EFFECTS OF NURSE TREE SPECIES ON GROWTH ENVIRONMENT AND
PHYSIOLOGY OF UNDERPLANTED *TOONA CILIATA* ROEMER IN SUBTROPICAL
ARGENTINEAN PLANTATIONS

by

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Abstract

Toona ciliata Roem. plantations require a nurse-tree overstorey to minimize damage from drought and frost in north-eastern Argentina. Nurse-species vary in their facilitative and competitive abilities, thus influencing trade-offs among *T. ciliata* establishment success, stem quality and productivity, and ultimately stand revenues. The first objective was to quantify the influence of nurse species (*G. robusta* A. Cunn., *Pinus elliottii* Englm. x *Pinus caribaea* Morelet, *P. taeda* L.) and thinning density on mortality, stem morphology and growth of under-planted *T. ciliata*. Trade-offs among performance traits were considered in developing recommendations for nurse species selection and density management. The second objective was to examine interspecific interaction mechanisms by determining the effects of nurse species and thinning intensities on light, soil water and nutrient availability to *T. ciliata*. The final objective was to link *T. ciliata* establishment success and early growth to soil water availability, by calibrating the two-dimensional forest hydrology model, ForWaDy. To develop a stand management tool for guiding establishment of *T. ciliata* plantations it was found that *T. ciliata* responded more to nurse species identity than density. *G. robusta* was less competitive with *T. ciliata* for soil nutrients and soil water than either of the pine species: *P. elliottii x P. caribaea* was an strong competitor for water while *P. taeda* was a strong competitor for nutrients. *G. robusta*, by contrast, increased water and phosphorus availability to *T. ciliata*. Density effects varied with nurse species and performance traits. ForWaDy had good predictive capability for early *T. ciliata* performance, and was especially discriminatory among nurse species effects. This study shows that nurse species and thinning effects depend on management objectives, but that nurse species choice can be more important than thinning for increasing early *T. ciliata* performance. Future research employing a greater range of overstorey species, thinning densities, tree ages and environmental conditions will improve predictions of mixed stand productivity under a broader range of conditions. The study contributes to a better understanding of competitive and facilitative interactions in nurse tree plantations and emphasize the need for long-term empirical and modeling studies of mixed species stand dynamics.

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Co-authorship statement

Chapter 2 was co-authored with Suzanne W. Simard, Jürgen Bauhus (Silviculture Institute, University of Freiburg, Germany), Brad Seely, Luciano J. Pozas (National University of Patagonia San Juan Bosco, Argentina), Cindy Prescott, and Hermann Hampel (Danzer Forestación S. A., Argentina). Suzanne Simard assisted with the manuscript preparation while all co-authors assisted with manuscript revisions. Herman Hampel provided expert advice and technical support at the study site. I designed and conducted the study, including plot selection, field and biomass sampling, light measurements, data analysis, and manuscript preparation. Diploma students from the University of Freiburg, Germany, interns from the National University of Patagonia San Juan Bosco, Argentina, as well as employees of Danzer Forestación S. A. Argentina, and Stefan Hodde assisted with field work. Johannes Stahr contributed some data on *T. ciliata* stem straightness. L. Jonatan Pozas assisted with field work, sample preparation and data entry.

Chapter 3 was co-authored with Suzanne Simard, Cindy Prescott, Jürgen Bauhus (Silviculture Institute, University of Freiburg, Germany), Rob Guy, Luciano Jonatan Pozas, and Brad Seely. Suzanne Simard assisted with the manuscript preparation while all co-authors assisted with manuscript revisions. Herman Hampel provided expert advice and technical support at the study site. I designed and conducted the study, including plot selection, field and biomass sampling, light and soil water measurements, live foliage and soil nutrient sampling, data analysis, and manuscript preparation. Diploma students from the University of Freiburg, Germany, interns from the National University of Patagonia San Juan Bosco, Argentina as well as employees of Danzer Forestación S. A. Argentina, Stefan Hodde and L. Jonatan Pozas, assisted with field work and sample preparation. Sofia Lizasoain conducted most of the leaf litter data collection. L. Jonatan Pozas assisted with the field work, data entry and sample preparation, and completed the stem wood δ ^{13}C sample preparation, which were analysed at UC Davis Stable Isotope Laboratory (Davis, CA, USA). Rob Guy assisted with the stem wood δ ^{13}C analysis and data interpretation. An Argentine laboratory, LANAIS N-15, Bahia Blanca, completed chemical analysis of the soil and foliar samples.

Chapter 4 was co-authored with Brad Seely and Suzanne Simard. Brad Seely and Suzanne Simard assisted with the manuscript preparation while Cindy Prescott provided advice on manuscript revisions. Brad Seely designed the computer model ForWaDy and guided me during the calibration process. Herman Hampel provided expert advice and technical support at the study site. For the empirical data collection, I designed and conducted the study, including field, light and soil water measurements. Climate data was provided courtesy of (INTA) Montacarlo, Argentina. Diploma students from the University of Freiburg, Germany, interns from the National University of Patagonia San Juan Bosco, Argentina as well as employees of Danzer Forestación S. A. Argentina, Stefan Hodde and L. Jonatan Pozas, assisted with field work. L. Jonatan Pozas also assisted with data entry.

1   Introduction

Context

Forest plantations in subtropical north-eastern Argentina have conventionally consisted predominantly of a single tree species. Recently, however, managers have started to plant *Toona ciliata* Roem. under young plantations of pine or other commercial conifers to increase their economic return. *T. ciliata* is a deciduous or, where growing conditions are favourable, evergreen tree species native to Australia. Because of its value for veneer and lumber products (Bahadur 1988, Edmonds 1995, Heinrich and Banks 2005), *T. ciliata* cultivation in north-eastern Argentina is expanding rapidly. However, in north-eastern Argentina, *T. ciliata* is subject to mortality losses and suppressed growth caused by frost or limited resource availability, especially in the first few years after planting. There is some evidence that establishment success and growth can be enhanced by planting *T. ciliata* under previously established nurse tree species (Bahadur 1988, Keenan et al. 1999, Ashton 1997, Rodríguez-Calcerrada 2008), also known as shelterwood (Rodríguez-Calcerrada et al. 2008). The influences of nurse species and stand density on understorey *T. ciliata* productivity and stem morphology (stem straightness and stability), however, are uncertain.

Nurse species can facilitate the establishment of understorey trees by protecting them against environmental extremes, and at the same time compete with them for soil water, nutrients and light. The balance between facilitation and competition can result in either positive or negative effects on mixture productivity. Positive mixture effects occur where productivity of the mixed stands is greater than that of monocultures of the composite species. They can result from one species protecting another against abiotic or biotic damage; interspecifc differences in soil resource utilization or canopy light capture; and competition avoidance through interspecific differences in shade tolerance, phenology or successional patterns (Chen et al. 2003, Man and Lieffers 1999). These positive mixture effects reflect both less intensive interspecific than intraspecific competition as well as interspecific facilitation (Montagnini et al. 1995, Kelty and Cameron 1995). Negative mixture effects result in reduced mixed stand productivity, and occur when interspecific competition for resources out-weighs facilitative effects. For example, nurse species can reduce light, water and nutrient availability to understory *T. ciliata*, causing losses in survival, growth and stem morphology. Understanding the facilitative and competitive mechanisms by which species interact is

fundamental to profitable species selection and density management in mixed plantations. Managing mixture dynamics for high-quality wood production is especially challenging where one or more of the species is outside of their natural range

In my PhD research, I investigated interspecific interactions in subtropical two-story mixed-species plantations, where the moderately shade-tolerant crop species, *T. ciliata*, was planted beneath one of three, previously established, shade-intolerant overstorey nurse species: *Grevillea robusta* A. Cunn., *Pinus elliottii* Englm. *x Pinus caribaea* Morelet or *Pinus taeda* L. The three nurse species were thinned to a range of densities one year after establishment of *T. ciliata*. The first specific objective was to quantify the influence of nurse species and density on establishment success, stem morphology and productivity of under-planted *T. ciliata.* Trade-offs among these influences were then considered in developing recommendations for nurse species selection and density management regimes for converting existing mid-value plantations to high-value *T. ciliata* plantations. The second objective was to examine mechanisms of interspecific interference between nurse trees and *T. ciliata*. Specifically, I examined the effects of nurse species and thinning intensity on light, soil water and nutrient availability to *T. ciliata*. These results provided an understanding of the growth-constraining resources in subtropical plantations in north-eastern Argentina. The final objective was to link *T. ciliata* establishment success and early growth to the availability of an important limiting resource, soil water. By calibrating the two-dimensional forest hydrology model, ForWaDy, I developed a stand management tool that can be used to guide management practices for successful establishment of *T. ciliata* plantations on drought-prone sites in north-eastern Argentina.

Literature review

Competition and facilitation mechanisms
Competition is a major structuring force in most terrestrial plant communities (Schoener 1983). It occurs when two or more plants or populations interact so that at least one exerts a negative effect on the other, expressed by reductions in survival or growth (Vandermeer 1989). The outcome of competition depends on the relative ability of the species or individual plants to obtain resources such as light (Donald 1958), water (Moore 1929, Riegel et al. 1995, Seabloom et al. 2003) or nutrients (Bartelheimer et al. 2006, Fargione and Tilman 2006). Historically, competition for light has been

considered the most significant process responsible for tree performance in forests, however, there is increasing evidence that below-ground competition can have at least as great an influence as aboveground competition (Coomes and Grubb 2000, Kajimoto et al. 2007). Belowground and aboveground competition can have different outcomes. While aboveground competition for light can severely reduce height growth and affect stem morphology of trees, belowground competition for soil water and nutrients can have immediate effects on plant survival and diameter or root growth (Ashton et al. 1997, Mahroof et al. 2000, Rodríguez-Calcerrada 2008). Managing mechanisms of interspecific competition by manipulating species composition and density can therefore critically influence the quality of performance of each species in mixture (DarHsiung et al. 2004).

Facilitation occurs when one species has a positive effect on another (Vandermeer 1989). One species may facilitate another, for example, through its ability to fix nitrogen (N) (Forrester et al 2005) or mobilize soil phosphorus (P) (Burgess et al. 1998, Radersma et al. 2005). In tropical climates where soil evaporative losses are high, canopy trees may facilitate establishment of understorey trees by providing shelter from irradiation, thus reducing understorey evapotranspiration and soil evaporation (Wallace et al. 1999, De Costa et al. 2007). Still other species may increase water availability by hydraulic lift, the nocturnal transport of water from deeper, moist soil layers to shallow, dry soil by plant roots (Caldwell et al. 1998). The stress-gradient hypothesis suggests that facilitation is more important in conditions of high abiotic stress, such as on drought-prone or nutrient-poor sites (Maestre et al. 2009). However, both the characteristics of the stress factors (or resource availability) on the site and the relative tolerance of the interacting species to the stress (or resource limitations) are important in predicting the strength of the facilitative effect.

There is generally a poor understanding of competition and facilitation mechanisms among plantation tree species, and this knowledge is of critical importance to successful cultivation of species mixtures (Wormald 1992).

Balancing competition and facilitation for meeting management objectives
Plantations are dynamic systems and resources for plant growth at a given site are always finite, which means that managers must carefully monitor species interactions to identify situations where competition starts to outweigh facilitation. This requires empirical study of shifts in the strength of pair-wise interactions between

species instead of relying on stress-gradient theories that have limited value as forests develop beyond the establishment phase. When the negative effects of competition from the growing nurse trees start to outweigh their facilitative effects, thinning may be necessary to increase the height and diameter growth rates of the understory crop species (Forrester et al. 2005). This competition threshold has been defined by Wagner at al. (1989) as "the level of vegetation abundance where there is an abrupt increase or decrease in the rate-of-change in tree growth or survival".

Competition thresholds vary with the attribute of stand growth being considered. Thus, tree survival, stem volume growth, height growth and basal-area growth respond differently to neighbour competition (Wagner 2000). For example, crop-tree volume growth starts to decline at a lower competition level (threshold) than at which crop tree survival declines (Wagner et al. 1989). Accordingly, choice of competition threshold for management depends on whether the objective is to maximize survival, height increment, basal-area growth, or biomass production (Wagner 2000). Consequently, the intensity or timing of thinning to reduce nurse competition depends on the specific management objectives. These objectives can be driven not only by the economics of timber production, but also for ecological, safety, visual, or predictability concerns (Wagner 2000). For example, conservation of wildlife species or maximizing total stand carbonstocks may be more important than thinning nurse trees below competition thresholds for maximizing crop tree productivity traits.

Manipulating nurse species composition and density influences resource availability and thus performance of both the understory trees and the remaining nurse trees. Quantifying mortality, biomass production, biomass allocation and stem morphology of the understorey trees, as well as the growth responses of the overstorey trees, is necessary to evaluate the effect of the manipulations on the value of the whole stand. It also provides insight into interference mechanisms, allowing for identification of thresholds for specific management objectives, design of stand-tending practices to best meet those thresholds, and improving predictive abilities for applying thresholds and practices under different conditions. Where there are multiple management goals, competition thresholds must be designed for balancing various performance traits, inevitably resulting in trade-offs for optimizing stand value. Although thinning potentially reduces the monetary revenues of one species by promoting growth of the remaining, more desirable species, failure to do anything may result in an unsuccessful mixture

(Turvey at al. 1984, Binkley and Gardia 1997, Hunt et al. 1999, Parotta 1999, Mahroof et al. 2000).

The relative importance of competition and facilitation in tree species mixtures, and thus their net effect on mixture productivity, is influenced by climate, soils, and the species involved. Competitive and facilitative interactions have been extensively studied in agroforestry systems in the tropics and subtropics (Rao et al. 1998), and the results from these systems can be applied to a certain extent to the juvenile stage of understorey crop development in nurse shelterwood systems. Research in agroforestry systems has shown that competition dynamics is different in humid than in dry environments. In humid and subhumid environments, where adequate rainfall favours rapid vegetation growth, competition is primarily for light, resulting in significant negative effects (crop shading) on intercrop species (Lawson and Kang 1990). In acidic, infertile soils of the humid tropics, however, there is intense competition for limited soil nutrients (Salazar et al. 1993). Intense belowground competition in acid soils can occur partly because tree roots are concentrated in same soil layer (0–0.2 m) as crop roots; this has been discovered in Peru (Salazar et al. 1993) and Nigeria (Ruhigwa et al. 1992). Tree species that root deeper, below the crop root zone, appear to be better suited for agroforestry systems in acid soils (Ruhigwa et al. 1992, van Noordwijk et al. 1995).

In contrast to humid environments, trees compete primarily for water in the semi-arid tropics. There, water competition can be intense, often negating the facilitative effect of the nurse shelter at low densities, resulting in lower crop production under shelter trees than in monoculture (Singh et al. 1989, Rao et al. 1990, Ong et al. 1991). Moreover, rapidly growing nurse species will deplete soil water more readily than slower-growing species (Govindarajan et al. 1996, McIntyre et al. 1997), negatively affecting crop-tree growth. Root studies of tree hedgerow and agricultural crops showed that roots of both species were concentrated in the top 0.5 m soil layer (Rao et al.1993). Such lack of niche partitioning can rapidly deplete soil water supply and limit stand growth.

A species mixture that is successful on one site can be less successful on another. For example, where N is limiting, an N-fixing species may benefit the growth of its neighbours. In a dry system replete in N but where water is scarce, this same species mixture can fail because of intense competition for water. These examples illustrate that understanding the site conditions (resource availability and site stresses),

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species resource requirements and stress tolerances, and the mechanisms by which species in mixture interact, are all important in species selection and density management for balancing competition and facilitation in species mixtures (Wormald 1992).

Modelling forest hydrological processes

Predicting productivity of species mixtures is difficult due to the complexity, dynamics and longevity of forests (Pacala 1996). Computer models can assist in predicting the future or unobserved cases, and to provide an understanding of processes underlying the predictions. However, models are only simplifications of the complex reality, and thus all models are imperfect (Holdaway and Brand 1983). No test will ever show that a model is perfectly valid or absolutely accurate. However, model evaluation can involve personal judgements based on the proposed use of the model. Furthermore, the user can decide on the level of acceptable errors, choice of the appropriate model among the alternatives, and other user-related practical considerations (Holdaway and Brand 1983). In some cases, models are evaluated mainly for their heuristic purposes.

Finding a model with the best fit for one purpose can prove to be quite difficult. According to the "principal of parsimony", Occam's razor suggests to "shave away all that is unnecessary". Also, as Albert Einstein said, "everything should be made as simple as possible, but not simpler" (Kimmins et al. 2008). Choosing a model that is too simple might leave out some important effects. A model that is too complex, however, runs the risk of over-fitting. That is, the model may respond to peculiarities in the particular data points that are being used to fit the model, which can increase uncertainty in the predictions (Kimmins et al. 2008). Complex models may have lower precision where many of the model parameters require estimation from a limited data set (Kimmins et al. 2008). Water stress has been modeled using various approaches.

Typically, models of forest growth that include water stress as a feedback to forest growth have quantified tree water stress using a summed measure of soil water deficit. One of the problems with this approach is that a summed water-deficit frequently fails to capture the dynamic interactions between different components of the hydrological cycle, resulting in inaccurate predictions of water stress and the net effect on tree productivity (Seely et al. 1997, Meyers 1988). It has been reported that hourly time-step models with a multi-layer soil moisture description and complete surface energy balance are better at accounting for short-term fluctuations in evapotranspiration

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(Daamen and Simmonds 1994), and thus tree water stress, than summed water deficits. This complexity, however, might increase the overall error of the model. By contrast, simple daily time-step models, which assume evaporation independent of evaporative demand, provide only an approximate description of soil evaporation under these conditions (Smith et al.1998). Nevertheless, it has been reported that a simple daily time-step model can obtain reasonable estimates of cumulative hydrological parameters over hydrologically-significant periods, like weeks or months (Smith et al. 1998).

Overview of thesis

The central purpose of my thesis was to examine the mechanisms by which the species (*G. robusta*, *P. elliottii x P. caribaea,* and *Pinus taeda*) and density (25, 50, 75 and 100% of the initial stand density) of nurse trees affected the establishment success, stem quality and productivity of under-planted *T. ciliata*. By examining interference mechanisms and outcomes, I sought to indentify the mixture composition and density at which facilitation and competition were balanced, resulting in optimal trade-offs among productivity traits of the crop and its nurse species. In Chapter 2, I tested the effect of nurse species and density on under-planted *T. ciliata* mortality, stem morphology, and biomass production. Based on my observations that *T. ciliata* performance varied with overstorey species and density, I went on in Chapter 3 to test the effects of nurse species and density on light, soil water and soil nutrient availability. These measures allowed me to identify the interference mechanisms underlying the performance differences. In Chapter 3, I determined that soil water was one of the most important limiting resources to *T. ciliata* survival and growth. Therefore, in Chapter 4, I calibrated and modelled *T. ciliata* drought stress (expressed as a Transpiration Deficit index (TDI)) using the two-dimensional forest hydrology model, ForWaDy. The model helped me predict water availability and tree water stress, and determine their effects on observed early mortality and growth of *T. ciliata*. Lastly, in Chapter 5, I summarized my most important findings in the light of the current literature, identified weaknesses in the field study and forest hydrology model, provided guidance for improving future studies, and suggested further avenues of inquiry, both for this project as well as generally in the field of mixed species plantations and facilitation and competition interactions. I end the thesis with general conclusions on the interactions and potential of success of growing

T. ciliata in mixture with *G. robusta*, *P. elliottii x P. caribaea*, and *Pinus taeda* in north-eastern Argentina.

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2   Trade-offs among establishment success, stem morphology and productivity of underplanted *Toona ciliata*: effects of nurse-species and thinning density[1]

Introduction

Intensive management of plantations is one means of meeting the increasing demand for forest products, while reserving large areas of native forests for biodiversity and other ecosystem services (Carnus et al. 2003). Production of high-quality timber from plantations has the potential to replace harvesting of valuable hardwoods from native forests. In northern Argentina, *Toona ciliata* (Australian red cedar) has been identified as a suitable species for production of high quality and economically valuable timber. Because of its value for veneer and lumber products (Bahadur 1988, Edmonds 1995, Heinrich and Banks 2005), *T. ciliata* cultivation is expanding rapidly. *Toona ciliata* has similar wood characteristics and uses to those of the highly sought-after north-eastern Argentina native, *Cedrela odorata*, and its cultivation may reduce the harvesting pressure on *C. odorata* in native forests (Mangialavori et al. 2003). Intensive plantation management of *C. odorata* in South America has had limited success due to damage by the shootborer, *Hypsipyla grandella*, to which *T. ciliata* appears resistant (Mangialavori et al. 2003).

　　T. ciliata is easily damaged by drought or frost in north-eastern Argentinean plantations, especially in the first few years after planting, although frost events were not severe enough to damage *T. ciliata* during the study period. There is some evidence that mortality and growth losses can be reduced by planting *T. ciliata* under previously established nurse-tree species (Buck and Imoto 1982, Bahadur 1988, Keenan et al. 1995 and 1999). Additionally, risks associated with growing single species stands due to market changes, pests or other calamities can be reduced by introducing an additional species. The three nurse-species evaluated in this study are *Pinus elliottii x Pinus caribaea, Pinus taeda* and *Grevillea robusta*. They are widely planted commercial species in the subtropics, especially northern Argentina (IPEC 2008, Montagnini et al. 2005).

　　The role of nurse-trees in tropical plantation forestry has received little attention to date. Interspecific competition can significantly influence the performance of each

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species in mixture (DarHsiung et al. 2004), so nurse-tree species must be selected carefully and kept at appropriate densities. For example, mahogany seedlings planted under mature pine experienced reduced growth and increasing mortality because of overstorey competition for nutrients and water (Mahroof et al. 2000). Choice of nurse-species may also influence *T. ciliata* stem morphology, which is an important determinant of wood quality and value, particularly for veneer products, and is an important factor in harvest, transport and processing costs and methods (Sierra-de-Grado et al. 1997). *P. caribaea* has been successfully used as a nurse-tree for growing late successional native species in the tropics (Ashton et al. 1997), while *G. robusta* has been used successfully as a nurse tree for *T. ciliata* in Australia (Keenan et al. 1995, Bygrave and Bygrave 2005).

The objective of this study was to evaluate the effects of overstorey nurse tree-species and density on *T. ciliata* sapling mortality, stem morphology, productivity and biomass allocation patterns. Further, the study provides insight into potential methods for converting existing mid-value plantations to high-value *T. ciliata* plantations. To this end, the following hypotheses were tested:

1) Mortality of individual *T. ciliata* saplings increases with decreasing overstorey density and increasing light availability;

2) *T. ciliata* stem morphology (stem straightness and stability) improves with decreasing overstorey density;

3) Productivity of established *T. ciliata* increases with decreasing overstorey density;

4) *T. ciliata* biomass allocation patterns change with light availability and overstorey basal area; and

5) There is an optimal nurse species and one or more thinning densities at which *T. ciliata* has the lowest mortality, the straightest stems and the highest productivity.

Material and methods

Study site
The study site was near the city of Posadas, in the Province Misiones, in north-eastern Argentina (about 55 55 13.46° W Longitude and 27 28 10.53° S Latitude). The Province of Misiones covers an area of approximately 30,000 km², which is less than 1% of the country total; however, it produces more than 60% of the country's timber (Rodrigo 2009). The native subtropical forests of Misiones have been reduced to less than 50%

of its original size (Burkart et al. 2002), mainly as a result of establishment of commercial plantations for pulpwood production (principally *Pinus elliotii* and *P. taeda*), and cash crops such as soybeans, yerba mate (*Ilex paraguariensis*), and tea (Montagnini et al. 2005). The elevation of the study site is 140 m to 155 m, slope is <4° and aspect south to southwest (160° to 240°). The subtropical climate has an average annual temperature of 21°C (hottest month average is 28°C and coldest month average is 16°C, with maximum and minimum daily temperatures of 40°C and -3°C). During the study period (July 2005 until August 2008), frost occurred on average 30 days (190 hours) per year. Mean annual precipitation was approximately 1700 mm; the wettest periods were spring and fall (~150 to >300 mm per month) and the driest months were December and January (often <100 mm per month). Soils are deep red and belong to the Kandihumult order after the US-Soil Taxonomy (Ligier et al. 1990), and are high in clay content (50%) with some silt (30%) and sand (10-15%). The soils are of low to intermediate fertility with low P and K.

After removal of the native forest (date unknown), the study area was used as cattle range for about 500 years. In the 1980's and 1990's, soy and/or maize were planted as intensive agricultural crops continuously for about 20 years. The site then fell fallow for a few years before the nurse plantation was established in 1999 followed by underplanting of *T. ciliata* in 2004 (Alberto Hennig, pers.comm.).

Experimental design
The study site comprised three adjacent 15-ha single nurse-species plantations (*Grevillea robusta*, *Pinus taeda,* and *Pinus elliottii x Pinus caribaea*), which were underplanted with 1-year-old *T. ciliata* 4m apart in every third row, when the nurse-trees were 6 years old. The underplanting was done when crowns of nurse-trees were large enough to offer shelter to *T. ciliata* but the canopy had not closed. *T. ciliata* were grown from seeds in pots at the company owned nursery. The original nurse-tree spacing was 4 x 3 m (*G. robusta*; 833 stems/ha) or 4 x 4 m (*P. taeda* and *P. elliottii x P .caribaea*; 625 stems/ha), and these densities were reduced by 25, 50, 75 and 0% (control plots) one year after underplanting (Figure 2.1). Treatment plot sizes varied between 0.1 and 0.6 ha, depending on distribution and previous mortality of underplanted T. ciliata. The density treatments were replicated in each plantation (experiment) three times, each using a randomized block design (Erskine et al. 2005). Blocking was applied according

to slope position, thus accounting for possible differences in soil moisture and nutrient regimes. About 10 months before light measurements were conducted, all overstorey trees were pruned to a height of 3.5 m in 2005 and 6.0 m in 2006, at ages 7 and 8, respectively.

One year after *T. ciliata* establishment and prior to thinning, 5 permanent subplots (PSP) per treatment unit (total of 180 PSPs) were established to monitor growth and development of *T. ciliata*. Each PSP included one *T. ciliata* and four nearby overstorey trees (some were subsequently removed by thinning) (Figure 2.1). In accordance with initial planting densities, plot-sizes were about 12 m^2 in the *G. robusta* experiment and 16m^2 in the two pine experiments. Subplots were randomly located, and were at least 12 m from adjacent PSPs or treatment plots, and at least 20 m from logging roads to avoid edge effects.

Mortality, growth and light measurements

Mortality of *T. ciliata* was assessed annually from 2005 to 2007 in a full inventory of each nurse-tree experiment. Mortality was assessed as *T. ciliata* "present" or "absent" on each planting spot. Height and diameter at 10 cm above ground-level (D10) of *T. ciliata* were measured annually from 2005 to 2007 in the 180 PSPs. We measured height and DBH (diameter at breast height (1.3 m) outside bark) of the surrounding four overstorey trees prior to and annually after thinning. In the last year of the study (2007), stem quality was evaluated based on straightness and stability. First, straightness of *T. ciliata* was visually characterized (crooked or not crooked) in a full inventory. We then quantified stem straightness of *T. ciliata* in the PSPs as the deviation (cm) from the vertical axis (cm/m). A rod with a weight was used to measure the distance and height (m) at which the tree pith exhibited the strongest deviation from the vertical going through the tree base. Deviation from the axis was then weighted according to the deviation per meter height (after Pretzsch 2002). Finally, we calculated height (m) to diameter (cm) ratio (H/D) as an index of stem stability and morphology.

Transmitted photosynthetically active radiation (PAR) was determined once on an annual basis in each PSP and related to understory tree growth response. PAR was measured under cloudless skies with a handheld ceptometer (SF-80, Decagon, Pullman,WA), Absolute PAR values were converted to relative values as a measure of the light environment of sampled seedlings using the percent of full sun (%FS):

%FS =Qi / Qo x 100

where Qi is the averaged PAR reading from the ceptometer and Qo is the PAR reading from the datalogger in the open (Chen 1997). The sensor was moved between the two paired locations, taking open-sky measurements several times during the sampling period in the nearest canopy gap. The time-span between below-canopy and open-sky readings was less than 5 minutes (Comeau, 2000). Light measurements were taken at midday between 11.00 and 13.00 hours under cloudless skies (Comeau, 2000). The below-canopy measures were taken in each of the cardinal directions at the top of the crown of the understory *T. ciliata.* The four cardinal measures were then averaged for each location. For trees taller than 1.5 m, an external sensor was attached to the ceptometer, which was elevated to *T. ciliata* crown height using a telescoping height pole and/or ladder. To compensate for the smaller measurement surface of the device, several measurements were taken horizontally: at the edges of the crown as well as in the center. All ceptometer and external sensor measurements taken during the last 2 years of the study were consistent with results from fisheye photos (Nikon Coolpix 8400 digital camera with a fisheye Lens FC - E9) from the same plots.

Biomass sampling

To estimate *T. ciliata* biomass in the *P. elliottii x P. caribaea* experiment, we harvested five *T. ciliata* from the PSPs in each density treatment (total of 20 trees harvested). For estimating *T. ciliata* biomass under *G. robusta* and *P. taeda*, we destructively sampled only nine undamaged individuals over a range of diameter and density treatments in each experiment. This was because many remaining *T. ciliata* in the PSPs were slightly damaged by deer or past pruning operations, malformed, or aphid-infested, to which *T. ciliata* responded with leaf shedding as the summer advanced.

Biomass sampling methods were modified from Wang et al. (1996). All trees to be cut were marked at D10 and DBH. Each tree was cut at the base and separated into stem, branches, and leaves. All leaves were bagged. For large trees with complex crown architecture, the crown was separated into top, middle and bottom sections for separate measurement and analysis. The stem, branches, and leaves were weighed separately. Freshly cut stems, branches and leaves were weighed on a digital scale (5 g precision). Stem discs (5-10 cm thick) were taken at D10 and DBH and weighed. Volume was determined using Archimedes principle by submerging the discs in a

graduated receptacle. The weight recorded by the scale equalled the amount of water displaced, and hence the volume. For each crown section, a 10-30 cm subsample was cut from at least one branch considered representative of the average length and diameter. The subsample was weighed and total length and diameter at both ends were recorded. Three leaves, representative of the size, shape and condition for the crown section, were selected, bagged and weighed. One of the leaves was scanned (Hewlett Packard Deskjet F4180) to allow subsequent LSA estimation. All subsamples were weighed on a digital scale with 2 g precision. Subsequently, all subsamples were oven-dried at 70 °C for 48 hours and weighed again.

Data analysis
T. ciliata LSA per leaf was determined using the computer software LAMINA (Bylesjö et al. 2008). LSA was related to dry weight per leaf and then multiplied with total tree leaf biomass (kg, ovendry) to obtain total tree LSA. Individual tree volume was estimated for trees taller than 1.3m based on the formula for a cone:

$$V = DBH^2 * \Pi/4 * Height * f_{1.3} * 100,$$

where V is individual tree volume (cm^3), DBH is diameter at breast height (cm), Height is total height (cm), and the constant $f_{1.3} = 0.33$ (Erskine et al. 2005). For all data, outliers per treatment plot were identified (> 2.7 standard deviations from the mean) and removed using stem and leaf plots, and data were natural-log-transformed where necessary. Tree growth parameters were compared among density treatments within each nurse-species experiment using Analysis of Variance (ANOVA) and Tukey HSD multiple comparison post-hoc test. Regression slopes were compared using Analysis of Co-variance (ANCOVA). Since the overstorey species were not replicated, only qualitative comparisons were made between species using means and standard errors. All data were analyzed using SYSTAT 11.0 (SYSTAT Inc., 2004).

Results

T. ciliata sapling mortality and light
T. ciliata sapling mortality rates were high in the first year after planting (2005) but less so in the years following thinning (Table 2.1). During the study, *T. ciliata* sapling mortality was >10% lower when grown under *G. robusta* than either of the pine overstories (Table 2.1) and generally lowest at light levels between 10-20% (Figure

2.2). Mortality of *T. ciliata* tended to increase with decreasing overstorey density in 2006, but differences among thinning treatments were not significant for either *G. robusta* or *P. elliottii x P. caribaea*. For *P. taeda*, however, mortality of *T. ciliata* increased significantly with decreasing stand density immediately after thinning (2006). In the subsequent year, *T. ciliata* mortality was greatest in the highest *P. taeda* overstorey density treatment. However, we could not distinguish mortality due to environmental factors versus mortality due to damage caused by the felling and pruning operations in 2005, and pruning in 2006.

During the first two years of the study, *T. ciliata* tree-top light levels were highest under *P. elliottii x P. caribaea* and lowest under *P. taeda*; they also increased with decreasing overstorey density under all nurse species in 2006 (Table 2.1, Figure 2.3). Based on the relationship between light and overstorey basal area estimated in 2005 and 2006, the lowest early mortality of *T. ciliata* (at light levels between 10-20%) occurred at basal areas of 14.0 – 18.5 m2/ha for *G. robusta*, 22.0 – 25.0 m2/ha for *P. elliottii x P. caribaea*, and 16.0 – 20.0 m2/ha for *P. taeda* (Figure 2.3). In 2007, most *T. ciliata* had grown into full sunlight with *G. robusta*, while some were in full sunlight with *P. elliottii x P. caribaea*. The *T. ciliata* growing under *P. taeda*, however, was still over-topped in 2007; thus, tree-top light levels increased with decreasing *P. taeda* density.

In the first year after planting (2005), *T. ciliata* mortality was positively correlated with light when it was grown beneath *G. robusta* and *P. elliottii x P. caribaea* (Pearson correlation coefficients = 0.76, R2 = 0.67 (Figure 2.2)), indicating mortality was related to exposure in open conditions. By contrast, pre-thinning *T. ciliata* mortality under *P. taeda* was associated with very low light levels and possibly competition for water. One year after thinning (2006), *T. ciliata* mortality was significantly positively correlated with light only with a *P. taeda* overstorey (Pearson correlation coefficient = 0.64, and linear regression R2 = 0.42 with a p-value of 0.024). Two years after thinning, mortality was highest in the densest, darkest *P. taeda* treatments (Table 2.1), and was generally weakly negatively correlated with light over all experiments (Pearson's correlation coefficient = -0.36).

T. ciliata stem morphology

The highest percentage of deformed *T. ciliata* with the strongest deviation from the vertical occurred under a *G. robusta* overstorey, while *T. ciliata* grew straightest under *P. taeda* (Figure 2.4, Table 2.2). The fewest deformed trees occurred where *G. robusta*

or *P. elliottii x P. caribaea* had been thinned by 50%, and where *P. taeda* had been thinned by 75%. The straightest stems occurred where the pine species had been thinned by 50% and where *G. robusta* had been thinned by 25 or 50%. However, differences among treatments were not statistically significant in the *G. robusta* or *P. taeda* experiments (Table 2.2).

Average H/D ratios of *T. ciliata* were greatest in the dense, un-thinned stands, and decreased with decreasing overstorey density, regardless of overstorey species (Table 2.2). The rate of deformation (across all overstorey species and densities) was positively correlated with H/D (Pearson's correlation coefficient = 0.59). At the individual-tree level, neither H/D nor deviation from the vertical were significantly correlated with light, but at the stand-level, the proportion of crooked trees was greater in treatments with higher average light levels measured over the study period (Pearson's correlation coefficient = 0.43).

Effects of overstorey species and density on the productivity of T. ciliata

One year after planting (2005), *T. ciliata* height and D10 (cm) were greatest under *G. robusta* and lowest under *P. taeda*, but did not vary among experimental thinning plots (Table 2.2). *T. ciliata* remained largest with the greatest growth increments under *G. robusta* over the course of the study. Height and diameter increment increased significantly with decreasing density of *P. taeda*, but growth rates remained lower than under *G. robusta* or *P. elliottii x P. caribaea* except in the 75% of thinning treatment. Although *T. ciliata* also tended to grow faster with increasing thinning intensity of *G. robusta* and *P. elliottii x P. caribaea*, differences among thinning treatments in these experiments were not statistically significant.

Volume of *T. ciliata* increased strongly with increasing tree-top light (measured over the study period) when grown under *P. taeda* and *P. elliottii x P. caribaea*, but it increased only weakly when grown under *G. robusta*. Differences among regression slopes were not significant based on ANCOVA (R^2 = 0.74, p–value = 0.157) (Figure 2.5).

T. ciliata biomass allocation patterns

Effects of thinning on *T. ciliata* biomass allocation were weak. There was no relationship between light and biomass allocation to stem-wood or foliage of *T. ciliata*. In keeping with this, overstorey density had no effect on *T. ciliata* foliage or stem-wood biomass in

either of the *G. robusta* and *P. elliottii x P. caribaea* experiments. However, we did find that *T. ciliata* allocated more biomass to foliage (R^2 = 0.62, p-value = 0.013) and less to stem-wood (R^2 = 0.88, p-value = 0.0008) with increasing density of *P. taeda* (Figure 2.6). That *T. ciliata* were still young and many had not yet developed branches contributed to the lack of relationships between light or overstorey basal area and branch biomass. We found that H/D ratios decreased with decreasing thinning density in all species combinations, indicating that *T. ciliata* allocated more biomass to height than diameter growth in dense stands (Table 2.2). As *T. ciliata* grew taller, it generally allocated more biomass to stem-wood than foliage (R^2 = 0.63, p-value < 0.001) (Figure 2.7).

In the final year of the study, LSA of *T. ciliata* increased with light availability when grown under *G. robusta* or *P. elliottii x P. caribaea* but not under *P. taeda* (Figure 2.8). Additionally, there was a positive relationship between height of *T. ciliata* and light in the final year of the study (y=6.22x0.46, R^2 = 0.75, p-value < 0.001), reflecting the fact that tall trees received the most light. Accordingly, *T. ciliata* LSA was strongly related to *T. ciliata* basal-area and light availability in the final year of the study ($(Y=x1/(a+b*x2^2)$, where Y=LSA, x1 = basal-area at D10, x2 = below-canopy light as a proportion of open-sky PAR, a = 0.1636E-03; b = 0.2882E-04; R2=0.84), indicating that large, tall trees whose canopy received high amounts of light had high LSA. These relationships did not exist before (2005) or one year after thinning, when most *T. ciliata* were still small.

Trade-offs

To grow *T. ciliata* in plantations in subtropical Argentina, our study indicates that seedlings should be planted under nurse-trees. The lowest mortality and maximum growth of *T. ciliata* occurred under *G. robusta* that had been thinned by 75% two years after planting (Table 2.4); however, stem morphology in this treatment was poor. *T. ciliata* stems grew straightest where thinning was lighter (50%) (Table 2.4), particularly under pine nurse species, but both *T. ciliata* growth rate and overstorey stand basal area suffered. These results clearly indicate that choice of nurse species and thinning density will entail a trade-off between volume production and stem quality.

In terms of overstorey value, *P. taeda* had greater DBH, total height, growth increment and stand basal than the other two nurse-species (Table 2.3). Increments of all three nurse-trees tended to be higher in more open treatments, indicating decreasing

intraspecific competition with decreasing density of nurse-species. An exception was decreasing height growth of *G. robusta* with decreasing stand density (Table 2.3). Revenue was earned from pine but not *G. robusta* sawn wood with thinning (Table 2.4). Generally, over the course of the study, both *T. ciliata* and average individual overstorey tree increments increased with decreasing overstorey density (Tables 2 and 3). The optimal trade-off between maximum *T. ciliata* stem-wood, most desirable *T. ciliata* stem morphology, and minimal loss of overstorey basal-area due to thinning occurred where the *G. robusta* overstorey was thinned by 50% (Figure 2.9, Table 2.4). However, choosing *G. robusta* over *P. taeda* and *P. elliottii x P. caribaea* for the lower *T. ciliata* mortality comes at the cost of lower overstorey stand basal area in the first year (Figure 2.3), lower overall overstorey growth increments (Table 2.3), and no early thinning revenues (Table 2.4).

Discussion

Toona ciliata sapling mortality

The high *T. ciliata* sapling mortality that occurred one year after planting (declining there after) indicates that conditions during the first year of establishment are critical for establishment of this species (Bahadur 1988). Mortality of *T. ciliata* was lowest under *G. robusta* followed by *P. taeda*, while mortality was highest beneath *P. elliottii x P. caribaea*. The mortality rate under *G. robusta* one year after establishment (11%) was higher than the 4.6% mortality found by Keenan et al. (1995), who also planted *T. ciliata* beneath five-year-old *G. robusta*. However, differences in mortality rates between these two studies may have been influenced by planting stock quality and other environmental factors at the time of establishment.

Mortality of *T. ciliata* increased with increasing light availability during the first two years after planting, which agrees with our first hypothesis and confirms that *T. ciliata* requires a canopy for shelter during the first one or two years of establishment. The mortality trend with overstorey density continued one year after thinning, but only significantly so under *P. taeda*. The tendency for sapling mortality to increase with canopy openness agrees with other studies (Rebbeck et al. 2004). One possible explanation is that exposure to high radiation levels and high vapour pressure deficits cause stress responses in *T. ciliata* that lead to early mortality. High mortality also occurred in the densest *P. taeda* overstories, however, and this may have been caused

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by insufficient light availability for net photosynthesis. That *T. ciliata* mortality occurs with both over- and under-exposure to light might explain why establishment success of *T. ciliata* was best under *G. robusta,* where initial understory light levels were intermediate to those of *P. taeda* and *P. elliottii x P . caribaea* as a result of its slower growth and lower stand basal area. Our results indicate that 10-20% light availability is most suitable for establishment and first-year growth of *T. ciliata* and that these conditions naturally occur under a *G. robusta* canopy planted at 4x3m spacing.

In the third year of the study, mortality increased again in the densest stands of *P. taeda*. Some mortality was possibly caused by intense competition for water, but some (to a low undetermined extent) was also caused by felling and pruning operations applied to *P. taeda*. Both of these mortality agents must be considered when choosing pine as a possible nurse tree. *G. robusta*, by contrast, facilitates sapling survival not only through overstorey protection (as measured by light availability) but also through less intensive belowground competition for water and nutrients than the pines (Bygrafe 2005, Mahroof 2000, Burns and Honkala 1990).

T. ciliata stem morphology

There was a higher proportion of malformed *T. ciliata* under *G. robusta* than the pine species. This may have resulted from post-thinning and post-pruning *T. ciliata* instability as observed on other sites in the study area (pers. observation). Although stem morphology was not strongly correlated with light availability, *T. ciliata* is a phototropic species, suggesting its stem morphology may have been influenced by the quality and heterogeneity of the light environment under *G. robusta*. The *T. ciliata* growing under *G. robusta* did not have higher H/D values than those under the pine species, but they were taller and may have been sheltered less efficiently from wind and side-light by the smaller broadleaved crowns than the larger crowns of the pine species. The positive effects of uniform protection from side and overhead light on producing straight, clean boles of established saplings have been reported by Bahadur (1988). Accordingly, stems were straightest in the 50% thinning treatments, where side protection was more uniform towards the North and East (direction to the sun in the southern Hemisphere, as well as the main wind direction during the summer) than in the 25% and 75% thinning treatments. The variable morphological responses of *T. ciliata* stems to overstorey density, also observed by Wick (1970), led us to reject our second

hypothesis that *T. ciliata* stem morphology (straightness) improves with decreasing overstorey density.

Effects of overstorey species and density on the productivity of T. ciliata

Lower diameter, height and volume of *T. ciliata* growing under the pines than *G. robusta* likely resulted more from competition for water and nutrients (Mahroof 2000) than light, because *P. taeda* had lower and the hybrid had higher understory light levels than *G. robusta*. Furthermore, where light levels were similar under nurse species, *T. ciliata* developed more volume under *G. robusta*. *Pinus* species can rapidly form extensive lateral root systems, which may allow them to compete more intensively with *T. ciliata* for water and nutrients than *G. robust*a (Burns and Honkala 1990). The effect of water competition on *T. ciliata* can be severe because of its low drought- tolerance (Bahadur 1988). That *G. robusta* also grew more slowly in height when thinned (which was also observed in the study area by Fassola et al. 2004) may also have benefited *T. ciliata* after the initial establishment period, when it is thought to require full overhead light for growth (Bahadur 1988).

The observation that *T. ciliata* was less productive under *P. taeda* than under *P. elliottii x P. caribaea* when thinned to similar light levels indicates the two nurse species differ in their competitiveness for soil resources. Additionally, the low nutrient demand and high P use efficiency of *G. robusta* may have contributed to the superior growth of *T. ciliata* in its understory (Radersma et al. 2005). Moreover, phosphatase activity in the rhizosphere soil of *G. robusta* is five times higher than in bulk soil (Radersma and Grierson 2004), suggesting its root system may be mobilizing P, thereby increasing P availability to *T. ciliata*. Thus, *G. robusta* may not only be less competitive than pines, it may also improve P nutrition of *T. ciliata*, perhaps contributing to the weak effect of thinning *G. robusta* on *T. ciliata* growth.

Reducing overstorey density generally improved productivity of *T. ciliata*. This pattern was strong only for *P. taeda*, however, probably because thinning reduced overstorey competition for light as well as nutrients and water as observed in other studies (Mangialavori et al. 2003, Buck and Imoto 1982). By contrast, thinning had little effect on *T. ciliata* biomass increment under the *G. robusta* and *P. elliottii x P. caribaea* overstories. Therefore, for *P. taeda*, we could not reject our third hypothesis that productivity of *T. ciliata* increases with decreasing overstorey density.

T. ciliata biomass allocation patterns

T. ciliata biomass allocation was little affected by thinning of *G. robusta* or *P. elliottii x P. caribaea* stands. This likely reflects the weak effect of light on *T. ciliata* growth or biomass allocation in these stands. The positive relationship between light and LSA under *G. robusta* and *P. elliottii x P. caribaea* in the final year of the study appeared to result from tall *T. ciliata* receiving more light and hence building more LSA than shorter trees. Even though thinning did not increase biomass allocation to stem wood, the decrease in H/D ratio with decreasing density suggests there was a shift in priority within stems toward diameter growth over height growth.

Thinning of *P. taeda* stands, by contrast, resulted in a biomass shift from foliage to stem-wood among large trees. A similar pattern as found by Wang et al. (1996) in *Betula papyrifera* stands, where biomass allocation to stem-wood increased with stand age (and hence tree size). Accordingly, we could not reject our fourth hypothesis that *T. ciliata* biomass allocation patterns change with overstorey basal area and light availability.

These observations, together with the general shift in biomass allocation to stem-wood with increasing *T. ciliata* tree height, suggest that different rates of development among density treatments may simply provide insight into changes in stem-wood allocation patterns due to ontogenetic development. The relatively stable allocation patterns we observed in different light environments agree with the weak structural and physiological response of *T. ciliata* along elevational and soil gradients in a study in Hawaii (Ares and Fownes 2000). Alternatively, the weak patterns we observed may also reflect the early stages of *T. ciliata* growth we investigated.

Trade offs, conclusions and management implications

To grow *T. ciliata* on similar sites in plantations in subtropical Argentina, our study indicates that seedlings should be planted under nurse-trees. We found greater establishment success and early biomass production under *G. robusta* than *P. elliottii x caribaea* or *P. taeda* overstories and at light levels between 10-20%; at these light levels, stand basal area was lowest for *G. robusta* and highest for *P. elliottii x P. caribaea* due to different architectural properties of the species. Accordingly, to improve the protective effect of nurse pines and reduce the necessity for replanting, *P. taeda* should be established at lower densities and *P. elliottii x caribaea* at higher densities than those investigated in this study. However, further research is needed to qualify the

effect of competition, particularly for soil moisture, on *T. ciliata* mortality under those growing conditions. If nurse pines are planted in the same densities as in the present study, then large-scale replanting of *T. ciliata* may be necessary to replace mortality losses after one year. Once *T. ciliata* seedlings are safely established, usually two to three years after planting, nurse-trees should be thinned to reduce overstorey competition and maintain rapid growth rates. Thinning will increase biomass increment not only of *T. ciliata* but also the remaining overstorey trees.

The timing and thinning intensity depends on competitive intensity of the nurse-species and the management objectives. In addition to maintaining adequate sapling growth rates and stability, thinning should also ensure that stems are of high quality. Therefore, early thinning one or two years after establishment of *T. ciliata* is required to create a homogenous light environment for increased *T. ciliata* stability. The optimal compromise between *T. ciliata* growth, stem quality and overstorey stand basal-area occurred where *G. robusta* and *P. elliottii x P. caribaea* were thinned by 50% following *T. ciliata* establishment. Where *P. taeda* was used as a nurse species, heavier thinning was required to achieve rapid *T. ciliata* growth rates; this came at a cost of reduced residual overstorey stand basal area, but at the benefit of higher and earlier revenues from the thinned sawn-wood and faster residual diameter increments.

Any thinning regime has to carefully consider that rapidly grown *T. ciliata* may have reduced value because of poor stem quality. Other studies suggest that early growth, form and wood quality are less desirable when of *T. ciliata* is grown rapidly in short rotations. For example, Otarola et al. (1976) found that wood density of rapidly grown *T. ciliata* was low, which may also increase its susceptibility to physical damage. However, wood quality early in the rotation may not reflect overall stem quality at the end of the rotation.

Our findings led us to reject our fifth hypothesis because we were unable to optimize all *T. ciliata* attributes (high establishment success, stem quality and productivity) under any single nurse species or thinning treatment. We conclude that the choice of nurse species depends on management objectives and recognize that market preferences change over time. Added to this, our results may apply only to the growth stage of *T. ciliata* that we studied, and the patterns we observed now may not be apparent at the end of the rotation. Rotation-length studies are needed to investigate

the long-term influences of different nurse-tree species and densities on *T. ciliata* mortality, stem morphology and productivity.

Table 2.1. Annual mortality during the two years after thinning (2005-2006 and 2006-2007), total survival in 2007 of *T. ciliata* by overstorey species and density and average light (% of Photosynthetic active radiation (PAR) below-canopy at top of *T. ciliata* crowns / PAR open-sky readings) measured one time per year from 2005-2007. Mortality caused by thinning and pruning operations could not be distinguished from mortality due to environmental factors. Values are means and 1 S.E. is in parentheses. Means with different letters are significantly different at α<0.05, and n/s = non-significant. Letters in bold indicate data that were square-root transformed prior to analysis. Values were determined from a full inventory in each treatment plot (n=3).

Overstorey Thinning (%)		*G. robusta*					*P. elliottii x P. caribaea*					*P. taeda*				
		0	25	50	75	p-value	0	25	50	75	p-value	0	25	50	75	p-value
T. ciliata planted (N 2004)		133	123	117	105	n/a	126	116	110	84	n/a	293	71	151	202	n/a
Pre-thinning (2005)	Mortality (%,)	11.8a (4.5)	12.3a (6.5)	7.0a (3.7)	14.2a (1.6)	0.707	35.2a (5.5)	32.1a (6.3)	33.8a (4.5)	39.1a (10.3)	0.903	30.3a (3.7)	23.1a (13.5)	37.8a (3.4)	13.1a (2.4)	0.931
	Light (%)	10.4 (2.6)	14.9 (5.4)	11.2 (2.4)	11.7 (3.9)	0.844	38.9 (10.8)	46.9 (6.2)	28.5 (5.4)	26.6 (1.9)	0.207	2.4 (0.3)	4.2 (1.9)	2.9 (0.4)	2.8 (0.9)	0.683
Post-thinning (2006)	Mortality (%)	0a (0)	0a (0)	0.1a (0.1)	0.9a (0.9)	0.470	1.9a (1.9)	0.5a (0.5)	4.6a (2.6)	4.3a (2.2)	0.428	0.9b (0.5)	0b (0)	3.4b (1.7)	17.2a (1.8)	0.000
	Light (%)	12.9b (4.6)	20.2ab (5.8)	15.3ab (2.2)	45.3a (11.2)	0.034	13.1b (2.8)	38.2ab (9.6)	37.0ab (12.5)	73.1a (10.6)	0.015	**4.7b (0.8)**	**9.1ab (3.3)**	**28.1ab (8.2)**	**39.6a (11.8)**	**0.012**
Post-thinning (2007)	Mortality (%)	0a (0)	0a (0)	0.4a (0.4)	0.9a (0.9)	0.554	0.8a (0.8)	1.3a (1.3)	0a (0)	1.0a (1.0)	0.774	5.3a (1.1)	0b (0)	1.4a (1.4)	0b (0)	0.009
	Light (%)	42.1a (13.9)	38.2a (16.6)	61.5a (10.7)	54.8a (13.8)	0.627	24.0a (9.5)	23.4a (3.6)	18.4a (5.3)	48.7a (7.8)	0.056	3.1b (0.2)	4.4b (1.0)	11.9b (1.7)	35.6a (7.0)	0.001

Table 2.2. *T. ciliata* diameter (D10), total height before and after thinning, and stem morphology two years after thinning (2007). Height : Diameter ratios (H/D) and occurrence of malformed trees (% crooked) were determined from a full inventory in each treatment plot (n=3). Deviation from the vertical axis (Form, cm/m), D10 and total height before and after thinning were measured in PSPs; here, the means were based on a tally from all PSPs in each treatment plot (n=3). Values are means and 1 S.E. in parentheses. Means with different letters are significantly different at α<0.05. Letters in bold indicate square-root transformance prior to analysis. The displayed data are untransformed.

Overstorey	*G. robusta*					*P. elliottii x P. caribaea*					*P. taeda*				
Thinning (%)	0	25	50	75	p-value	0	25	50	75	p-value	0	25	50	75	p-value
D10 2005(cm)	0.7a (0.07)	0.8a (0.10)	0.7a (0.07)	0.9a (0.09)	0.594	0.7a (0.05)	0.6a (0.10)	0.5 (0.01)	0.6 (0.06)	0.229	0.3a (0.03)	0.3a (0.02)	0.3a (0.02)	0.3 (0.02)	0.676
D10 2007(cm)	4.0a (0.01)	5.2a (0.39)	4.8a (0.43)	5.8a (0.73)	0.155	3.5a (0.48)	3.2a (0.25)	3.1a (0.45)	4.6a (0.39)	0.11	0.6b (0.20)	1.4b (0.14)	3.6a (0.31)	4.6a (0.65)	0.000
D10 incr. 2005-2007 (cm)	3.3a (0.1)	4.3a (0.4)	4.1a (0.4)	4.9a (0.6)	0.134	2.7a (0.5)	2.6a (0.3)	2.7a (0.5)	4.0a (0.3)	0.111	0.4b (0.2)	1.1b (0.2)	3.1a (0.4)	4.3a (0.7)	0.000
Height 2005(m)	0.62a (0.05)	0.70a (0.11)	0.67a (0.05)	0.80a (0.60)	0.375	0.64a (0.10)	0.45a (0.04)	0.50a (0.10)	0.53a (0.05)	0.378	0.29a (0.02)	0.23a (0.01)	0.26a (0.03)	0.28a (0.02)	0.294
Height 2007(m)	4.4a (0.4)	5.1a (0.3)	4.7a (0.4)	5.2a (0.5)	0.503	3.7a (0.6)	3.2a (0.4)	2.5a (0.3)	3.7a (0.4)	0.227	1.0c (0.1)	1.7bc (0.1)	3.1ab (0.2)	3.8a (0.6)	0.001
Height incr. 2005-2007 (m)	3.7a (0.3)	4.4a (0.3)	4.0a (0.4)	4.4a (0.5)	0.630	3.0a (0.5)	2.7a (0.4)	2.0a (0.4)	3.1a (0.3)	0.255	0.7c (0.1)	1.5bc (0.1)	2.7ab (0.3)	3.5a (0.6)	0.002

Table 2.2, continued

Overstorey	*G. robusta*					*P. elliottii x P. caribaea*					*P. taeda*				
Thinning (%)	0	25	50	75	p-value	0	25	50	75	p-value	0	25	50	75	p-value
H/D 2007	138.7a (2.7)	132.5a (3.6)	128.2a (9.9)	126.8a (5.7)	0.555	181.3a (30.9)	154.4a (10.4)	125.4a (6.0)	135.2a (6.0)	0.173	205.8a (5.4)	175.6a (16.7)	136.8b (2.4)	121.7b (2.1)	0.001
Deformation 2007 (%)	25.8a (7.8)	45.4a (9.6)	25.7a (6.4)	39.9a (7.9)	0.273	21.6a (3.8)	23.5a (11.8)	11.5a (5.8)	20.0a (12.0)	0.796	6.7a (3.2)	7.3a (1.9)	4.9a (2.5)	1.1 a (0.6)	0.283
Dev. from vertical 2007 (cm/m)	17.3a (8.1)	9.5a (0.2)	10.5a (0.8)	13.4a (3.6)	0.621	**5.2ab (1.6)**	**11.5a (2.3)**	**3.6b (1.4)**	**11.6a (2.1)**	**0.026**	4.0a (4.0)	8.1a (4.1)	3.9a (1.3)	9.6a (2.5)	0.518

Table 2.3. Individual nurse-tree DBH, total height, and relative basal-area increment two years after thinning (2006 and 2007) and stand-level nurse-tree basal-area before and after thinning. Values were compared between thinning treatments separately for each nurse-tree species. Values are means and 1 S.E. is in parentheses. Values are based on tallies of all PSPs in each treatment plot (n=3). Means with different letters are significantly different at α<0.05. Letters in bold indicate data that was square-root transformed prior to analysis. The displayed data are untransformed.

Species	*G. robusta*					*P. elliottii x P. caribaea*					*P. taeda*				
Thinning (%)	0	25	50	75	p-value	0	25	50	75	p-value	0	25	50	75	p-value
Stems/ha	833	625	417	208	n/a	625	469	313	156	n/a	625	469	313	156	n/a
DBH 2005 (cm)	14.5 (1.1)	13.4 (0.7)	14.8 (0.7)	15.0 (0.4)	0.523	18.1 (0.2)	16.4 (1.0)	17.9 (1.5)	18.0 (1.1)	0.68	20.3 (0.3)	20.6 (0.2)	20.4 (0.6)	20.9 (0.9)	0.886
DBH 2007 (cm)	18.9 (1.0)	17.8 (0.6)	19.4 (1.0)	20.7 (1.2)	0.275	21.5 (0.4)	21.8 (0.7)	23.4 (1.3)	23.9 (1.2)	0.295	24.0a (0.5)	25.2a (0.3)	25.5a (0.6)	29.3b (1.6)	0.014
DBH increment (cm) 2005-2007	4.3a (0.1)	4.4a (0.1)	4.6a (0.3)	5.7a (0.8)	0.162	3.4b (0.2)	5.4b (0.3)	5.5a (0.3)	5.9a (0.1)	0.001	3.7b (0.3)	4.6b (0.1)	5.1b (0.2)	8.4a (0.9)	0.001

Table 2.3., continued

Species Thinning (%)	G. robusta					P. elliottii x P. caribaea					P. taeda				
	0	25	50	75	p-value	0	25	50	75	p-value	0	25	50	75	p-value
Ht 2005 (m)	10.5 (0.7)	10.6 (0.6)	11.1 (0.2)	11.1 (0.2)	0.725	10.7 (0.9)	9.9 (0.6)	9.9 (0.9)	10.3 (0.5)	0.821	12.3 (0.3)	12.2 (0.5)	11.7 (0.4)	12.2 (0.5)	0.736
Ht 2007 (m)	14.1 (0.6)	13.0 (0.7)	13.1 (0.6)	12.5 (0.7)	0.456	12.1 (0.5)	13.0 (0.7)	11.7 (0.6)	11.4 (0.5)	0.268	14.0 (0.5)	14.6 (0.3)	14.1 (0.1)	14.5 (0.4)	0.55
Height increment (m) 2005-2007	3.5a (0.2)	2.3ab (0.2)	2.0ab (0.4)	1.4b (0.6)	0.026	1.3a (0.4)	3.1a (0.8)	1.8a (0.4)	1.1a (0.2)	0.095	1.8a (0.4)	2.4a (0.3)	2.4a (0.3)	2.4a (0.2)	0.434
Stand BA 2005 (m²/ha)	14.4 (2.1)	12.3 (1.2)	14.9 (1.4)	15.1 (0.5)	0.524	16.6 (0.5)	13.7 (1.7)	16.2 (2.7)	16.2 (2.1)	0.709	20.3 (0.5)	21.2 (0.3)	20.7 (1.3)	21.9 (1.6)	0.782
Stand BA 2007 (m²/ha)	**24.1a (2.4)**	**16.1b (1.1)**	**12.7b (1.3)**	**7.2c (0.7)**	**0.000**	23.5a (1.0)	18.0b (1.2)	13.7b (1.5)	7.2c (0.7)	0.000	28.4a (1.2)	23.9b (0.4)	16.2c (0.8)	10.7d (1.0)	0.000

Table 2.4. Decision table displaying advantages and disadvantages of growing *T. ciliata* under different nurse species and overstorey densities.

Overstorey Thinning (%)	*G. robusta*				*P. elliottii x P. caribaea*				*P. taeda*			
	0	25	50	75	0	25	50	75	0	25	50	75
Mortality[1]	Low				High				Medium			
Stem morphology[2]	Poor				Medium				Good			
	Very poor	Poor	Medium	Poor	Poor	Very poor	Good	Poor	Poor	Very poor	Medium	Medium
T. ciliata stem-wood volume[3]	High				Medium				Medium			
	High	High	High	High	Medium	Medium	Medium	High	Low	Low	Medium	High
Revenues first thinning	No	No	No	No	No	Yes	Yes	Yes	No	Yes	Yes	Yes
Residual overstorey stand basal area[4]	High	High	Medium	Low	High	High	Medium	Low	High	High	High	Medium
Residual individual overstorey tree diameter increment[5]	Medium	Medium	Medium	High	Medium	High	High	High	Medium	Medium	High	High

[1] *T. ciliata* mortality (%) determined 1 year after planting (2005), with "Low" = 0-15%, "Medium" = >15-30%, and "High" = >30% mortality

[2] *T. ciliata* stem morphology incorporation stability (H/D) and stem form on a individual tree and thinning experiment basis (table 2), rated and averaged on a scale of 1-3 between species, with "Good" having the lowest and "Poor" the highest score, and on a scale of 1-4 within species and between thinning experiments, with "Good" = 1, "Medium" > 1-2, "Poor" > 2-3, and "Very poor" => 3-4.

[3] *T. ciliata* conical volume (cm^3) calculated as $V = DBH^2 * \Pi/4 * Height * f_{1.3} * 100$, with f = 0.33 (Erskine et al,. 2005), with "Low" = <500, "Medium" = 500-1000, and "High" = >1000

[4] Residual overstorey stand basal area (m2/ha), with "Low" < 10, "Medium" 10-15, "High" = >15

[5] Residual individual overstorey tree diameter increment (cm), with "Low" = < 3, "Medium" 3-5. "High" = >5

Figure 2.1. The arrangement of permanent subplots (PSP) in each nurse-tree experiment (PSP sizes were 12 m^2 for *G. robusta* and 16m^2 for the pine overstories). The numbers above each plots represent the thinning intensity (0, 25, 50, 75 % removal).
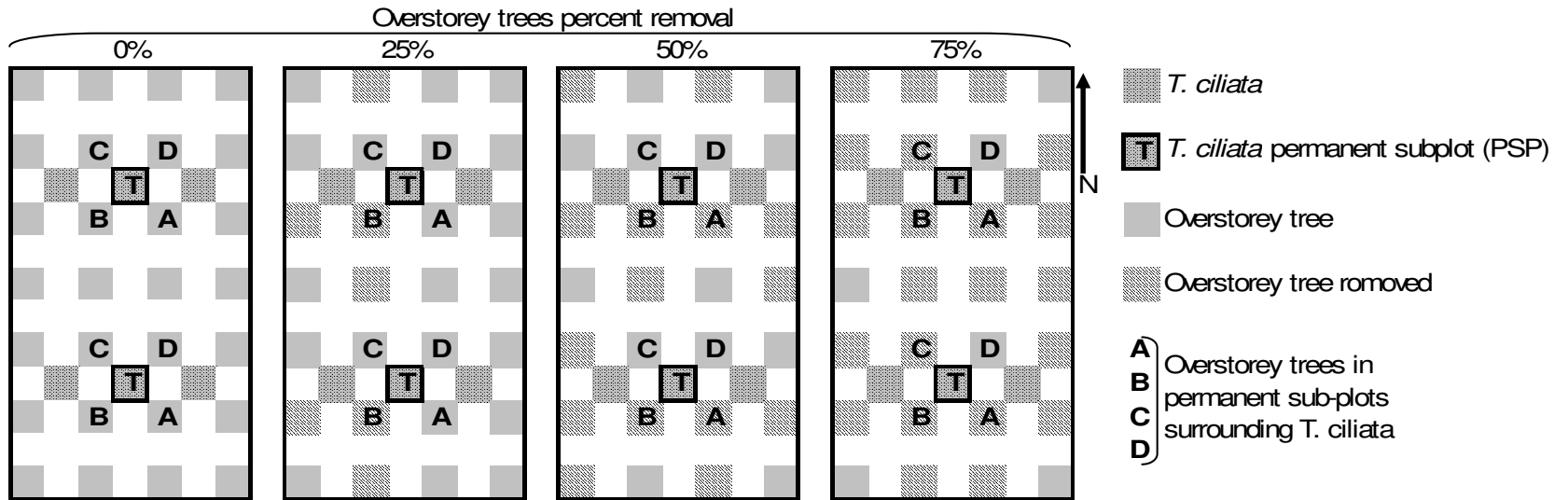
Figure 2.2. Relationship between *T. ciliata* sapling mortality one year after planting and average understory light (PAR below-canopy at top of *T. ciliata* crowns / PAR open-sky readings) prior to thinning (2005). The regression includes data from the *G. robusta* and *P. elliottii x P. caribaea* stands only because *T. ciliata* mortality responded similarly to over-exposure. Data for *P. taeda* is presented separately because mortality also resulted from low light availability. Mortality means were determined from a full sapling inventory in each treatment plot (n=3), while means for light (%) are based on measurements in all PSPs in each treatment plot (n=3). Regression (y=a*ln(x)-b) coefficients and statistics are: a = 16.1, b = 30.9, R^2 = 0.67, p-value < 0.001.
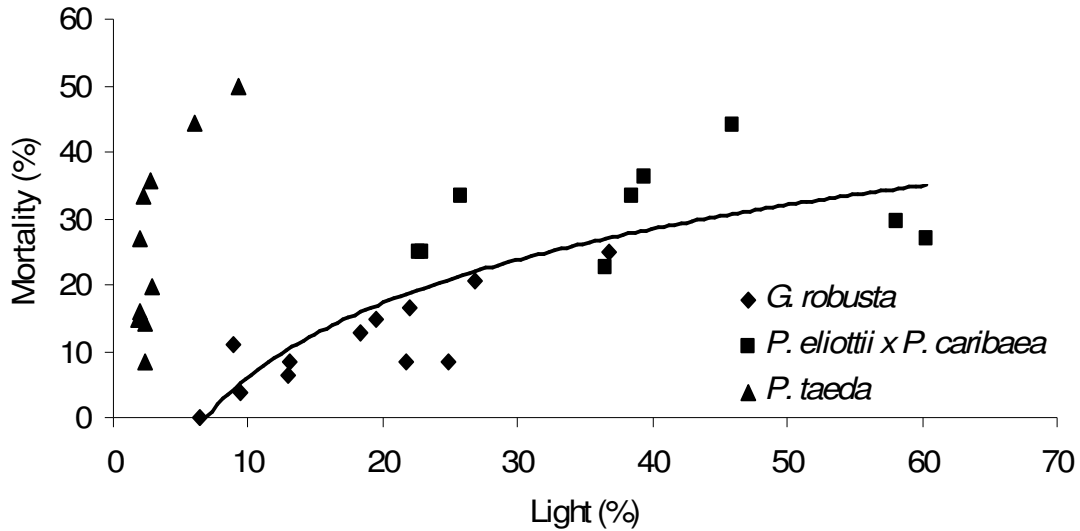
Figure 2.3. Relationship between nurse species stand basal area and light. Data was collected before and one year after thinning. The vertical and horizontal lines indicate the overstorey basal area at which *T. ciliata* mortality is lowest, assuming mortality is lowest at light levels between 10-20%. Regression coefficients and statistics for *G. robusta* are: a = -2.0, b = 46.6, R^2 = 0.70, p-value 0.010; for *P. elliottii x P. caribaea* are: a = -2.7, b = 80.5, R^2 = 0.71, p-value = 0.009; and for *P. taeda* are: a = -2.1, b = 52.3, R^2 = 0.83, p-value = 0.002. Slopes of the linear regressions (y = a*x+b) were not significantly different from each other (R^2 = 0.86, p – value = 0.586).
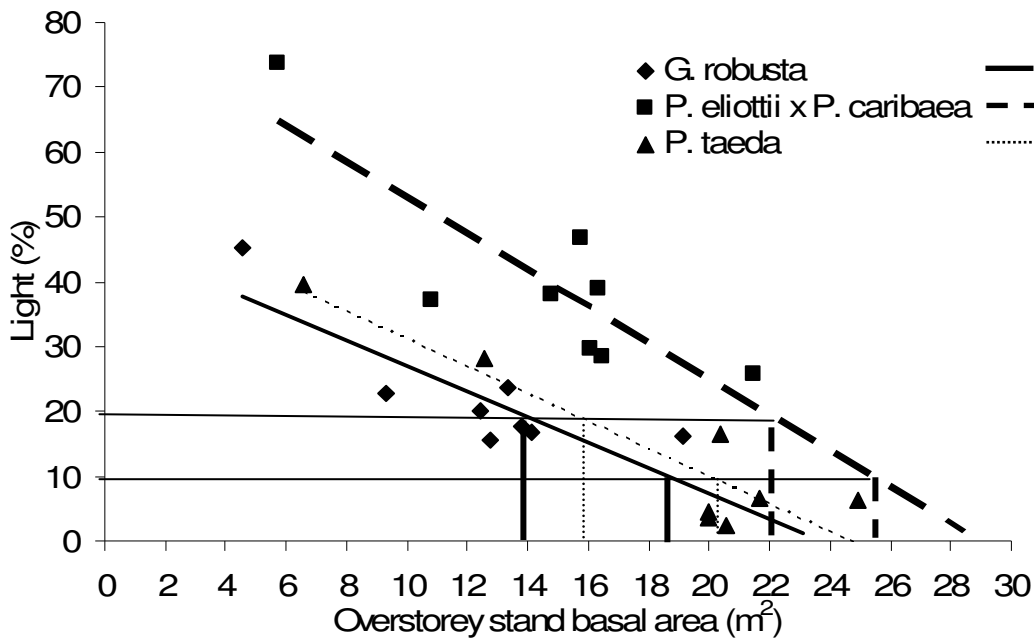
Figure 2.4. Mean percentage of deformed *T. ciliata* per overstorey species, and mean percentage deviation from the vertical measured 2 years after thinning. Values are means $\pm$ 1 SE. The percent of deformed *T. ciliata* was determined from a full inventory in each treatment plot (n=3), while deviation from the vertical (cm/m) was based on tallies trees in all PSPs in each treatment plot (n=3).
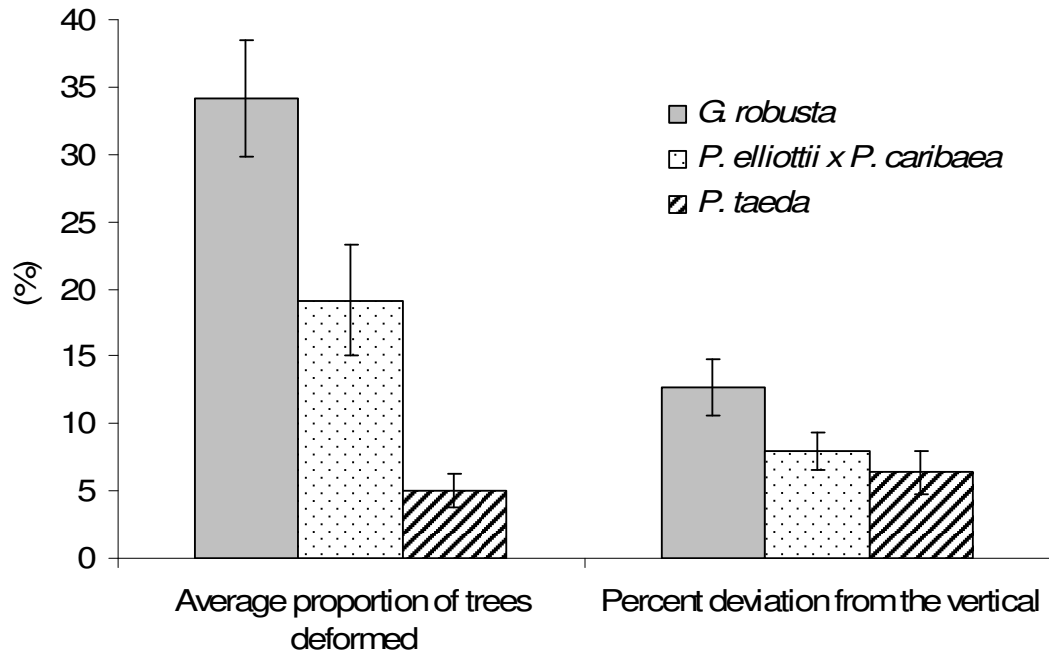
Figure 2.5. Relationship between *T. ciliata* conical volume (cm^3) and tree-top light (%) averaged over the study period (2005-2007). Values are means for each treatment plot derived from PSP tallies. The volume index was measured for trees taller than 1.3m and was based on the formula: V = DBH^2*Π/4*Height*f$_{1.3}$*100, with f = 0.33 (Erskine et al. 2005). Linear regressions (y=a*x+b) coefficients and statistics for *G. robusta* are: a = 70.9, b = 303.1, R^2 = 0.39, p-value = 0.029; for *P. elliottii x P. caribaea* are: a = 41.6, b= 693.2, R^2 = 0.77, p-value < 0.001; and for *P. taeda* are: a = 94.9, b = 768.8, R^2 = 0.80, p-value < 0.001. Slopes of the regressions were not significantly different from each other (R^2 = 0.74, p − value = 0.157).
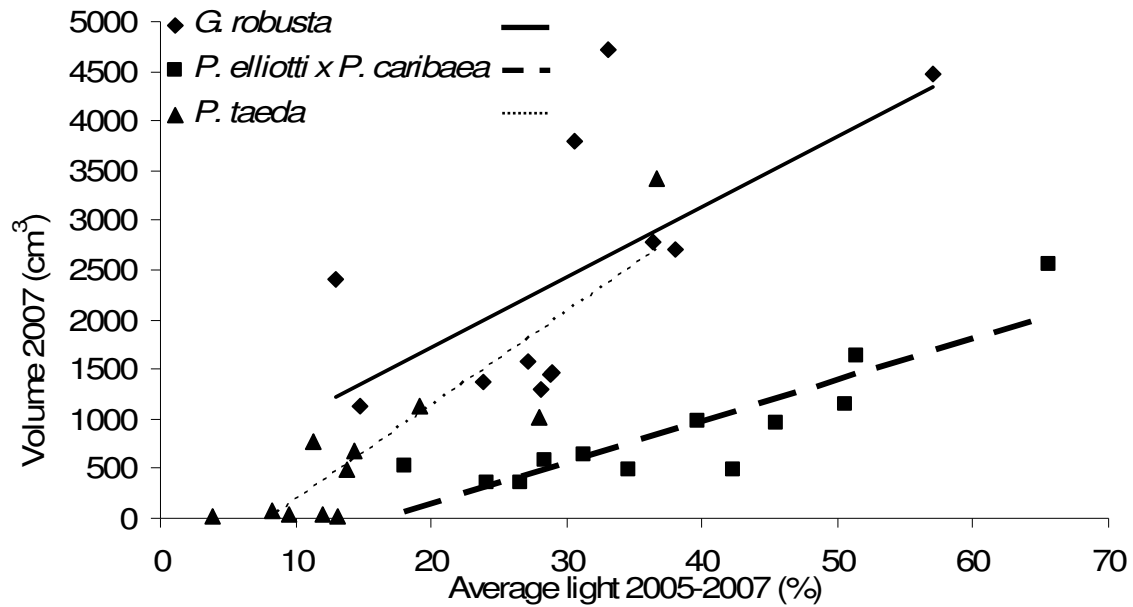
Figure 2.6. Relationship between *T. ciliata* foliar biomass/total biomass or stem-wood biomass/total biomass ratios and P. taeda basal area (m2/ha) two years after thinning. *T. ciliata* were harvested randomly from PSPs over a range of diameters, heights and overstorey densities. Linear regressions (y=a*x+b) coefficients and statistics for stem-wood biomass/total biomass ratios are: a = -0.015, b = 0.81, R^2 = 0.88, p-value = 0.0008; biomass/total biomass ratio are: a = 0.013, b= 0.20, R^2 = 0.62, p-value = 0.013.
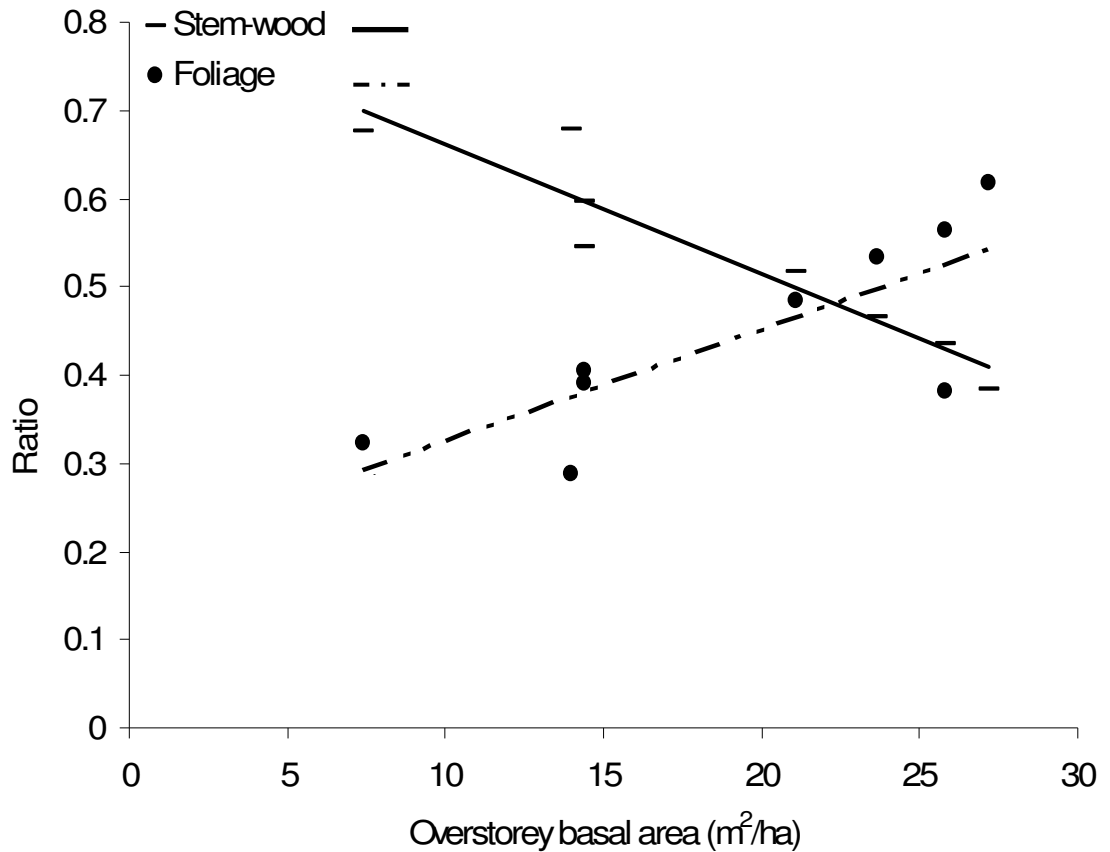
Figure 2.7. Relationship between stem-wood/foliar biomass ratio and height of *T. ciliata* two years after thinning. *T. ciliata* were harvested randomly from PSPs over a range of diameters, heights and overstorey densities. Regression ($y=a*x^b$) coefficients and statistics are: a = 0.92, b = 0.51, R^2 = 0.64, p-value < 0.001.
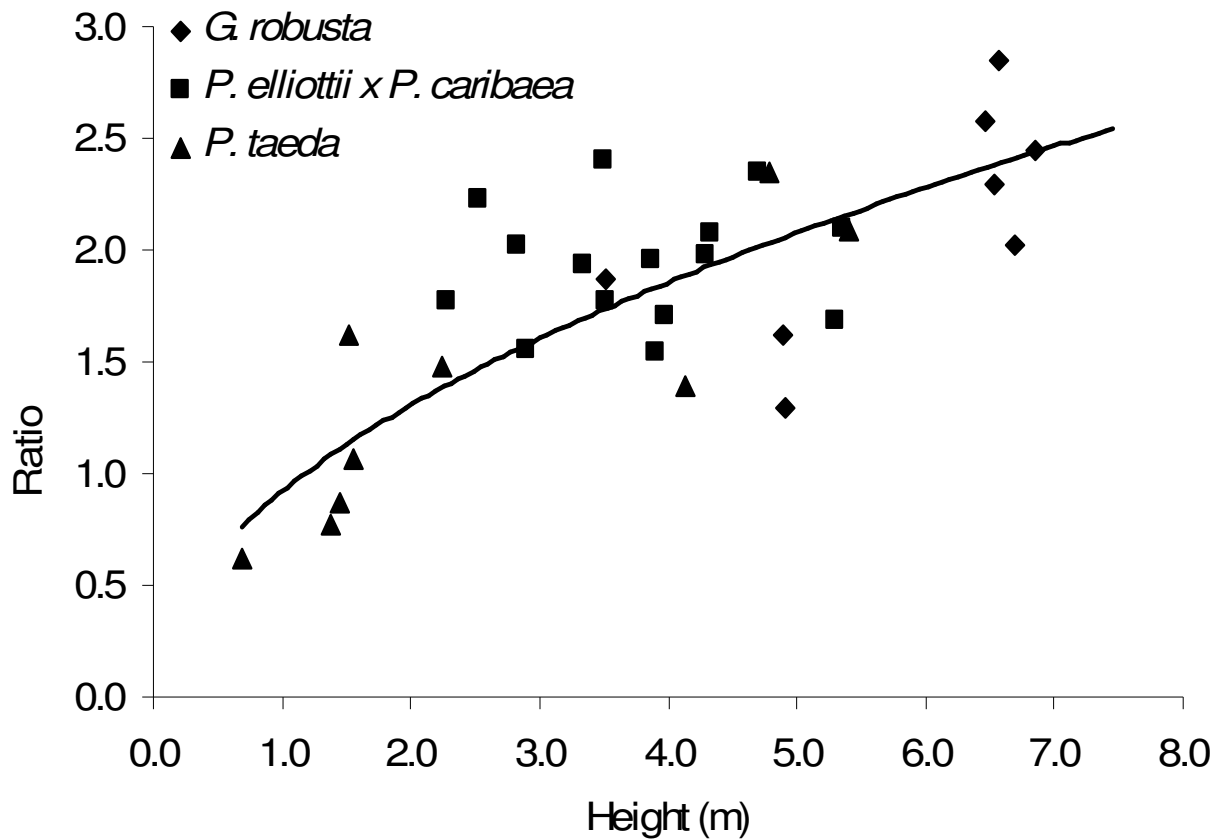
Figure 2.8. Relationship between *T. ciliata* leaf surface area (LSA, m^2) and light availability (%) two years after thinning.). Linear regressions (y=a*x+b) coefficients and statistics for *G. robusta* are: a = 0.31, b = 5.5.1, R^2 = 0.62, p-value = 0.022; for *P. elliottii x P. caribaea* are: a = 0.24, b = 2.04, R^2 = 0.48, p-value = 0.001.Slopes did not differ significantly from each other (R^2 = 0.62, p-value = 0.583)
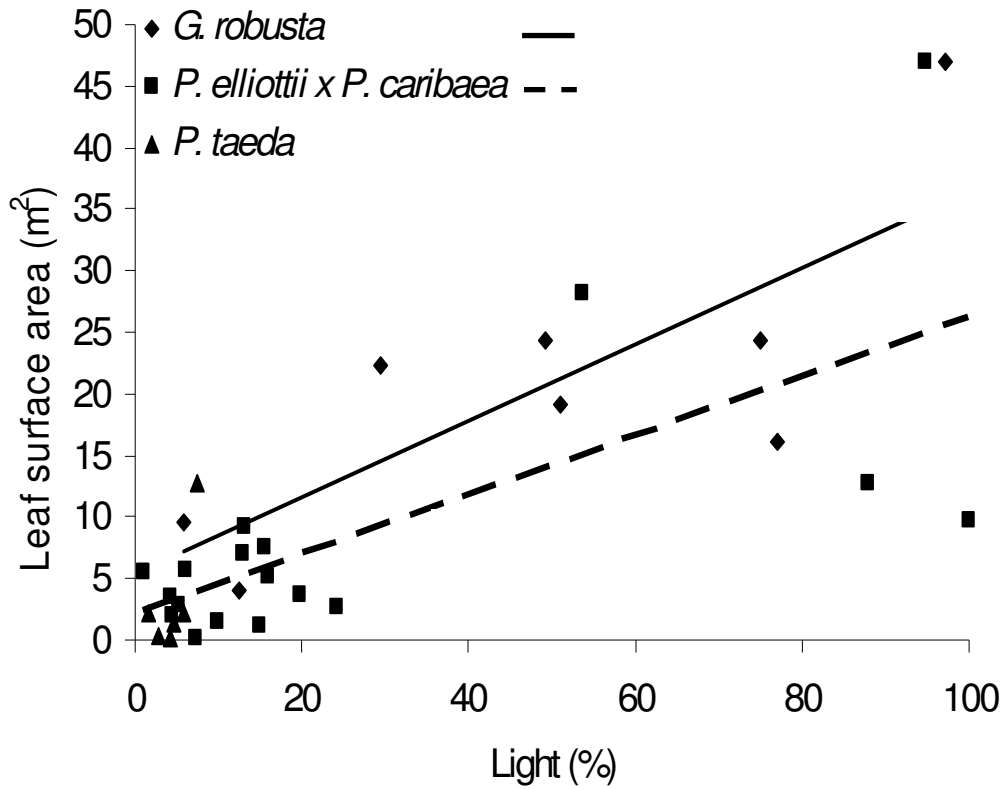
Figure 2.9. Effect of overstorey basal area (m^2/ha) on *T. ciliata* volume (cm^3) two years after thinning. The volume index was measured for trees taller than 1.3m and was based on the formula: V = DBH^2*Π/4*Height*$f_{1.3}$*100, with f = 0.33 (Erskine et al. 2005). Nurse species are: G = *G. robusta*, H = *P. elliottii x P. caribaea*, T = *P. taeda*. The number associated with the species codes indicates the thinning intensity (0-75%). Values are means + 1 SE and are based on tallies of all PSPs in each treatment plot (n=3).
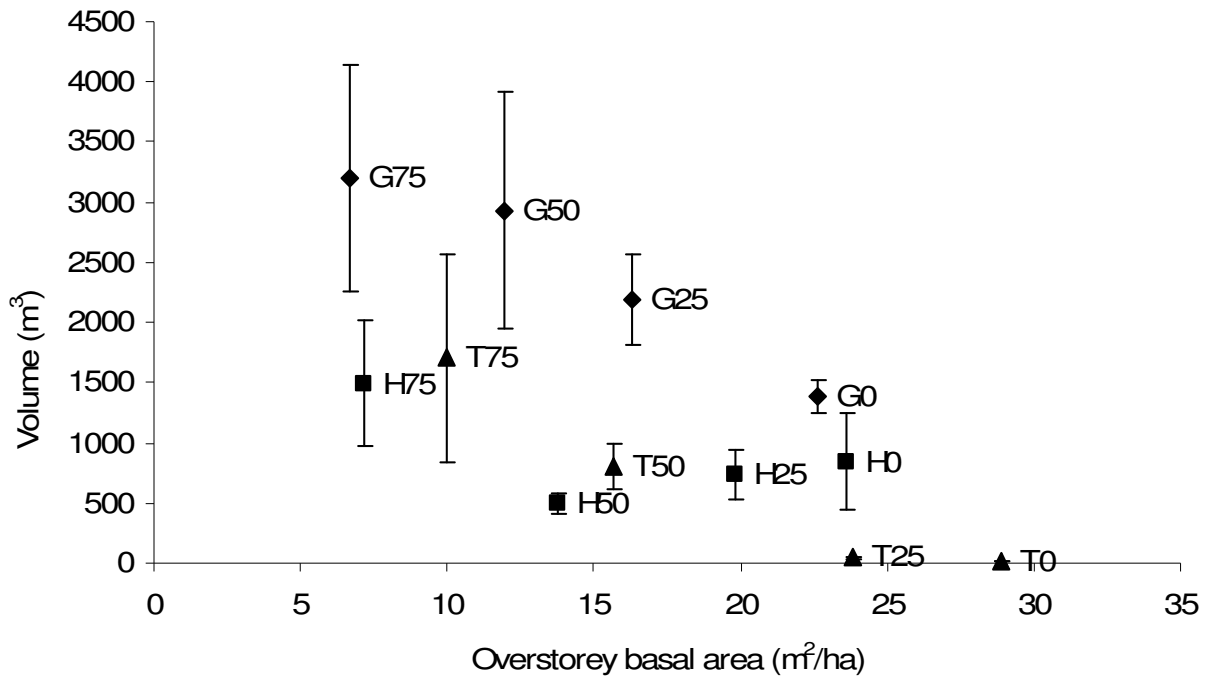
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3   Soil water and nutrient availability influence early establishment of *Toona ciliata* grown under three nurse species in north-eastern Argentina[2]

Introduction

Large areas of the world's tropical forests are being harvested with consequent losses in productivity and biodiversity. Tree plantations are one of the few management approaches by which converted lands are reforested and productivity or ecosystem services are restored. On some sites, establishing a nurse overstorey species in advance is necessary to protect underplanted crop species against abiotic or biotic damage and hence establish productive plantations. While the facilitative effects of nurse trees can be necessary for initial crop establishment, their competitive effects can also reduce juvenile growth rates of the main crop species. Although the net effects of facilitation and competition on productivity are often well documented (Dordel et al. 2009), the physiological mechanisms underlying these interactions are not (Balandier et al. 2006). Moreover, competition and facilitation mechanisms differ among nurse species and densities, and change over time and space. By understanding interspecific interaction mechanisms, nurse-crop tree species mixtures can be designed and managed so that trade-offs between crop-tree establishment and productivity are optimized. Understanding the facilitative and competitive mechanisms by which overstorey nurse species interact with understory crop species is necessary for predicting species composition and density effects on stand productivity over time and on different sites in subtropical plantations. This information is necessary to design and manage species mixtures that optimize forest productivity and ecosystem services.

In north-eastern Argentina, the Province of Misiones covers an area of approximately 30,000 km², which is less than 1% of the country total but produces more than 60% of the country's timber (Rodrigo 2009). The native subtropical forests of Misiones have been reduced to less than 50% of its original size (Burkart et al. 2002) due to establishment of commercial plantations for pulpwood production (principally *Pinus elliottii* Engelm*., P. taeda* L. and also *Pinus elliottii x P. caribaea,* and *Grevillea robusta* A. Cunn.) and cash crops such as soybeans, yerba mate (*Ilex paraguariensis*), and tea (IPEC 2008, Montagnini et al. 2005). One of the commercial tree species

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rapidly being planted on degraded lands is *Toona ciliata* Roem. (Australian red cedar) because of its value for veneer and lumber products (Bahadur 1988, Edmonds 1995, Heinrich and Banks 2005). However, *T. ciliata* is easily damaged by drought or frost during the establishment period, and therefore is being planted under previously established nurse-tree species. *Pinus elliottii x P. caribaea, P. taeda* and *Grevillea robusta* are promising nurse tree candidates.

Initial research in these novel mixtures suggests that *T. ciliata* survival and growth are greater under *G. robusta* than under *P. elliottii x P. caribaea* or *P. taeda* overstories (Dordel et al. 2009). *G. robusta*, a native species of Australia, is an evergreen broadleaf tree with a period of pronounced litterfall followed by immediate emergence of new leaves in the spring (Webb et al. 1967). It forms cluster roots (Skene et al. 1996), which are thought to increase acquisition of phosphorus (Dinkelaker et al., 1995), which is often limiting plant growth in subtropical soils. Its tap root system is thought to be capable of hydraulic lift (Burgess et al. 1998). *Pinus taeda* is a native conifer to the southeastern United States, which grows and rapidly develops strong branches (Dordel et al. 2009). *P. elliottii x P. caribaea* is a hybrid between *P. elliottii*, a native of the southeastern United States, and *P. caribaea,* a native to a few islands in the Caribbean Sea (Zheng and Ennos 1999). This hybrid has a narrow crown, which results in open canopies and allows for planting at high densities. Although overexposure to light appears to be a major factor in *T. ciliata* mortality during the first year after planting, subsequent *T. ciliata* growth is not well correlated with light availability (Dordel et al. 2009).

The overall objective of this study was to examine the effects of nurse tree species and density on light, water and nutrient availability to *T. ciliata.* We tested three hypotheses regarding the facilitative and competitive mechanisms by which overstorey nurse species interact with *T. ciliata.*

First, we hypothesized that competition for soil water and soil nutrients is a more important determinant of *Toona ciliata* growth than light availability. To test this hypothesis we determined soil water content, as well as *T. ciliata* foliar nutrients, biomass, and stemwood $\delta^{13}C$. Stemwood $\delta^{13}C$ can be a useful indicator of water availability and drought stress in seasonally dry climates, and can thus serve as seasonally integrated measure of water use efficiency (WUE; Warren et al. 2001). Accordingly, we expected to find higher $\delta^{13}C$ when soil water was more abundant

(Dupouey et al. 1993, Walcroft et al. 1997) and increases in *T. ciliata* biomass where stemwood δ ^{13}C was high. Foliar nutrient concentrations are related to the rate of photosynthesis and can thus also influence stemwood δ ^{13}C (Warren et al. 2001). Thus, we expected to find a positive relationship between *T. ciliata* stemwood δ ^{13}C and foliar nutrients, and ultimately between *T. ciliata* foliar nutrients and biomass. In tropical systems, light can be less responsible for growth dynamics (Akeyeampong et al. 1999) where soil nutrients or water are the most limiting resources; in those cases below-ground competition is considered most important (Smith et al. 1998). Consequently, we expected to find only weak relationships between light availability and *T. ciliata* stemwood δ ^{13}C, foliar nutrients and biomass.

Second, we hypothesised that *G. robusta* is more facilitative and less competitive with *T. ciliata* than the pines because of possible positive effects on soil nutrient and water availability. It has been observed that *T. ciliata* growth is higher underneath *G. robusta* (Dordel et al. 2009). Because of its reported positive effects on P (Radersma and Grierson 2004), and water availability (Smith et al. 1998, Burgess et al. 1998), *G. robusta* could compete less with *T. ciliata* in its understory. In contrast, pine species compete agressivley with understory plants for soil water and nutrients (Ashton et al. 1997, Mahroof et al. 2000, Rodríguez-Calcerrada 2008). Accordingly we expected to find taller *T. ciliata* with higher foliar nutrient contents, and moister soils with higher nutrient contents beneath a *G. robusta* overstorey than beneath the pines. We also expected to find higher soil nutrient concentrations and water contents closer to *G. robusta* than to pine or *T. ciliata*. We also assumed that *G. robusta* would either: a) have higher leaf-litter quality (lower litter C:nutrient ratios) and would return more nutrients to the soil than the pines, or b) would be more P efficient and thus have foliage and foliar litter with lower P concentrations (Vitousek 1984) than the pine species.

Finally, we tested the hypothesis that soil water and soil nutrient availability would increase with decreasing overstorey density by comparing *T. ciliata* growth, foliar nutrient contents and soil water availability among different overstorey densities. The underlying rationale was that lower densities of the overstorey would require less nutrients and soil water, so that more of these resources should then be available to the understory and result in increased soil water and taller *T. ciliata* with higher foliar nutrient contents (Rodríguez-Calcerrada 2008).

Material and methods

Study site

The study site was near the city of Posadas, in the Province Misiones, in north-eastern Argentina (about 55 55 13.46° W Longitude and 27 28 10.53° S Latitude). The elevation of the study site is 140 m to 155 m, slope is <4° and aspect south to southwest (160° to 240°). The subtropical climate has an average annual temperature of 21°C (hottest month average is 28°C and coldest month average is 16°C, with maximum and minimum daily temperatures of 40°C and -3°C). During the study period, frost occurred on average 30 days (190 hours) per year. Mean annual precipitation was approximately 1700 mm; the wettest periods were spring and fall (~150 to >300 mm per month) and the driest months were December and January (often <100 mm per month). Soils are deep red and belong to the Kandihumult order according to US Soil Taxonomy (Ligier et al. 1990), and are high in clay content (50%) with some silt (30%) and sand (10-15%). The soils are of low to intermediate fertility with low P and K availability.

After removal of the native forest (date unknown), the study area was used as cattle range for about 500 years. In the 1980s and 1990s, soy and/or maize were planted as intensive agricultural crops continuously. The site then fell fallow for less than ten years before the nurse plantation was established in 1999 followed by underplanting of *T. ciliata* in 2004 (Alberto Hennig, pers.comm.).

Experimental design

The study site comprised three adjacent 15-ha single-nurse-species plantations (*Grevillea robusta*, *Pinus taeda,* and *Pinus elliottii x Pinus caribaea*), which were underplanted with 1-year-old *T. ciliata* when the nurse trees were 6 years old. The underplanting was done when crowns of nurse trees were large enough to offer shelter to *T. ciliata* but the canopy had not closed. *T. ciliata* was planted in ploughed rip lines between every third rip line of overstory trees. The overstorey trees were originally planted in ploughed rip lines that were 4 m apart and with 3 or 4 m within-row spacing, resulting in stand densities of 833 stems/ha for *G. robusta* and 625 stems/ha for *P. taeda* and *P. elliottii x P .caribaea*. These densities were reduced by 25, 50, 75 and 0% (control plots) one year after underplanting. The density treatments were replicated three times in each experiment, each using a randomized block design (Erskine et al. 2005). Blocking was applied according to slope position, thus accounting for possible

differences in soil water and nutrient regimes. About 10 months before light measurements were conducted, all overstorey trees were pruned to a height of 3.5 m in 2005 and 6.0 m in 2006 (at ages 7 and 8, respectively).

One year after planting and prior to thinning, five permanent subplots (PSP) per treatment unit (total of 180 PSPs) were established to monitor growth, physiology and resource availability of *T. ciliata*. Each PSP included one *T. ciliata* and four nearby overstorey trees (some were subsequently removed by thinning). In accordance with initial planting densities, plot sizes were about 12 m^2 in the *G. robusta* experiment and 16m^2 in the two pine experiments. Subplots were randomly located, and were at least 12 m from adjacent PSPs or treatment plots, and at least 20 m from logging roads to avoid edge effects.

Growth and light measurements

Height of *T. ciliata* was measured annually from 2005 to 2007 in a full inventory. Diameter at breast height (DBH), diameter at 10 cm above ground level (D10).

Transmitted photosynthetically active radiation (PAR) was determined once on an annual basis in each PSP and related to understory tree growth response. PAR was measured under cloudless skies with a handheld ceptometer (SF-80, Decagon, Pullman,WA), Absolute PAR values were converted to relative values as a measure of the light environment of sampled seedlings using the percent of full sun (%FS):

%FS =Qi / Qo x 100

where Qi is the averaged PAR reading from the ceptometer and Qo is the PAR reading from the datalogger in the open (Chen 1997). The sensor was moved between the two paired locations, taking open-sky measurements several times during the sampling period in the nearest canopy gap. The time-span between below-canopy and open-sky readings was less than 5 minutes (Comeau, 2000). Light measurements were taken at midday between 11.00 and 13.00 hours under cloudless skies (Comeau, 2000). The below-canopy measures were taken in each of the cardinal directions at the top of the crown of the understory *T. ciliata.* The four cardinal measures were then averaged for each location. For trees taller than 1.5 m, an external sensor was attached to the ceptometer, which was elevated to *T. ciliata* crown height using a telescoping height pole and/or ladder. To compensate for the smaller measurement surface of the device,

several measurements were taken horizontally: at the edges of the crown as well as in the center. All ceptometer and external sensor measurements taken during the last 2 years of the study were consistent with results from fisheye photos (Nikon Coolpix 8400 digital camera with a fisheye Lens FC - E9) from the same plots.

Biomass, stemwood δ 13C and foliar nutrient sampling and analysis of T. ciliata trees

To estimate *T. ciliata* biomass in the *P. elliottii x P. caribaea* experiment, we harvested five *T. ciliata* from the PSPs in each density treatment (total of 20 trees harvested). For estimating *T. ciliata* biomass under *G. robusta* and *P. taeda*, we destructively sampled only nine undamaged individuals over a range of diameter and density treatments in each experiment. This was because many remaining *T. ciliata* in the PSPs were slightly damaged by deer or past pruning operations, malformed, or aphid-infested, to which *T. ciliata* responded with leaf shedding as the summer advanced.

Biomass sampling methods were modified from Wang et al. (1996). Each tree was cut at the base and separated into stem, branches, and leaves. All leaves were bagged. The stem, branches, and leaves were weighed separately. Freshly cut stems, branches and leaves were weighed on a digital scale (5-g precision). Stem discs (5-10 cm thick) were taken at D10 and DBH and weighed. Volume was determined using Archimedes principle by submerging the discs in a graduated receptacle. The weight recorded by the scale equalled the amount of water displaced, and hence the volume. All subsamples were oven-dried at 70 °C for 48 hours and weighed again.

For determining *T. ciliata* foliar nutrient content, the oven-dried foliar samples were combined by overstorey tree species and density treatment prior to analysis. Foliage was sent to LANAIS N-15, Bahia Blanca, Argentina, and analyzed for C, N, P, K, Ca, Mg concentrations, using an automated carbon analyser for C (LECO Model CR12), N Kjeldahl digestion for N (Bremner and Mulvaney 1982), and liquid pre-digestion with HNO_3+HClO_4 (2:1) and an ICP-AES (Inductively Coupled Plasma - Atomic Emission Spectrometer) for Ca, Mg, P and K. Foliar nutrient content was determined using the derived biomass equations.

Stemwood of all harvested *T. ciliata* was assessed for natural abundance ^{13}C for a seasonally integrated measure of water use efficiency. Wedges of stemwood were cut from oven-dried D10 stem discs, ground in a ball-mill, and 1-mg subsamples sent to the UC Davis Stable Isotope Laboratory (Davis, CA, USA) for analysis. At the lab, the

samples were combusted, CO_2 was liberated, and the gas was analyzed for the $^{13}C/^{12}C$ ratio with a continuous-flow isotope-ratio mass spectrometer.

Foliar and litter nutrient analysis of the overstorey trees

For three overstorey trees per control plot, current-year foliage was sampled from four branches, one from each of the cardinal directions, located in of the upper third of the crown. The sample trees were climbed using ropes and so-called "trepadores" (adjustable devices for climbing posts), and the branches were cut and returned to ground level. Ten leaves or fascicle bundles of needles were harvested at the second lateral whorl of each branch. All foliage was bagged and oven-dried at 70 ^{o}C for 48 hours (Wang et al. 1996). The oven-dried samples were composited for each control plot and overstorey species for a total of 9 samples per species. The samples were sent for analysis of C, N, P, K, Ca, and Mg as described above.

Leaf-litter was sampled under ten randomly selected overstorey trees in each control plot (ten leaves of *G. robusta* or ten needles per pine species). Only un-decomposed, recently shed leaf-litter was sampled from the soil surface. Similar to the fresh foliar samples, the litter samples were composited for each overstorey species and control plot (n= 9) analysed for total C, N, P and K.

Litterfall

Litter traps measuring 1 m^2 and lined with 2-mm mesh were placed in three locations in control plots near three of the PSPs (PSP 1, 3 and 5). The traps were placed under the northern crown-edge of one overstorey tree in each PSP. Overstorey litter was collected monthly over the course of one year. After separating the foliage from other materials (i.e., bark, seeds, plant material from other species, insects, and bird faeces), it was oven-dried for 48 hours at 70°C and weighed (after Palma et al. 2002). For each litterfall sample tree, height to green crown, pruning height, and crown diameter in the four cardinal directions were recorded, along with distance and cardinal direction to each litter trap.

Soil nutrients and bulk density

Mineral soils were sampled in *T. ciliata* and overstorey rip lines at the edge of each PSP (about 2 m away from the nearest *T. ciliata*) in control plots. Surface vegetation and organic matter was first removed and soil was then collected at 0-10 cm (n=3) and 20-50cm (n=6) depths using a shovel and knife. Samples were composited

by rip line and soil depth and mixed. Samples were stored at <5°C and shipped in a cooler to LANAIS N-15, Bahia Blanca, Argentina, using the methods outlined in Tiessen and Moir (1993) for total C, McGill and Figueiredo (1993) for total N, and Kalra and Maynard (1991) for available P.

Bulk density was estimated at 0-10 cm after the methods of Macadam (1987). The soil was sampled using a slide hammer and thin-walled metal rings with an internal diameter of 5.5 cm and a height of 4 cm (Vtot=100 cm^3).The samples were oven-dried at 105°C for 48 hours and weighed (Mtot). Using a 2-mm sieve, organic debris (e.g., roots, Mr) and coarse soil fragments (Mcf) were removed. The bulk density of the fine (<2mm) soil fraction (Df) was estimated as follows:

Df= (Mtot-MCf-Mr)/Vtot.

Rooting depths and soil water

Rooting depth was measured in two soil pits per treatment plot (30 pits per overstorey species = 90 pits). Each soil pit (1 m long and 60 cm deep) traversed a *T. ciliata* rip line and bordered an overstorey rip line. Rooting depths were determined along the vertical profile of the soil pits using a measuring tape. *G. robusta* cluster roots were observed in the upper 10 cm of mineral soil under the *G. robusta* overstorey; cluster roots generally form in the top soil layers (Lambers 2003). Soil water content was measured in 20-cm sections along the vertical profile of a subsample of soil pits using a soil water meter (Moisture Meter type HH2 readout unit with moisture sensor ThetaProbe Theta Probe, Delta-T Devices, Cambridge). It was not possible to measure soil water in all soil-pits due to difficulties inserting the probe into the compacted clay soil. Additionally, we measured soil water by inserting the soil water meter to 7-cm depth along transects in the *T. ciliata* rip line at 0.5- m, 1-m, and 1.5-m distances from the *T. ciliata*.

Data analysis

T. ciliata foliar nutrient content was calculated from individual tree leaf nutrient concentrations and foliar biomass of destructively harvested *T. ciliata* (n=38) as follows:

Y = a + b x D^2 x Ht,

where a and b are constants based on regression analysis, D = DBH (outside bark, cm), Ht = total height (m), and Y = foliar biomass (kg, oven-dry mass) (after Standish et al. 1985, modified). For trees shorter than 2.5 m, we used D10 instead of DBH, and applied this equation to trees in the corresponding height range.

For all data, outliers per treatment plot were identified (> 2.7 standard deviations from the mean) and removed using stem and leaf plots. Data were natural-log or square-root-transformed where not normally distributed. Tree growth parameters were compared among density treatments within each nurse-species experiment using Analysis of Variance (ANOVA) and Tukey HSD multiple comparison post-hoc test, Kruskal-Wallis non-parametric tests, and paired t-tests. Regression slopes were compared using Analysis of Co-variance (ANCOVA). All data were analyzed using SYSTAT 11.0 (SYSTAT Inc., 2004).

Results

Relationships between T. ciliata growth and environmental parameters
T. ciliata biomass increased with increasing stemwood $\delta^{13}C$ (Figure 3.1) and foliar nutrient contents (N, P, K, Mg, Ca) (Figure 3.2). Accordingly, foliar nutrients were positively related to stemwood $\delta^{13}C$ (Figure 3.3). P and K in particular had strong positive relationships with both biomass and stemwood $\delta^{13}C$. Linear regression slopes between *T. ciliata* foliar nutrient contents and stemwood $\delta^{13}C$ or biomass differed significantly among nutrients (Figures 2 and 3). Overall, *T. ciliata* stemwood $\delta^{13}C$ was lowest under *P. taeda* and highest under *G.robusta*, and increased with tree height ($y=1.0Ln(x)-29.6$, $R^2=0.58$, p-value < 0.001; Pearson's correlation coefficient = 0.72) and with soil water content at 20-40cm soil depth of the overstorey rip lines ($y = 5.7x+201.1$, $R^2 = 0.42$, p-value = 0.022; Pearson's correlation coefficient: 0.65). *T. ciliata* stemwood $\delta^{13}C$ also increased with average percent light measured over the period of the study period (Figure 3.4). There was no relationship between percent light measured at the top of *T. ciliata* crowns prior to harvesting and foliar N, P, K or Mg contents, with the exception of a positive relationship between light and foliar Ca content ($y = 0.85x – 50.1$, $R^2=0.70$, p – value = 0.003; Pearson's correlation coefficient = 0.83).

Overstorey species effects

T. ciliata growth and foliar nutrients

The height, leaf biomass and foliar nutrient contents of *T. ciliata* saplings were all greatest under *G. robusta* and least under *P. taeda* (Figure 3.5, Table 3.1), though foliar nutrient concentrations (%) were similar in all treatments (Table 3.1). Among the overstorey species, foliar P concentration was lower in *G. robusta* than the pines, whereas Mg, K and Ca concentrations were higher (Table 3.2). Leaf-litter of *G. robusta* was also lower in P but higher in N and K than that of the pines (Table 3.2). Litter C:N ratio was lowest in *G. robusta*, but litter C:P ratios were lowest in *P. taeda* (Table 3.2).

Mean annual foliar litterfall mass was highest under *P. taeda,* and with its high foliar P concentration, cycling of P back into the soil was highest under this species (Table 3.3). Return of N and K in litter was more similar among the nurse species because the high concentrations in *G. robusta* offset the greater masses of *P. taeda* litter. Litterfall from the pine species peaked in April (fall), while *G. robusta* litterfall peaked in October (spring) (Figure 3.6).

Soil nutrients

The nutrient contents of soil in the rip lines in which the overstorey species were planted were greater than those in the rip lines in which *T. ciliata* was planted, where bulk density was lowest (Table 3.4). Total and available soil P tended to be greater at 0-10 cm depth than 20-50 cm depth, particularly in the *G. robusta* rip lines. Total P was similar among all nurse species, but available P (0-10 cm depth) was much greater under *G. robusta* than either of the pine overstories (Table 3.4). Total K was intermediate beneath *G. robusta* and highest beneath *P. taeda*, but available K was highest beneath *G. robusta* (Table 3.4).

Soil water

Soil water content was generally greater under *G. robusta* than under the pine overstories (Table 3.5). For all nurse species, top-soils (0-20cm) were drier in *T. ciliata* rip lines than in the overstorey rip lines, but more so under the pines, especially *P. elliottii x P. caribaea*, than under *G. robusta* (Table 3.5). Soil water content generally increased with soil depth, but nevertheless, soils remained relatively drier under the pines than *G. robusta* and drier in the *T. ciliata* versus overstorey rip lines at 20-40 cm; these differences diminished at 40-60 cm depth (Table 3.5). There tended to be less

water at 20-40 cm depth under *P. taeda* than *P. elliottii x P. caribaea*. In correspondence with these results, average rooting depths in overstorey rip lines were generally greatest under *P. taeda* (Table 3.6). In addition, rooting was deeper in the *T. ciliata* than the overstorey rip lines of the un-thinned treatments (Table 3.6).

Overstorey density effects

T. ciliata growth and foliar nutrients

Height growth of *T. ciliata* increased with decreasing density of *P. taeda*. These trends were weaker with *G. robusta* and *P. elliottii x P. caribaea* (Figure 3.5). Likewise, *T. ciliata* nutrient contents generally increased with decreasing overstorey density for all three overstorey species, with significant differences among density treatments only with a *P. taeda* overstorey, for K under *P. elliottii x P. caribaea* (Table 3.1).

Soil water

Soil water content in *T. ciliata* rip lines decreased with decreasing overstorey density of *G. robusta,* particularly at 0-20 cm depth (Table 3.5). In contrast, soil water content in *T. ciliat*a rip lines generally increased with decreasing overstorey density of the pines, although the trend was not strong (Table 3.5). Total biomass of *T. ciliata* increased with soil water content of the upper 7 cm and 20-40cm of the mineral soil (Figure 3.7).

Discussion

Relationships between T. ciliata growth and environmental parameters

Growth of *T. ciliata* was strongly correlated with foliar nutrient content and wood natural abundance ^{13}C, suggesting nutrient availability was an important growth-regulating factor to *T. ciliata* at our study site. The positive correlations between natural abundance ^{13}C, foliar nutrient content and soil water content, combined with faster growth rates and higher foliar nutrient contents of *T. ciliata* under *G. robusta* than the pines, suggest that *T. ciliata* had greater photosynthetic capacity under *G. robusta* and at lower overstorey densities (Kranabetter et al. 2009). The greater photosynthetic capacity of the faster growing and nutrient-rich *T. ciliata* under *G, robusta* and in the more open stand conditions appeared to result from greater soil phosphorus, potassium and water contents. However, since foliar nutrient content naturally increased with foliar and stem biomass, and foliar nutrient concentrations were relatively stable across

species and density treatments, caution is needed in in interpreting soil nutrient limitations to growth.

Soil water availability was also an important determinant of *T. ciliata* growth rate as indicated by the positive, significant correlation between *T. ciliata* natural abundance ^{13}C and soil water content. The importance of water availability to growth of *T. ciliata* is further underscored by the drier surface soils and greater rooting depth in the *T. ciliata* than overstorey rip lines, presumably resulting from greater soil water availability at depth in the *T. ciliata* rip lines; in the overstorey rip lines, by contrast, intense interspecific water competition likely caused niche partitioning between the understorey and overstorey species for enhanced overall water uptake. Soil water availability probably interacted strongly with nutrient availability since litter decomposition and soil nutrient distribution are inhibited by drought (Radersma et al. 2005). Light availability appeared to be of lesser importance to early growth of *T. ciliata*, as has been reported elsewhere in the tropics (Akeyeampong et al. 1999), but may increase in importance as the trees reach more open conditions in the upper nurse canopy. These findings support our first hypothesis that competition for soil nutrients and water and are more important determinants of *T. ciliata* growth than light availability. We argue further that water may be more limiting than nutrients because foliar nutrient concentrations were fairly similar across treatments, suggesting nutrient contents simply increased linearly with growth of *T. ciliata*.

Overstorey species effects

Foliar nutrients and water availability appeared to be less limiting to *T. ciliata* growth under *G. robusta* than under the pines. This corresponded with higher nitrogen, magnesium, potassium and calcium concentrations in fresh foliage of *G. robusta* as opposed to the pine species, and lower concentrations of phosphorus. It is possible that higher foliar nitrogen contents interacted with lower water stress under *G. robusta* to enhance *T. ciliata* growth (Fife and Nambiar, 1997). In general, *T. ciliata* foliar nutrient concentrations were high compared with other studies of *T. ciliata* in the tropics (Thompson et al., 1992, Ares and Fownes, 2000, Specht and Turner 2006).

The lower phosphorus concentration in fresh foliage of *G. robusta* than the pines may mean that this species has lower phosphorus demand and is more phosphorus efficient, and thus is less competitive with *T. ciliata* for this nutrient. The higher phosphorus use efficiency of *G. robusta* is illustrated by its much lower foliar

phosphorus content, as well as higher N:P and lower C:N ratios (in live foliage and monthly litterfall, which is suggestive of faster decomposition rates (Vitousek 1984)), compared with the pines, especially *P. taeda*. High phosphorus use efficiency of *G. robusta* has been noted in other studies (Radersma and Grierson 2004). Greater nitrogen availability under *G. robusta* is also suggested by the lower litter C:N and higher N:P ratios. Prescott (2002) indicates that rates of turnover and nutrient release may be less associated with rates of litter decomposition, however, than the mass of nutrients a tree species returns in its litterfall. *G. robusta* sheds most of its leaves in spring, returning a pulse of nutrients to the soil at a time that is most beneficial for *T. ciliata* growth. Strong positive relationships between the initial concentrations of N or P and the rate of release of nutrients during the initial stages of decay have been reported elsewhere (Prescott 2002), stressing the importance of the timing of litterfall. The pines, on the other hand, shed the bulk of their needles in the fall, when *T. ciliata* growth and nutrient demand are low. In the pine stands, nutrients may be leached from the soil before *T. ciliata* can take it up.

Proteoid roots (cluster roots) were observed in the *G. robusta* stands in our study, and may explain why available soil phosphorus was significantly higher under *G. robusta,* particularly in the top 10 cm near *G. robusta* individuals, even though total soil phosphorus did not differ from the pine overstories. Other studies report phosphatase activity five times higher in the rhizosphere soil of *G. robusta* than in bulk soil (Radersma and Grierson 2004), suggesting its root system may be mobilizing phosphorus, thereby increasing phosphorus availability to *T. ciliata*. High phosphorus concentrations in leaves and litter of *P. taeda* and lower phosphorus contents in *T. ciliata* foliage indicated that *P. taeda* competed strongly with *T. ciliata* for phosphorous and might thus negatively effect its growth. Out of the three overstorey species, *P. elliottii x P. caribaea* was intermediate with respect to its soil, leaf and litter nutrient contents and *T. ciliata* growth. The low nutrient demand, high phosphorus use efficiency and phosphorus mobilization by *G. robusta* (Radersma et al. 2005) suggests that it is not only less competitive than the pines, but that it facilitates phosphorus nutrition of *T. ciliata* and may help explain the superior growth of *T. ciliata* in its understory. Cluster roots may not only increase phosphorus but also availability of other nutrients, such as potassium. Available soil potassium was highest under *G. robusta* but total soil potassium was lower, even relative to *P. taeda*.

All soil nutrients tended to be more abundant in the overstorey rip lines than the *T. ciliata* rip lines (top 10 cm). These results suggest that *T. ciliata* and the nurse species together more fully exploited the soil profile, suggestive of niche packing, and probably also competed with each other. Alternative explanations for the greater nutrient availability in the overstorey rip lines may be greater nutrient input via stem-flow (Rao et al 1988) or the observed higher bulk-densities of the soil.

The wetter soils under the *G. robusta* than pine stands, especially at shallow depths, suggest that *G. robusta* competes with *T. ciliata* for water less strongly than do the pine species, especially *P. elliottii x P. caribaea,* though sample numbers underneath the latter were low and more research is needed to confirm this observation. This could be the result of soil resource partitioning, where the two species exploit different horizontal or vertical rooting zones (Leuschner et al. 2004). Smith et al. (1997) found that when the top of a soil profile was drier than the underlying soil layers, uptake of water by *G. robusta* was dominated by the activity of vertical roots. Thus, complementary water use by *G. robusta* and the crop it was grown with was maximised when most water was available from below the crop (Smith et al 1997). Thus, the severity of competition for water between *G. robusta* and *T. ciliata* may have depended on soil water rather than root distribution. Alternatively, the considerably higher water content of surface soils under *G. robusta* than the pines, and the increasing soil water content with increasing *G. robusta* density, could indicate hydraulic lifting by *G. robusta.* Hydraulic lift could also partly explain the enhanced nutrient availability under *G. robusta* (Burgess et al. 1998).

Because of the positive effects of *G. robusta* on soil water and nutrient availability to *T. ciliata*, we failed to reject our second hypothesis that *G. robusta* is more facilitative and less competitive with *T. ciliata* than the pines. Our findings agree with other studies reporting low competitiveness of *G. robusta* in plantations (Rao et al. 1998, De Costa et al. 2007). *G. robusta* has been successfully used as a nurse tree in other parts of the world with *T. ciliata* (Buck and Imoto 1982, Keenan et al. 1995, Bygrave and Bygrave 2005) as well as with agricultural crops on various sites in Rwanda (Kalinganire 1996) and with tea plantations (De Costa et al. 2007). The success of tea grown under *G. robusta* in Sri Lanka is attributed to reduced evaporation and transpiration rates, thus contributing to higher soil water content and greater growth (De Costa et al. 2007). Conversely, in agro-forestry studies in Kenya, competition by *G.*

robusta for water led to reduced crop yields of cowpea (Lott et al. 1999) and maize (Lott et al. 1999, Radersma et al. 2005). Radersma et al. (2005) suggested that the reduced crop growth was not due to direct water limitation but the decreased phosphorus diffusion to roots caused by low soil water content.

Overstorey density effects

T. ciliata foliar nutrients and soil water generally increased with decreasing overstorey pine density, leading to increased *T. ciliata* growth. Thus, for pine nurse species, we could not reject our third hypothesis that soil water and soil nutrient availability to *T. ciliata* increased with decreasing overstorey density. However, soil water content increased with density of *G. robusta*, most likely due to hydraulic lift or niche complementarity, resulting in low interspecific interference. Consequently, we reject our third hypothesis for a *G. robusta* overstorey.

Conclusions

Our results suggest that *G. robusta* is less competitive with *T. ciliata* for soil nutrients and soil water compared to the pine-nurse species on mesic sites in north-eastern Argentina. *G. robusta* may facilitate *T. ciliata* growth by providing shelter and increasing P and potentially K availability, possibly through cluster roots, and by increasing soil water, possibly by hydraulic lift or complementary water use. *P. taeda* compete predominantly with *T. ciliata* for nutrients while *P. elliottii x P. caribaea* competes especially strongly for water. *G. robusta* may be less effective as a nurse species, however, on sites where soil phosphorus, potassium and water are less limiting. Our results indicate that choosing *G. robusta* as a nurse species can be more important than thinning for maximizing early *T. ciliata* growth. More empirical observations, including from different sites and densities and at different growth stages of all four species in this study, are needed to confirm these observations.

Table 3.1. Foliar nutrient contents (g/dry weight per tree) of individual *T. ciliata* trees in each overstorey species and thinning treatment two years after thinning and foliar nutrient concentrations (%). Nutrient contents were calculated using an equation relating individual-tree foliar biomass (leaf biomass; kg, ovendry) with height and diameter of destructively subsampled *T. ciliata* (n=38) (y = a + b x D^2 x Ht) . Values are means (and 1 S.E. in brackets) and are based on tallies from all PSPs in each treatment plot (n=3). Samples were compared between overstorey species using ANOVA. Means with different letters are significantly different at α=0.05. Letters in bold indicate data that had been square root-transformed for analysis. The displayed data are untransformed.

Overstory	*G. robusta*					*P. elliottii x P. caribaea*					*P. taeda*				
Thinning (%)	0	25	50	75	p-value	0	25	50	75	p-value	0	25	50	75	p-value
Leaf biomass (kg)	0.64a (0.04)	0.78a (0.11)	0.97a (0.22)	1.0a1 (0.22)	0.405	0.29a (0.04)	0.2a (0.05)	0.28a (0.10)	0.53a (0.17)	0.219	0.03a (0.00)	0.05a (0.01)	0.26b (0.04)	0.52b (0.14)	0.005
C (g)	290.02a (17.19)	362.45a (50.33)	447.58a (99.89)	485.06a (107.52)	0.353	134.10a (18.77)	95.27a (23.32)	127.75a (46.66)	246.17a (78.66)	0.213	15.10b (0.71)	22.34b (3.55)	117.53ab (16)	239.23a (65.27)	0.005
N (g)	23.03a (1.37)	23.96a (3.33)	28.32a (6.32)	31.17a (6.91)	0.646	8.98a (1.26)	6.18a (1.51)	6.76a (2.47)	13.85a (4.43)	0.254	0.97b (0.05)	1.43b (0.23)	8.17ab (1.15)	15.32a (4.18)	0.005
P (g)	0.93a (0.05)	1.23a (0.17)	1.59a (0.35)	1.58a (0.35)	0.304	0.41a (0.06)	0.33a (0.08)	0.40a (0.14)	0.74a (0.24)	0.265	0.05b (0.00)	0.07b (0.01)	0.40ab (0.06)	0.87a (0.24)	0.004
K (g)	4.94a (0.29)	6.91a (0.96)	5.70a (1.27)	7.04a (1.56)	0.528	**2.01ab (0.28)**	**1.22ab (0.28)**	**1.02b (0.37)**	**4.23a (1.35)**	**0.031**	0.36b (0.02)	0.59b (0.09)	2.17ab (0.30)	4.42a (1.21)	0.006
Ca (g)	10.61a (0.63)	13.73a (1.91)	16.82a (3.75)	17.30a (3.83)	0.378	4.62a (0.65)	3.2a (0.8)	4.30a (1.57)	7.76a (2.48)	0.265	0.48b (0.02)	0.52b (0.08)	3.87ab (0.54)	8.52a (2.32)	0.004
Mg (g)	1.93a (0.11)	2.52a (0.35)	3.32a (0.74)	2.74a (0.61)	0.354	1.05a (0.15)	0.71a (0.18)	1.04a (0.38)	1.53a (0.49)	0.427	0.11b (0.01)	0.14b (0.02)	0.79ab (0.11)	1.66a (0.45)	0.005

Table 3.1., continued

Overstorey Thinning (%)	*G. robusta*				*P. elliottii x P. caribaea*				*P. taeda*			
	0	25	50	75	0	25	50	75	0	25	50	75
N within sample	4	3	1	1	5	5	5	5	3	2	3	1
C (%)	45.62	46.20	46.21	47.88	46.46	46.57	45.31	46.45	43.67	44.84	45.70	46.00
N (%)	3.62	3.05	2.92	3.08	3.11	3.02	2.40	2.61	2.80	2.88	3.18	2.95
P (%)	0.15	0.16	0.16	0.16	0.14	0.16	0.14	0.14	0.14	0.13	0.16	0.17
K (%)	0.78	0.88	0.59	0.69	0.70	0.59	0.36	0.80	1.05	1.19	0.84	0.85
Ca (%)	1.67	1.75	1.74	1.71	1.60	1.56	1.52	1.46	1.40	1.04	1.51	1.64
Mg (%)	0.30	0.32	0.34	0.27	0.36	0.35	0.37	0.29	0.32	0.29	0.31	0.32
C/N (%)	12.59	15.13	15.80	15.56	14.93	15.42	18.90	17.77	15.60	15.58	14.39	15.62
C/P (%)	313.32	293.74	282.01	307.00	330.75	290.48	322.65	331.71	319.97	336.81	292.05	274.38
N/P (%)	24.88	19.42	17.84	19.73	22.15	18.84	17.07	18.67	20.52	21.62	20.29	17.57

Table 3.2. Fresh foliar and litter nutrient concentrations (mg/g) of nurse tree species sampled in unthinned stands. Values are means (and 1 S.E. in brackets) and are based on tallies from subsamples (n=3) per treatment plot (n=3). Samples were compared between overstorey species using ANOVA. Means with different letters are significantly different at $\alpha<0.05$.

Species	Fresh Foliage				Overstorey litter			
	G. robusta	*P. elliottii x P. caribaea*	*P. taeda*	p-value	*G. robusta*	*P. elliottii x P. caribaea*	*P. taeda*	p-value
C	473.83a (4.14)	474.77a (4.39)	473.87a (3.66)	0.983	469.67c (1.20)	485.00a (2.08)	478.33b (1.20)	0.001
N	13.86a (0.70)	11.88a (0.15)	12.66a (0.96)	0.205	7.87a (0.28)	6.73ab (0.41)	3.80b (0.30)	0.000
P	0.42b (0.02)	0.58ab (0.06)	0.67a (0.05)	0.023	0.18b (0.01)	0.16b (0.01)	0.36a (0.01)	0.000
K	4.64a (0.09)	3.36b (0.11)	3.82ab (0.44)	0.037	2.90a (0.17)	1.63b (0.03)	1.43b (0.15)	0.000
Ca	7.80a (0.20)	1.61b (0.41)	1.61b (0.07)	0.000	n/a	n/a	n/a	n/a
Mg	1.26a (0.06)	0.68b (0.05)	0.75b (0.02)	0.000	n/a	n/a	n/a	n/a
C/N	34.32a (1.45)	39.97a (0.73)	37.85a (2.78)	0.176	59.86b (2.19)	72.58b (4.54)	127.62a (11.04)	0.001
C/P	1132.40a (54.97)	835.37ab (96.59)	710.37b (46.85)	0.013	2688.47a (217.30	2995.81a (1547.03)	1340.36b (45.23)	0.001
N/P	33.06a (1.67)	20.85b (2.09)	18.79b (0.23)	0.001	45.12a (4.52)	41.64a (3.48)	10.66b (0.98)	0.001

Table 3.3. Mass (kg/ha) and nutrient contents (kg/ha) of annual aboveground litter of the three nurse-tree species sampled monthly in unthinned stands. Values are means and 1 S.E. in brackets (n=3). Samples were compared between overstorey species using ANOVA. Means with different letters are significantly different at α<0.05.

Species	G. robusta	P. elliottii x P. caribaea	P. taeda	p-value
Mass	5304.67b (736.95)	4867.00b (1120.00)	12408.43a (846.22)	0.002
C	2489.23b (341.61)	2360.03b (545.55)	5933.90a (400.27)	0.002
N	41.50a (4.72)	32.13a (6.00)	47.50a (6.46)	0.244
P	0.93b (0.13)	0.80b (0.21)	4.47a (0.32)	0.000
K	15.27ab (2.69)	7.87b (1.95)	17.67a (0.84)	0.030

Table 3.4. Nutrient contents and bulk densities in the mineral soil of rip lines in which the three overstorey species (OS) were planted and in the rip lines in which *T. ciliata* (TC) was planted. Samples were taken at 0-10 and 20-50-cm soil depths and calculated using values for soil nutrient concentrations and bulk densities. We did not determine soil bulk densities in 20-50-cm soil depths (n/a), however assumed that values are similar, since these sample locations were still in the ploughed rip lines. Values are means (and 1 S.E. in brackets) and are based on soil samples from unthinned stands (n=3). Means with different letters are significantly different at α=0.05. Letters in bold indicate that data were log-transformed for analysis. The displayed data are untransformed.

Overstorey	*G. robusta*				*P. elliottii x P. caribaea*				*P. taeda*			
Depth (cm)	0-10		20-50		0-10		20-50		0-10		20-50	
Rip line	OS	TC	OS	TC	OS	TC	OS	TC	OS	TC	OS	TC
Total C (mg/g)	24.53 (0.91)	20.79 (1.68)	18.08 (1.23)	16.18 (0.83)	24.17 (0.98)	23.00 (1.82)	18782.45 (579.79)	17601.06 (508.61)	25.12 (0.96)	22.86 (0.90)	17.93 (1.15)	17.20 (0.25)
Total N (mg/g)	1.91 (0.052)	1.69 (0.095)	1.40 (0.127)	1.39 (0.141)	1.89 (0.057)	1.73 (0.093)	1.48 (0.074)	1.39 (0.099)	1.96 (0.069)	1.71 (0.034)	1.44 (0.97)	1.40 (0.034)
Total P (mg/g)	0.40 (0.012)	0.35 (0.033)	0.32 (0.032)	0.28 (0.018)	0.38 (0.033)	0.34 (0.024)	0.29 (0.045)	0.27 (0.023)	0.39 (0.011)	0.37 (0.019)	0.28 (0.014)	0.25 (0.011)
Available P (mg/kg)	**11.41 (5.01)**	**7.61 (2.38)**	**1.06 (0.20)**	**1.05 (0.18)**	3.30 (0.20)	3.35 (0.76)	2.51 (0.50)	3.51 (2.26)	**6.12 (2.02)**	**3.85 (0.60)**	**0.80 (0.10)**	**1.28 (0.58)**

Table 3.4., continued

Overstorey	G. robusta				P. elliottii x P. caribaea				P. taeda			
Depth (cm)	0-10		20-50		0-10		20-50		0-10		20-50	
Rip line	OS	TC	OS	TC	OS	TC	OS	TC	OS	TC	OS	TC
Total K (mg/g)	1.35 (0.28)	1.23 (0.22)	1.65 (0.21)	1.42 (0.19)	1.21 (0.19)	1.05 (0.12)	1.18 (0.22)	1.38 (0.18)	1.57 (0.14)	1.37 (0.078)	1.51 (0.24)	1.30 (0.20)
Exchangeable K (mg/kg)	83.26 (4.25)	66.26 (9.82)	29.80 (1.84)	27.03 (4.79)	67.49 (4.40)	63.97 (9.63)	35.48 (4.46)	29.91 (4.75)	71.99 (16.29)	70.20 (4.65)	27.09 (9.19)	26.19 (9.29)
Soil Bulk density	1.20 (0.026)	1.08 (0.027)	n/a	n/a	1.15 (0.026)	1.07 (0.027)	n/a	n/a	1.23 (0.021)	1.09 (0.026	n/a	n/a

Table 3.5. Soil water content (kg m^{-2} 60cm depth^{-1}) at three different depths (0-20, 20-40, and 40-60 cm) of the mineral soil of rip lines in which the three overstorey species (OS) were planted and in the rip lines in which *T. ciliata* (TC) was planted in the four thinning treatments (0-75% overstorey removal). Samples were taken during one day in the winter (July 30, 2007). No samples were taken in 0 and 75% thinning treatments of *P. elliottii x P. caribaea*. Values were compared between thinning treatments (horizontal, Kruskal Wallis and Mann-Whitney U tests) and rip lines (vertical, paired t-test) separately for each nurse-tree species. Values are means (and 1 S.E. in brackets) and are based on different n per thinning treatment, with *G. robusta* and *P. elliottii x P. caribaea*: n=2 per treatment, and *P. taeda*: n=4 for 0 and 50%, n=5 for 25%, and n=4 for 75% thinning of the overstorey. Means with different letters are significantly different at α=0.05. Capital letters indicate differences between rip lines using t-tests, while small letters indicate differences between thinning treatments using non-parametric tests.

Overstorey species		*G. robusta*					*P. elliottii x P. caribaea*			*P. taeda*				
Soil depth (cm)	Thinning treatment	0	25	50	75	p-value	25	50	p-value	0	25	50	75	p-value
0-20	OS	79.7Aa (18.3)	76.4Aa (8.2)	63.9Aa (1.3)	74.9Aa (3.1)	0.729	52.9Aa (8.5)	52.2Aa (7.2)	0.956	60.6Aa (2.2)	58.36Aa (5.3)	62.2Aa (1.4)	68.5Aa (1.6)	0.146
	TC	67.3Aa (4.3)	56.7Aab (1.9)	52.1Ab (0.5)	44.9Bb (0.7)	0.012	30.4Aa (2.6)	43.9Ba (7.5)	0.231	37.7Ba (2.4)	46.9Ba (4.2)	46.4Ba (3.0)	43.1Ba (1.2)	0.158
	p-value	0.539	0.302	0.096	0.08		0.163	0.023		0.004	0.154	0.025	0.008	
20-40	OS	87.1Aa (3.3)	84.8Aa (0.6)	76.8Aa (1.6)	77.6Aa (2.6)	0.074	65.3Aa (2.7)	77.6Aa (3.4)	0.105	63.7Aa (2.3)	62.2Aa (3.4)	70.9Aa (3.0)	66.8Aa (2.7)	0.274
	TC	73.2Aa (12.8)	57.5Aa (12.5)	49.2Aa (8.2)	60.2Aa (4.6)	0.489	45.5Aa (5.9)	50Aa (9.8)	0.732	39.7Ba (3.5)	38.8Ba (2.1)	49.7Ba (3.1)	46.3Ba (5.3)	0.136
	p-value	0.382	0.285	0.217	0.25		0.261	0.145		0.011	0.003	0.022	0.108	
40-60	OS	84.8Aa (0.0)	82.8Aa (2.6)	80.4Aa (0.8)	83.9Aa (2.5)	0.459	86.6Aa (7.6)	61.2Aa (2.6)	0.087	69.6Aa (3.9)	73.4Aa (1.4)	71.1Aa (4.0)	71.4Aa (1.3)	0.801
	TC	85.1Aa (1.7)	74.2Aa (12.4)	77.8Aa (1.4)	76.3Aa (8.7)	0.772	74.9Aa (4.1)	64.9Aa (1.5)	0.149	66.8Aa (6.9)	64.4Aa (6.8)	79.2Aa (2.2)	69.6Aa (6.6)	0.104
	p-value	0.889	0.669	0.447	0.62		0.500	0.533		0.486	0.299	0.108	0.841	

Table 3.6. Rooting depths in rip lines in which the three overstorey species (OS) were planted and in the rip lines in which *T. ciliata* (TC) was planted and in the four thinning treatments (0-75% overstorey removal). Values were compared between thinning treatments (ANOVA) and rip lines (paired t-test) separately for each nurse tree species (n=3; with 1-2 subsamples (soil-pits) per replicate. Means with different letters are significantly different at α<0.05. Capital letters indicate differences between rip lines using t-test (vertical), while small letters indicate differences between thinning treatments using ANOVA (horizontal).

Overstorey species	*G. robusta*					*P. elliottii x P. caribaea*					*P. taeda*				
Thinning treatment	0	25	50	75	p-value	0	25	50	75	p-value	0	25	50	75	p-value
OS	36.5Ba (2.5)	42.2Aa (5.5)	34.8Aa (5.2)	34.2Aa (5.8)	0.665	33.8Ba (0.7)	42.5Aa (2.0)	38.0Aa (1.9)	37.5Aa (4.8)	0.257	36.3Aa (2.7)	42.5Aa (0.6)	46.5Aa (2.4)	36.5Aa (5.0)	0.128
TC	40.8Aa (2.9)	38.7Aa (3.1)	40.0Aa (2.8)	39.7Aa (2.0)	0.953	37.5Aa (1.4)	39.2Aa (3.3)	35.8Aa (2.2)	42.2Aa (0.7)	0.271	42.8Aa (1.1)	38.2A (1.9)	42.0Aa (0.8)	41.2Aa (1.2)	0.141
t-test p-value	0.010	0.395	0.170	0.292		0.035	0.135	0.281	0.373		0.214	0.158	0.210	0.349	

Figure 3.1. Relationship between stemwood δ ^{13}C and total aboveground biomass of *T. ciliata* trees grown beneath the three overstorey species, y=8E+18e$^{1.54x}$, R^2 = 0.62, p-value < 0.001, Pearson's correlation coefficient = 0.60.
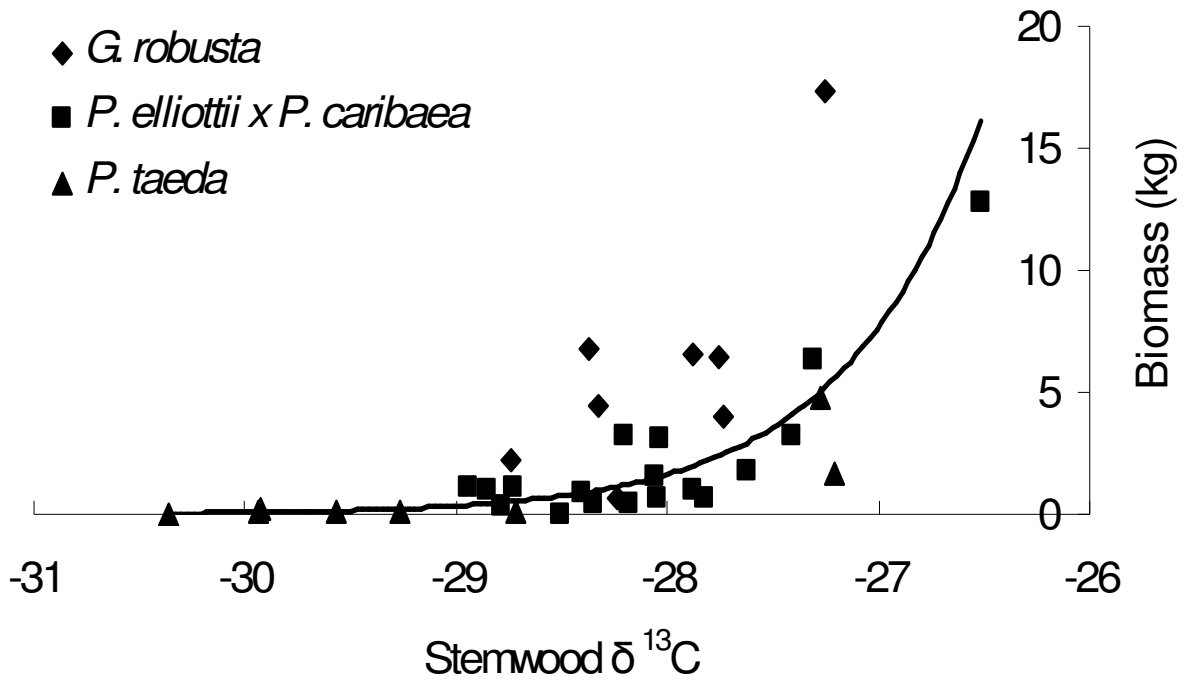
Figure 3.2. Relationship of individual *T. ciliata* total aboveground biomass (kg, oven-dry) and their nutrient contents of Mg, P, Ca, N and K (g/m^2). Values are means of each treatment plot derived from PSP tallies. Linear regressions (y=a*x+b) coefficients and statistics are: for Mg: a =0.007, b = 0.19, R^2 = 0.53, p-value = 0.019; for P: a = 0.0045, b= 0.082, R^2 = 0.52, p-value = 0.019; for Ca: a = 0.049, b = 0.86, R^2 = 0.57, p-value = 0.012; for N: a = 0.071, b = 1.67, R^2 = 0.46, p-value = 0.025; and for K: a = 0.61, b = 0.74, R^2 = 0.91, p-value < 0.001;. Slopes of the regressions were significantly different from each other (p – value = 0.000).
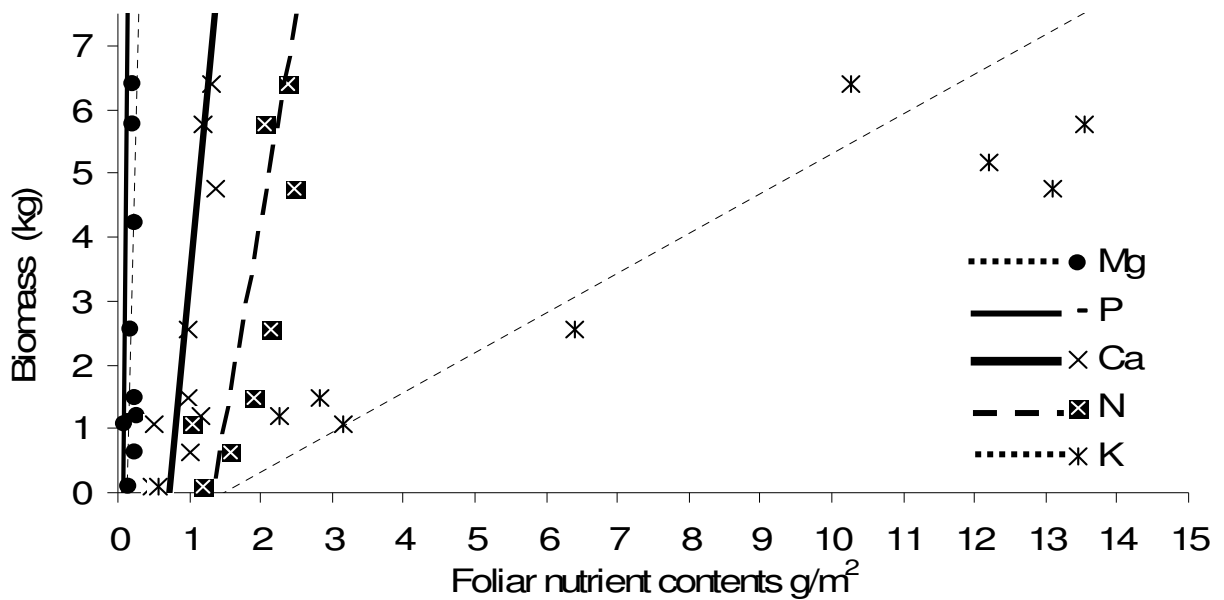
Figure 3.3. Relationship between *T. ciliata* stemwood δ ^{13}C and foliar contents of Mg, P, Ca, N and K (g/m^2). Values are means for each treatment plot derived from PSP tallies. Linear regressions (y=a*x+b) coefficients and statistics are: for Mg: a = 0.07, b = 2.2, R^2 = 0.64, p-value = 0.006; for P: a = 0.041, b= 1.25, R^2 = 0.80, p-value = 0.001; for Ca: a = 0.43, b = 13.0, R^2 = 0.81, p-value=0.000; for N: a = 0.60, b= 18.8, R^2 = 0.62, p-value = 0.004; and for K: a = 0.099, b = 29.1, R^2 = 0.70, p-value = 0.002;. Slopes of the regressions were significantly different from each other (p – value = 0.000).
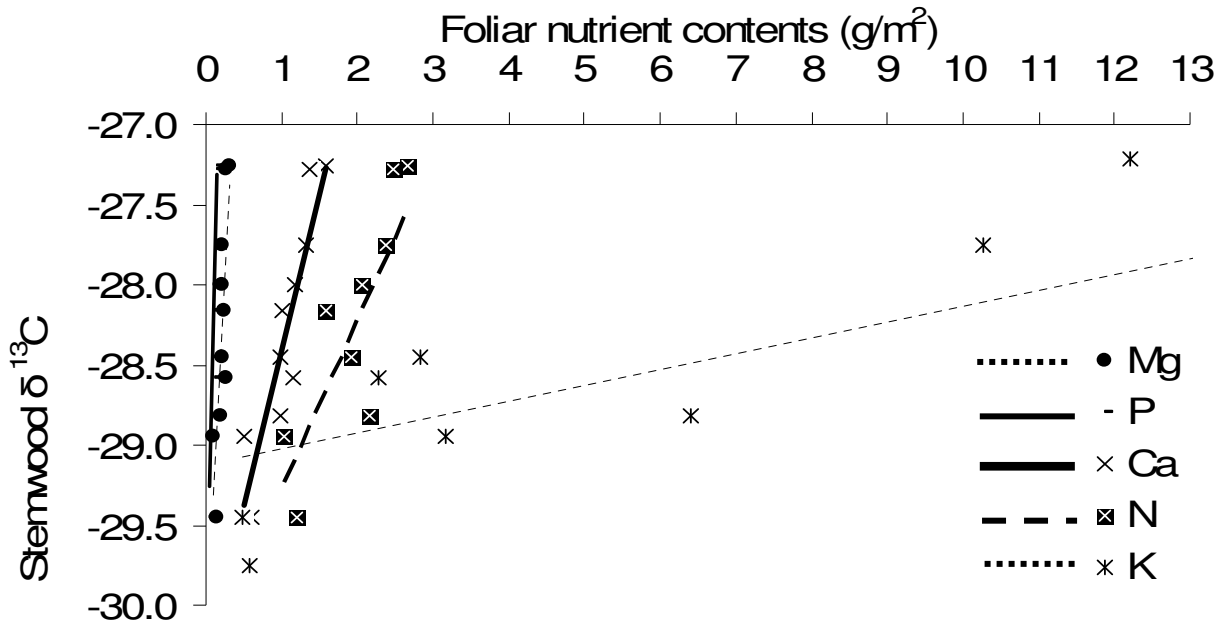
Figure 3.4. Relationship between stemwood δ ^{13}C of *T. ciliata* and average light (% of Photosynthetic active radiation (PAR) below-canopy at top of *T. ciliata* crowns / PAR open-sky readings) measured one time per year from 2005-2007, y = 0.0044x-29.5, R2 = 0.57, p-value < 0.001, Pearson's correlation coefficient = 0.75.
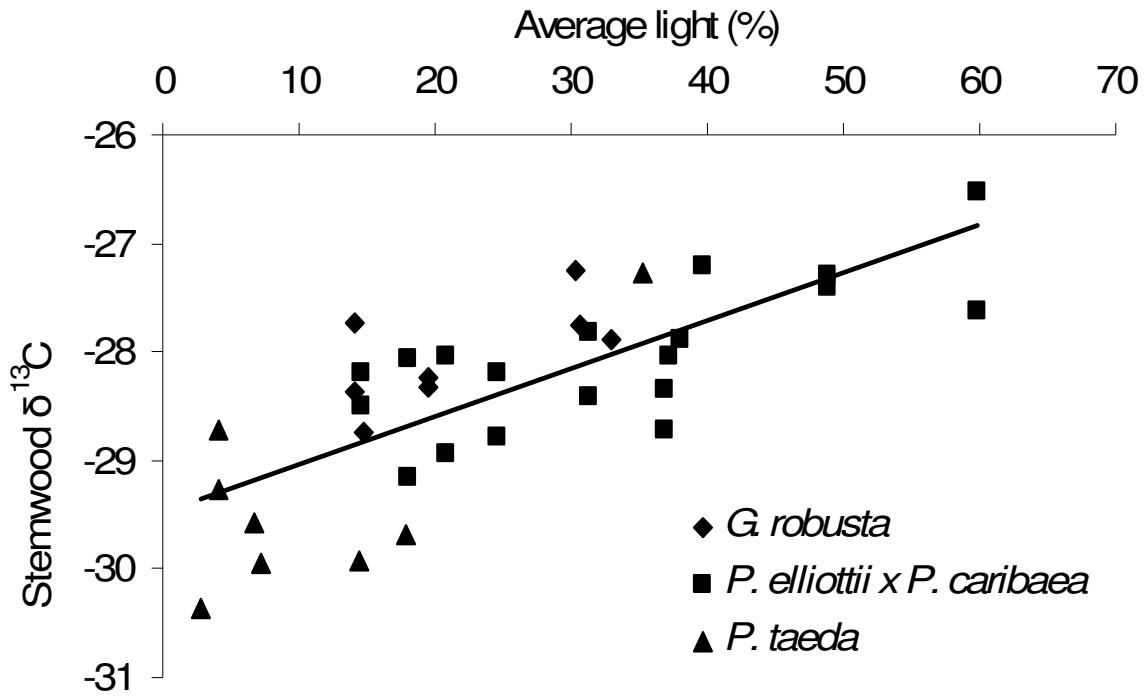
Figure 3.5. *T. ciliata* total annual heights. Values are means and standard errors in each overstorey species and thinning density treatment one year after planting (2005) and two years after thinning (2006 and 2007). Numbers underneath the bars indicate overstorey thinning treatment (%). Values are based on a full inventory of all three replicates in each overstorey experiment.
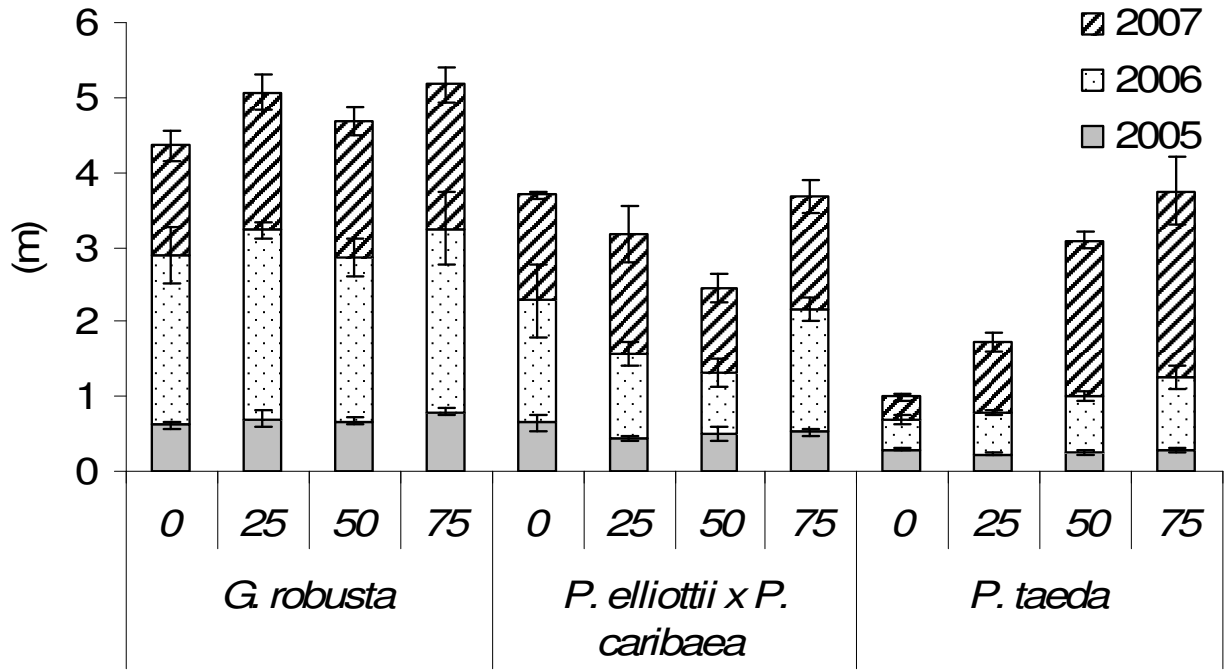
Figure 3.6. Timing of litterfall of the three overstorey species. Leaf-litter mass (kg/ha) in monthly litterfall over the course of one year. Values are means (and 1 S.E.) and are based on samples from unthinned stands (n=3).
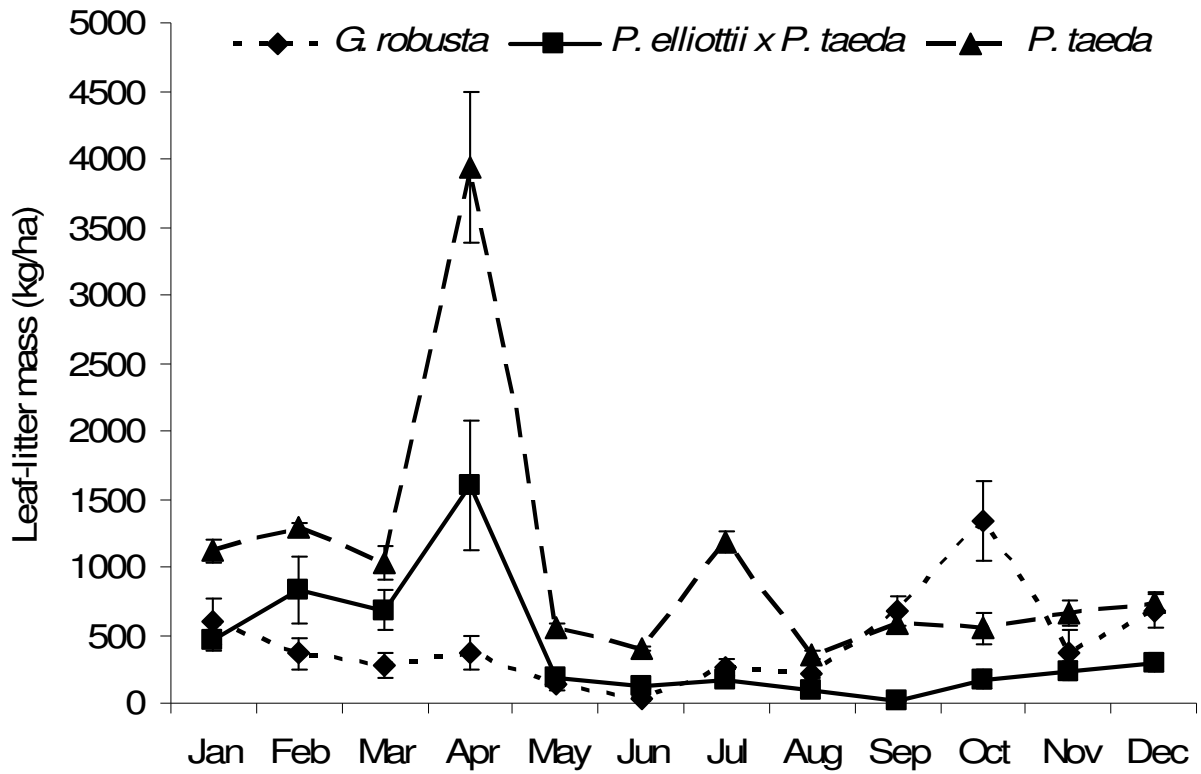
Figure 3.7. Relationship between *T. ciliata* total biomass (kg, oven-dry) and volumetric soil water content (%). Regression coefficients for the top 0-7cm of the mineral soil: y = 0.13x-23, R^2 = 0.78, p < 0.001, Pearson's correlation coefficient = 0.88 and for 20-40cm soil depths: y = 0.12x-3.42, R^2 = 0.42, p = 0.022, Pearson's correlation coefficient = 0.65. Soil moisture was measured on the same day in the winter (July 30, 2007) in a subsample (n=11) of permanent sub plots (PSP) where the corresponding *T. ciliata* was subsequently harvested for biomass determination. The *T. ciliata* were selected over a range of diameters underneath the three nurse species and with varying overstorey densities. Nurse species are: G = *G. robusta*, H = *P. elliottii x P. caribaea*, T = *P. taeda*. The numbers associated with each species indicate the soil depths at which soil water contents were sampled.
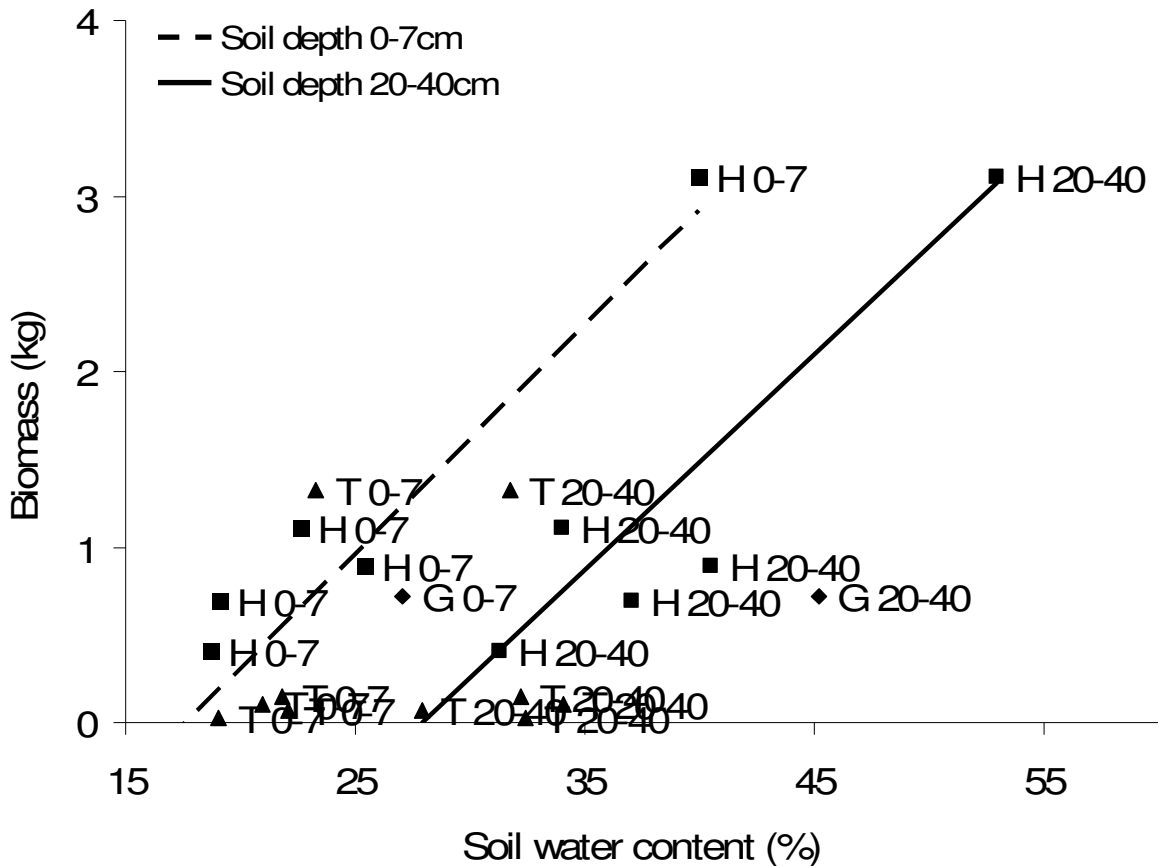
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4 Predicting transpiration deficits that govern early mortality and growth of underplanted Toona ciliata Roem. in subtropical Argentinean plantations with the two-dimensional forest hydrology model, ForWaDy[3]

Introduction

Toona ciliata Roem. (Australian red cedar) is a valuable timber species that is planted in the understory of nurse tree shelterwoods, to protect it from early drought and irradiation damage in the subtropical forests of north-eastern Argentina (Buck and Imoto 1982, Bahadur 1988, Keenan et al. 1995 and 1999). Survival and early growth of *T. ciliata* have been shown to increase substantially when planted in the understory of *Grevillea robusta* A. Cunn. and, to a lesser degree, *Pinus elliottii* Englm. *x Pinus caribaea* Morelet or *Pinus taeda* L. (Dordel et al. 2009). Nurse trees also have high resource demands, requiring careful selection of nurse species and management of overstorey density to minimize productivity losses caused by competition. Soil water is one of the most limiting factors for the early development of *T. ciliata,* and nurse tree competition for water can cause stress to understory trees to varying degrees and at different times of the growing season. *G. robusta* is thought to have a tap root system, capable of switching water uptake patterns from lateral to vertical roots when top soils are drier than deeper soil layers (Smith et al. 1998). It is also capable of hydraulic lift (Burgess et al. 1998), which could reduce early mortality and improve growth of *T. ciliata* in its understory. In contrast, pine species are known to compete strongly with understory plants for soil water in dense stands (Ashton et al. 1997, Mahroof et al. 2000, Rodríguez-Calcerrada 2008). As a result, nurse tree management can have important effects on forest hydrology and ultimately on tree water stress and stand development.

Describing the dynamics of forest hydrology in nurse tree mixtures requires extensive measurements of soil moisture and hydrological fluxes, including precipitation, throughfall, evapotranspiration, and stream flow. In addition, such measurements need to be conducted over multiple years and at different times of the year to account for interannual and seasonal variation. The implementation of such field studies is often prohibitively expensive. Short-term data sets may miss key hydrological events with respect to the timing of plantation development, thereby making it difficult to

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identify critical periods for applying management interventions to reduce drought mortality. One alternative is to use a forest hydrology model in combination with forest ecosystem models to simulate the effects of forest water dynamics on stand growth and development.

The fundamental goal of this study was to use the existing forest hydrology model, ForWaDy (Seely et al. 1997), to examine the temporal patterns in soil moisture and water stress in *T. ciliata* planted under different overstory species, including *Grevillea robusta, Pinus elliottii x Pinus caribaea,* and *Pinus taeda,* on drought-prone sites in subtropical Argentina. This involved model calibration, model evaluation and fitting, and the simulation of alternative shelterwood systems to assess hydrologic dynamics and the development of water stress in *T. ciliata* plantations (A detailed description of the model can be accessed at the UBC Forest Ecosystem Simulation Research Group webpage from URL: http://www.forestry.ubc.ca/ecomodels/moddev/forwady/forwady.htm.)

The first objective was to calibrate ForWaDy for the climate, soil, and vegetation types in the study area. By employing a cumulative transpiration deficit index (TDI), defined by Seely et al. (1997) as a measure of cumulative water stress, we sought to develop a decision making tool for management of nurse species and densities for cultivation of high-value *T. ciliata*. Our second objective was to evaluate model results against field measurements, and to improve the model fit for site-specific soil conditions by adjusting initial soil parameters. Our third objective was to simulate the alternative *T. ciliata* shelterwood scenarios (as defined below) to test for relationships between *T. ciliata* mortality and growth, and modelled TDI and other hydrological variables. To this end, the following hypotheses were tested:

1) Empirically measured soil water contents correspond to predicted ForWaDy soil water contents in the corresponding soil layers.

2) Predicted TDI is lower and soil water content is higher under *G. robusta* than the pines.

3) Predicted TDI decreases and soil water content increases with decreasing stand density of pines but increasing stand density of *G. robusta*.

4) *T. ciliata* early survival and growth are highest at low TDI and high soil water content.

Material and methods

Study site

The study site was near the city of Posadas, in the Province Misiones, in north-eastern Argentina (about 55 55 13.46°W Longitude and 27 28 10.53°S Latitude). The elevation of the study site is 140 m to 155 m, slope is <4° and aspect south to southwest (160° to 240°). The subtropical climate has an average annual temperature of 21°C (hottest month average is 28°C and coldest month average is 16°C, with maximum and minimum daily temperatures of 40°C and -3°C). During the study period, frost occurred on average 30 days (190 hours) per year. Mean annual precipitation was approximately 1700 mm; the wettest periods were spring and fall (~150 to >300 mm per month) and the driest months were December and January (often <100 mm per month). Soils are deep red and belong to the Kandihumult order after the US-Soil Taxonomy (Ligier et al. 1990), and are high in clay content (50%) with some silt (30%) and sand (10-15%). The soils are of low to intermediate fertility with low P and K.

After removal of the native forest (date unknown), the study area was used as cattle range for about 500 years. In the 1980's and 1990's, soy and/or maize were planted as intensive agricultural crops continuously for about 20 years. The site then fell fallow for a few years before the nurse plantation was established in 1999 followed by underplanting of *T. ciliata* in 2004 (Alberto Hennig, pers.comm.).

Experimental design

Three experiments were established in three adjacent 15-ha single nurse-species plantations (*Grevillea robusta*, *Pinus taeda,* and *Pinus elliottii x Pinus caribaea*). The nurse species were under-planted with 1-year-old *T. ciliata* when the nurse-trees were 6 years old. The original nurse-tree spacing was 4 x 3 m (*G. robusta*; 833 stems/ha) or 4 x 4 m (*P. taeda* and *P. elliottii x P .caribaea*; 625 stems/ha), and these densities were reduced by 25, 50, 75 and 0% (control plots) one year after underplanting. The density treatments were replicated in each plantation (experiment) three times, each using a randomized complete block design (Erskine et al. 2005). Blocking was applied according to slope position, thus accounting for possible differences in soil moisture and nutrient regimes. About 10 months before light measurements were conducted, all overstorey trees were pruned to a height of 3.5 m in 2005 and 6.0 m in 2006, at ages 7

and 8, respectively. One year after planting and prior to thinning, 5 permanent subplots (PSP) per treatment unit (total of 180 PSPs) were established to monitor mortality and growth of *T. ciliata*. Each PSP included one *T. ciliata* and four nearby overstorey trees (some were subsequently removed by thinning). In accordance with initial planting densities, plot-sizes were about 12 m^2 in the *G. robusta* experiment and 16 m^2 in the two pine experiments. Subplots were randomly located, and were at least 12 m from adjacent PSPs or treatment plots, and at least 20 m from logging roads to avoid edge effects.

Model description

The ForWaDy (Forest Water Dynamics) model was constructed using the Stella[TM] dynamic system modelling environment. It provides a mechanistic representation of above and belowground interactions in forest stands with multiple canopy layers, with an emphasis on belowground water resource capture (Figure 4.1). Only a brief description of the model is provided here. For a more detailed description, see Seely et al. (1997).

The energy budget approach employed in ForWaDy, based on the well-tested Priestly-Taylor evapotranspiration equation, allows the model to partition evapotranspiration into its primary components, thereby facilitating the capacity to simulate water competition. The daily energy available for evapotranspiration is divided among canopy trees, understory trees, minor vegetation and the forest floor based on the proportional interception of incoming solar radiation by each vertical layer. These values are adjusted for reflection depending on surface albedo and a canopy resistance term related to stomatal conductance. Subsequently, a passive competition for available soil moisture is simulated through the use of an algorithm that combines species-specific root occupancy information with energy-limited transpiration and evaporation demands. Canopy water stress is determined as a function of energy-limited canopy transpiration demand and soil-limited actual canopy transpiration through the calculation of a cumulative daily transpiration deficit index (TDI) over a desired time frame. ForWaDy allows the simulation of snowfall and snowpack dynamics based on the RHYSSys Snow Model (RSM) (Coughlan and Running 1997); however, this feature was disabled in the simulation for this study due to the lack of snowfall in the study area. All equations describing water flow within the model are solved using a simulation

a time step (dt) of 0.25 days. The use of time steps (dt) less than one day enables the model to divide the flux of water from a particular soil reservoir among competing outflows.

Empirical data inputs to ForWaDy include daily climate, vegetation, and forest floor and soil parameters (Table 4.1). One of the strengths of ForWaDy is its portability and flexibility for use in forest management. Accordingly, climate and site-specific soil and vegetation data requirements are kept to a minimum. The Stella^TM modelling environment allows the model to be accessible to users that are unfamiliar with modelling techniques. The structure of the model is presented graphically as a flowchart in the "map-layer", which is linked to the "equation-layer". The equation-layer contains the mathematical relationships between parameters. The input-data (Table 4.2 and 4.3) can be easily changed using the interface layer, which is linked to specific variables in other layers. Specifically the interface layer allows for modification of key vegetation response parameters including canopy resistance, Permanent Wilting Point, root occupancy, rooting depths, Leaf Area Index (LAI) and minor vegetation cover, can be modified for each experiment.

Model calibration, evaluation and fitting

An initial calibration of ForWaDy for the study site was conducted with respect to the input requirements described in Table 4.1. Following the initial calibration, the model was run and parameterized using field measurements of soil moisture to improve the model fit. A detailed description of the data collected and assembled for calibration is provided in the following section.

Climate data

Daily climate data (precipitation, as well as minimum, maximum and average air temperatures) collected at a weather station about 10 km from the study site (INTA Montecarlo, Argentina) was used to drive the model. Slope and aspect were measured to provide input for the estimation of incoming shortwave solar radiation using an algorithm developed by Nikolov and Zeller (1992) and modified to represent the effect of site location on solar geometry.

Light measurements

Transmitted photosynthetically active radiation (PAR) was determined once on an annual basis in each PSP and related to understory tree growth response. PAR was measured under cloudless skies with a handheld ceptometer (SF-80, Decagon, Pullman,WA), Absolute PAR values were converted to relative values as a measure of the light environment of sampled seedlings using the percent of full sun (%FS):

%FS =Qi / Qo x 100

where Qi is the averaged PAR reading from the ceptometer and Qo is the PAR reading from the datalogger in the open (Chen 1997). The sensor was moved between the two paired locations, taking open-sky measurements several times during the sampling period in the nearest canopy gap. The time-span between below-canopy and open-sky readings was less than 5 minutes (Comeau, 2000). Light measurements were taken at midday between 11.00 and 13.00 hours under cloudless skies (Comeau, 2000). The below-canopy measures were taken in each of the cardinal directions at the top of the crown of the understory *T. ciliata.* The four cardinal measures were then averaged for each location. For trees taller than 1.5 m, an external sensor was attached to the ceptometer, which was elevated to *T. ciliata* crown height using a telescoping height pole and/or ladder. To compensate for the smaller measurement surface of the device, several measurements were taken horizontally: at the edges of the crown as well as in the center. All ceptometer and external sensor measurements taken during the last 2 years of the study were consistent with results from fisheye photos (Nikon Coolpix 8400 digital camera with a fisheye Lens FC - E9) from the same plots.

Vegetation and litterfall

Mortality and height growth of *T. ciliata* were assessed annually in a full inventory. Slope, aspect, litter depth, and minor vegetation cover were determined at the centre of each PSP. *T. ciliata* diameter at breast height (DBH) and total height were recorded annually in each PSP over the course of three years. Individual tree volume was estimated for trees taller than 1.3m based on the formula for a cone:

$$V = DBH^2 * \Pi/4 * Height * f_{1.3} * 100,$$

where V is individual tree volume (cm^3), DBH is diameter at breast height (cm), Height is total height (cm), and the constant $f_{1.3} = 0.33$ (Erskine et al. 2005). For all data,

outliers per treatment plot were identified (> 2.7 standard deviations from the mean) and removed using stem and leaf plots

Litter traps measuring 1 m^2 and lined with 2 mm mesh were placed in three locations in control plots near three of the PSP's (PSP 1, 3 and 5). The traps were placed under the northern crown-edge of one overstorey tree in each PSP. Overstorey litter was collected monthly over the course of one year. After separating the foliage from other materials (bark, seeds, plant material from other species, insects, bird faeces), it was oven-dried for 48 hours at 70°C and weighed (after Palma et al. 2002).

Overstory and *T. ciliata* Leaf Area Index (LAI) were estimated annually for each combination of overstory species and thinning level based on rates of light transmission measured at varying levels of the canopy (see Light measurements). Specifically, LAI was calculated from PAR measurements using the following formulation of the Beer-Lambert light extinction equation (after Vose and Swank 1990):

LAI = ln(Qi/Qo)/k),

where Qi=canopy PAR transmittance, Qo = total incoming PAR, and k= light extinction coefficient. Literature values were used for k and modified to meet the conditions at the study site: *G. robusta* = 0.75 (Yoneda 1993), *P. elliottii x P. caribaea* = 0.5 (Jarvis and Leverenz 1983), and *P. taeda* = 0.69 (Sampson and Allen 1998) (Table 4.2). Overstorey LAI was estimated from Qi/Qo measured on top of *T. ciliata* crowns in control plots, while *T. ciliata* LAI was determined by subtracting LAI at the top of the *T. ciliata* from LAI at 1m above the ground. LAI for the nurse species was assumed to be relatively constant over the period of the study; to that end, continuous LAI growth on top of the crown was negated by the frequent pruning at the base. LAI derived for control plots was reduced by 25, 50 and 75% to simulate the thinning treatments. Seasonal fluctuations in LAI were estimated from observed seasonal patterns in sampled litterfall over the course of a year (Table 4.3).

Soil and rooting and canopy parameters

Soil texture, clay content, and bulk density were measured in treatment plots using samples from soil pits. Estimates of coarse fragment content, including layers with bulk densities high enough to reduce root occupancy, were made for each layer. This variable acts to reduce available porosity in soil layers represented in ForWaDy. Each soil pit (1m long and 60cm deep) traversed a *T. ciliata* rip line and bordered an

overstorey rip line. Rooting depth was measured in two soil pits per treatment plot (30 pits per overstorey species = 90 pits). Rooting depths were determined along the vertical profile of the soil pits using a measuring tape. *G. robusta* cluster roots were observed in the upper 10cm of mineral soil under the *G. robusta* overstorey; cluster roots generally form in the very top soil layers (Lambers 2003). Trees and most of their roots were growing in rip lines with lower bulk densities, and we accounted for different soil bulk density of lower soil layers and adjacent areas by applying their lower coarse fragment contents. Rooting depths increased with growth of *T. ciliata* but not with growth of the overstorey, which was assumed to occupy the whole soil profile over the whole study period.

ForWady uses a canopy resistance term (RCan) for each canopy type to account for the effect of stomatal conductance on effective transpiration rates. This term is used to quantify the amount of potential energy consumed by resistance. Estimates of RCan and of species-specific permanent wilting point soil moisture contents are shown in Table 4.2. The use of an approximated RCan will undoubtedly lead to some error in the calculation of canopy PET (Seely et al 1997), but it should provide a reasonable estimate suitable for the intended use of the model, estimating the *T. ciliata* Transpiration Deficit Index (TDI).

Soil water content measures for model fitting

To evaluate the model and to improve its fit for local soil conditions, we measured soil moisture content of different soil layers in the summer and winter of the last year of the study. Soil water content was measured in 20 cm sections along the vertical profile of a subsample of soil pits using a soil water meter (Delta-T Devices, Cambridge). It was not possible to measure soil water in all soil-pits due to difficulties in inserting the probe into the compacted clay soil. In the final winter and final summer of the study (year 3), we also measured soil water by inserting the soil water meter vertically to 7 cm depth in transects along the *T. ciliata* rip line at 0.5 m, 1 m, and 1.5 m from the *T. ciliata*.

Simulation of alternative shelterwood scenarios

To assess the suitability of ForWaDy as a management tool in these forest types, we examined the relationship between model output (TDI and other variables) and field-measured *T. ciliata* mortality and height growth during the three years after planting. For

each nurse species and its associated thinning experiment, we modelled the different scenarios with various parameters, which we changed accordingly. These parameters were canopy resistance (RCan), permanent wilting point for the upper two soil layers, maximum tree root occupancy, also for the upper two soil layers, the light extinction coefficient (k), and tree rooting depths (Table 4.2). Additionally, we varied the maximum leaf area index (LAI) for the three nurse trees scenarios and the understorey *T. ciliata,* and maximum understorey vegetation cover (%) (Table 4.3). These values were slightly reduced during the course of the year according to seasonal fluctuations. While fluctuations of overstorey LAI was derived from empirical litterfall data collected in unthinned stands at the study site over the course of a year, the small seasonal fluctuations of understorey vegetation cover were estimated.

Results

Model evaluation

As expected, simulated soil water content of the A1 soil layer (0-25 cm) closely followed patterns of precipitation throughout the 3-year simulation period (Figure 4.2). Peaks in monthly cumulative TDI tended to follow periods with low soil water content (A1 layer) and were more pronounced during periods of high maximum air temperatures. Modeled soil water contents in the three soil layers, A1, A2 and B, also corresponded closely with measured soil water content measured during one day in winter, on December 30, 2007 (Figures 4.3 and 4.4). Fluctuations in soil water content were best modelled for the ForWaDy A1 Layer in the winter, corresponding best to measurements in the topsoil 0-20cm (Pearson's correlation coefficient = 0.85) (Figure 4.3 and 4.4). All empirical data measured in 0-20, 20-40 and 40-60 cm soildepths during winter corresponded well to the the corresponding soil layers A1, A2 and B. Linear regression (y=a*x+b) coefficients and statistics are: a = 0.90, b = 4.18, R^2 = 0.75, p-value < 0.001, and Pearson's correlation coefficient 0.87.

For the five measurement days in the summer, simulated soil water content for the A1 layer (0-25cm) was consistently greater than field measured values in the surface layer (0-7cm) (Figure 4.3 and 4.5). Measurements taken at the same locations (upper 7cm) during a wetter period in the winter (Figure 4.4) were closer to the A1 layer values predicted by ForWaDy. We did not measure soil water content in deeper soil layers in summer.

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Generally, the model predicted differences in soil water content among sites with different nurse species, with the most available soil water under *G. robusta,* particularly in winter (Figures 4.4 and 4.5 and Table 4.4) and in the deepest soil layer B (Table 4.4). Soil water measured during five days in the summer differed little between the two pine species, with *P. elliottii x P. caribaea* soils slightly drier than *P. taeda* (Figure 4.5). Overall, modelled soil moisture was slightly higher underneath *P. taeda* than *P. elliottii x P. caribaea*, both in summer and winter (Table 4.4). However, soil moisture in the B-layer was similar (Table 4.4). Those trends were similar to the short term measurements, where we found little difference in soil water beneath the pines in winter, although we had no empirical soil water measures for the 0 and 75% density treatments in *P. elliottii x P. caribaea* (Figure 4.4).

ForWaDy predicted an decrease in soil water content with decreasing density of *G. robusta*, while variation in soil water contents underneath the pine overstorey were very slight (Table 4.4), roughly corresponding with trends measured in the field (Figure 4.4 and 4.5). Predicted trends varied between *G. robusta* and the pine overstories (Table 4.4) because of different physiological and vegetation parameters used for each nurse-tree and *T. ciliata* scenario (Table 4.2 and 4.3).

Mortality

T. ciliata mortality increased with increasing simulated TDI the first year, and this relationship was stronger when considered over the whole 3-year study period (Figure 4.7). Most of the mortality occurred in the first year, with very little additional mortality in the second and third year (Figure 4.7). ForWaDy explained a large amount of the variation in *T. ciliata* mortality over the thinning treatments, performing poorly only in the *P. taeda* 50% density when modelled over the whole study period (Figure 4.7), most likely due to mortality caused by the annual pruning activities. It accurately predicted greater mortality of *T. ciliata* under the pines than *G. robusta*, and increasing mortality with increasing thinning intensity for all three nurse species (Figure 4.7).

Growth

Both height growth and volume of *T. ciliata* decreased with increasing TDI (Figure 4.8 and 9). TDI was negatively correlated with height increment growth on an annual basis and between the different nurse species thinning treatments ($R^2 = 0.58$; p-value <

0.001; Pearson's correlation coefficient = -0.76). As with mortality, the greatest height growth occurred in the first year with a TDI of 170, where the overall TDI was much higher than in the following years, due to *T. ciliata* shallower roots (Table 4.2) and a period of low rainfall during the summer (Figure 4.2). Overall, *T. ciliata* height increments were highest with an annual cumulated TDI below 50 (Figure 4.8). *T. ciliata* average stem volume among all overstorey species and densities was also negatively correlated with a TDI cumulated over the three years of the study period (R^2 = 0.42; p-value = 0.023; Pearson's correlation coefficient = -0.65) (Figure 4.9).

Predicted TDI was lowest under *G. robusta* and highest under *P. elliottii x P. caribaea* (Figure 4.8 and 4.9), corresponding with the highest and lowest average height growth and volume of *T. ciliata*, respectively (Figure 4.8). Predicted TDI and *T. ciliata* growth also generally increased slightly with increasing thinning intensity for *G. robusta* and *P. elliottii x P. caribaea* overstories (Figure 4.8 and 4.9), but was uniform for a *P. taeda* overstorey.

Discussion

Model evaluation

Modelled soil moisture content in the A1 layer (0-25 cm) was a good predictor of measured soil water contents at 0-20 cm measured in winter. ForWaDy performed well considering that the model operates on a daily time-step and was only evaluated for a single day. Often, daily models will be slightly out of phase with empirical data while still projecting correct trends. Ideally the model should be evaluated against field data spanning a longer period of time.

A comparison of simulated A1 layer (0-25) moisture content relative to measurements in the uppermost 7cm suggest that the model tended to overestimate summer soil water. Several reasons for this discrepancy were possible. Firstly, the higher model estimates of soil water content could have resulted from higher precipitation at the weather station relative to that occurring at the study sites. The sensitivity of the model to precipitation is indicated by the rapid response of soil moisture content in the A1 layer to precipitation. Secondly, we measured soil water content only in the top 7cm, while the model predicted values for the top 25cm. Differences between these two would be expected as the model provides an estimate of moisture content for the whole A1 layer with the assumption that the moisture is evenly

distributed throughout the layer. In reality, there is often a gradient of moisture content that develops from differential drying patterns. Brady and Weil (1996) observed that soil moisture content at greater soil depths is less sensitive to precipitation and less prone to fluctuations relative to surface layers.

The model also performed slightly less well in predicting specific soil water moisture contents in the deeper soil layers, A2 (25-45cm) and B2 (45-195cm). However, these differences should be considered in the context of the limited field sampling for model evaluation and the fact that moisture gradients may exist in sampling points relative to the whole-layer moisture content that the model is simulating. When all layers and treatments are considered (Figure 4.3), the model is clearly able to reasonably predict broader trends in moisture content. Based on this result, we failed to reject our first hypothesis that empirically measured soil water content correspond with modelled ForWaDy soil water content in the corresponding soil layers. Small differences in simulated moisture contents in the deeper layers may be of minor importance to *T. ciliata* water stress and productivity, however, since it uses water resources mainly from the upper soil layers (Table 4.2 and Dordel et al 2009), and is less directly influenced by soil water at depth. Nevertheless, the overstorey draws water from deeper soil layers, especially the modelled A2 layer, and thus errors in the simulation of canopy transpiration from both deep and shallow soil water resources would ultimately influence the *T. ciliata* TDI values.

Nurse species and density effects

ForWaDy predicted lower cumulative TDI and higher soil water content under *G. robusta* than the pines; thus, we also failed to reject our second hypothesis. The model was also more predictive of soil moisture fluctuations in the *G. robusta* than the pine overstories, but it was generally less sensitive at detecting soil water content changes with thinning regardless of overstorey species. The model accurately predicted increasing soil water content with increasing density of *G. robusta,* as observed in the field, likely resulting from hydraulic lift (Burgess et al. 1998), and water uptake predominantly by vertical roots from deeper soil layers (Smith et al. 1998). It was less predictive of decreasing soil water content with increasing density of the competitive pines, however, leading us to partially reject our third hypothesis.

The variation in predicted trends for TDI and soil water contents between *G. robusta* and the pines were due to differences in access to deeper soil layers, and the estimated canopy resistance, permanent wilting point and other parameters. Thinning density effects, on the other hand, were driven by differences in LAI and understorey vegetation cover of the treatments. Lower goodness of fit of the predictions for density effects could have been due to a low sensitivity of the model to those changes; however, weak or heterogenous responses to thinning were also observed in the field. This could mean that the ecological differences were not very strong between density treatments and less important than overstorey species effects (Dordel et al. 2009). Better results may be obtained with actual measured values of LAI in the field, although this would increase the calibration effort for the model.

It has been reported that hourly time-step models with a multi-layer soil moisture description and complete surface energy balance account better for short-term fluctuations in evapotranspiration (Daamen and Simmonds, 1994). This may be caused by a return of soil evaporation to the potential rate in the early part of a day due to re-hydration of the soil surface layer overnight (Daamen and Simmonds 1996). Simple daily time-step models, which assume evaporation independent of evaporative demand, will only be able to give an approximate description of soil evaporation under these conditions (Smith et al.1998). Furthermore, it has been reported that even a simple daily time-step model can obtain reasonable estimates of cumulative hydrological parameters over hydrologically significant periods, like weeks or months (Smith et al 1998). For the purpose of this study, we were primarily interested in modelling intermediate effects of soil moisture and transpiration on *T. ciliata* growth and mortality, for which cumulative values are sufficient.

Mortality and growth

Modelled TDI was a good predictor of *T. ciliata* first year mortality and early height growth and volume, and these relationships improved when modelled over the whole study period. The increased precision of the model over the longer term may have resulted from delayed responses of sapling survival and growth to drought stress. That TDI predicted height growth with less accuracy than it predicted mortality suggests that water was not the only limitation to *T. ciliata* growth at the study site (Dordel et al 2009). By contrast, water appeared to be the main limitation to early *T. ciliata* mortality. TDI

accurately predicted greater survival and faster growth of *T. ciliata* under *G. robusta* than the pine overstories, but was poorer at predicting density effects under pine than *G. robusta*. The better performance of the model in *G. robusta* stands may have resulted in the moister surface soils than in pine stands. The positive relationship between TDI and *T. ciliata* early performance supports our fourth hypothesis that *T. ciliata* survival and growth are greatest at low TDI and high soil water content. The lowest mortality and greater growth of *T. ciliata* occurred at annual TDI values of approximately 170 and 50, respectively.

Conclusions

ForWaDy accurately predicted early *T. ciliata* mortality and growth from TDI under *G. robusta*, *P. elliottii x P. caribaea* and *P. taeda* nurse overstories on drought-prone sites of subtropical Argentina. The model results suggest that water stress was an important limitation to *T. ciliata* survival and growth on our study sites. The modelled TDI and soil water contents could be improved, however, for deeper soils, during summer, and for fluctuations between different overstorey densities. Collection of more calibration data, especially climate data directly at the study site, is required for predicting *T. ciliata* mortality and growth at later growth stages, on different site qualities (soil moisture regimes), or under different nurse species.

Acknowledgements

Table 4.1. Data requirements for ForWaDy (modified after Seely et al. 1997).

Data Requirements		
Climate data (daily)	Vegetation data	Forest floor & soil data
• Mean, Max and Min air temperature	• Percent cover by conifers & hardwoods	• LF layer mass (kg/ha)
• Solar radiation	• Seasonal conifer and hardwood Leaf Area Index (LAI)	• Humus depth and bulk density
• Total precipitation	• Seasonal understory % cover	• Depth of soil layers (rooting zone)
	• Rooting depths for trees	• Soil texture class of each soil layer
	• Rooting depths for understory	• Coarse fragment content of layers
	• Root occupancy in each layer	
	• Canopy resistance	

Table 4.2. Parameters used to calibrate ForWaDy for the three nurse trees scenarios and the understorey *T. ciliata*. Canopy resistance (RCan) based on values of *α* (modified after Seely et al. 1997). Soil layers describe different soil depths from the soil surface of the mineral, where A1 = 0-25 cm, A2= 20-45 cm, and B = 45-195 cm, each year in ForWaDy starts in July 1st, (the southern Hemisphere winter) and runs to June 31st.

Overstorey species	*G. robusta*	*P. elliottii x P. caribaea*	*P. taeda*	*T. ciliata*
Canopy resistance (Rcan)	0.3	0.25	0.35	0.15
Permanent wilting point (%) A1	0.23	0.17	0.18	0.23
Permanent wilting point (%) A2	0.23	0.17	0.18	0.23
Max. tree root occupancy A1	0.15	0.65	0.65	0.95
Max. tree root occupancy A2	0.3	0.9	0.9	0.7
Max. tree root occupancy B	0.8	0.2	0.2	0.0
Light extinction coefficient (k)	0.75	0.5	0.69	0.4
Tree rooting depths (cm)	195	75	75	Year 1=15, Year 2=25, Year 3=40

Table 4.3. Maximum leaf area index (LAI) for the three nurse trees scenarios and the understorey *T. ciliata* and maximum understorey cover (%). Values were reduced during the course of the year according to seasonal fluctuations. Each year in ForWaDy starts in Ju ly 1st, (the southern Hemisphere winter) and runs to June 31st.

Overstorey species		*G. robusta*				*P. elliottii x P. caribaea*				*P. taeda*			
Thinning treatment		0	25	50	75	0	25	50	75	0	25	50	75
Max. Overstorey Leaf Area Index (LAI)	Year 1	3.00	3.00	3.00	3.00	2.20	2.20	2.20	2.20	5.40	5.40	5.40	5.40
	Year 2	3.00	2.50	2.00	1.50	2.20	1.83	1.47	1.10	5.40	4.50	3.60	2.70
	Year 3	3.00	2.25	1.50	0.75	2.20	1.65	1.10	0.55	5.40	4.05	2.70	1.35
Max. *T. ciliata* Leaf Area Index (LAI)	Year 1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1
	Year 2	0.4	0.4	0.2	0.2	0.5	1.0	1.2	0.5	0.4	0.3	0.2	0.3
	Year 3	1.0	1.2	1.1	1.4	0.8	1.4	1.3	1.1	0.4	0.4	0.5	0.6
Max. Understorey cover (%)	Year 1	0.44	0.44	0.44	0.44	0.36	0.36	0.36	0.36	0.00	0.00	0.00	0.00
	Year 2	0.41	0.39	0.51	0.72	0.31	0.37	0.49	0.55	0.00	0.24	0.34	0.32
	Year 3	0.30	0.32	0.46	0.45	0.23	0.27	0.54	0.63	0.00	0.27	0.31	0.44

Table 4.4. ForWaDy simulated soil water contents (%) during the coolest months (winter; July and August) and the hottest months (summer; January and February) during the study period underneath the three nurse species and four thinning treatments. Soil layers, were A1 (25 cm), A2 (25-45 cm) and B (45-195 cm). Values are means and 1 S.E. in parenthesis.

| Overstorey species		G. robusta				P. elliottii x P. caribaea				P. taeda			
Thinning (%)		0	25	50	75	0	25	50	75	0	25	50	75
Year 1 Winter	A1		32.24 (0.15)				23.63 (2.69)				24.77 (2.52)		
	A2		30.16 (1.61)				22.98 (5.44)				23.13 (4.77)		
	B		35.35 (3.61)				39.74 (0.74)				39.66 (0.76)		
Summer	A1		30.92 (1.89)				22.88 (0.77)				24.22 (0.69)		
	A2		28.12 (0.16)				18.56 (0.93)				20.17 (1.27)		
	B		29.42 (1.52)				38.98 (0.39)				39.03 (0.37)		
Year 2 Winter	A1	35.50 (4.82)	35.34 (4.92)	34.82 (5.34)	33.68 (6.06)	31.21 (7.98)	31.00 (8.00)	30.82 (7.95)	30.82 (7.95)	32.68 (7.87)	32.71 (7.87)	32.69 (7.89)	32.69 (7.89)
	A2	35.73 (6.79)	35.76 (6.82)	35.52 (7.00)	34.84 (7.58)	32.56 (9.98)	32.53 (9.92)	32.42 (9.90)	32.37 (10.05)	33.13 (9.58)	33.11 (9.60)	33.10 (9.61)	33.10 (9.61)
	B	40.53 (2.47)	40.65 (2.35)	40.66 (2.34)	40.73 (2.27)	41.89 (1.11)	41.89 (1.11)	41.85 (1.15)	41.90 (1.10)	41.90 (1.10)	41.89 (1.11)	41.89 (1.11)	41.89 (1.11)
Summer	A1	29.85 (2.23)	29.03 (2.31)	27.71 (2.10)	26.05 (1.71)	21.97 (1.53)	21.92 (1.62)	21.92 (1.65)	21.78 (1.66)	23.64 (1.19)	23.63 (1.21)	23.63 (1.21)	23.63 (1.21)
	A2	25.88 (1.01)	25.49 (0.98)	24.53 (1.04)	22.69 (0.36)	17.24 (0.19)	17.27 (0.19)	17.29 (0.21)	17.32 (0.17)	18.46 (0.30)	18.46 (0.30)	18.46 (0.30)	18.46 (0.30)
	B	23.25 (0.04)	23.24 (0.06)	23.14 (0.13)	23.00 (0.00)	30.12 (0.11)	30.15 (0.15)	30.20 (0.19)	30.63 (0.39)	30.12 (0.11)	30.14 (0.13)	30.14 (0.13)	30.14 (0.13)
Year 3 Winter	A1	32.65 (0.61)	32.02 (0.56)	30.08 (0.15)	27.52 (0.13)	25.24 (0.11)	24.98 (0.37)	24.82 (0.53)	24.90 (0.71)	26.15 (0.05)	26.13 (0.03)	26.13 (0.06)	25.98 (0.11)
	A2	29.53 (0.37)	29.32 (0.55)	29.02 (0.82)	28.56 (1.53)	24.24 (2.89)	24.48 (2.90)	24.44 (2.66)	25.02 (2.37)	24.84 (1.87)	24.89 (1.85)	25.02 (1.95)	25.10 (2.00)
	B	28.08 (1.5)	28.21 (1.50)	28.34 (1.40)	27.53 (1.05)	31.00 (0.00)	31.00 (0.00)	31.00 (0.00)	31.00 (0.00)	31.00 (0.00)	31.00 (0.00)	31.00 (0.00)	31.00 (0.00)
Summer	A1	38.37 (1.27)	37.85 (1.32)	36.83 (1.74)	35.59 (2.03)	36.81 (1.39)	36.24 (1.59)	35.34 (1.99)	34.75 (2.14)	38.25 (0.82)	38.19 (0.79)	38.14 (0.84)	37.85 (0.94)
	A2	38.54 (0.62)	38.27 (0.70)	37.56 (0.74)	37.25 (0.62)	38.44 (0.49)	38.27 (0.56)	37.86 (0.89)	37.71 (1.12)	40.15 (0.06)	40.12 (0.01)	40.12 (0.01)	39.92 (0.19)
	B	40.42 (1.57)	40.20 (1.64)	39.93 (1.83)	40.37 (1.51)	42.58 (0.03)	42.53 (0.01)	42.44 (0.08)	42.42 (0.10)	42.88 (0.04)	42.88 (0.04)	42.88 (0.04)	42.86 (0.03)

Figure 4.1. Schematic of the forest hydrology model indicating the various flow pathways and storage compartments in the model (after Seely et al. 1997, modified). Canopy transpiration and transpiration deficit index are calculated separately for the overstory species and *T. ciliata*.
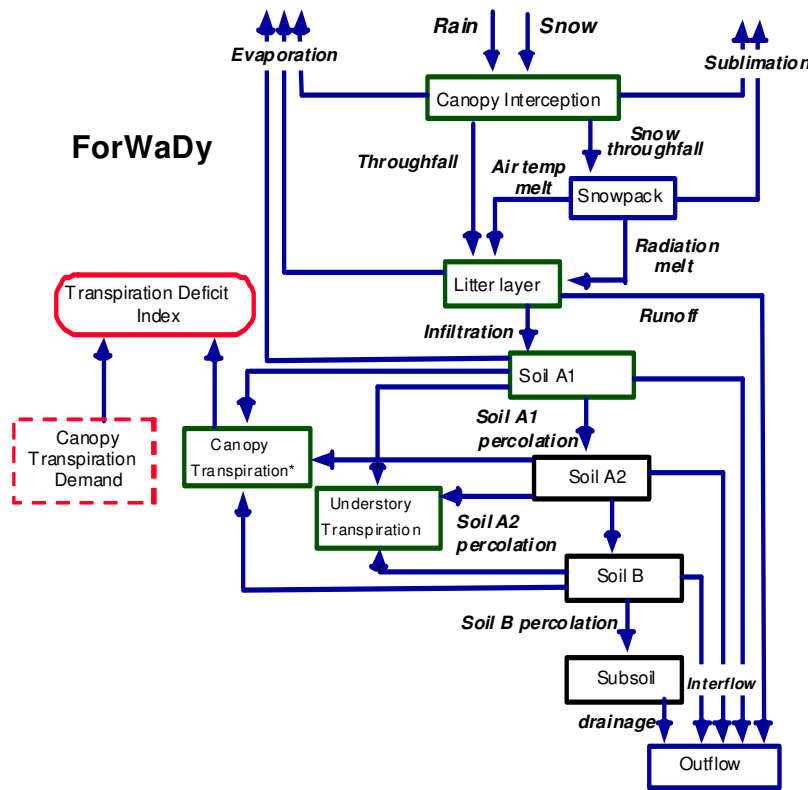
Figure 4.2. Relationships between the estimated average monthly ForWaDy soil water content (%) in the A1 layer (0-25 cm depth from the soil surface of the mineral soil), average monthly maximum air temperature (ºC), cumulative monthly precipitation (cm, for better graphical display), and monthly cumulative ForWaDy Transpiration Deficit Index (TDI) for *T. ciliata.* The empirical air temperature and precipitation data were collected over the course of the study period, while the ForWaDy soil water content and TDI were estimated for the 75% density treatment in the *G. robusta* experiment. Each year in ForWaDy starts in July 1st, (the southern Hemisphere winter) and runs to June 31st.
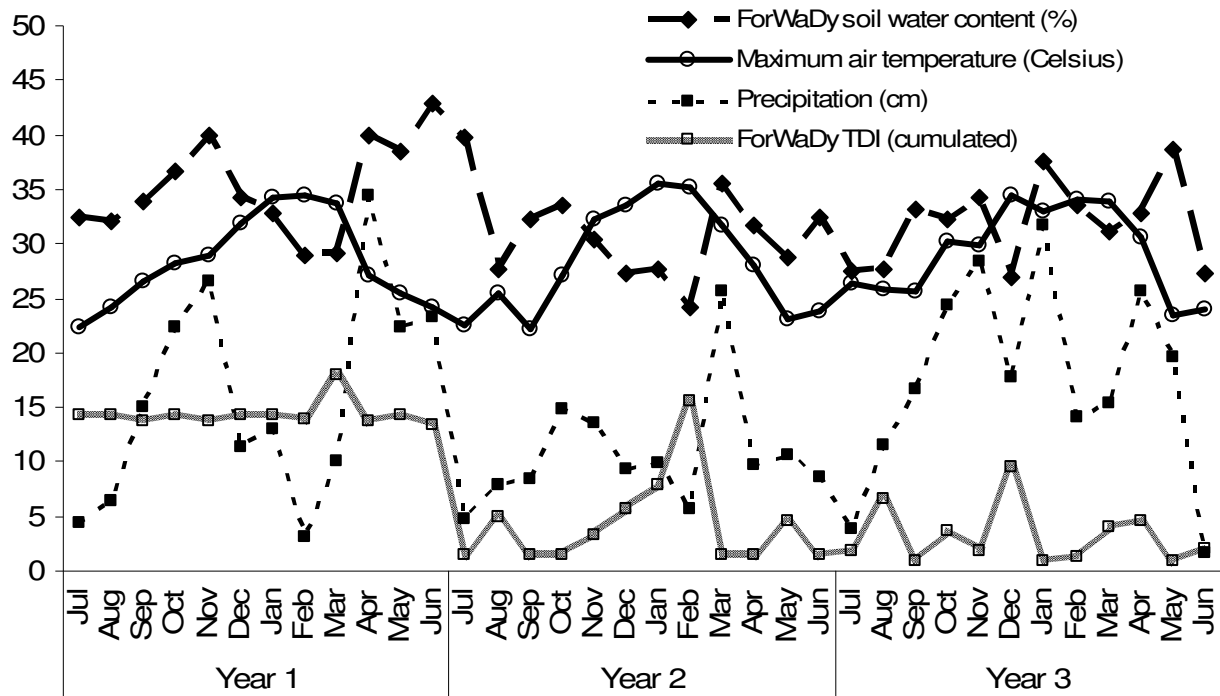
Figure 4.3. Model evaluation. Differences between ForWaDy estimated and empirical soil water content data (%). The data was sampled in 0-7-cm, 0-20-cm, 20-40-cm, and 40-60-cm depths from the soil surface of the mineral soil and compared with ForWaDy layers A1 (25 cm), A2 (25-45 cm) and B (45-195 cm). The empirical soil water data was sampled in the winter on one day (July 30, 2007), and in the summer over five consecutive days (December 18-22, 2007). ForWaDy modelled data was well correlated with the empirical data, with Pearson's correlation coefficients of 0.47 (summer 0-7 cm and A1 layer), 0.79 (winter 0-7 cm and A1 layer), 0.85 (winter 0-20 cm and A1 layer), 0.54 (winter 20-40 cm and A2 layer), -0.64 (winter 40-60 cm and B layer).
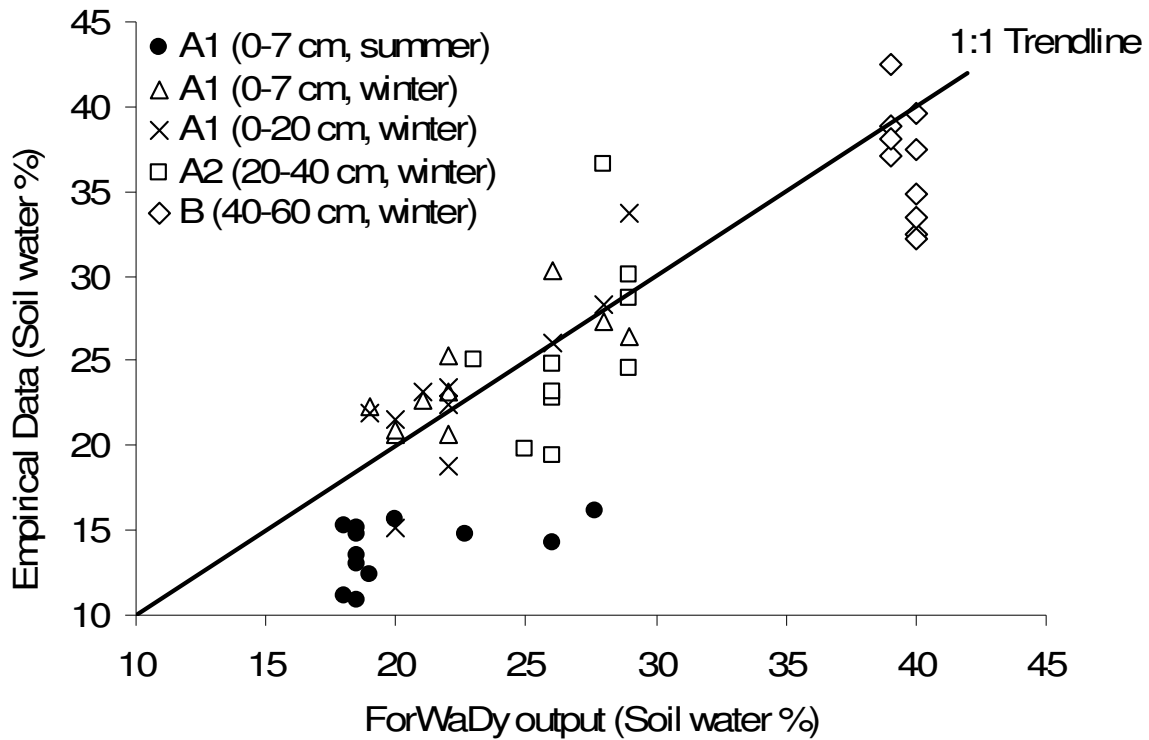
Figure 4.4. Model evaluation. Relationships between empirically measured soil water content at 0-7, and 0-20-cm depths from the soil surface of the mineral soil and ForWaDy model estimates for 0-25 cm depth (A1 layer). Nurse species are: G = *G. robusta*, H = *P. elliottii x P. caribaea*, T = *P. taeda*. The numbers associated with each species indicate the thinning intensity (0-75%). Soil data was collected during one day during the winter (July 30, 2007), with n= 2 (*G. robusta* and *P. elliottii x P. caribaea*) and n = 4 (*P. taeda*) in the 0 and 50% density treatments, n=5 in the 25% density treatment, and n=3 in the 75% density treatment. Missing empirical data for density treatments 0 and 75% in *P. elliottii x P. caribaea*.
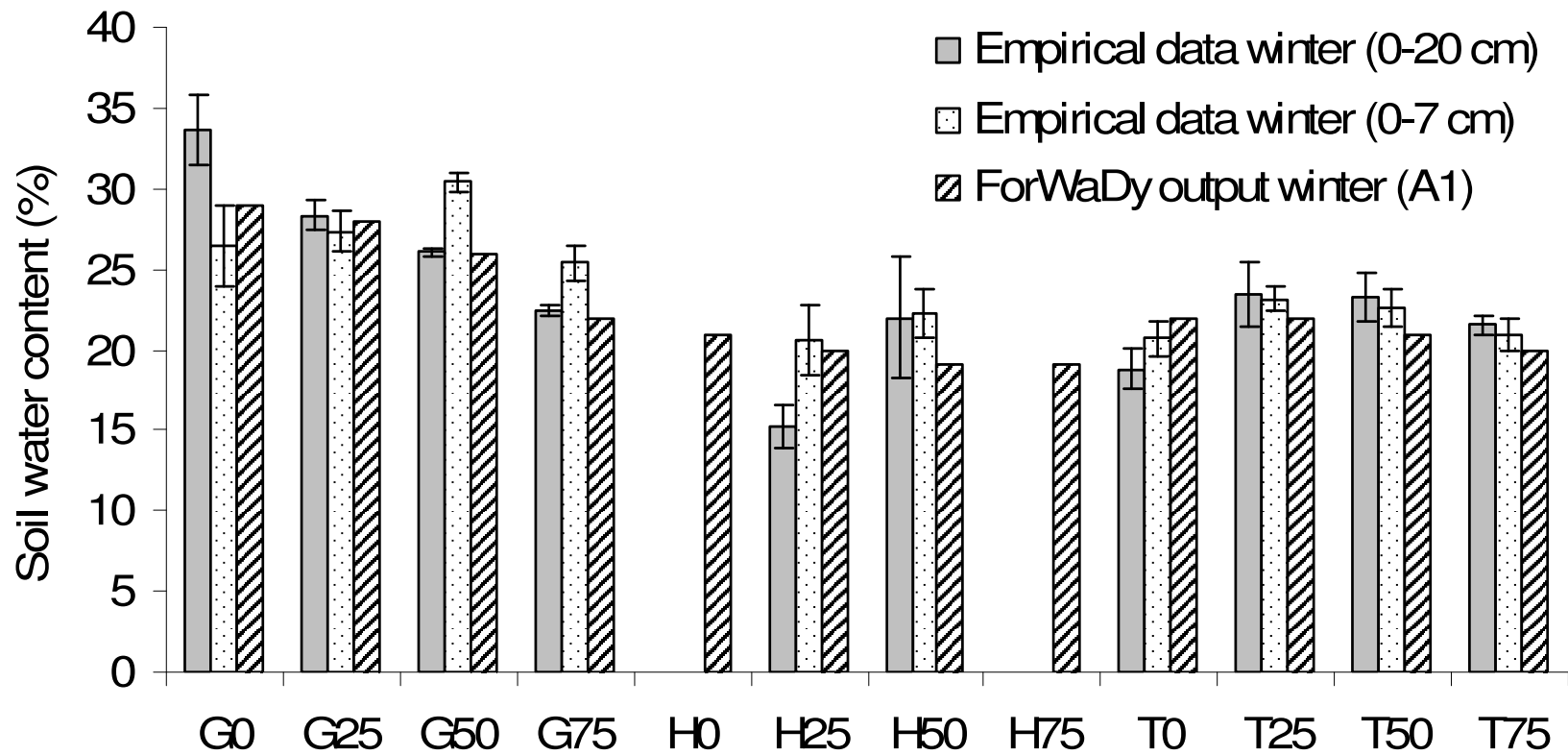
Figure 4.5. Model evaluation. Relationship between empirically measured soil water content at 0-7 cm depth and ForWaDy model estimates for 0-25 cm depth (A1 layer) in summer of 2007. Nurse species are: G = *G. robusta*, H = *P. elliottii x P. caribaea*, T = *P. taeda*. The numbers associated with each species indicate the thinning intensity (0-75%). All soil data was collected during over five consecutive days during the summer (December 18-22, 2007) in the three thinning experiments (n=3).
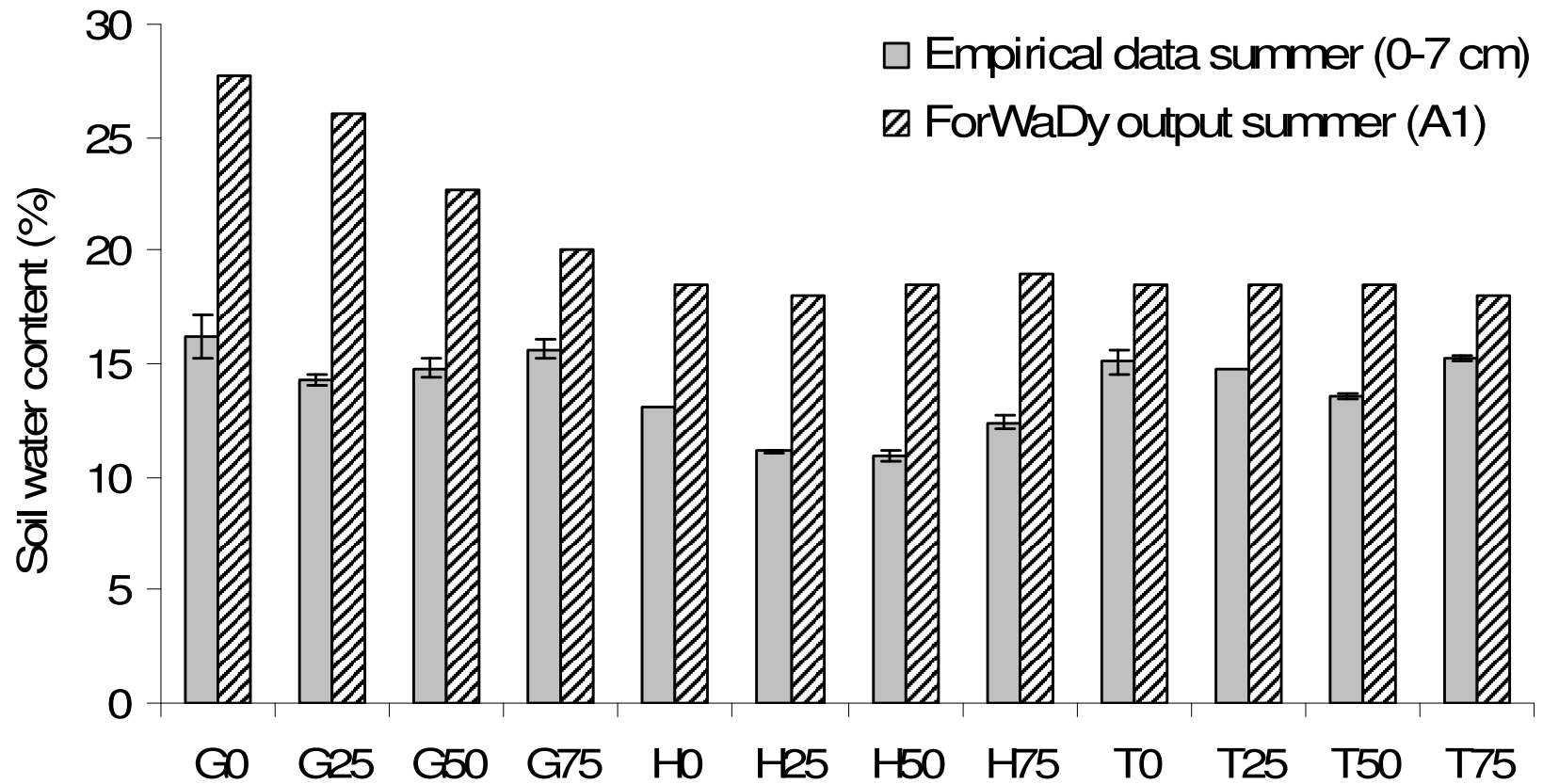
Figure 4.6. Relationships between one-year and three-year observed mortality (%) of *T. ciliata* grown under the three nurse species and density treatments and modelled TDI (cumulated Transpiration Deficit Index). Regression coefficients and statistics for the relationship in year 1 (pre-thinning) were: Y = 1.31x + 166.49; R^2 = 0.68; p-value = 0.001; Pearson's correlation coefficient of 0.82. For the three year cumulative period (before and after thinning), the regression coefficients and statistics were: Y = 6.14x + 168.34; R^2 = 0.92; p-value < 0.001; Pearson's correlation coefficient = 0.92. Mortality means were determined from a full sapling inventory in each treatment plot (n=3). Nurse species are: G = *G. robusta*, H = *P. elliottii x P. caribaea*, T = *P. taeda*. The numbers associated with each species indicate the thinning intensity (0-75%). Each year in ForWaDy starts in July 1st, (the southern Hemisphere winter) and runs to June 31st.
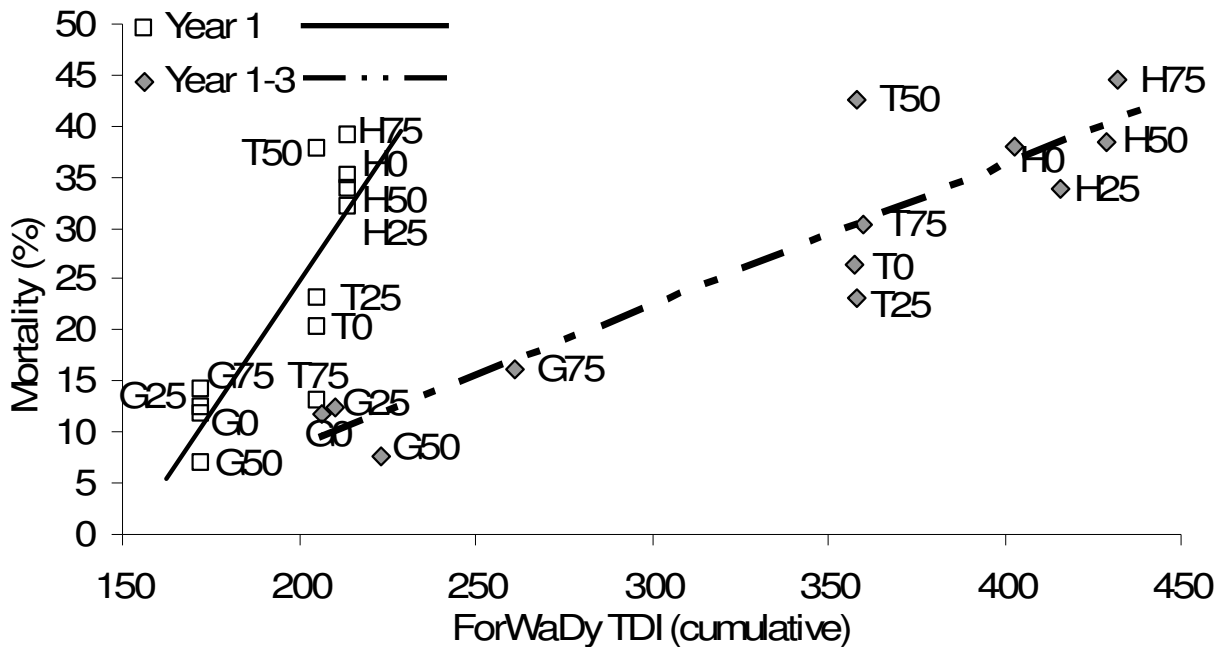
Figure 4.7. Relationship between average annual height increment of *T. ciliata* and annual cumulative ForWaDy Transpiration Deficit Index (TDI). Regression coefficients and statistics are: $Y=-73.17x+196.53$; $R^2 = 0.58$; p-value < 0.001; Pearson's correlation coefficient = -0.76. *T. ciliata* height averages were determined from a full sapling inventory in each treatment plot (n=3). Nurse species are: G = *G. robusta*, H = *P. elliottii* *x P. caribaea*, T = *P. taeda*. The number associated with the species codes indicates the thinning intensity (0-75%). Each year in ForWaDy starts in July 1st, (the southern Hemisphere winter) and runs to June 31st.
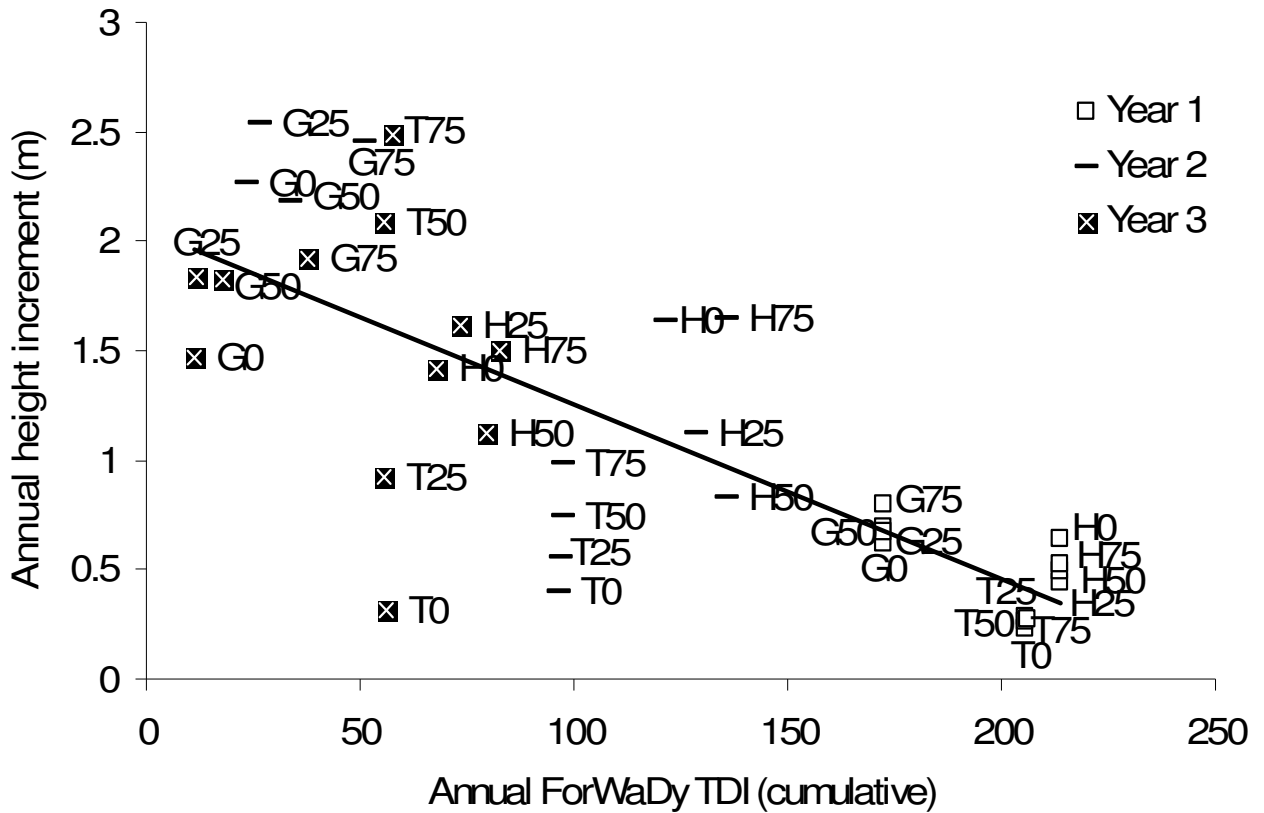
Figure 4.8. Relationship between cumulative ForWaDy TDI over the three-year study period and average *T. ciliata* aboveground stem volume in the final year of the study among the nurse species and density treatments. For the three-year cumulative period (before and after thinning), the regression coefficients and statistics were: Y=-0.0534x + 405.16; R^2 = 0.42; p-value = 0.023; Pearson's correlation coefficient = -0.65. The volume index was measured for trees taller than 1.3m and was based on the formula: V = $DBH^2 * \Pi/4 * Height * f_{1.3} * 100$, with f = 0.33 (Erskine et al. 2005). Nurse species are: G = *G. robusta*, H = *P. elliottii x P. caribaea*, T = *P. taeda*. The number associated with the species codes indicates the thinning intensity (0-75%). Values are means are based on tallies of all PSPs in each treatment plot (n=3).
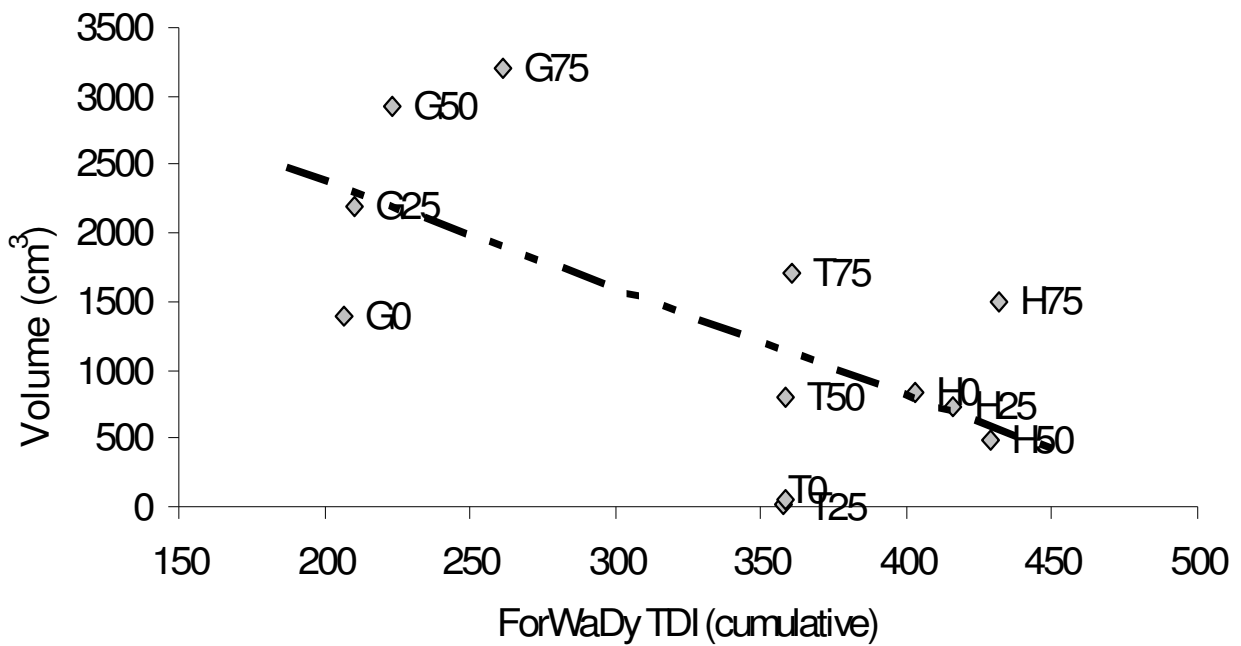
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5   Summary and conclusions

Nurse tree species facilitate establishment of under-planted *T. ciliata*, but also compete with them for resources, in plantations in subtropical Argentina. Interspecific interactions between the overstory nurse trees and *T. ciliata* are managed by manipulating composition and density of the nurse trees. In this thesis, I examined trade-offs among *T. ciliata* performance traits with varying overstorey species composition and density, and studied the underlying interference mechanisms affecting *T. ciliata* growth. I then predicted *T. ciliata* establishment success and growth over the growing season and over the long term by employing a forest hydrology model.

My general objectives were:

- To quantify the influence of nurse species and density on establishment success, stem morphology and productivity of under-planted *T. ciliata,* and to consider trade-offs among these influences when developing recommendations for nurse species selection and density management regimes.
- To examine mechanisms of interspecific interference between nurse tree species and *T. ciliata* in terms of light, soil water and nutrient availability to *T. ciliata*.
- To link *T. ciliata* establishment success and early growth to the availability of the limiting resource, soil water, by calibrating the two-dimensional forest hydrology model, ForWaDy, and use this stand management tool for guiding successful establishment of *T. ciliata* plantations on drought-prone sites in north-eastern Argentina.

My most important findings were:

Choice of nurse species and thinning intensity results in trade-offs among *T. ciliata* performance traits as well as overstorey productivity, and therefore depends on management objectives.

T. ciliata establishment success was greater when planted under *G. robusta* than the pines, and mortality increased with decreasing overstorey density and increasing exposure to solar radiation. Increased performance of *T. ciliata* seedlings with shelter has been observed in other studies (Keenan et al. 1995, Bygrave and Bygrave 2005),

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but it has also been recognized that overstorey species can be competitive, particularly among pine species, requiring application of thinning treatments once understory *T. ciliata* is established (Ashton et al. 1997, Mahroof et al. 2000, Rodríguez-Calcerrada 2008). I found that once established, *T. ciliata* grew faster under *G. robusta* than the pines, and generally grew most where any of the nurse species were thinned by 75%.

Total overstorey basal area was highest in *P. taeda* stands and individual overstorey tree growth generally increased with decreasing stand density, except for slower height growth of *G. robusta* in more open stands. Slower height growth of *G. robusta* in more open stands has been observed before (Fassola et al. 2004). However, it is well established that thinning generally increases resource availability and thus growth of the remaining trees (Mangialavori et al. 2003, Buck and Imoto 1982), as was observed for *T. ciliata* and the overstorey pines.

T. ciliata had the straightest stems where growing under *P. taeda* and stem morphology was best in stands thinned by 50%, regardless of nurse species. This result suggests that light played a role in influencing stem form. With the exception of early mortality, however, light levels appeared to have limited further effects on *T. ciliata* growth dynamics. Neither growth rate nor stem morphology were strongly correlated with light transmission to *T. ciliata* crowns. That light availability was not strong related to vegetation growth has been observed in other ecosystems where water limits productivity (Akeyeampong et al. 1999, Lawson and Kang 1990). However, plants are phototrophic, and it can therefore be assumed that *T. ciliata* morphology was influenced more by light distribution than average light availability under the different overstorey species and densities, with straighter stems growing under uniform rather than heterogeneous light conditions (Bahadur 1988, Wick 1970).

Thinning operations resulted in sawn-wood revenue for the pine species only. Taken together, these results show that choice of nurse-species and thinning densities leads to different trade-offs between *T. ciliata* establishment success, stem quality and productivity. Depending on current market conditions, it can also affect revenue from intermediate and final harvests of the nurse and crop species.

Water and nutrients are more limiting than light to *T. ciliata* growth in these subtropical forests, and choosing *G. robusta* rather than pine as a nurse species

is more important than thinning for increasing water and nutrient availability to *T. ciliata.*

Rapid growth of *T. ciliata* under *G. robusta* was associated with higher soil water and nutrient availability than under the pine species, and resource availability tended to increase with decreasing overstorey density of all overstorey species. Growth was highly correlated with wood $\delta^{13}C$ and foliar nutrient contents (N, P, K, Mg, Ca), suggesting that both soil water and nutrients limited growth (Warren et al. 2001, Dupouey et al. 1993, Walcroft et al. 1997). Light was not strongly correlated with *T. ciliata* growth or foliar nutrient content, suggesting that light was of secondary importance to soil factors in influencing *T. ciliata* growth. The more limiting effects of soil resources than light on *T. ciliata* productivity have been observed in other subtropical forests (Mangialavori et al. 2003, Buck and Imoto 1982, Akeyeampong et al. 1999, Lawson and Kang 1990, Salazar et al. 1993).

Soil water content increased with soil depth under all three overstorey species, but was highest under *G. robusta*. Soil water content tended to increase with decreasing overstorey density of the pine species. In *G. robusta* soils, by contrast, soil water content increased with increasing *G. robusta* density, possibly because *G. robusta* predominantly accesses water from deeper soil layers by vertical roots (Smith et al. 1998) and can increase soil surface water content through hydraulic lift (Burgess et al. 1998). Rooting was deeper in *T. ciliata* rip lines than in the overstorey rip lines of un-thinned treatments, indicating that resource partitioning was induced by nurse tree competition for water (Leuschner et al. 2004).

The foliage of *T. ciliata* had higher P and K concentrations and N, Mg and Ca contents when grown under *G. robusta* than the pine species, whereas only P and K were more available in the mineral soil under *G. robusta*. These results suggest greater niche packing when *T. ciliata* is mixed with *G. robusta* than the pines. Interestingly, foliar P was lower and foliar K was higher for *G. robusta* than the other nurse species. *G. robusta* is considered highly P-efficient (Radersma and Grierson 2004), and its proteoid (cluster) roots are thought to facilitate P nutrition of *T. ciliata* (Radersma et al. 2005). Litterfall peaked in the spring for *G. robusta*, with *G. robusta* returning most of its nutrients to soils at the beginning of the growing season. For the pine species, however, litterfall peaked in the fall, and although nutrient return via litterfall was highest under *P. taeda*, litter C:N and C:P were also high. These results confirm earlier studies showing

that pine species interfere with soil water and nutrient availability to its understorey (Ashton 1997, Mahroof et al. 2000, Rodríguez-Calcerrada 2008), but that *G. robusta* is less competitive and even appears to facilitate uptake of soil nutrients and water by *T. ciliata*. While these results apply to drought-prone and nutrient-deficient sites in subtropical forests, the mechanisms and strength of interference among these species may differ on other sites. My findings stress the importance of careful nurse tree species selection for *T. ciliata* establishment, but also show that an understanding of interference mechanisms is necessary to predict the best species and density management regimes for particular site qualities.

The calibrated two-dimensional forest hydrology model ForWaDy is a good predictor of *T. ciliata* establishment success and growth under different overstorey species.

ForWaDy was a good predictor of winter soil water content in the upper soil layer, and early *T. ciliata* mortality and growth under the different overstorey species. However, it was less precise at predicting soil water content in the upper soil layer in summer and soil water content in deeper soil layers throughout the year. ForWaDy accurately predicted lowest early mortality under a *G. robusta* overstorey, corresponding with the lowest predictions for TDI (Transpiration Deficit Index, defined by Seely et al. (1997) as a measure of cumulative water stress) and the highest predictions of soil water content in the top soil layer in intermediate and high overstorey densities. It also accurately predicted the highest *T. ciliata* mortality under a *P. elliottii x P. caribaea* overstorey, corresponding with the highest modelled TDI. *T. ciliata* grew tallest in low density treatments with low TDI, but differences between treatments were not very pronounced and effects were mainly due to overall species rather than thinning effects. This trend matched my field observations.

It has been reported that hourly time-step models with a multi-layer soil moisture description and complete surface energy balance account for short-term fluctuations in evapotranspiration (Daamen and Simmonds, 1994) better than simple daily time-step models (Smith et al.1998), like ForWaDy. However, daily time-step models can reasonably estimate cumulative hydrological parameters over longer periods, like weeks or months (Smith et al 1998). This was sufficient for the purpose of this study,

where my primary interest was to model the intermediate effects of soil water content and transpiration on *T. ciliata* growth and mortality.

Discussion and conclusions relating the manuscript chapters to each other and to the overall field of study

I addressed my first objective in Chapter 2, where I quantified the effects of nurse species and thinning density on early establishment and growth of *T. ciliata*. I found that performance of *T. ciliata* varied greatly with overstorey species and density. In Chapter 3, I unravelled the interference mechanisms that governed the *T. ciliata* performance responses. I found that nurse species influences on soil water and soil nutrient availability was more important than their ability to compete for light, and that *G. robusta* was more facilitative and less competitive for soil resources than either of the pine species. In Chapter 3, I also determined that overstorey thinning effects on soil resource availability varied dramatically between *G. robusta* and the pines, but that thinning density was less important than species choice for increasing early *T. ciliata* growth (Chapter 2 and 3).

My findings agree with other studies reporting low competitiveness of *G. robusta* in plantations (Rao et al. 1998, De Costa et al. 2007). *G. robusta* has been successfully used as a nurse tree in other parts of the world with *T. ciliata* (Buck and Imoto 1982, Keenan et al. 1995, Bygrave and Bygrave 2005). In addition to its positive effects on soil water content resulting from hydraulic lift and complementary water use, *G. robusta* could contribute to improved *T. ciliata* growth through reduced evaporation and transpiration rates (Chapter 3), similar to observation made in tea plantations with *G. robusta* in Sri Lanka (De Costa et al. 2007). *G. robusta* has been shown to access water from deeper soil layers by vertical roots (Smith et al. 1998) and hydraulic lift (Burgess et al. 1998), contributing to the improved growth of *T. ciliata* in its understory. In contrast, pine species compete strongly with understory plants for soil water and nutrients (Ashton et al. 1997, Mahroof et al. 2000, Rodríguez-Calcerrada 2008). Our results suggest that *P. taeda* competes predominantly with *T. ciliata* for soil nutrients while *P. elliottii x P. caribaea* competes especially strongly for soil water (Chapter 3).

In Chapter 4, in recognition that soil water was one of the most important resources limiting early establishment and growth of *T. ciliata* at the study site, I calibrated the two-dimensional forest hydrology model, ForWaDy. In validating the model, I found that it had good predictive capability for *T. ciliata* performance, water

stress, and winter soil water content in upper soil layers. I therefore concluded that the calibrated ForWaDy model could serve as a planning tool to guide managers in species selection and thinning regimes for *T. ciliata* and nurse tree plantation establishment in drought-prone areas of north-eastern Argentina.

The overall significance and contribution of the thesis research to the field of study

To my knowledge, the influences of multiple nurse species and a wide range of thinning densities on *T. ciliata* early establishment and growth have never been compared on a single site before. I was able to show how dramatically the choice of nurse species influences *T. ciliata* early establishment and growth, and could link those observations to the underlying interaction mechanisms influencing *T. ciliata* performance. I found that nurse trees were competitive for soil resources, but that facilitation by *G. robusta* was of primary importance in improving soil water and nutrient availability, and thus performance of *T. ciliata*. This finding agrees with the stress-gradient hypothesis of facilitation (Maestre et al. 2009), that facilitation is of primary importance on impoverished sites. In studying these interactions, I came to the understanding that the net effect and mechanisms of nurse tree interactions are not easy to predict, and therefore must be empirically studied for specific site conditions if the results are to be applied in a productive manner to forest management. In my research, I was also able to demonstrate the importance of early thinning to promote *T. ciliata* growth, especially where *P. taeda* was used as a nurse tree, and to explain the processes by which thinning influenced resource availability. I found that thinning generally increased soil resource availability, but that its effects on *T. ciliata* growth depended greatly on choice of nurse tree species. Finally, I was able to link *T. ciliata* water stress to one of the most important limiting resources, soil water, by employing the two dimensional forest hydrology model, ForWaDy. In calibrating and verifying the model, I was able to develop a useful management tool that can be applied to guide successful establishment of *T. ciliata* in nurse-tree plantations. My study was the first demonstration of ForWaDy as an accurate, predictive management tool.

Strengths and weaknesses of the thesis and research related to the project

Along with the strengths of my research discussed above, there were several weaknesses as well. Firstly, the short-term nature of my experiment, and the fact that it

was conducted on a single site, limit the general applicability to a wider range of environmental conditions. Current patterns in growth and stem morphology of the understorey *T. ciliata* may change over time, resulting in different outcomes over the long term. In addition, growth constraints and interactions with nurse tree species may change as the stands develop, and they may be more dynamic than indicated by initial results. Correspondingly, the identified importance of water and nutrients to *T. ciliata* development might be valid only for establishment and early growth periods, but competition for light may become increasingly important with time, especially where overstorey stand density is not controlled. Related to this is the limitation of the study to a single growth stage of *T. ciliata*. By examining different growth stages of both *T. ciliata* and the nurse species, and by monitoring dynamics over a whole rotation, from the moment of planting to the final harvest, I would have gained a deeper insight into the facilitative and competitive interactions between and within species. As with variation with stand development, species interactions are also likely vary across sites, such as where soil phosphorus, potassium and water are less limiting.

Secondly, the generally weak responses of *T. ciliata* survival and early growth to overstorey density manipulations of *G. robusta* and *P. elliottii x P. caribaea* may have been influenced by the lack of very low and very high density treatments for comparison. Without including density extremes, the full effects of nurse-tree competition and facilitation on *T. ciliata* may not have been fully expressed.

Thirdly, the study design could have been improved by including a range of site qualities and climatic conditions. This would have allowed testing of the stress-gradient hypothesis (SGH; see below) (Bertness and Callaway 1994), and for a variety of interacting stress factors. It may also have allowed me to examine interactions between facilitation and competition over stress gradients, testing whether facilitative effects decrease with increasing competition for resources (Michalet et al. 2006). This kind of analysis would be useful in predicting changes in species interactions under different site and climate scenarios. Similarly, by exploring a wider variety of species over the long-term, I could also have determined whether the magnitude and direction of interactions change with the ontogeny of the interacting species (Miriti 2006).

Fourth, the low sensitivity of ForWaDy at detecting differences among thinning treatments was a short-coming of the calibrated model (Chapter 4). The fit of predicted versus empirical summer soil moisture data in the different thinning treatments would

have benefited from fine-tuning, including utilization of climate data obtained from on or near my study site rather than from a site at distance. This would increase the value of the management tool for *T. ciliata* early establishment and growth. Also, the model did not include or predict soil nutrient availability, another important resource influencing growth of *T. ciliata*. Light, though of lesser importance at my study site, was also not considered. Including both soil nutrient and light availability in the model could improve its predictability of *T. ciliata* performance at the study site. Linking ForWaDy to FORECAST (Seely at al. 1997) would achieve this and likely improve the accuracy of the *T. ciliata* growth predictions as well as those of the associated overstorey.

Finally, the general applicability of the results of my study are limited due to the unique situation where non-native *T. ciliata* is planted in subtropical Argentina. Although growing conditions are comparable to other parts of the world, results of this study would not apply to ecosystems where the shoot borer insect, *Hypsipyla robusta*, occurs. The presence of this insect in Australia and India makes establishment of economically viable *T. ciliata* plantations difficult so far (Bygrave and Bygrave 2005, Bahadur 1988).

Future research directions in the field of mixtures competition and facilitation; and evaluation of current knowledge and proposals for new ideas related to the field of study

Different categories of stress may affect shifts between competition and facilitation. Abiotic stress may come from either non-resource-related conditions such as heat, cold, wind, salinity or soil structure, or resource-related conditions such as water, light and nutrients (Maestre et al. 2009). Grime (1977) argued that stressful environments are best defined as those in which producers are limited by the environment in their ability to convert energy to biomass, and it is under this focus on productivity that most community ecologists examine stress (Lortie et al. 2004, Brooker 2006, Callaway 2007). It is thought that the relative frequency of facilitation and competition will vary inversely across gradients of physical stress or ecosystem productivity, which is expressed as the SGH (stress-gradient hypothesis) (Bertness and Callaway 1994). The SGH, however, makes a broad prediction for general patterns across species and systems, and might be refined by incorporating species traits to explain why co-occurring species may not show the same response, either in magnitude or direction, to a common neighbour under the same environmental conditions (Maestre et al. 2009), as observed in my study.

Similar to what I observed with *G. robusta*, it is thought that plants in arid environments generally improve soil fertility and microclimate under their canopies (Cortina and Maestre 2005). Therefore, when a limited resource is the only fundamental abiotic stress factor, facilitation can only occur when neighbours increase the availability of this resource (Maestre and Cortina 2004); this appeared to be operative with *G. robusta*, which increased water as well as soil nutrient availability to *T. ciliata*. Such facilitation did not occur under the pine species in my study. Maestre et al (2009) suggest that there are circumstances where one might expect facilitation to occur, such as with *G. robusta* at my study site. For example, in an arid environment, a plant with the capacity for hydraulic lifting can provide water to a neighbour (Ludwig et al. 2004). Shade from nearby canopy shrubs and trees can also help retain soil moisture at the soil surface and facilitate neighbours with shallower roots (Maestre et al. 2003), and can indirectly facilitate the water-relations of understorey neighbours by decreasing the vapour pressure difference between the leaf of the beneficiary and ambient air. However, if the below-ground spatial niches of interacting species overlap substantially, and there is more than one factor driving stress – situations potentially found in environments such as arid and semi-arid areas (e.g. Reynolds et al.2000, Carrick 2003, Hipondoka et al. 2003, Ludwig et al. 2004) – then shifts in the balance of net interactions from competition to facilitation with increasing stress are less likely to occur. I observed this beneath the pine overstories, where pines competed intensively for water and soil nutrients, which both became even more limiting to *T. ciliata*.

My study shows that the shift between facilitation and competition depends on nurse species and density. In a sense, the nurse species and density manipulations in my study created an experimental stress gradient governed by resource availability. In combination with other studies, my results might contribute to a better understanding of species interactions along stress gradients and may help formulate the conceptual framework of the SGH more explicitly. Specifically, future empirical studies examining mixed species plantations, including nurse trees, should incorporate, to the fullest extent possible, a stress gradient where *T. ciliata* or another crop tree is present, and include nurse-species with different competitive-stress tolerance capacities. Further, the type of stress needs to be identified and responses related to the type of stress (i.e., resource limitations, such as soil water and nutrients vs. non-resource limitations, such as temperature and irradiation (Maestre et al. 2009). After explicit definition of the

stress-factors, the experiments need to be designed accordingly. This might also facilitate future synthetic efforts to contrast the relative importance of different types of stress gradients (Maestre et al. 2009) and employ computer models to predict species-interaction adaptations with climatic change.

Final conclusions

I have demonstrated some tools that are effective for understanding and predicting the resource limitations and species interactions that drive establishment success and early growth of *T. ciliata* under previously established nurse tree species and across gradients of overstorey density. These include the empirical study of tree and environmental responses to manipulated treatment factors in an experimental setting, but also the development of a modeling tool for predicting *T. ciliata* performance using calibration data (growth, physiological and environmental) collected from the study site for estimating transpiration deficits. Clear relationships between *T. ciliata* early establishment and growth, and soil water and nutrient availability, as influenced by nurse species, provided a more thorough framework for describing dynamics of *T. ciliata* performance beneath *G. robusta*, *P. elliottii x P. caribaea*, and *P. taeda*. Future research with longer-term studies employing different nurse species and density treatments over a wide range of sites and climatic conditions will clarify, confirm and provide deeper insight into these species interactions across stress gradients.

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