene Equal Variance test (Hintze, 1997). Data were $\log_e$ transformed to meet assumptions of normality. Chlorophyll *a* and *b* content was analyzed with a multivariate analysis of variance (MANOVA) with light treatment and population in the model. Significant effects were then analyzed with one-way ANOVAs for chlorophyll *a* and *b* content, total chlorophyll, and chlorophyll *a* to *b* ratio. Photosynthesis rates were calculated in three ways: on a leaf area basis as measured and on a mass basis calculated using mean SLA_{plant} or SLA_{leaf} values. Photosynthesis rates were analyzed with a GLM ANOVA with light treatment (full sun or shade) and shading (whether measured under full sun or a 30% shade cloth) as fixed effects.

Models were developed for plants from each light treatment and harvest separately, using path analyses (Schumacker and Lomax, 1996). Log_e of net assimilation rate and leaf area ratio were used to meet the assumptions of normality and homoscedasticity of the regression analyses. Total relative growth

rate and net assimilation rate were used as response variables. Leaf weight ratio, $\log_e$ of total plant biomass, and leaf area ratio were variables allowed in the models. Only significant relationships and correlations are shown in the models. All analyses were conducted using NCSS 97 (Hintze, 1997).

Results

Light

Amount of light available in the shade treatment was significantly lower than full sun ($Z = 7.79$, $P < 0.001$). The mean photon flux density in the shade treatment was about 6% of full sun (shade = 124 ± 6.4 μmol $m^{-2} \cdot s^{-1}$; sun = 2020 ± 25.8 μmol $m^{-2} \cdot s^{-1}$).

Effect of light on plants

In the first harvest, there was no effect of light or population on any biomass measure (Table 3.1). The only significant effect was a light by population interaction for stem biomass due to a change in ranking order among populations (Table 3.1). In the second harvest, full sun plants were larger than shade plants for all variables measured except coarse root biomass (Table 3.1). Fine and coarse root biomass had a significant population effect and the only significant light by population interaction was for coarse root biomass (Table 3.1).

In the first harvest, only LAR, SLA, and NAR were affected by light treatment in the first harvest (Table 3.2) with LAR and SLA greater and NAR lower in low light (Figure 3.2). In the second harvest, most weight ratios (except fine root weight ratio), R:S, SLA_{leaf} and RGR_{below} were all affected by light

environment (Table 3.2). Plants in low light had higher LWR, SWR and SLA, but lower RWR, R:S, and RGR_{below} (Figure 3.1, 3.2).

Photosynthesis rates, taken on a per leaf area basis responded significantly to effects of the light treatment in which plants were grown and the light availability during measurement (Figure 3.3a; $F = 34.86$, $P < 0.001$ - light treatment; $F = 16.78$, $P < 0.001$ - shading). However, since leaves of plants grown in full sun were much thicker than those in shade, these differences between light treatment are eliminated if calculated on a per dry gram of leaf basis estimated either using SLA_{plant} or SLA_{leaf}. Photosynthesis measured on a per gram basis only showed an effect of light availability at the time of measurement, not of light treatment in which plants were grown (Figures 3b, 3c; SLA_{plant}, $F = 23.53$, $P < 0.001$; SLA_{leaf}, $F = 21.90$, $P < 0.001$).

Chlorophyll content of leaves was also calculated on a per leaf area and wet weight basis. The MANOVA showed only a significant light treatment effect. When chlorophyll content was calculated on a per leaf area basis, shade plants had lower chlorophyll content (0.018 ± 0.001 mg $\cdot$ cm^{-2}) than those in full sun (0.025 ± 0.001 mg $\cdot$ cm^{-2}; $F = 27.52$, $P < 0.0001$). When calculated on a weight basis, this trend was reversed (1.81 ± 0.08 mg $\cdot$ g^{-1}, 1.28 ± 0.07 mg $\cdot$ g^{-1} shade and full sun respectively; $F = 27.52$, $P < 0.0001$). The ratio of chlorophyll *a* to *b* in leaves was always greater in plants in the full sun treatment than those in shade (4.47 ± 0.06, 3.73 ± 0.02, sun and shade plants respectively; $F = 165.03$, $P < 0.0001$).

Effects of ontogeny

Leaf area ratio and specific leaf area increased from first to second harvests (Figure 3.2). Relative growth rates decreased from first harvest to second harvest (Figure 3.2), although beta coefficients were always positive (Table 3.2). Comparison of beta coefficients further reveals the shift in biomass allocation from aboveground biomass in the first harvest to belowground biomass in the second harvest. Leaf weight ratio was negatively related to biomass in the first harvest, but positively related in the second harvest (Table 3.2). Root measures including RWR, FrWR, CrWR, and R:S, were positively related to plant size in the first harvest and negatively related to plant size in the second harvest (Table 3.2).

Differences between populations

Notwithstanding differences found between light treatments and through ontogeny, the ANCOVA revealed differences among populations. Significant differences among populations were found for LWR, RWR, FrWR, R:S, SLA_{leaf}, and RGR_{below} in the first harvest (Table 3.2; Figures 3.1, 3.2). There were continued population effects of RWR, CrWR, R:S, SLA_{leaf}, and RGR_{below} in the second harvest. When there was a significant effect of population, the planned comparisons between the Ohio and West Virginia population compared to the North Carolina population were also significant in support of our hypothesis (Table 3.2). There were significant light by population interactions in the first harvest with SLA_{leaf} only and in the second harvest, there were marginally significant interactions with CrWR, R:S, RWR, and RGR_{below}.

Allometric analysis

Three significant relationships were found between $\log_e$-transformed variables. Leaf area ratio and SLA_{plant} were positively related to each other (R^2 = 0.92; $P < 0.01$). Also, net assimilation rate was negatively related to both LAR and SLA (R^2 = 0.88; $P < 0.01$; R^2 = 0.96; $P < 0.01$, respectively). There was no change in relationship due to light treatment, population, or harvest date.

Some relationships were only found in the first or second harvests. A positive linear relationship was found for $\log_e$ transformed aboveground biomass and belowground biomass in first harvest (R^2 = 0.86; $P < 0.05$; β = 1.23). This relationship was less clear in the second harvest due to shade plants obscuring the trend (R^2 = 0.21; $P < 0.05$; β = 0.57).

The second harvest data showed significantly different relationships of full sun and shade plants between RGR_{total} and its components. Log_e of net assimilation rate for shade plants was positively correlated to RGR_{total}, with the regression line explaining almost 80% of variation (Figure 3.4a). Leaf area ratio and SLA_{plant} for shade plants were negatively correlated with RGR_{total}; the regression line had high R^2 for LAR but low for SLA_{plant} (Figures 3.4b, 3.4c). Log_e of net assimilation rate for full sun plants had a slight, but significant, positive relationship to RGR_{total} with a low R^2 (Figure 3.4a). RGR_{below} data were only significantly related to SLA_{plant} (R^2 = 0.26; $P < 0.05$; not shown). Relationships of RGR_{above} to LAR and NAR were similar to those found for RGR_{total}. However, RGR_{above} was only significantly related to SLA_{plant} in full sun (R^2 = 0.12; $P < 0.05$, not shown).

Growth models

Models using RGR_{above} and RGR_{below} were very similar in their relationships between variables, so only models with RGR_{total} will be reported here. The first harvest model for full sun plants showed a weak relationship between LAR and RGR (Figure 3.5a). This was the only model that had a significant relationship between LWR and RGR (Figure 3.5a). In this model, net assimilation rate and, to a lesser extent LWR and plant total biomass, are most important in determining RGR.

In the first harvest model for shade plants, leaf weight ratio was only related to NAR (Figure 3.5b). There were strong relationships between LAR and NAR with RGR. However, LAR and NAR were strongly negatively related (Figure 3.5b).

For plants from the second harvest, leaf weight ratio was correlated to all variables of full sun plants and to NAR and LAR of shade plants; however, the path analyses for these plants did not have any significant relationships with LWR (so it is left out; Figure 3.6). Models for plants in both light treatments had high values relating LAR and NAR to RGR and a strong negative relationship between LAR and NAR (Figure 3.6).

Discussion

Paulownia tomentosa responded as a typical sun-adapted species when grown in shade. Leaves were thinner and there was a greater investment in leaf area per unit biomass (SLA and LAR) when grown in the shade as predicted by Grime (1979) and Givnish (1988). However, leaves of plants grown in either light

treatment were able to photosynthesize at similar rates (when calculated on a per weight basis) when newly exposed to high or low light. That is, there was no physiological change in photosynthetic rate at the light levels measured, only a morphological difference between leaves.

The results of this study are somewhat different than those found for mid-successional trees grown at different light levels (Bazzaz and Carlson, 1982). The difference in results could be due to differences in the light treatments between studies. Our study changed overall light availability and provided sunflecks of varying light intensity similar to forest understories (Canham et al., 1996; Robison and McCarthy, 1999). Plants in the shade had long lasting sun flecks of up to 35% of full sun. This may have limited the physiological response of *P. tomentosa*.

The ratio of chlorophyll *a* to *b* was significantly different between light treatments and as expected sun plants had greater ratios than shade plants (Givnish, 1988). The lack of chlorophyll ratio response has been reported (Chow, Adamson, and Anderson, 1991; Wayne and Bazzaz, 1993; Robison and McCarthy, 1999), as well as higher chlorophyll ratios for seedlings grown in low light (Lei and Lechowicz, 1998). However, this change in chlorophyll *a* to *b* ratio did not translate into different rates of photosynthesis.

All plants regardless of light treatment originally invested a high proportion to belowground structures. There was a shift in emphasis from belowground biomass accumulation early in development to aboveground biomass accumulation in the second harvest. This shift in biomass allocation has been

shown previously for this species (Chapter 2). Relative growth rates were high for woody seedlings in both harvests compared to other tree species (Canham et al., 1996; Cornelissen, Castro Díez, and Hunt, 1996; Swanborough and Westoby, 1996; Wang, Hawkins, and Letchford, 1998; Wright and Westoby, 1999).

Research on tropical tree seedlings and saplings has shown that pioneer species are often more flexible in plant traits such as leaf area ratio, specific leaf area, and relative growth rates (Veneklaas and Poorter, 1998; Valladares et al., 2000). A study of North American hardwood species found that slow growth rates were correlated to low survivorship and that shade intolerant species showed greater leaf area ratio and specific leaf area than shade tolerant species (Walters and Reich, 1996). This is well supported with this study of *P. tomentosa*, further evidence of its ecological niche as an early successional plant intolerant of shade.

The overall positive relationship between specific leaf area and leaf area ratio is a relationship that holds across woody species (Cornelissen, Castro Díez, and Hunt, 1996; Hunt and Cornelissen, 1997; Wright and Westoby, 1999). In the phenotypic response of *P. tomentosa*, relative growth rates were negatively correlated with leaf area ratio and specific leaf area. However, relationships among taxa suggest that fast-growing species have high leaf area ratio and specific leaf area (*e.g.*, Hunt and Cornelissen, 1997). Other researchers have also noted that phenotypic response is opposite to the evolutionary relationship (Walters, Kruger, and Reich, 1993a; Kitajima, 1994). Evolutionarily, plants with

high investment in leaf area per unit biomass also have high relative growth rates; however, since *P. tomentosa* is a sun-adapted plant, it increases leaf area ratio and specific leaf area in response to low light, but this does not increase its growth rate, since light is limited. In fact, plants grown in low light had lower photosynthetic rates per leaf area. Greater thickness of leaves produced by plants in high light accounted for the greater photosynthetic rates in high light.

Growth models show similar patterns to others (Poorter, 1989; Poorter and Remkes, 1990). Correlations derived from the models closely resemble correlations found between variables (as per Schumacker and Lomax, 1996). This suggests that the changes in relationships found in growth models are due to the interaction of variables in the model. Other studies have also shown that net assimilation rate and leaf area ratio are important in determining relative growth rate, but due to a negative relationship between them, only one of these is significantly correlated to growth rate (Poorter, 1989; Poorter and Remkes, 1990). Relative growth rate is often not related to net assimilation rate (Poorter and Van Der Werf, 1998; Wright and Westoby, 1999; but see Walters, Kruger, and Reich, 1993b). Instead, relative growth rate is most often related to leaf area ratio or specific leaf area (Walters, Kruger, and Reich, 1993a,b; Cornelissen, Castro Díez, and Hunt, 1996; Hunt and Cornelissen, 1997; Lusk, Contreras, and Figueroa 1997; Cornelissen, Castro-Díez, and Carnelli, 1998; Poorter and Van Der Werf, 1998; Wang, Hawkins, and Letchford, 1998; Wright and Westoby, 1999). In this study, only plants grown in shade in the first harvest show leaf area ratio to be more important than net assimilation rate in determining relative

growth rate. We found leaf weight ratio not to be important in determining growth rate, in contrast to other studies that have found significant relationships between these variables (Walters, Kruger, and Reich, 1993a,b; Lusk, Contreras, and Figueroa, 1997; Cornelissen, Castro-Díez, and Carnelli, 1998; Poorter and Van Der Werf, 1998).

Paulownia tomentosa plants showed significant population and genotype (population) by environment interactions, thus indicating phenotypic plasticity in various allocation and growth traits measured in high and low light. However, the species was clearly more morphologically plastic than physiologically plastic. Early successional habitats may be considered relatively resource rich (Bazzaz, 1979). These results and others suggest that *P. tomentosa* is an early successional species, intolerant of shade (Chapters 1 & 2). Our results support the model that in resource rich environments, plants will tend to be more morphologically plastic than physiologically plastic (Grime, Crick, and Rincon, 1986; although morphology obviously has a basis in physiology; Bradshaw, 1965).

Paulownia tomentosa seedlings die back to ground level over the winter unless their stems are thick and woody (A. C. W. Longbrake, pers. obs.). Since seedlings are sensitive to cold winter weather, it is interesting that variables relating to future resprouting success (see Chapter 2), specifically root weight ratio and growth rate of roots, were significantly different among populations (Table 3.2). The North Carolina population may not have invested enough biomass in roots to resprout the following season. Green stems die back each

winter and plants must resprout from energy invested in the root system (A. C. W. Longbrake, pers. obs.). Thus, the species shows evidence of rapid adaptability to a range of environmental conditions. Notwithstanding the adaptability and phenotypic plasticity of *P. tomentosa*, its response to low light suggests that it will not be an invasive tree in intact forest canopies. Small-scale disturbances such as a tree fall, may allow enough light availability to allow seeds to germinate, but, despite high growth rates, *P. tomentosa* may not be able to reach the canopy before it closes. The species can persist by resprouting for several years (Chapter 1). However, a single tree-fall gap may not be a large enough in space and time for *P. tomentosa* establishment. Larger gaps of several trees, repeated canopy openings, or a longer growing season may allow enough light for germination and time before canopy closure for this fast-growing species to be established in secondary forests. This possibility will need further study.

Even though *P. tomentosa* is not currently an invasive species in Ohio, an increase in temperature of a few degrees may allow the species to establish and persist. Some evidence of this is suggested by the establishment of trees within cities farther north of its range, such as Athens, Ohio (because urban areas are heat islands). Further, the presence of mature trees further north of its naturalized range has allowed for their occasional establishment in natural areas. Therefore, its current naturalized range may expand northward, given appropriate environmental conditions.

Paulownia tomentosa is a shade intolerant species. However, it shows a rapid ability to acclimate to low light conditions. Whether it will be able to persist in habitats of low light remains to be seen, although some persistence in low light is suggested by other studies (Chapter 1) and field observations. *Paulownia tomentosa* seems to be most successful occupying the niche of an early successional species with high morphological phenotypic plasticity and high growth rates. We have shown that the species can form locally adapted populations in only 160 years (approximately 20 generations). This adaptability and phenotypic plasticity may be important for non-native plant species to invade new ecosystems. Since it has only been in the United States for a short time, this study suggests that it may continue to expand its range.

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Table 3.1. ANOVA of biomass measures for all plants[a].

	Effect in the Model					
	Light		Population		Light × Pop	
Variable	*F*	*P*	*F*	*P*	*F*	*P*
FIRST HARVEST						
Total biomass	21.27	ns	1.49	ns	2.27	ns
Above-ground biomass	23.75	ns	1.95	ns	2.02	ns
Leaf biomass	28.81	ns	2.15	ns	3.12	ns
Stem biomass	19.75	ns	2.29	ns	4.22	*
Below-ground biomass	16.71	ns	1.23	ns	2.21	ns
Fine root biomass	18.99	ns	0.60	ns	2.88	ns
Coarse root biomass	<0.01	ns	1.46	ns	0.20	ns
Leaf area	0.04	ns	3.25	ns	2.07	ns
SECOND HARVEST						
Total biomass	228.48	**	0.48	ns	0.14	ns
Above-ground biomass	256.23	**	0.70	ns	0.05	ns
Leaf biomass	178.37	**	1.02	ns	0.19	ns
Stem biomass	157.13	**	1.50	ns	1.89	ns
Below-ground biomass	367.37	**	1.85	ns	0.81	ns
Fine root biomass	404.05	***	5.06	***[b]	0.74	ns
Coarse root biomass	29.62	ns	8.05	***[b]	7.14	***
Leaf area	55.94	*	0.87	ns	1.87	ns

[a]Biomass measures were $\log_e$ transformed to meet assumptions of normality and homoscedasticity. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = not significant.
[b]Significant single degree of freedom planned comparison (see text for details)

Table 3.2. ANCOVA of allometric measurements of phenotypic plasticity experiment. Beta (*b*) is the standardized regression coefficient.

	Light		Population		L × P		Biomass		
Variable	*F*	*P*	*F*	*P*	*F*	*P*	*b*	*F*	*P*
FIRST HARVEST									
Leaf weight ratio	10.92	ns	6.16	**[a]	1.81	ns	-0.269	1.74	***
Stem weight ratio	2.52	ns	1.57	ns	0.97	ns	-0.400	27.43	***
Root weight ratio	9.51	ns	6.26	**[a]	1.96	ns	0.338	19.38	***
Fine root weight ratio	8.29	ns	5.38	**[a]	2.23	ns	0.273	12.19	***
Coarse root wt ratio	0.40	ns	1.78	ns	1.71	ns	0.570	72.63	***
Root/shoot	9.46	ns	5.81	**[a]	1.96	ns	0.325	17.69	***
Leaf area ratio	65.40	*	2.23	ns	1.04	ns	-0.030	0.03	ns
SLA_{plant}	213.45	**	1.46	ns	0.52	ns	0.042	0.51	ns
SLA_{leaf}	113.95	**	4.60	*[a]	4.70	*	-0.050	1.56	ns
Net assimilation rate	8.58	*	2.89	ns[a]	0.99	ns	0.180	8.17	**
RGR_{total}	6.74	ns	1.72	ns	2.15	ns	0.733	237.35	***
RGR_{above}	9.29	ns	1.98	ns	2.76	ns	0.640	155.63	***
RGR_{below}	4.85	ns	3.16	*[a]	0.90	ns	0.779	266.67	***
SECOND HARVEST									
Leaf weight ratio	105.93	**	2.47	ns	1.50	ns	0.733	245.89	***
Stem weight ratio	142.62	**	0.58	ns	0.18	ns	-0.503	63.38	***
Root weight ratio	75.32	*	3.96	*	2.17	†	-0.707	223.85	***
Fine root weight ratio	22.28	ns	0.25	ns	0.66	ns	-0.819	317.58	***
Coarse root wt ratio	46.47	*	4.12	*	2.87	†	-0.208	14.25	***
Root/shoot	97.46	*	4.75	*	1.27	†	-0.731	301.90	***
Leaf area ratio	16.37	ns	1.94	ns	1.80	ns	-0.707	255.39	***

Table 3.2. continued.

SLA_{plant}	29.51	ns	1.39	ns	1.66	ns	-0.755	333.48	***
SLA_{leaf}	1405.1	***	16.79	***[a]	3.56	*	-0.010	0.50	ns
Net assimilation rate	24.39	ns	0.13	ns	0.84	ns	0.835	313.96	***
RGR_{total}	20.09	ns	2.48	ns	1.60	ns	0.856	1423.06	***
RGR_{above}	9.31	ns	2.71	ns	1.00	ns	0.922	1745.09	***
RGR_{below}	83.55	*	4.50	*[a]	3.16	†	0.296	52.26	***

† = $P < 0.10$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = not significant.
[a]Significant single degree of freedom planned comparison (see text for details)

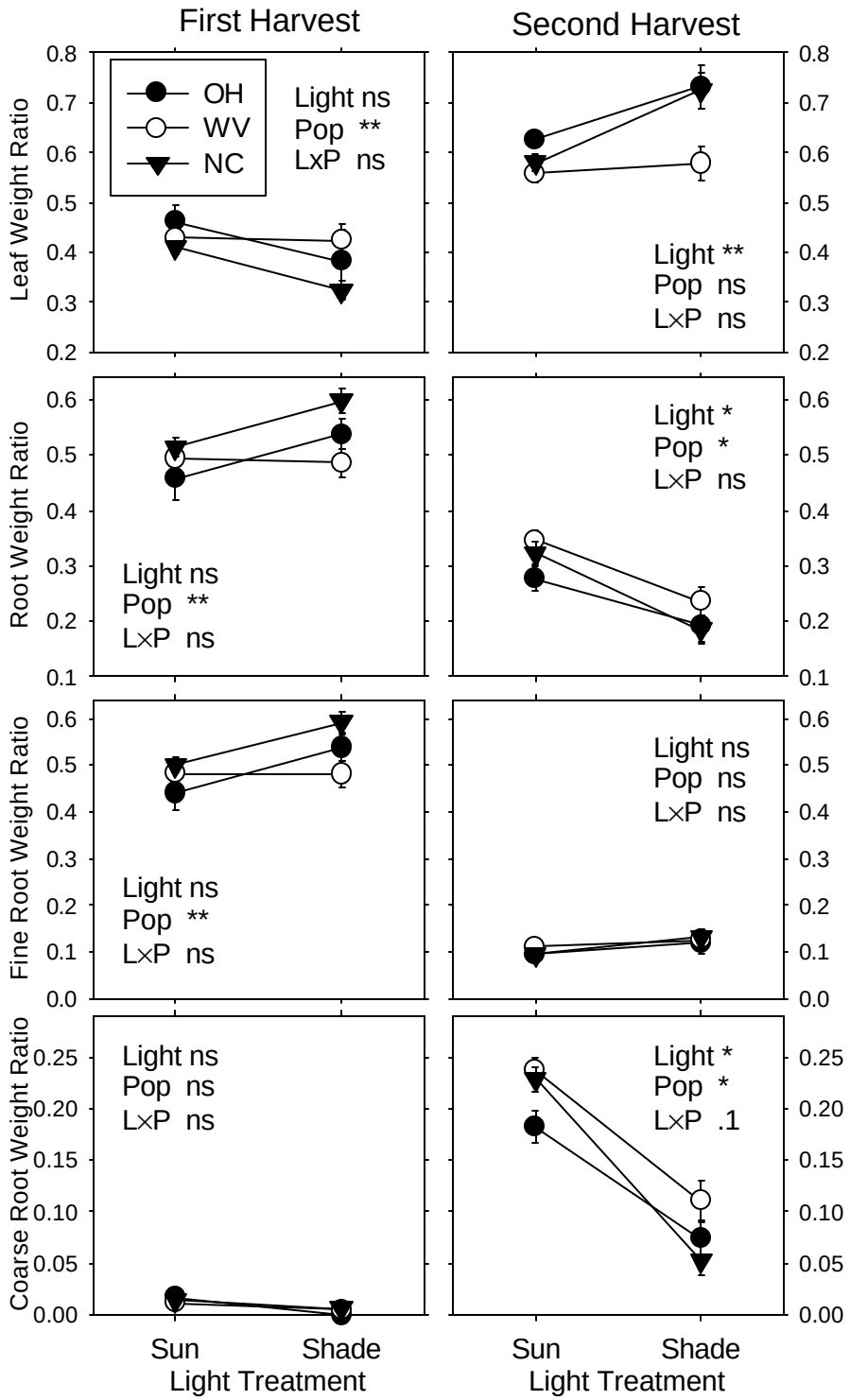


Figure 3.1. Weight ratio measures for plants in the first and second harvests. Different symbols show the mean (± SE) for each population. Partial results of ANCOVAs are given in each panel.

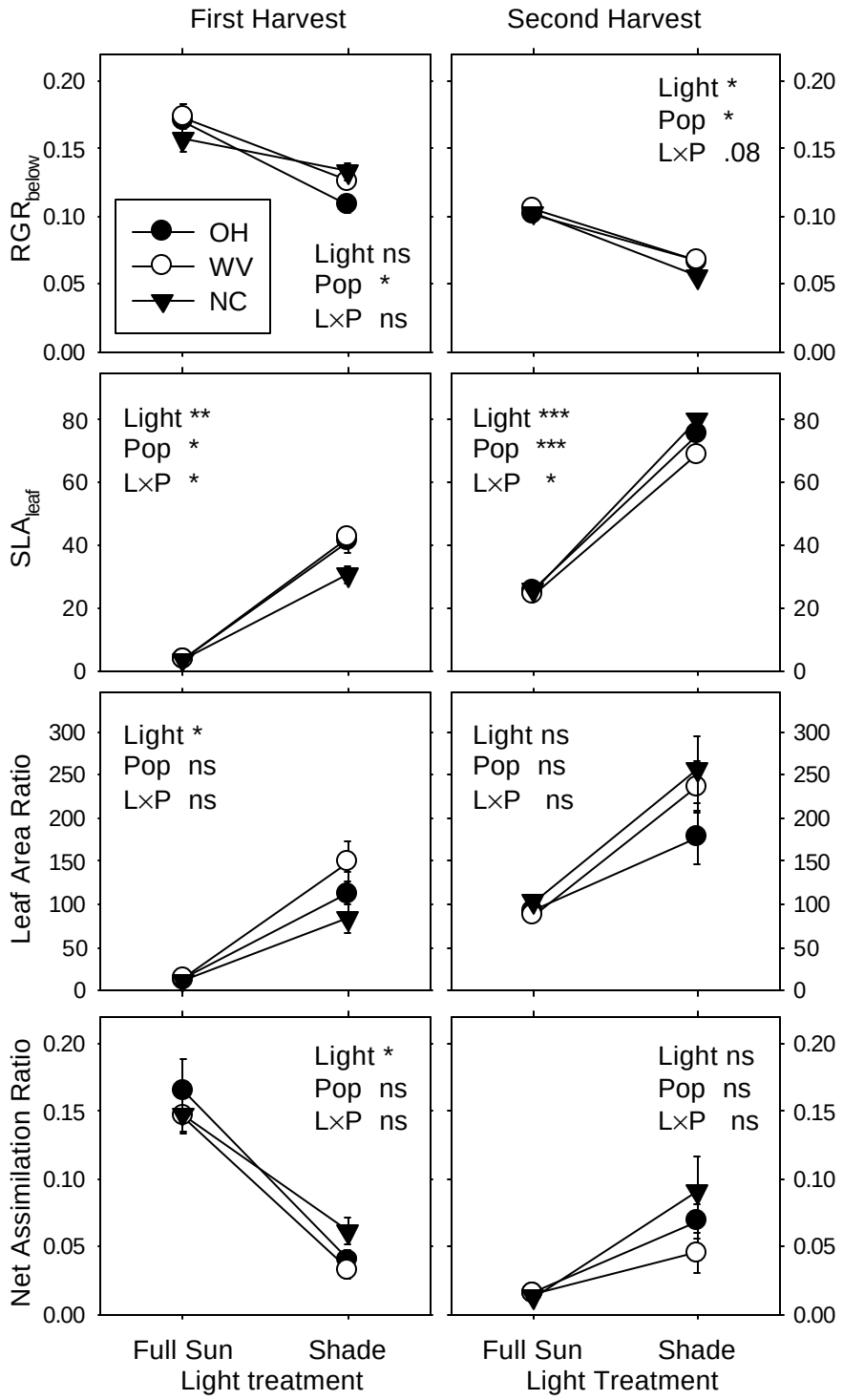


Figure 3.2. Growth and leaf measures for plants in the first and second harvests. Different symbols show the mean (± SE) for each population. Partial results of ANCOVAs are given in each panel.

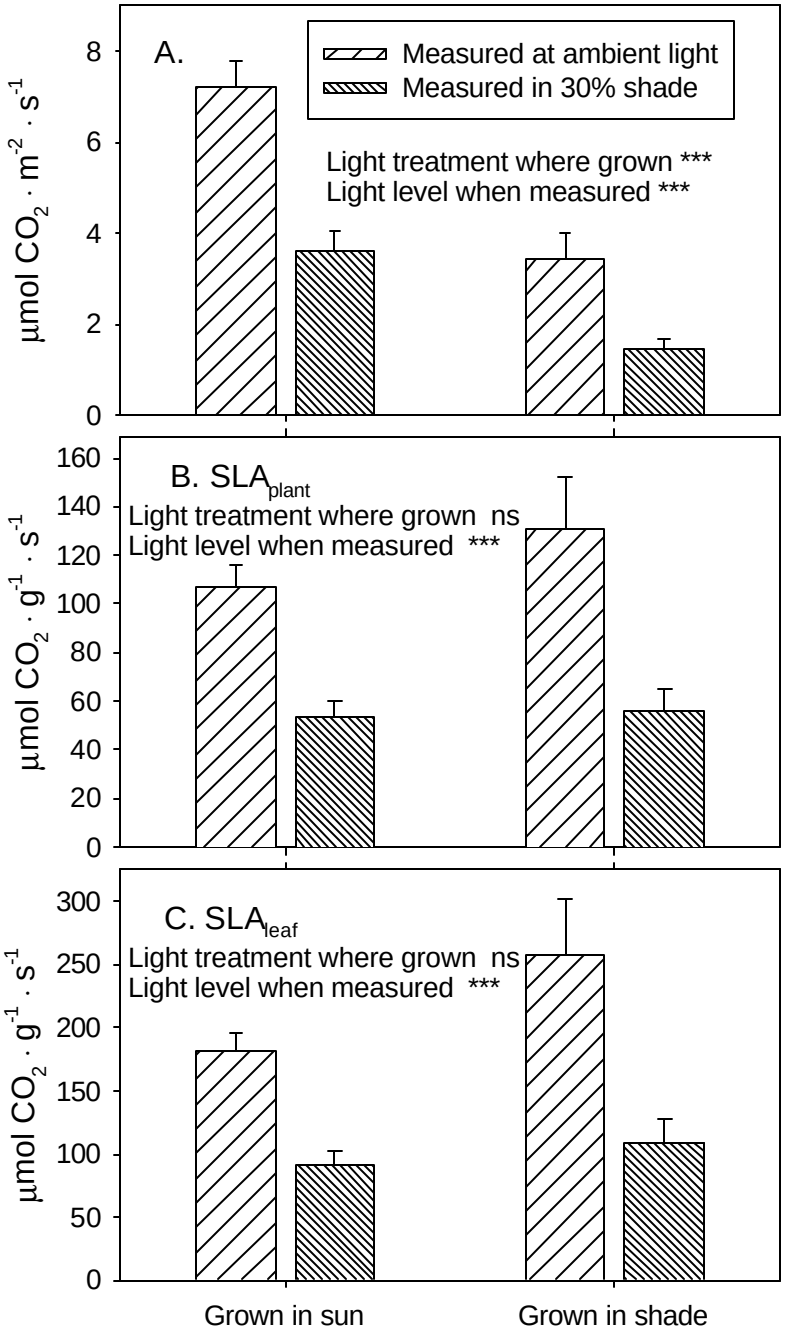


Figure 3.3. Rate of photosynthesis (± SE) calculated on a per area basis (a), on a gram dry weight basis using SLA_{plant} data (b), and on a gram dry weight basis using SLA_{leaf} data (c) for plants either grown in full sun or shade treatments. Plants were removed from their light treatment and readings were taken in full sun (open striped bars) or under a 30% shade cloth (densely striped bars). Significant terms of the ANOVA are shown in each panel. *** = $P < 0.001$.

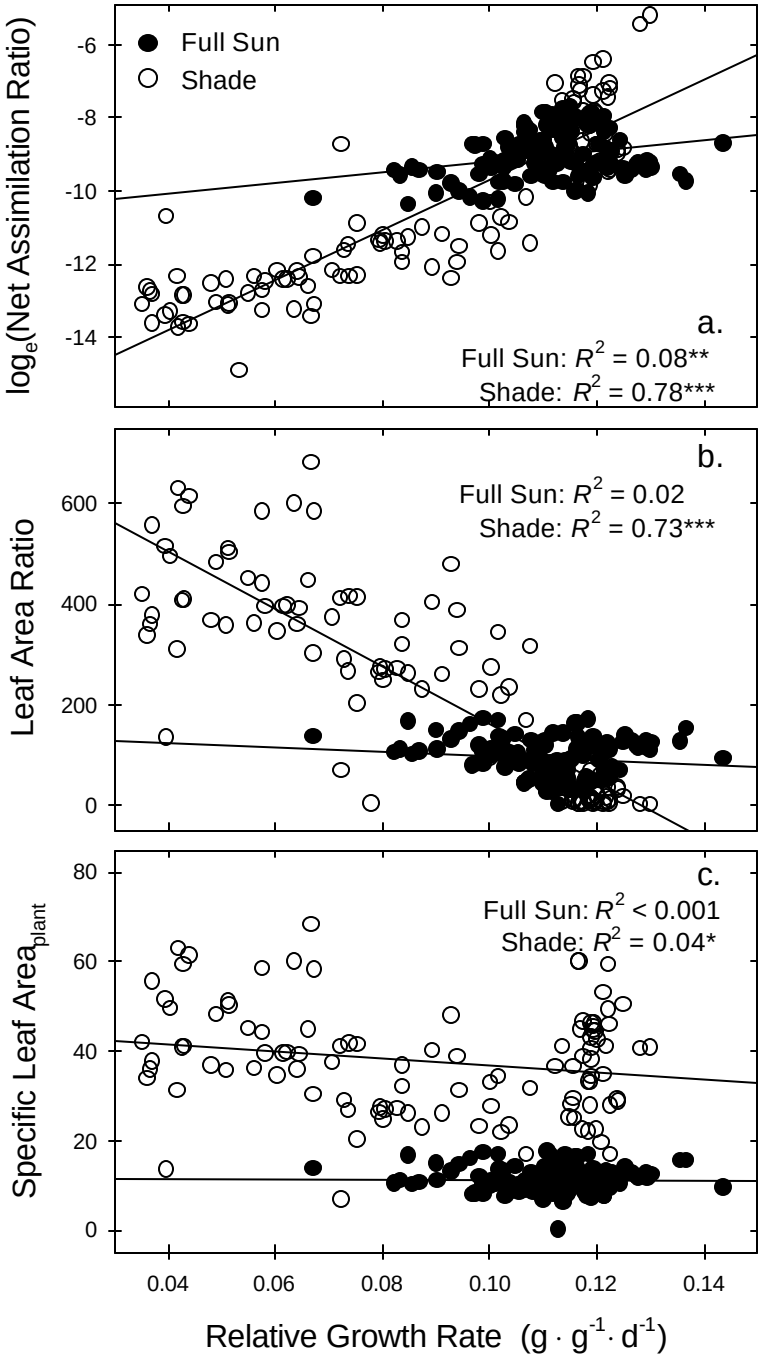


Figure 3.4. Relationships found for second harvest data using a Type II regression analysis between relative growth rate of plants (all parts) and $\log_e$ net assimilation rate, leaf area ratio, and specific leaf area calculated for whole plant. Relationships differed among light treatments. Closed circles represent data from full sun plants and open circles represent data from shade treatment plants.

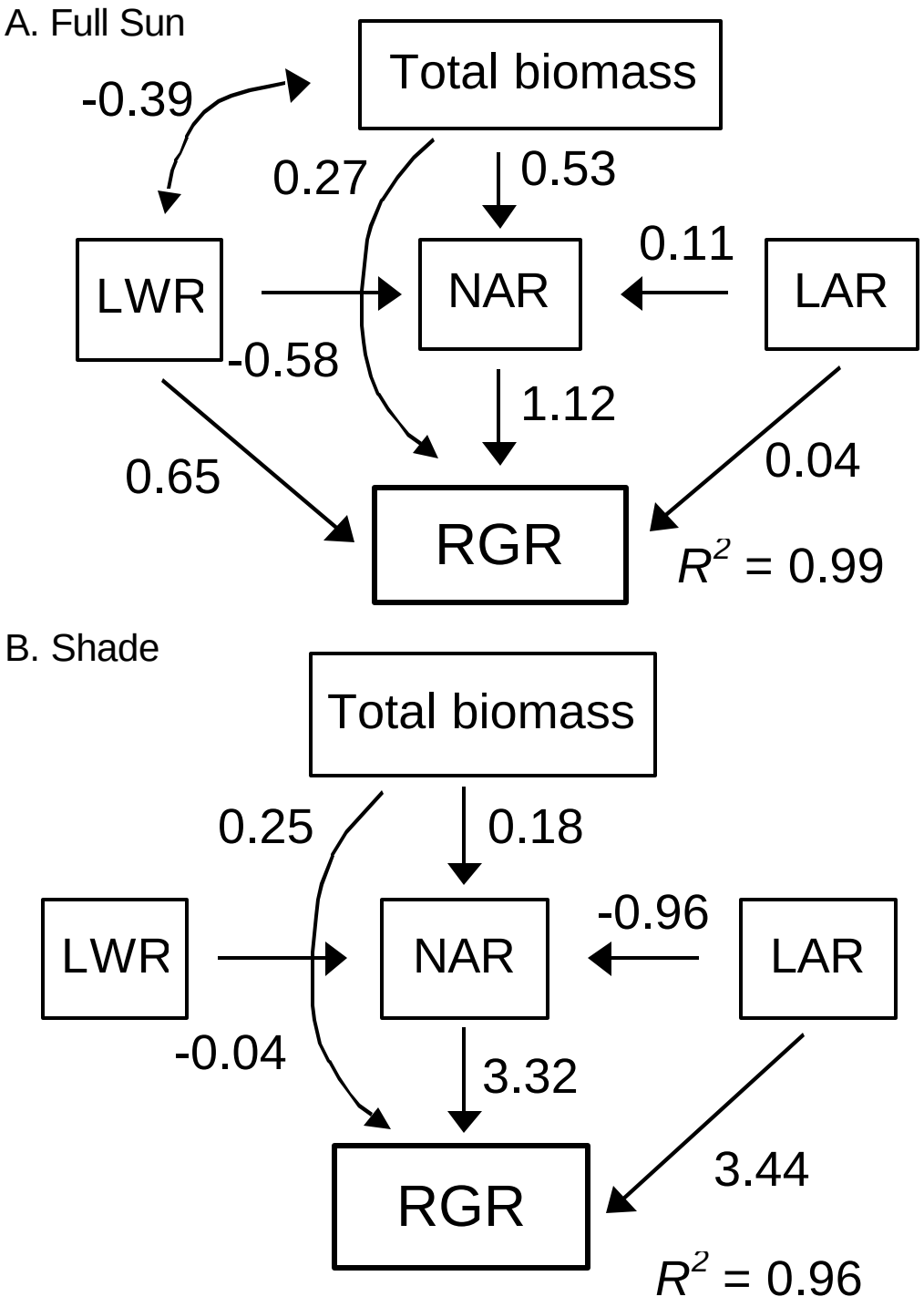
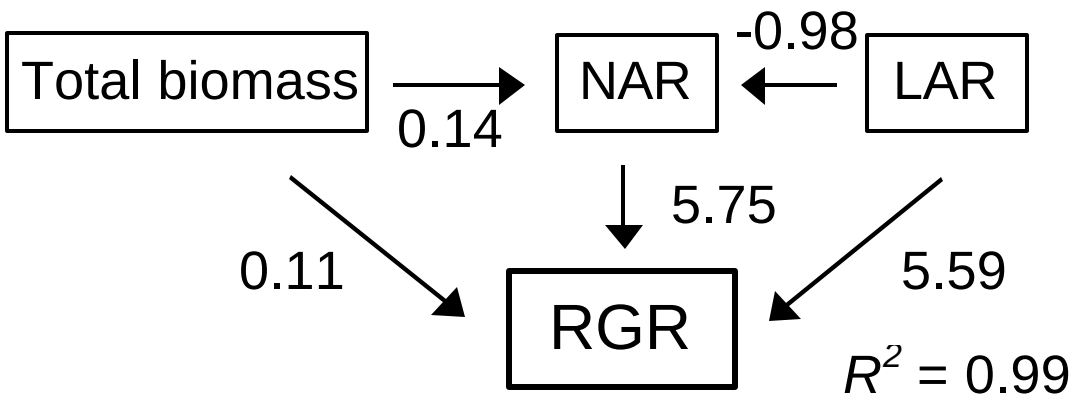


Figure 3.5. Growth models developed for first harvest plants separately for full sun and shade plants. Only significant effects were entered in the model. Single headed arrows are regression coefficients found in the path analysis. Double headed arrows are significant correlations between variables.

A. Full Sun



B. Shade

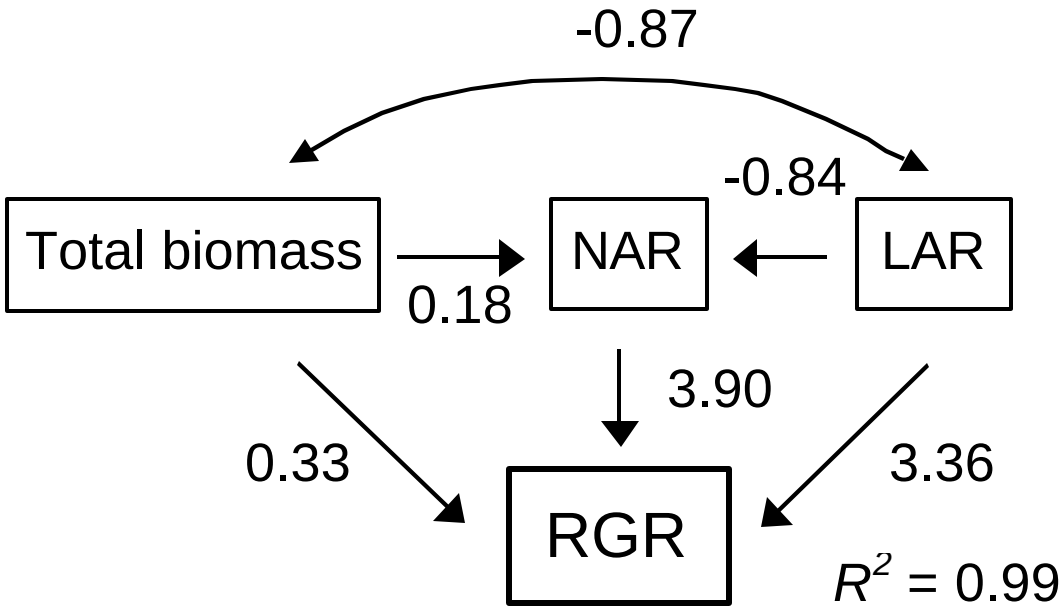


Figure 3.6. Growth models developed for second harvest plants separately for full sun and shade plants. Only significant effects were entered in the model. Single headed arrows are regression coefficients found in the path analysis. Double headed arrows are significant correlations between variables.

Chapter 4 : Seed germination, persistence, and microsite requirements of *Paulownia tomentosa* (Scrophulariaceae) in a managed forest

Introduction

Paulownia tomentosa (Thunb.) Sieb. & Zucc. ex Steud. (Scrophulariaceae) is a tree native to China that was brought to North America in the 1840's. Mature *P. tomentosa* trees have terminal inflorescences that appear before the foliage in early spring. The fruits do not mature until late fall when capsules open to release 2,000 or more seeds each. Seeds are small (2.25 mm long and 0.2 mg) and winged. Because *P. tomentosa* can invade strip-mined land (Melhuish et al., 1990) and can germinate in soil with pH as low as 4 (Turner et al., 1988), researchers have suggested using it for reclamation of surface mined land (Carpenter & Smith, 1979; Tang et al., 1980). However, *P. tomentosa* is considered a significant threat to native species diversity in Great Smokey Mountains National Park (Langdon & Johnson, 1994) and can become established after flooding into natural streamside ecosystems in Virginia (Williams, 1993).

Much is known about the physiology of seeds and germination of *P. tomentosa* under controlled conditions. Seed germination is phytochrome controlled (Borthwick et al., 1964) and dormancy can be induced by long imbibition in darkness (Grubisic et al., 1985). The amount of light needed to break induced dormancy is reduced with the application of the following:

gibberellins, abscisic acid, fusicoccin, and chloro-choline chloride (Grubisic et al., 1988), exposure to low temperatures (Grubisic & Konjevic, 1992), organic nitrate addition (Grubisic et al., 1992), diammonium phosphate addition (Cunningham & Carpenter, 1980), nitrate application (Grubisic & Konjevic, 1990), and an increase in electron acceptors in soil (Giba et al., 1994). Application of deuterium oxide prolonged induced dormancy and increased the light requirement for germination (Grubisic & Konjevic, 1986). Seeds soaked in hypochlorite or ethanol and hypochlorite had high germination rates (Ho et al., 1995). Seeds will germinate given sufficient light in warm temperature when they are released from fruits (A. C. W. Longbrake, pers. obs.). This study is intended to add to the literature by examining seed germination rates and requirements under field experimental conditions in a managed forest landscape.

Dispersed seeds may germinate immediately or have some type of dormancy (enforced dormancy or dormancy) that delays germination (Harper, 1977). For example, in the northern hardwood forests, it has been shown that many dominant species rely on yearly seed inputs from surrounding intact vegetation rather than a seed bank in order to colonize a disturbed site (Hughes & Fahey, 1988). Seed which exhibit enforced dormancy will germinate if given basic requirements for germination, such as light or water (Harper, 1977). Some seeds may be deeply dormant and not germinate under any conditions until one or more complex signals or requirements are met, such as months of cold, wet stratification (Baskin & Baskin, 1998). Moreover, seeds may shift between being dormant to nondormant or change their type of dormancy through time (Baskin &

Baskin, 1989). In the present study, we tested for germination and viability at different times over the course of the year, so that such changes could be noted.

Because *P. tomentosa* seeds can be induced into dormancy and since seeds are shed from adults in late fall or early winter, it seems likely that seeds will persist in the soil at least several months. However, we are unable to find evidence in the literature that this species can form a persistent seed bank. The ability to form a seed bank will have implications for the management of the species and help to understand its niche in the ecosystems it has invaded. A seed bank allows species to specialize in environments that occur infrequently across an ecosystem (Chesson, 1986; Pake & Venable, 1995). In previous chapters, we have shown that *P. tomentosa* is an early successional species, probably specializing in high light environments. Thus, some mechanism is probably needed to maintain populations of *P. tomentosa* throughout a heterogeneous forest mosaic. However, it has been proposed that there is a trade-off between dispersability of seeds and seed longevity (Venable & Brown, 1988). This trade off suggests that *P. tomentosa* seeds, having very high dispersability, may not be able to form a long-lived, persistent seed bank.

Soil microsite requirements for germination ("safe site" as per Harper et al., 1961) is another factor that is not well understood for this species. *Paulownia tomentosa* is often found on steep cobbley soils along highways and waterways. The establishment of naturalized *P. tomentosa* populations in a few habitats in the United States is undoubtedly due to a complex interaction of factors that influence seed germination and establishment, such as microsite conditions,

herbivory rates, and so forth (Facelli, 1994). We wanted to understand the microsite conditions favorable to germination for *P. tomentosa*. Such studies have been used for other invasive plants to understand germination requirements and predict where they may be most problematic (*e.g.*, Hamrick & Lee, 1987).

We have shown in previous work that *P. tomentosa* has many characteristics of an invasive non-native, and forests, particularly those that are human-disturbed, are potentially at risk. There is also a growing literature that suggests that disturbed plant communities, particularly those with human-caused disturbance, have higher proportions of invasive, non-native species (Rejmánek, 1989). Our study uses a gradient of anthropogenic disturbance common to managed forests of the southeastern United States. We used intact secondary forest, forest edge, and aggrading clear cuts to compare seed survival and germination.

We were interested in understanding the seed ecology of *P. tomentosa*, particularly as it relates to its invasive potential into a managed forest landscape. Specifically, we pose the following questions: (1) Can *P. tomentosa* form a seed bank that will persist in one or more of the habitats of a managed forest landscape? (2) Which habitats will be best suited to germination? and (3) What are the most favorable substrate conditions that promote germination?

Methods

Field sites

Field sites were located at the Waterloo Wildlife Experiment Station forest (39° 21'N, 82° 16'W). The forest is oak-hickory in the mid and upper slopes with

more mesic species at the lower slope position. The Ohio Department of Natural Resources, Division of Wildlife currently maintains clear cuts for game management. In the spring of 1997, at each of five clear cuts (replicate sites), we set up a transect perpendicular to the edge of the clear cut and forest. Transects were chosen so that they were all close to the midslope position and such that slope aspect was as consistent among plots as possible. On each transect, plots were delineated in three habitats: clear cut, edge, and forest. Plots in clear cuts were set up 25 m from the forest edge. Edge plots were placed in the edge of the forest, but within the forest canopy. Forest plots were placed 60 m from the edge of the clear cut in the intact forest (henceforth, forest).

Cages were constructed in each of the three habitats at the five replicate transects over fall and winter of 1997-98. Cages were 1×2 m and consisted of 61 cm high hardware cloth buried 15 cm to prevent access to burrowing animals. Wire mesh 1.2 m high with 2.5 cm openings was added above the hardware cloth to prevent deer browsing. All wire was attached firmly to corner fence posts. A door was cut into the wire mesh to allow investigator access and could be secured when not in use.

Seed bank study

Seeds were collected from a single tree in Athens, OH (39° 22' N, 82° 06' W) each autumn and kept in cold (5°C), dry storage until they were used. We chose to use a single tree as a seed source because variation was found among populations and we wanted to minimize that variation (Chapter 3). Small mesh bags made of nylon were made to contain 100 seeds. Five such bags were tied

to a single metal marker, so one seed bag could be retrieved at each of five harvest dates. Three transects at Waterloo were used. At each transect, bags were placed in each habitat (clear cut, edge, and forest). At each habitat, three sets of bags with their marker were placed at the soil surface under the litter layer and three sets were placed at 5 cm depth. Thus, at each harvest date, three sets of habitats were visited and three bags were removed from the litter layer and three from 5 cm depth in each habitat for a total of 54 bags per visit.

Seed bags were placed in the field in January 1998. They were collected in mid June and mid August of 1998, again in mid June and August of 1999, and in mid June of 2000, for a total of 270 seed bags (2700 seeds) over five harvest dates. Seeds were counted, spread on petri plates with moist filter paper, and placed in a germination chamber (Percival Scientific, Boone, IA) with 12 hours of light (20 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and 12 hours of dark at 25°C / 15°C respectively. Germination after 25 days was recorded. Ungerminated seeds were tested for viability using a tetrazolium viability test (Baskin & Baskin, 1998). Data recorded included (1) number of germinants, (2) number of dormant seeds, and (3) mortality, which was calculated as 100 minus the sum of germinants and dormant seeds. Percents were calculated using the original number of seeds placed in the field to account for losses while in the field as well as non-viable seeds recovered from bags.

One seed bag was found to have a large hole through which seeds were lost. This replicate was omitted from the analysis. Seed bank data (percent mortality and dormancy) were analyzed with a General Linear Model Analysis of

Variance (GLM ANOVA). To prevent possible losses of bags to mammal activity, two markers with bags were placed inside the cage at each transect (one set under litter layer and one set at 5 cm depth). However, seed bags were not disturbed and no difference was found between those in cages and outside cages, so this factor was dropped in the analysis. Harvest date, habitat (clear cut, edge, forest), and depth (litter layer, 5 cm) were entered in the model as fixed factors. All analyses were done in NCSS 2000 (Hintze, 2000).

Field germination study

At each of the three habitats in the five replicate sites, four 0.25 $\times$ 0.25 m plots were established with half inside and half outside cages (see description in "Field sites"). In early June of 1997, 100 seeds were sprinkled into plots. A total of 60 plots were monitored. Plots were weeded monthly and germination was recorded for each plot. Seedlings were removed at the end of the growing season. Field germination data were analyzed using a log linear analysis.

Substrate microsite study

In 1999, sod was removed from a 1.8 $\times$ 1.5 m plot in an experimental garden at Ohio University (39° 20' 22" N, 82° 6' 25" W) and a mosaic 30 substrate treatment quadrats (0.3 $\times$ 0.3 m) was delineated. Six substrate treatments were used: (1) bare mineral soil (no addition), (2) sand (river sand), (3) gravel (limestone 2-4 cm diam.), (4) cobble (limestone 10-15 cm diam.), (5) leaf litter from oak-hickory forest, and (6) potting mix (Sunshine Mix II, Sun Gro Horticulture Inc., Bellevue, WA). Each substrate treatment was replicated five

times in a Latin Square design. The entire plot was fenced using 61 cm high wire mesh with 2.5 cm openings. Wire mesh was also placed on top of the organic matter treatments (leaf litter and potting mix) to keep organic matter in the designated quadrat. The location of substrate treatments was assigned randomly, but so each treatment was replicated once in each row and column. In mid May, 100 seeds were sprinkled evenly in the center 0.25 x 0.25 m area of each quadrat. Quadrats were weeded weekly and checked for germinants. Germinants were counted and removed from quadrats.

In the year 2000, the experiment was repeated. This time, two 1.8×1.8 m fenced plots were prepared. In each of these, the six substrate treatments described above were replicated six times and quadrats were randomly located as before. Seeds were added in late April. A month later, all substrate treatment quadrats in one of the plots were disturbed using a three prong garden tool (disturbance treatment). For the cobble treatment, rocks were removed, soil was disturbed, and then rocks were replaced. The other plot received no treatment (undisturbed). All quadrats were watered daily for the first two weeks and then weekly as needed thereafter. Quadrats were weeded weekly and seedlings were allowed to grow until mid September when all seedlings were counted and harvested. All plant parts, including roots, were collected and dried until a constant weight.

Soil samples were taken from each quadrat in September of 2000 before plants were harvested. Within a few hours of taking the soil sample, a small subsample was used to determine soil moisture gravimetrically. The rest of the

soil samples were sieved through a 2 mm mesh, dried, and pH was measured (pH/Ion Analyzer 350, Corning Inc.) using a 2:1 water to soil mixture. Microsite data were analyzed using GLM ANOVA with substrate and disturbance treatment as fixed factors. Soil pH values were converted to hydrogen ion concentration before analysis. All data were tested for normality and heteroscedasticity. Biomass data were $\log_e$ transformed prior to analysis, although untransformed data are shown in figures. For analyses with more than two factors, Bonferroni post hoc analyses were used to determine significant differences between treatments. A single degree of freedom planned comparison was used to compare the pH of the organic substrate treatments against the other treatments to determine if organic matter would lower soil pH.

Results

Seed bank study

Seeds had relatively low mortality rates throughout the study (Figure 4.1A). As expected, seed mortality increased through time from the first harvest date in June of 1998 to the last in June of 2000 (Table 4.1). The first harvest had 8.9% (± 1.8% SE) mortality and only 21% (± 3.3% SE) mortality after three years in the field. Mortality was also significantly affected by habitat and depth, and there was a significant habitat by depth interaction (Table 4.1), since the greatest mortality was found for clear cut and edge sites where, particularly seeds in the litter layer, had greatest mortality (Figure 4.1). Germination percents were very high overall, usually over 80% (Figure 4.1). There was some germination of

seeds observed in bags the at the first harvest date and mostly for bags under the litter layer (Figure 4.1).

Dormancy of seeds was also affected by harvest date, habitat, and depth (Table 4.1). Harvest date had significant interactions with all other effects (Table 4.1). This is because dormancy of seeds was very low the first year of the study, but in August of the second year, seeds, especially those in the clear cuts and at the litter layer, had high percent dormancy (Figure 4.1). Seed collected in June of 2000 showed much lower percent dormancy similar to the other June harvests (Figure 4.1). Seeds in the litter layer had greater dormancy than those at 5 cm depth in the soil, however, this effect was more pronounced in clear cut sites, thus causing a significant habitat by depth interaction (Table 4.1; Figure 4.1).

Field germination study

Field percent germination was extremely low and patchy. Only three transects had any germinants and all were in clear cut habitats (9 plots of 60). Germination was first noted inside cages ($3.8 \pm 1.5\%$) in late July. About equal germination was observed inside ($3.8 \pm 1.9\%$) and outside ($2.5 \pm 1.3\%$) of cages by late September, however seedlings outside cages did not persist. Where germination was observed, it was ~10%, but the plot means are much lower due to the patchiness of germination.

Substrate microsite study

The year 1999 was a drought year in SE Ohio (National Climatic Data Center and National Oceanic and Atmospheric Administration, 2001). Probably due to low moisture, we observed germination in quadrats only in early June.

The cobble treatment had the greatest number of germinants (52.4 ± 9.7%), followed by the gravel treatment (27.8 ± 2.8%). No germination was observed in any other substrate treatments.

Substrate treatment and disturbance significantly affected soil moisture and there was a significant treatment by disturbance interaction (Table 4.2; Figure 4.2A). Soil pH also varied significantly due to substrate treatments and disturbance treatment (Table 4.2; Figure 4.2B). The organic substrate treatments (leaf litter and potting mix) had lower pH values than soils in all other treatments (planned comparison $t = 10.6$, $P < 0.0001$; Figure 4.2B).

Unlike the 1999 data, 2000 data show greatest germination in the bare soil treatment (Figure 4.3A). The bare soil, disturbed treatment had greater germination than any other treatment, which accounted for the significant substrate treatment by disturbance interaction (Table 4.2; Figure 4.3A). Substrate treatment and disturbance also significantly affected biomass of quadrats (Table 4.2; Figure 4.3B). However, biomass per individual differed significantly only by disturbance treatment (Table 4.2; Figure 4.3C).

Discussion

An invading plant must overcome several barriers to become naturalized in a new ecosystem (Williamson, 1996). Of these barriers, the most important are seed dispersal and germination, since these factors will determine if and how rapidly a species can spread into a new region. A clear understanding of seed physiology and germination has important implications for the management of an invasive species, particularly since non-native species can have greater

reproductive output in newly invaded habitats compared to where they are native (Nobel, 1989).

Paulownia tomentosa shows many traits associated with an early successional species. Seed dormancy is broken by light (Borthwick et al., 1964) and by stimuli that indicate disturbance (Pons, 1989), such as nitrate addition (Grubisic et al., 1992). Contrary to conclusions of Hyatt and Casper (2000), *P. tomentosa* can form a persistent seed bank. There is often a high proportion of early successional species represented in the seed bank even of a late successional forest (Pickett & McDonnell, 1989). Hyatt and Casper (2000) found high numbers of *P. tomentosa* seeds in the soil where it was not a dominant species, but they concluded that seeds were short-lived in the soil because they did not germinate. However the lack of germination of *P. tomentosa* could be due to dormancy that they were unable to measure. Even though a trade off between dispersability and persistence of seeds has been proposed, other studies have found evidence to the contrary (Marks, 1974; Thompson et al., 1998). *Paulownia tomentosa* has both high dispersability and the ability to form a persistent seed bank.

Habitat and position in the soil profile affected seed dormancy. It is clear that buried seeds will need disturbance to bring them up to the surface to get enough light to germinate, as the case with other species (Grime, 1989; Houle & Payette, 1990; Hyatt, 1999). *Paulownia tomentosa* seeds exhibit enforced dormancy when released from fruits, since seeds will germinate given mild temperatures, light, and water. Early summer collections of seeds, which were in

the field over winter, showed they germinate readily with light and water. However, later in the year, some seeds became physiologically dormant and did not germinate in light and high temperatures. Thus, *P. tomentosa* seeds cycle between dormancy states.

A small, but significant, proportion of seeds remained physiologically dormant and did not germinate with simple addition of light and water. Variability in seed response within the seed population may allow the species greater flexibility in its establishment and lead, in part, to its success. Seeds buried 5 cm in soil had a greater tendency to become dormant. Buried seeds also had less mortality. Increased dormancy in these seeds could be an effective mechanism to maintain a persistent seed bank.

If we extrapolate the data from this experiment, we predict that *P. tomentosa* seeds may remain viable in the soil for about 15 years using the highest percent mortality found in this experiment. This does not compare with other species that are known to persist much longer (*e.g.,* pin cherry (*Prunus pensylvanica*), Tierney & Fahey, 1998). However, this is only a preliminary estimate since it is based the highest average mortality over a three year period. The study, nonetheless, shows that *P. tomentosa* seeds can persist in the soil profile and their continued viability is dependent upon their location within the ecosystem and in the soil profile.

The niche of *P. tomentosa* in American forests can be compared to that of *Cecropia* in neotropical rainforests, since *Cecropia* seeds also remain viable for several years (Holthuijzen & Boerboom, 1982). Unlike their rainforest

experiment, our seeds were exposed to natural environmental conditions and seed predators. Nonetheless, we had very little herbivory or disturbance of seeds in our field sites.

The herbivory that we did see was greater in the leaf litter and clear cut and edge sites. This probably reflects the patchy and, perhaps, habitat-dependent distribution of seed predators. We did find that in some seed bags, all or most of seeds were missing with many seed wings remaining. There was never a trace of a hole in the nylon mesh material (< 1 mm), which indicates the small size of the granivore.

It is interesting that despite the high viability of seeds and high light environment of the clear cut sites, only a very small number of seeds in a small proportion of plots germinated in field sites. Seeds were probably buried over the course of a year and only a few were still able to germinate. It may be that seeds in forest and edge sites will need a canopy disturbance to trigger germination. It is surprising that no seeds germinated in forest edges even though these habitats get much more light than forest sites. However, given the positive response of seed germination to small disturbance after only one month as we found in the microsite study, disturbance may be necessary to trigger germination.

The substrate treatments provided microsite variability. As expected, the sand treatment was much drier than the other sites. However, even though the organic matter treatments were greatest in moisture, they did not have the highest rates of germination. Moisture, it appears was not an overriding factor for

germination. The organic matter treatments were lowest in pH, while the gravel limestone treatment was greatest. Inasmuch as the germination rate of *P. tomentosa* is reduced in soils with pH values below 5 (Turner et al., 1988), the low pH of microsite treatments may help to account for low germination rates in this case. The differences in soil moisture between disturbed and undisturbed quadrats were probably due to the presence of seedlings in the disturbed plot leading to more shade, since three month old seedlings can reach 1-2 m tall.

The inter-year variation in seed germination was due to dramatic climate differences between the two years. The dry year restricted germination to the gravel and cobble sites. Under the cobble and gravel treatments, we observed moist conditions through the beginning and middle of summer during the drought.

The microsite experiments also emphasized the importance of animals in germination and establishment success of a species both in the role of creating disturbances (McCarthy & Facelli, 1990), as well as their impact on seeds and seedlings from herbivory (Facelli, 1994). Although we did find germination in field sites not protected from mammals, these seedlings often did not persist to the end of the season. Also, the high germination rates on bare mineral soil, particularly in the disturbed quadrats, suggests that *P. tomentosa* would respond well to small disturbances created by animals, such as turkeys and burrowing rodents that are common in Appalachia, in conjunction with a canopy gap.

Interestingly, a recent paper identifying species guilds in the Central Hardwood Forest has no clear guild for *P. tomentosa* (Sutherland et al., 2000). It does not fit the pioneer, spring-dispersed guild because seeds are not dispersed

in spring, nor do they have short viability. It may be that *P. tomentosa*, like sycamore (*Plantanus occidentalis*), would be an outlier in the opportunistic guild of long-lived and intermediate shade tolerant group. Like *P. tomentosa*, sycamore sheds seeds in the fall, germinates in the spring, has high seed dispersal potential, and is shade intolerant (Sutherland et al., 2000). However, the uniqueness of *P. tomentosa* in the ecosystem may allow it to invade early successional habitats in the United States.

The ecology of the seeds compliments work done with seedlings to show that *P. tomentosa* will be able to invade high light environments, such as recent clear cuts and large forest gaps (see Chapter 1). In areas under threat from invasion by *P. tomentosa*, large-scale disturbances that expose bare mineral soil should be avoided. Also, the removal of existing *P. tomentosa* stands may promote resprouting of stumps (see Chapter 2) and germination of seeds from the seed bank. Planting of shade tolerant species in the understory of existing stands may allow native species to increase dominance while preventing germination of *P. tomenosa* from the seed bank.

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Table 4.1. ANOVA results for seed mortality and seed dormancy. Seed mortality is the loss of seeds in the field and nonviable seeds recovered from seed bags. There were five harvest dates: June 1998, August 1998, June 1999, August 1999, and June 2000. Seed bags were placed in three habitats (clear cut, edge, forest) and at two depths (under litter and 5 cm in soil).

		Variable			
		Seed mortality		Seed dormancy	
Effect in Model	df	*F*	*P*	*F*	*P*
Harvest Date	4	4.85	***	20.07	***
Habitat	2	8.84	***	13.00	***
Depth	1	41.99	***	15.33	***
Habitat × Depth	2	7.49	***	3.16	*
Harvest Date × Depth	4	1.93	ns	3.24	*
Harvest Date × Habitat	8	1.18	ns	3.69	***

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = not significant

Table 4.2. ANOVA results comparing soil conditions, germination, and plant biomass on various substrate microsite quadrats. Soil treatments used were: bare mineral soil, sand, gravel, cobble, leaf litter, and potting mix (see text for details). A soil disturbance treatment was applied to half of quadrats. 'Interaction' refers to the interaction between the disturbance treatment and soil treatment.

	Effect in Model					
	Substrate df = 5		Disturbance df = 1		Interaction df = 5	
Variable	*F*	*P*	*F*	*P*	*F*	*P*
Soil moisture	59.61	***	5.81	*	2.63	*
pH	12.93	***	17.12	***	1.17	ns
Germination	6.14	***	21.93	***	4.94	***
Total biomass	3.39	**	13.29	***	0.46	ns
Biomass/plant	2.21	ns	20.96	**	0.27	ns

* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$

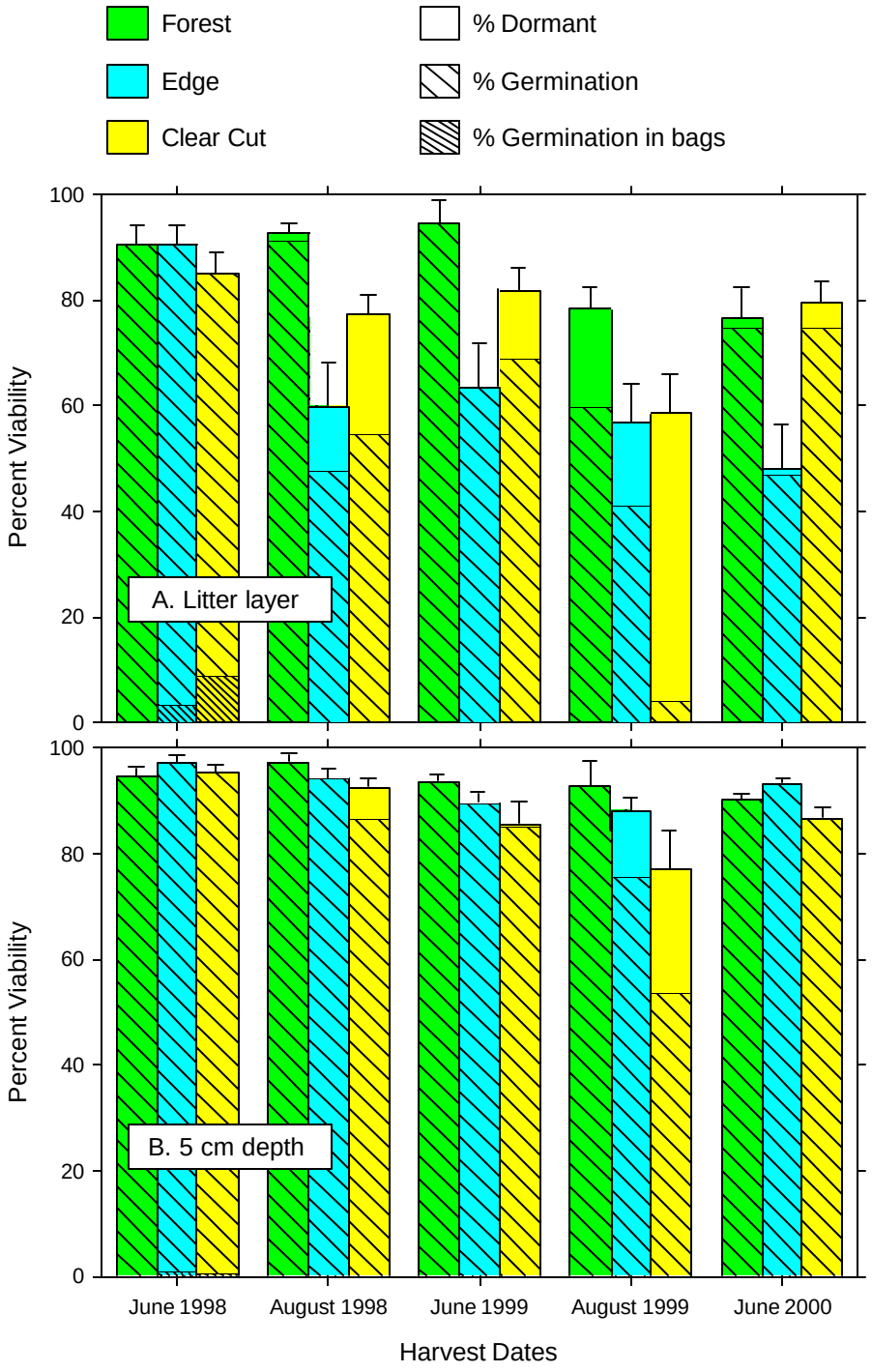

Figure 4.1. Percent viability split between seeds that germinated in seed bags, germinated in controlled conditions, and those that were dormant for bags placed under the leaf litter layer (A) and at 5 cm depth (B) in three habitats over five harvest dates. Seeds that did not germinate were tested for viability (see text for details). Each stacked bar represents percent seed viability and error bars correspond to standard error of viability.

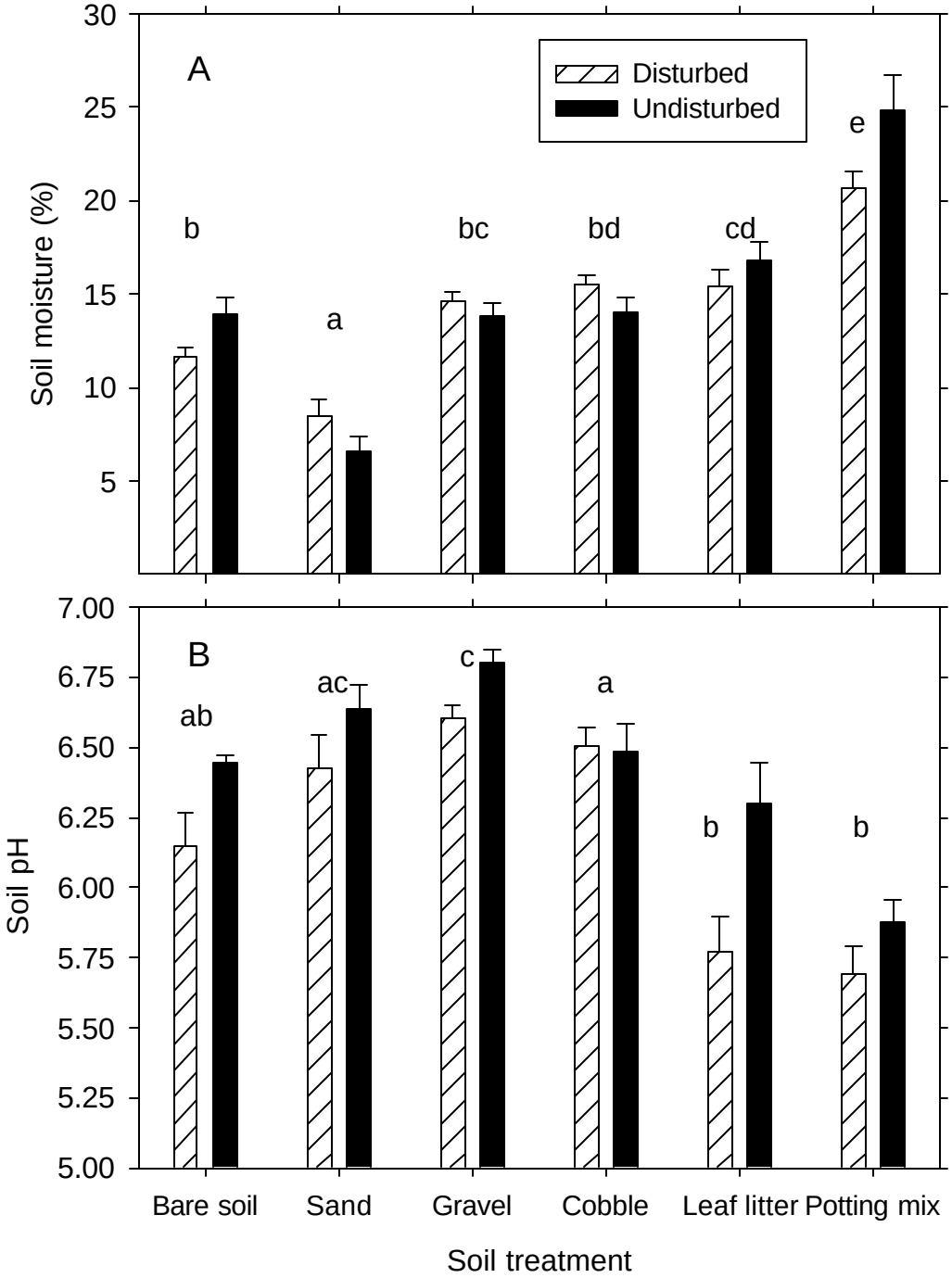

Figure 4.2. Percent soil moisture (A) and pH (B) for soils under soil treatments used in the soil microsite experiment. Soil samples were taken at the end of the growing season before plants were harvested. Different letters above the group of bars indicate an overall significant difference among soil treatments.

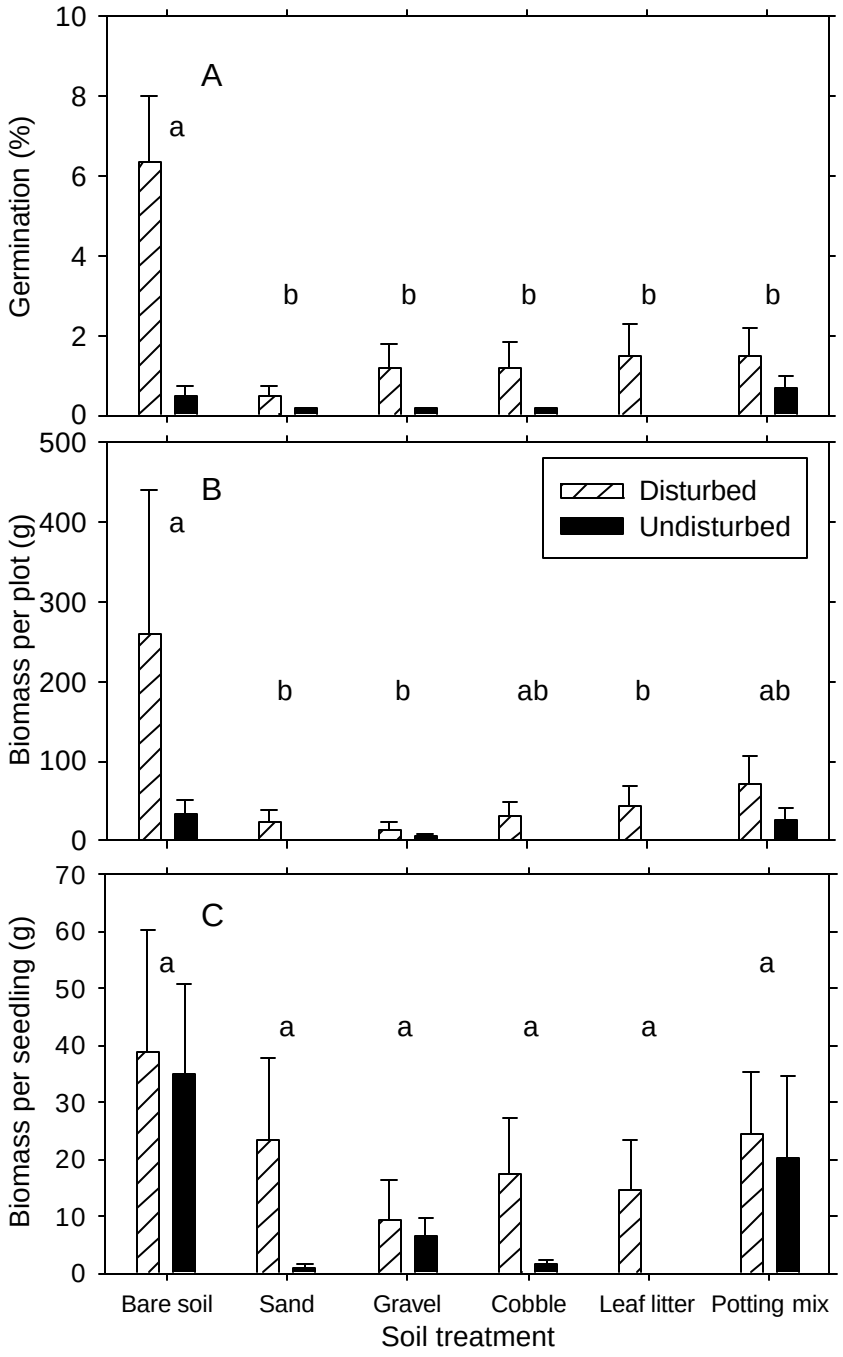

Figure 4.3. Percent germination (A), total biomass in the quadrat (B), and biomass per plant (C) for *Paulownia tomentosa* seedlings on substrate treatments used in the soil microsite experiment. Final counts and harvests were done in late September after a season of germination and growth. Different letters above the group of bars indicate an overall significant difference among substrate treatments.

Chapter 5 : A new index of interspecific competition for replacement and additive designs

Introduction

There are many indexes of competition found in the literature. In this paper, we will compare indexes of interspecific competition typically used with replacement experiments such as those outlined by De Wit (1960). Some of these indexes are adequately defined and are easy to understand. Others, however, are somewhat vague and obscure. We will introduce some of the most commonly used indexes and discuss their meaning using a hypothetical data set.

The indexes that we will review are used in replacement series experimental designs. In these replacement designs, species of plants are grown in pots or plots of a given size. Plants are grown in monocultures and mixtures. Plants are grown at a single overall density while proportions of plants in mixtures are varied. Plants are often grown at several densities, since extrapolation of data from experiments done at a single density in replacement experiments has been widely criticized (Taylor & Aarssen 1989; Firbank & Watkinson 1985; Connolly 1986; Jolliffe *et al.* 1984; *e.g.*).

Since density is known to have effects on plant yields, density is usually held constant to calculate indexes of yield. Other indexes of competition that compare different densities of pots such as Relative Efficiency Index (REI), Land

Area Ratio (LAR), and Relative Resource Total (RRT) (Connolly 1987) will not be covered in this paper.

The indexes discussed in this paper may be adapted for additive designs where the competitor species density is varied and target species density remains constant. Some researchers consider these experiments more appropriate since they partition the inter- and intraspecific competition (Connell 1983). The design of the experiment and how the indexes are used should be explicitly stated when computing and reporting the index in question.

For the purposes of illustration, we will use yield or biomass as the variable being measured although other variables, such as flower number, fruit set, seed production, and so forth, may be more meaningful to measure in a given study. Such data may be easily substituted in these equations for biomass.

First, we will outline the basic terms by which we will define all indexes (notation modified from Fowler, 1982). Let

Y_A = the yield of species *A* in monoculture,

Y_B = the yield of species *B* in monoculture,

Y_{AB} = the yield of species *A* in presence of species *B*, and

Y_{BA} = the yield of species *B* in presence of *A*.

Since researchers often grow plants at different densities, we use a superscript after the Y to denote the density at which the plants are grown, such that,

Y^D_A = the yield of species *A* grown at an overall density of D.

Yields, as defined above, denote total yield of the pot; however, they can be easily modified to represent yield on a per plant basis (by dividing by the product of density and proportion). Further, since researchers often also vary the proportion at which these plants are grown together, let

p_A = the proportion which species *A* was sown and

p_B = the proportion at which *B* was sown,

such that the following equation is always true:

$$p_A + p_B = 1.$$

Some indexes will work with more than two species (this will be discussed in the text) and always the addition of all proportions in a given pot will sum to 1.

We will use a hypothetical data set from a replacement design at a single density to illustrate many common competition indexes. For the purpose of illustration, there are two species A and B. They were grown together in mixtures of 40% A and 60% B with a total density of 20 plants, so that $p_A = 0.4$, $p_B = 0.6$, and density = 20. When grown in monoculture at a density of 20, species A yields 200 g and species B 1000 g. We have only used a single density since all indexes are calculated at a constant density and changing density uniformly does not affect any of the indexes presented here. Moreover, since all pots were grown at a density of 20, we will drop this superscript from the text. However, it would be important to differentiate the values if density were varied.

For our hypothetical example, we have outlined most possible outcomes of a competition experiment between two species (cases 1-11 in Table 5.1). The first case is that in which the species grow equally well with each other as they

do in monoculture (case 1, Table 5.1). That is, their respective yields in mixture will differ from yields in monoculture only to the degree that there are differences in size and proportions at which each species was planted. A good index of yield should take these differences into account. The next two situations are cases in which both species do worse in combination (case 2) or better in combination (case 3). We have chosen to increase or decrease yield by 30% for all examples except the last two cases that illustrate a more extreme example, where we used an improvement in yield of 200%. In the other eight situations, we have shown a variety of conditions to allow a direct comparison of competitive indexes.

Usually, indexes of competition take the yield of a species and divide this by some expected yield usually derived from a yield in monoculture. By so doing, it becomes an index of relative yield, not absolute yield (for discussion see Grace, 1995). One need not use the yield in monoculture since this method can be criticized for only comparing strength of inter- and intra-specific competition and these interactions can not, then, be directly compared. However, this paper is not concerned with this debate rather with the proper calculation, use, and interpretation of the indexes. Any number of variables can be used to create a relative index. For example, yield of species grown without competitors adjusted by density or the species with a different neighborhood of competition can be used. Naturally, interpretation of the data will vary according to the application of these indexes, but the basic nature of the indexes remains unchanged.

Relative Yield (RY)

Relative Yield as defined by De Wit (1960) measures yield in mixture over yield in monoculture taking into account proportions at which the species are grown (equation 1 in Table 5.2). Whether calculations are made at the pot level or the individual plant level, the RY value remains the same. In the first case, when species grow as well with each other as when alone, Relative Yield values are 1.0 for each species.

A Relative Yield value of 1.0 means that for species A, the intra- and inter-specific competition is equal. That is, species A does just as well competing against plants of its own species as with species B. A value > 1.0 means that species A does better competing against the other species than with its own species, *i.e.* intraspecific competition > interspecific competition. An RY_A value < 1.0 means that for species A, interspecific competition is greater than intraspecific competition, *i.e.*, the biomass of species A is reduced in the presence of species B.

The meaning of RY is illustrated by the hypothetical examples. When a species has been reduced by 30% in mixture, its RY value is 0.7. When a species has increased by 30% in mixture, its RY value is 1.3. In the last cases when a species has increased 200% over expected yield in monoculture, the RY value is 3.0. The interpretation of specific RY values is clear and well defined. RY can be calculated for any number of species in a competition experiment.

If one were to plot RY_A values versus RY_B values in space, there would be six main areas of interest in the graph (Fig. 5.1). The first main division in the

graph is at the $RY_A = RY_B$ line. Values above this line indicate that species A has the competitive advantage (if RY_A is plotted on the y-axis) over species B. Below the line, species B has competitive advantage over species A. Furthermore, if the RY values are below 1, then that species is declining in mixture compared to monoculture. Thus you can have areas of mutual interference or facilitation, or areas where one species is increasing and the other is declining (Fig. 5.1).

Relative Competition Intensity (RCI)

Grace (1995) used an index similar to RY called the Relative Competition Index. He takes the yield in mixture and subtracts the yield in monoculture and then divides this by the yield in monoculture (equation 2 in Table 5.2). Like RY, RCI is a relative index and is equivalent to

$$RCI^D_A = 1 - RY^D_A$$

and thus is somewhat inverse to the values given for RY. If $RCI_A = 0$, there is no effect of a competitor. If RCI_A is positive, species A has less biomass in that treatment than B and therefore competition is indicated. If the measure is negative, A has more biomass in the mixture and therefore there is no competition with species B. Moreover, this number is the proportion of decrease (if positive) or increase (if negative) of species A in mixture with respect to monoculture. Campbell & Grime (1992) modified RCI by multiplying by 100, which merely changes the proportion to a percent.

In the first case, the RCI values for species A and B calculated as percent show no increase or decrease in either species (Table 5.1). Due to the way we set up the example, whenever species A or B decreases by 30% (cases 2, 4, 5,

and 8-11) the RCI value is 0.3 (Table 5.1). When a species does better in mixture than monoculture (cases 3, and 6-9), its RCI value is -0.3 (Table 5.1). The last two cases, which show larger increases (A in case 10 and B in case 11), give RCI values of -2.0 and in these cases, the yield of the species was tripled in mixture to what was expected in monoculture (Table 5.1). Due to the inversion of sign and subtraction by one, the numbers are not entirely intuitive and no information has been gained by changing the original RY formula.

Relative Yield Total (RYT)

Since researchers often want a single number from each pot replicate in the experiment that includes all species, many indexes use data from both species to generate a single value. One such index is Relative Yield Total (RYT). Several formulae have been used to determine this index (formulae 3-5 in Table 5.2). The idea expressed in the literature is that when RYT = 1.0 the species are competing for the same resources, if the value is > 1.0 then there is some kind of avoidance of competition occurring, and if the value is < 1.0 then there is mutual antagonism (Silvertown & Lovett Doust, 1993). Let us examine the results of the three formulae. In the first case, where there is no change in yield as compared to monocultures, RYT1 and RYT3 have a value of 1.0 while RYT2 has a value of 2.0 (Table 5.1). It seems more accurate to conclude that the species are competing for the same resources since they are equivalent in mixture. The meaning of RYT2 is, so far, unclear. When both species are reduced by 30% in the second case, RYT1 and RYT3 are 0.7 and in this case RYT2 is 1.4 (case 2, Table 5.1). In this case, it seems logical to assume that the

species are mutually antagonistic and so again, RYT2 is unclear. RYT1 differs from RYT2 in that while they both sum the RY values for each species, RYT1 divides the sum in half. If the number is not divided by two, then as we have seen in the first few cases, RYT2 is not reflecting what RYT is intended to mean.

RYT1 and RYT3 differ in all the remaining hypothetical cases (cases 3-11, Table 5.1). RYT3 has some additional variables which seem to allow the inclusion of the proportion at which the species are grown, however, these expressions fall out of the equation since proportions are already taken into account in the formula for RY (see Appendix I for mathematical proof). In the other hypothetical cases, RYT1 gives the average of the RY values for both species. Because of this, we do not think that it can be given the meaning as intended in the literature. If both RY_A and RY_B were equal to 1, then species are competing for the same resource, or they are equivalent to each other. Since together their yield is the same as when grown in monoculture, there is some factor limiting both of their growth in the mixture equally as when in monoculture at the same density. Likewise, if both RY_A and RY_B were greater than one, then there is avoidance of competition and when grown in mixture, the yield of plants is greater than when grown in monoculture. When RY_A and RY_B are both less than one, that is evidence for mutual antagonism between competitors. If one species decreases, then there are more resources available for the other species or conversely, if one increases there may be fewer resources available for the other species. In these cases, it would be difficult to determine if the species are antagonistic or are using the same resources. Summing the relative yields

obscures the behavior of each species. We recommend keeping RY values for each species separate so that the researcher can assess what is occurring in their experiment.

The use of RYT values in the De Wit diagrams has meaning, only because these diagrams include RY values for each species and thus one can visually determine the proportional contribution of each species. However, analyzing RYT values for each plot alone will not allow the researcher make conclusions about the competitive abilities of the species in the experiment. This is because an infinite number of combinations of RY_A and RY_B can yield the same RYT value (Fig. 5.2a). The function curves of RYT cross through the different competitive scenarios between species A and B (Fig. 5.2a), thus masking the interaction between the two species.

Aggressivity (AG)

There are two indexes called Aggressivity (AG) which presumably quantify how aggressively a species behaves in mixture. The calculations of AG are similar to the calculations for RYT. AG1 is half of the difference between RY_A and RY_B (formula 7 in Table 5.2). AG2 is calculated for each species. $AG2_A$ is the difference between RY_A and RY_B, and $AG2_B$ is the inverse of $AG2_A$, so only one value needs to be calculated. This makes AG1 one half the value of $AG2_A$. In the first three cases, when the species are changing in the same way (increase equally, decrease equally, or remain in original proportions), all AG values are equal to 0. For AG1 and $AG2_A$, the value is positive if RY_A is greater than RY_B. Inversing the situation for the species (going from case 4 to 5 or 6 to

7, etc.) inverses the value of either Aggressivity index. In both calculations of AG, relative yields are used. Thus, these calculations suffer from the same problems as RYT1. When relative yields are subtracted, it is unclear what is happening between the two species whereas RY clearly explains the differences in relative yield of each species. Moreover, the function curves for values of AG are parallel to the diagonal (where $RY_A = RY_B$) and thus, also cross through different competitive scenarios (Fig. 5.2b).

Relative Yield of Mixture (RYM)

An index that shows the proportion of yield attained in mixture as compared to what could be attained in monoculture is the Relative Yield of Mixture (RYM). This measure takes the yield of both species in mixture and divides by the yield that was attained in monoculture while taking into account the proportion at which the species were grown (equation 6 in Table 5.2). This value is identical to the value for RYT1 for the first three hypothetical cases and differs in the rest of the cases (Table 5.1). This is because RYT uses RY values that give each species equal weight. RYM, however, is concerned with total biomass so that when species A is reduced, but not B (case 4, Table 5.1), the value of RYM is still close to 1. When species B is reduced, the RYM value is 0.735 (case 5, Table 5.1), which shows a reduction of about 27% in total biomass. This is because species B contributes more biomass to the pot (1000 g in monoculture) than does species A (200 g in monoculture). When RYM values are equal to 1.0, then the biomass in the pot is equal to what was expected in the pot (although the relationship between species is unclear). When the value is

greater than 1.0, there is some kind of facilitation or avoidance of competition to get more biomass than expected when grown in monoculture. When the value is less than 1.0, there is less biomass than expected from the monocultures, which suggests antagonism between the competitors. RYM - 1 gives a proportion and (RYM - 1)*100 will give the percentage increase (if positive) or decrease (if negative) in overall biomass in the plots.

Although this accurately describes the total biomass from both species attained in mixture compared to monoculture, it does not illustrate the competitive interaction between the two species since the function curves cross competitive scenarios (Fig. 5.2c). The slope of the line is determined by the proportional contribution of species A and B to total biomass. This index can be calculated for any number of species in a competition experiment.

Competition Intensity (CI)

Competition Intensity (CI) as defined by Wilson (1988) was designed for a 1:1 mixture of species only in an additive experimental design. We modified the equations to account for different proportions possible in replacement designs (see Appendix IV). Thus, the measure is equivalent to the reciprocal of RYM - 1. Modified Competitive Intensity (CI), or sometimes called Intensity of Competition, takes the possible yield in monoculture and divides by the yield in mixture (equation 10 in Table 5.2). If there is no change in performance of either species in mixture compared to monoculture, CI = 0. If there is more biomass in mixture than monoculture, then the index is less than zero (case 3, 6, 7, 9, and 11; Table 5.1). If there is less biomass in mixture than monoculture, the index is greater

than zero (case 2, 4, 5, 8, and 10; Table 5.1). The measure, however, cannot clearly identify conditions of competition since it is looking at the effects of both species together and thus, like RYM, can only identify cases when there is an overall reduction or increase in total biomass in the mixture treatment (Fig. 5.2d).

Competitive Balance (CB)

Competitive Balance (CB) as defined by Wilson (1988) was also designed for a 1:1 mixture of species in an additive experiment. We have modified his equations to account for different proportions (see Appendix II). CB is an index of competition in the mixture such that, if CB = 0 there is no competition and the more negative the value of CB, the more competition in the mixture (Wilson 1988). CB takes the natural logarithm of the yield in mixtures of both species (corrected for difference in proportion) divided by their yield in monocultures (equation 9 in Table 5.2). Since CB uses the natural log, if the value is 0, then the change in either species is the same (cases 1-3, Table 5.1). If the yield in mixture is greater than the expected yield in monoculture, CB will be less than 0 and if the yield in mixture is less than expected in monoculture, CB will be greater than 0. In case 4, when the proportion of species A is reduced by 30% and species B remains the same, the value of CB_A is -0.357 and +0.262 if species A increases by 30% while B remains the same (case 6). Not only is CB_A negative if species A is reduced, but also if it is reduced relative to species B, so that if A stays equivalent to monoculture and B increases (case 7), CB_A = -0.262. Likewise, if species A is increased relative to species B, CB_A will be positive (cases 5,6,8, and 10). A higher number relates to greater disparity between the

relative yield of the two species. Notice that $CB_A = -CB_B$, so only one value needs to be computed. If the natural logarithm is not taken, then the measure is equivalent to Relative Crowding Coefficient (RCC) as defined by De Wit and Goudriaan (1974) (These RCC values not shown in Table 5.1). In that case, the value equals 1.0 if the proportional change of both species is the same. The value will be greater than 1.0 if species A is greater in mixture than species B and less than 1.0 if species A is less than B.

There is an easier way to compute and define CB. The alternative formula for CB is as follows (see Appendix III for mathematical proof):

$$CB = \ln (RY_A/RY_B)$$

This formula uses the Relative Yields of both species, so that when $RY_A > RY_B$, CB will be greater than 0 and when $RY_A < RY_B$, CB will be less than 0. And CB will equal 0 if the two relative yields are equal. Since this index uses RY of each species, unlike RYM, it gives equal weight to each species regardless of the amount of biomass they contribute. Note that although the function curves cross competitive scenarios, they do differentiate clearly between situations above and below the diagonal (Fig. 5.2e). Unfortunately, since this index uses the ratio of RY values for two species, it cannot be computed for more than two species.

Relative Replacement Rate (RRR)

Relative Replacement Rate (RRR) is the product of two ratios: the ratio of the proportions the species were planted and the ratio of yield in mixture of the species (equation 11 in Table 5.2). Notice that RRR_A is the reciprocal of RRR_B, so only one value needs to be computed.

When both species did as well with each other as in monoculture or did proportionally well or worse (cases 1-3), RRR_A value was 0.2. This is because the yield of A is less than that of B and in monoculture of species A is 200 and species B is 1000 (200/1000 = 0.2). The idea in the literature is that when RRR = 1, species are competing for the same space. If RRR < 1, A is replacing B, and if RRR > 1, then B is replacing A. It is unclear how this meaning is assigned given the variables used to compute it. This value does not compare a yield in mixture with that in monoculture. It compares the yields in mixture of the two species in the experiment. If plants are larger or produce more biomass, they are likely to do so at a range of densities and proportions. This, however, does not explain what is going on in the experiment between the two species since the function curves cross competitive scenarios and the values (unlike CB) are not intuitive (Fig. 5.2f).

Another definition of RRR (De Wit & Van Den Bergh 1965), looks at the change in biomass of species A over time *t* divided by the change in biomass of species B over time *t*. In this way, this measure is correctly called a rate and may show the intended meaning of the term.

Relative Crowding Coefficient (RCC)

The only other index that individually calculates performance of each species separately is Relative Crowding Coefficient (RCC). RCC is calculated as a product of two ratios. The first ratio is the ratio of the proportions planted ([1 – proportion of species A] [proportion of species A]$^{-1}$). The second ratio is the ratio of biomass the species produced in the mixture divided by the biomass the

species produced in monoculture minus the amount produced in mixture. Thus the generalized form of the formula is as follows:

$$RCC_A = \left(\frac{1 - p_A}{p_A} \right) \left(\frac{Y_{AB}}{Y_A - Y_{AB}} \right)$$

(modified from equation 12 in Table 5.2). The expectation is that the greater the value of RCC, the better a species does in competition (Firbank & Watkinson 1985).

RCC equals 1.0 when the species does as well with the other species as with itself, as in the first case and whenever the RY index equals 1.0 (Table 5.1). RCC will equal unity when the two ratios given in the equation are reciprocals of each other. So that, if the planting ratio is the same as the ratio of the yield of species A, then RCC for species A will equal 1.0. When the species is producing less biomass in the mixture than expected from the monoculture, then RCC is less than one. When a species is producing more biomass in mixture than expected from monoculture yields, RCC is greater than one. Thus, the interpretation that a greater RCC value implies greater competitive ability seems justified.

A strength of this index is that by using the equation as we have presented it, this formula will work to calculate the species' RCC value with one or more competitors. However, there are some problems with this index that should not be overlooked. If the amount of biomass in mixture is exactly equal to the biomass in monoculture, this index cannot be calculated (that situation will give a zero in the denominator). Further, if the biomass in mixture exceeds the biomass

in monoculture, then the number becomes negative. The index relies on the comparison of two ratios. A negative number in the denominator inverses the function curve of this index (the ratio of planting proportion must, by definition, always be a positive number). Thus, the function of RCC across RY values is discontinuous (Fig. 5.3).

Further, the value of RCC is dependent upon the proportion at which the species was grown. For example, take case 2 where both species are decreased by 30%. In that example, species A has an RCC value of 0.583 and species B has a value of 0.483. Both species have been reduced in mixture and this is reflected in the fact that the RCC values are less than one. However, although they are proportionally reduced equally, species A has a higher RCC value than species B. Does this mean that species A is a better competitor than species B? If we change only the proportion at which species A and B are planted by inverting the values (that is, $p_A = 0.6$ and $p_B = 0.4$), then species A would have an RCC value of 0.483 and species B would have an RCC value of 0.583. Moreover, RCC_A will be greater than RCC_B only while RY_A and RY_B are less than one and this relationship inverses when RY_A and RY_B are greater than one (inset of Fig. 5.3). Therefore, comparing the absolute value of RCC between species at different proportions is not appropriate. RCC values can be compared if the species were planted at the same proportions only and then they would show the intended meaning of RCC.

Change in Contribution (CC)

We shall introduce a measure, Change in Contribution (CC) defined by equation 13 in Table 5.2. CC is calculated for each species separately. This value is the proportion of biomass a species attained in mixture divided by the expected proportion from monoculture data. Subtracting one from this value will give the proportional change (increase if positive and decrease if negative) in contribution of biomass in mixture as compared to monoculture. This index may be of some use in describing the changes in biomass of species in different competitive situations.

In the first three hypothetical cases, neither species is changing in proportion to what was expected in monoculture, so CC for both species equal zero. In the case 4, where species A was reduced by 30% and species B stayed the same, CC_A = -0.274 and CC_B = 0.037, so the proportional loss of species A was about 27% and the proportional increase of species B was only about 4% of total biomass. Unlike CB, notice that the absolute CC values for species B are lower than those for species A. This shows that species B has a higher proportion of biomass in the plots, so the decreases and increases do not change the proportion of total biomass composed of species B greatly. Species A, on the other hand, undergoes dramatic changes in proportion since it contributes less overall biomass.

The main difference between this index and the others described that can be calculated for a single species, is that it does not use RY values. This index defines the change in proportion of biomass contributed by each species in the

mixture. Therefore, the absolute amount of biomass attained for a species relative to the other species will affect this value (unlike RY, which is affected only by the biomass by the same species attained in monoculture). If CC_A values are plotted with Y_{AB} and Y_{BA} allowed to vary, the highest value for CC_A (determined by the monoculture proportions – see denominator in Appendix V) is where $Y_{BA} = 0$ and where Y_{AB} is high. (Note that if both Y_{AB} and Y_{BA} are equal to zero, the index is undefined). CC_A decreases as Y_{BA} increases and as Y_{AB} decreases. CC values can be computed for a single species with any number of competitors (see Appendix V for a generalized equation).

Discussion

There are two types of indexes of competition for replacement or additive experiments: indexes computed for species individually (RY, RCI, AG, RRR, RCC, and CC) and indexes for entire treatment replicates (RYT, RYM, CI, CB). The category of indexes that represent entire treatment replicates had several poorly defined and unclear indexes. This is due mostly to the fact that a single number will not be able to describe the interaction between two species to differentiate competitive scenarios shown in Figure 5.1. At best, the index CB was able to define situations above and below the diagonal, which at least distinguishes the performance of one species over another.

RYT, AG1 and RRR as defined in the above sections are not providing the information implied in the literature and should not be used. AG2 calculated for species separately is a poor index since its meaning is unclear.

RYM and CI show what is happening to actual biomass yield in the plots as compared to what might have been obtained in monoculture, although the behavior of each species is masked in this value and therefore should not be used to try to describe competition between species. If a researcher is interested in a single value to represent a replicate treatment, RYM is a valid, clear, although limiting, choice.

The values generated for Relative Yield (RY) are very helpful and easy to understand. This index explains what each species is doing in mixture relative to their performance in monoculture. Change in Contribution (CC) explains the proportional change in biomass of a species in the mixture compared to expected values from monoculture and takes into account the differences in biomass of the species.

Indexes used in competition experiments must be clearly defined and have some meaning relevant to the analysis. An incomplete understanding of the indexes of competition may lead to misinterpretation of competition data. We have developed a consistent notation with which all indexes can be understood and the hypothetical data set was effective in directly comparing indexes in different competition scenarios and assessing their meaning.

The most serious problems with the indexes are with those that cannot differentiate between the success of one species over the other (above or below the diagonal in Figure 5.1) such as RYT, AG, RYM, and CI (see Fig. 5.2). The other indexes that combine the outcomes of more than one species (CB and RRR) are still problematical because they can only determine the success of one

species over another and the distance from the $RY_A = RY_B$ diagonal (CB and, although less intuitive, RRR).

It is clear from this review, that an important question researchers need to address is whether their question of interest is better answered using an index which treats species equally or differentially due to their contribution in absolute amount of biomass. Indexes that treat each species equally are RY and RCI for single species or CB for two species. Indexes that weigh species by total biomass produced are CC for single species or RYM and CI for more than one species.

Since RY values seem very versatile and clear in meaning, we suggest plotting RY values in the RY space as shown in Figure 5.1. This may help illustrate the pattern of competitive outcomes in the experiment. It may also be appropriate to analyze competition data using RY values for each species together in a multivariate analysis of variance with a range of density and proportion (if a replacement experiment) or density (if additive). The applicability of using RY values in a multivariate analysis, however, needs to be more explicitly addressed.

There are other practical problems that must be dealt with when using these indexes. Since they are ratios, there may be problems with their use in statistical tests (Jasienski & Bazzaz, 1999). These issues need further consideration. Regardless of the index used, we must keep in mind the biological meaning of the data and clearly define and calculate indexes. In this article, we have only taken a first small step towards a better understanding of

competition indexes. Our hope is that, in the future, obscure indexes may be discarded and more appropriate indexes may be adopted which have a clear, relevant meaning to experimenters.

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Appendix I

The formula for RYT3 is as follows:

$$RYT3^D = p_A RY^D_A + p_B RY^D_B \qquad \text{(equation 6 in Table 5.2)}$$

Although the proportions are used in the above equation, if we substitute the formulae for RY (equation 1 in Table 5.2) and simplify, we get:

$$\begin{aligned} RYT3^D &= p_A (Y^D_{AB} / p_A Y^D_A) + p_B (Y^D_{BA} / p_B Y^D_B) \\ &= Y^D_{AB} / Y^D_A + Y^D_{BA} / Y^D_B \end{aligned}$$

The ratios in the final equation are the yield of plants in mixture divided by the yield of plants in monoculture without taking into account proportions at which they were grown.

Appendix II

The original equation for CB given in (Wilson, 1988):

$$CB = \ln \left[\frac{\left(\frac{Y^D_{AB}}{Y^D_{BA}} \right)}{\frac{Y^D_A}{Y^D_B}} \right]$$

To correct for different proportions, we modified the equation to be as follows:

$$CB = \ln \left[\frac{\left(\frac{Y^D_{AB} \left(p_B \right)}{Y^D_{BA} \left(p_A \right)} \right)}{\frac{Y^D_A}{Y^D_B}} \right]$$

There is no need to correct the denominator since the species were grown at equal densities in monoculture.

Appendix III

The mathematical proof that shows the alternative equation for modified CB.

$$CB = \ln\left[\frac{\left(\frac{Y_{AB}^{D}(p_B)}{Y_{BA}^{D}(p_A)}\right)}{\frac{Y_A^D}{Y_B^D}}\right]$$

$$= \ln\left(\frac{Y_{AB}^{D}(p_B Y_B^D)}{Y_{BA}^{D}(p_A Y_A^D)}\right)$$

$$= \ln\left(\frac{RY_A^D}{RY_B^D}\right)$$

Appendix IV

The original equation for CI from Wilson (1988) is as follows:

$$CI = \left[\frac{Y_A^D + Y_B^D}{Y_{AB}^D + Y_{BA}^D}\right] - 1$$

The modified equation is as follows:

$$CI = \left[\frac{(p_A)Y_A^D + (p_B)Y_B^D}{Y_{AB}^D + Y_{BA}^D}\right] - 1$$

(Notice that this is the reciprocal of RYM less 1.)

Appendix V

The generalized equation of the index Change in Contribution that can be used for more than two species. The calculation below is for species 1 which has been grown in a mixture with species 2, 3, … n. The proportion at which species were grown is indicated by p_i, where i is the species number.

$$CC_1^D = \frac{Y_{1(2,3,..n)}^D \Big/ \sum_{i=2}^{n} Y_{i1}^D}{(p_1)Y_1^D \Big/ \sum_{i=2}^{n} (p_i)Y_i^D} - 1$$

Table 5.1. Competition indexes in different hypothetical scenarios. (Values in bold were designated by the authors for the different scenarios, = means the species grew as well in mixture at in monocultures, << means species the is reduced by 30%, >> means the species increased by 30%, >>> means species did twice as well in mixtures as in monocultures).

	CASE 1 A = B =	**CASE 2 A << B <<**	**CASE 3 A >> B >>**	**CASE 4 A << B =**	**CASE 5 A = B <<**	**CASE 6 A >> B =**	**CASE 7 A = B >>**	**CASE 8 A >> B <<**	**CASE 9 A << B >>**	**CASE 10 A >>> B <<**	**CASE 11 A << B >>>**
Y^{20}_{AB}	**80**	**56**	**104**	**56**	**80**	**104**	**80**	**104**	**56**	**240**	**56**
Y^{20}_{BA}	**600**	**420**	**780**	**600**	**420**	**600**	**780**	**420**	**780**	**420**	**1800**
RY^{20}_{A}	1.0	0.7	1.3	0.7	1.0	1.3	1.0	1.3	0.7	3.0	0.7
RY^{20}_{B}	1.0	0.7	1.3	1.0	0.7	1.0	1.3	0.7	1.3	0.7	3.0
RCI^{20}_{A}	0.0	0.3	-0.3	0.3	0.0	-0.3	0.0	-0.3	0.3	-2.0	0.3
RCI^{20}_{B}	0.0	0.3	-0.3	0.0	0.3	0.0	-0.3	0.3	-0.3	0.3	-2.0
$RYT1^{20}$	1.00	0.70	1.30	0.85	0.85	1.15	1.15	1.00	1.00	1.85	1.85
$RYT2^{20}$	2.00	1.40	2.60	1.70	1.70	2.30	2.30	2.00	2.00	3.70	3.70
$RYT3^{20}$	1.00	0.70	1.30	0.88	0.82	1.12	1.18	0.94	1.06	1.62	2.08
$AG1^{20}$	0.00	0.00	0.00	-0.15	0.15	0.15	-0.15	0.30	-0.30	1.15	-1.15
$AG2^{20}_{A}$	0.00	0.00	0.00	-0.30	0.30	0.30	-0.30	0.60	-0.60	2.30	-2.30
$AG2^{20}_{B}$	0.00	0.00	0.00	0.30	-0.30	-0.30	0.30	-0.60	0.60	-2.30	2.30
RYM^{20}	1.000	0.700	1.300	0.965	0.735	1.035	1.265	0.771	1.229	0.971	2.729
CI^{20}	0.000	0.429	-0.231	0.037	0.360	-0.034	-0.209	0.298	-0.187	0.030	-0.634
CB^{20}_{A}	0.000	0.000	0.000	-0.357	0.357	0.262	-0.262	0.619	-0.619	1.455	-1.455
CB^{20}_{B}	0.000	0.000	0.000	0.357	-0.357	-0.262	0.262	-0.619	0.619	-1.455	1.455
RRR^{20}_{A}	0.200	0.200	0.200	0.140	0.286	0.260	0.154	0.371	0.108	0.857	0.047
RRR^{20}_{B}	5.000	5.000	5.000	7.143	3.500	3.846	6.500	2.692	9.286	1.167	21.429
RCC^{20}_{A}	1.000	0.583	1.625	0.583	1.000	1.625	1.000	1.625	0.583	-9.000	0.583
RCC^{20}_{B}	1.000	0.483	2.364	1.000	0.483	1.000	2.364	0.483	2.364	0.483	-1.500
CC^{20}_{A}	0.000	0.000	0.000	-0.274	0.360	0.256	-0.209	0.687	-0.431	2.091	-0.744
CC^{20}_{B}	0.000	0.000	0.000	0.037	-0.048	-0.034	0.028	-0.092	0.057	-0.279	0.099

Table 5.2. List of indexes with formulae used for comparison of indexes in hypothetical example.

Name of index	No.	Abbreviation	Formulae	Source
Relative Yield	1	RY^D_A RY^D_B	$RY^D_A = Y^D_{AB} / (p_A Y^D_A)$ $RY^D_B = Y^D_{BA} / (p_B Y^D_B)$	Notation after Fowler 1982
Relative Competitive Intensity	2	RCI^D_A RCI^D_B	$RCI^D_A = (p_A Y^D_A - Y^D_{AB})/(p_A Y^D_A)$ $RCI^D_B = (p_B Y^D_B - Y^D_{BA})/(p_B Y^D_B)$	Grace 1995
Relative Yield Total	3	$RYT1^D$	$RYT1^D = (RY^D_A + RY^D_B)/2$	McGilchrist and Trenbath 1971
Relative Yield Total	4	$RYT2^D$	$RYT2^D = RY^D_A + RY^D_B$	De Wit and Van Den Bergh 1965
Relative Yield Total	5	$RYT3^D$	$RYT3^D = p_A RY^D_A + p_B RY^D_B$	Fowler 1982
Relative Yield of Mixtures	6	RYM^D	$RYM^D = (Y^D_{AB} + Y^D_{BA})/(p_A Y^D_A + p_B Y^D_B)$	Wilson 1988
Aggressivity	7	$AG1^D$	$AG1^D = 0.5(RY^D_A – RY^D_B)$	McGilchrist and Trenbath 1971
Aggressivity	8	$AG2^D_A$ $AG2^D_B$	$AG2^D_A = RY^D_A – RY^D_B$ $AG2^D_B = RY^D_B – RY^D_A$	Snyder *et al*. 1994
Competitive Balance	9	CB^D_A CB^D_B	$CB^D_A = \ln(((p_B Y^D_{AB})/(p_A Y^D_{BA}))/(Y^D_A/Y^D_B))$ $CB^D_B = \ln(((p_A Y^D_{BA})/(p_B Y^D_{AB}))/(Y^D_B/Y^D_A))$	Modified from Wilson 1988 (App. II)
Competition Intensity	10	CI^D	$CI^D = (p_A Y^D_A + p_B Y^D_B)/(Y^D_{AB} + Y^D_{BA}) - 1$	Modified from Wilson 1988 (App. IV)
Relative Crowding Coefficient	11	$RCC_A{}^D$ $RCC_B{}^D$	$RCC_A{}^D = (p_B Y^D_{AB})/(p_A(Y^D_A – Y^D_{AB}))$ $RCC_B{}^D = (p_A Y^D_{BA})/(p_B(Y^D_B – Y^D_{BA}))$	Firbank and Watkinson 1985
Relative Replacement Rate	12	$RRR_A{}^D$ $RRR_B{}^D$	$RRR_A{}^D = (Y^D_{AB}/p_A)/(Y^D_{BA}/p_B)$ $RRR_B{}^D = (Y^D_{BA}/p_B)/(Y^D_{AB}/p_A)$	Dekker *et al*. 1983
Change in Contribution	13	CC^D_A CC^D_B	$CC^D_A = (Y^D_{AB}/(Y^D_{AB}+Y^D_{BA}))/((p_A Y^D_A)/(p_A Y^D_A+p_B Y^D_B))-1$ $CC^D_B = (Y^D_{BA}/(Y^D_{AB}+Y^D_{BA}))/((p_B Y^D_B)/(p_A Y^D_A+p_B Y^D_B))-1$	

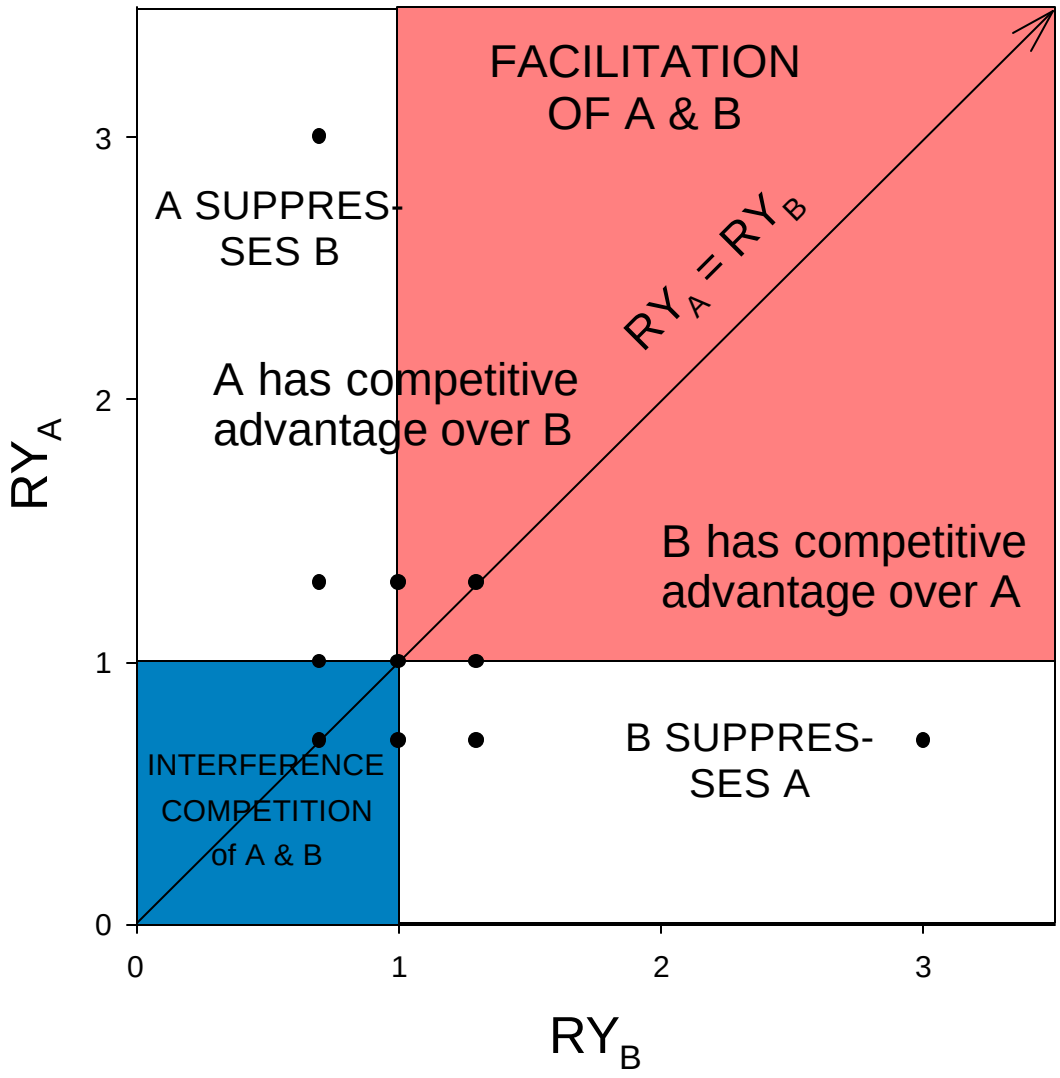

Figure 5.1. Graphical representation of all possible outcomes of a competition experiment between two species. The eleven points on the figure are values from all hypothetical data cases (Table 5.1). Note that these dots span a wide range of outcomes. The diagonal reference line denotes the areas of the graph in which species A has a competitive advantage over B (area above the line) and where B has a competitive advantage over A (below the line). Moreover, the area in dark gray in the lower left corner shows when both species A and B are suppressed in mixture. In the area defined to the right by $RY_B = 1$ to the y-axis, is an area where species B is reduced in competition, but species A is doing better in mixture, so A has a clear advantage over B. The light gray area is where both species are doing better in the mixture than they did in monoculture showing facilitation of both species. The area defined on top by $RY_A = 1$ to the x-axis is where species B is doing better in mixture and is suppressing A.

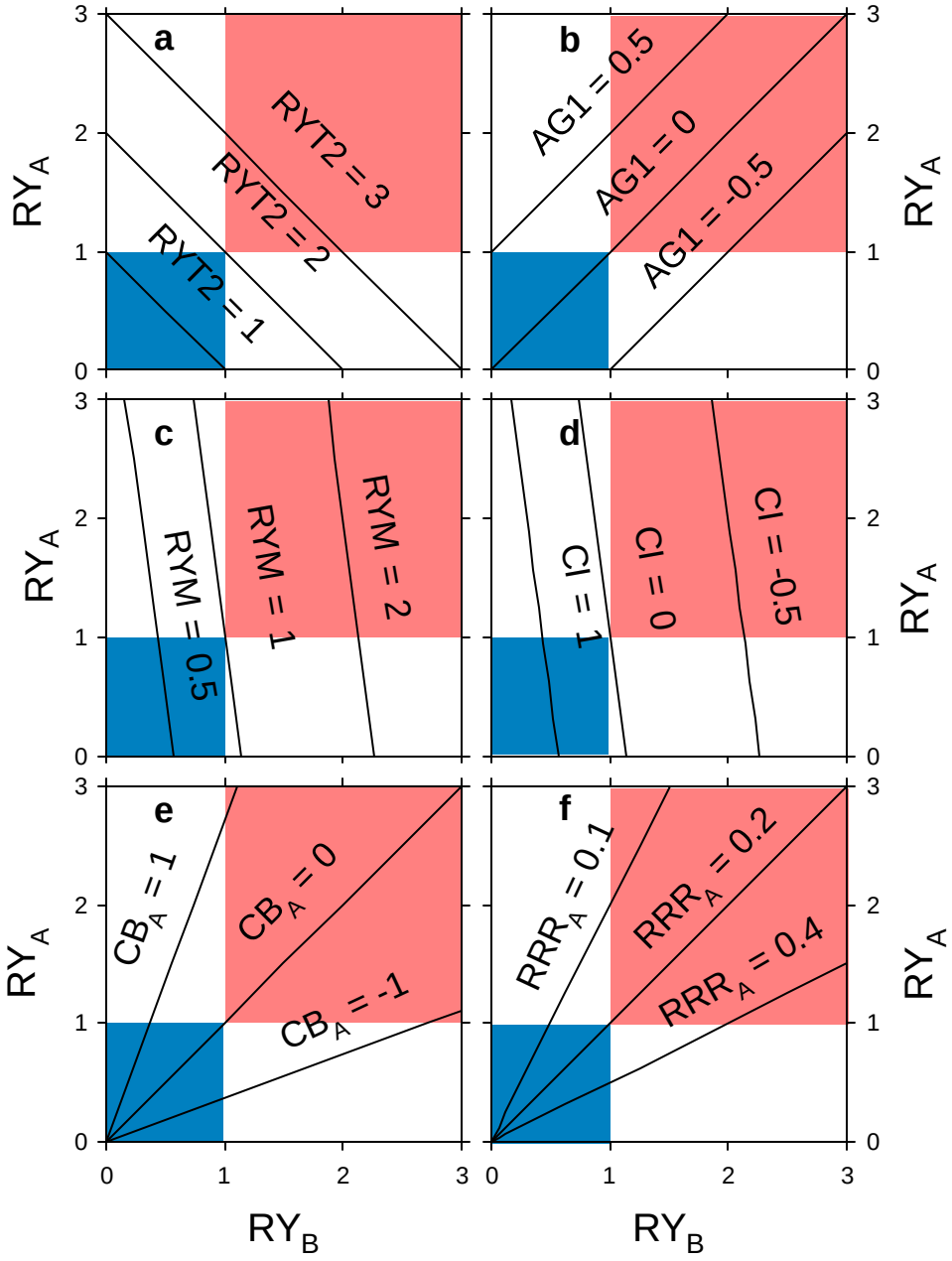

Figure 5.2. Using the same graphic background used in Fig. 5.1, we have plotted function curves of all measures that seek to describe the interaction of two species in a single index. The function curves plotted are for (a) RYT2, (b) AG1, (c) RYM, (d) CI, (e) CB_A, and (f) RRR_A. Note that function curves for RYT1 would be similar to those plotted for RYT2 and function curves for AG2 would be similar for those plotted for AG1. All function curves cross through a range of competitive scenarios while only CB and RRR_A differentiate between above and below the diagonal. This illustrates the problem of using a single number to understand the interaction between two species.

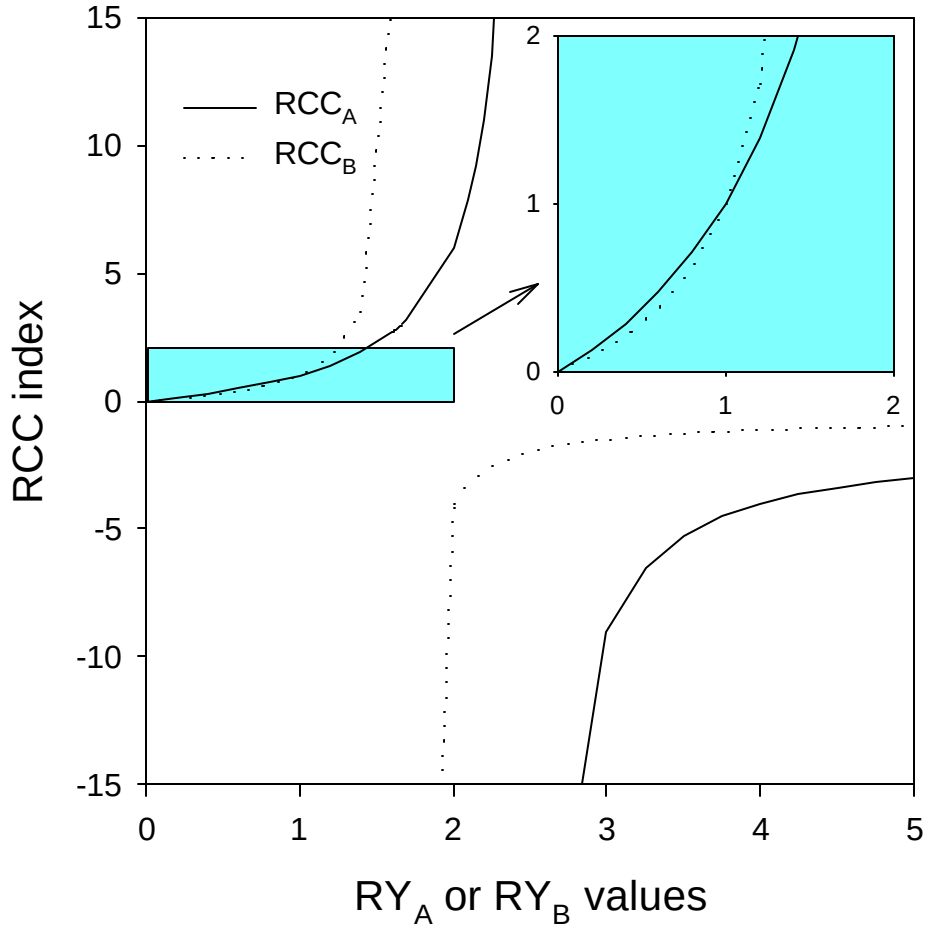

Figure 5.3. This shows the discontinuous function of RCC across a range of RY_A and RY_B values using the conditions given in the hypothetical example where $p_A = 0.4$ and $p_B = 0.6$. The inset portion of the graph further illustrates the shift from $RCC_A > RCC_B$ to $RCC_A < RCC_B$ at RY values of one.