UNIVERSIDAD DE CÓRDOBA

Departamento de Ingeniería Forestal

Área de Ingeniería Agroforestal

Producción de biomasa en plantaciones intensivas de *Eucalyptus* spp. en Uruguay

Biomass production in intensive plantations of *Eucalyptus* species in Uruguay

Tesis Doctoral

Fernando Resquin Pérez

TITULO: *Producción de biomasa en plantaciones intensivas de Eucalyptus spp. en Uruguay*

AUTOR: *Fernando Resquín Pérez*

© Edita: UCOPress. 2019
Campus de Rabanales
Ctra. Nacional IV, Km. 396 A
14071 Córdoba

https://www.uco.es/ucopress/index.php/es/
ucopress@uco.es

Departamento de Ingeniería Forestal

Área de Ingeniería Agroforestal

Producción de biomasa en plantaciones intensivas de *Eucalyptus* spp. en Uruguay

Biomass production in intensive plantations of *Eucalyptus* species in Uruguay

Tesis Doctoral presentada por

Fernando Resquin Pérez

Para la obtención del título de

DOCTOR POR LA UNIVERSIDAD DE CÓRDOBA

Director

Dr. Rafael Maria Navarro Cerrillo

(Catedrático de la Universidad de Córdoba)

Córdoba, Marzo 2019

TÍTULO DE LA TESIS: "PRODUCCIÓN DE BIOMASA EN PLANTACIONES INTENSIVAS DE EUCALYPTUS SPP. EN URUGUAY."

DOCTORANDO: Fernando Resquin Pérez

INFORME RAZONADO DE LOS DIRECTORES DE LA TESIS

La diversificación de la matriz energética es una de las políticas impulsadas en los últimos años en Uruguay con el objetivo de reducir la dependencia de los combustibles fósiles y al mismo tiempo contribuir a las reducciones de gases de efecto invernadero. Esto se ha traducido en la promoción para el desarrollo del uso de fuentes alternativas del petróleo como ha sido el caso de las energías eólicas, solar fotovoltaica y la proveniente de distintos tipos de biomasa.

La biomasa de origen forestal ha generado interés teniendo en cuenta la importante expansión que han tenido las plantaciones forestales y en particular la de algunas especies de eucaliptos. Esto se ha basado en el alto potencial productivo que es posible obtener en plazos relativamente cortos para la producción de celulosa y madera sólida. La historia reciente del manejo de ese tipo de plantaciones ha permitido generar conocimientos tanto científicos como empíricos en cuanto a al comportamiento de las especies en los distintos tipos de suelos forestales del país. La instalación de este tipo de cultivos con destino a la producción de biomasa, por tanto, genera expectativas en cuanto a la obtención de distintos tipos de combustibles (sólidos, líquidos o gaseosos). No obstante, debido a las particularidades de los sistemas de producción de biomasa en turnos relativamente reducidos, se generan una serie de interrogantes que deben ser respondidos para que puedan ser considerados como sistemas viables de producción de biocombustibles.

En ese sentido la tesis doctoral aporta información sobre aspectos del crecimiento, contenido energético y extracción de nutrientes de tres especies de eucaliptos plantadas a cuatro espaciamientos con destino a la producción de biomasa. Este trabajo fue desarrollado en cinco capítulos cuyos contenidos se describen a continuación:

El primero analiza los parámetros del sitio (suelo, clima y topografía) que muestran mayor asociación con el crecimiento de las especies de eucaliptos evaluadas en las diferentes regiones de Uruguay y la proyección de hábitat a futuro en función de diferentes escenarios de cambio climático. Con los ensayos instalados a campo se obtuvo información de sobrevivencia y crecimiento en los primeros seis años de crecimiento. Esto permitió evaluar los efectos de la competencia entre individuos sobre la tasa de mortalidad, el crecimiento individual y por hectárea, así como analizar las curvas de crecimiento y su relación con el momento óptimo de cosecha. Con las mediciones del peso y la densidad de la madera se estimó la productividad de biomasa en función de la especie y la densidad de plantación. Fueron identificadas las variables que mejor relación mostraron tanto con el volumen como con el peso individual las cuales fueron utilizadas para obtener modelos para cada sitio, especie y densidad de plantación. Esta información, a su vez, fue utilizada para analizar los parámetros energéticos de la madera tales como el poder calórico, densidad energética y rendimiento energético para cada especie y densidad de plantación, así como su evolución procurando identificar la máxima producción de energía por unidad de superficie y de tiempo.

Finalmente fueron evaluadas la producción de cada fracción de biomasa (Madera, corteza y hojas) y la extracción de nutrientes de las mismas asumiendo un turno de cosecha próximo a los seis años de crecimiento. Estos aspectos cobran importancia desde el punto de vista de la sostenibilidad de este tipo de cultivos teniendo en cuenta que los suelos forestales son los de menor fertilidad natural del país y que los sistemas de producción de este tipo de cultivos prevén la cosecha del árbol entero con la consiguiente remoción de fracciones con altos contenidos de nutrientes.

La Tesis se presenta como un compendio de 5 artículos científicos, dos de los cuales ya han sido publicados, y los restantes se encuentran en proceso de finalización para ser enviados a revistas relacionados con la temática de los mismos.

Artículos publicados:

Resquin, F., Navarro-Cerrillo, R. M., Rachid-Casnati, C., Hirigoyen, A., Carrasco-Letelier, L. and Duque-Lazo, J. (2018) 'Allometry, Growth and Survival of Three Eucalyptus Species (*Eucalyptus benthamii* Maiden and Cambage, E. dunnii Maiden and *E. grandis* Hill ex Maiden) in High-Density Plantations in Uruguay', Forests, 9(745), pp. 1–22. doi: 10.3390/f9120745. Índice de Impacto: 0.89 Q1 posición 22/159 según ranking SJR.

Resquin, F., Navarro-Cerrillo, R. M., Carrasco-Letelier, L. and Casnati, C. R. (2019) 'Influence of contrasting stocking densities on the dynamics of above-ground biomass and wood density of *Eucalyptus benthamii*, *Eucalyptus dunnii*, and *Eucalyptus grandis* for bioenergy in Uruguay', Forest Ecology and Management. Elsevier, 438(January), pp. 63–74. doi: 10.1016/j.foreco.2019.02.007. Índice de Impacto: 1.62 Q1 posición 4/159 según ranking SJR.

Artículos enviados:

Modelling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunni*i in Uruguay. Resquin, F.; J. Duque-Lazo; R.M. Navarro-Cerrillo; C. Acosta Muñoz; C. Rachid-Casnati; L. Carrasco-Letelier. New Forest (en evaluación).

Influence of age and planting density on the energy content of *Eucalyptus benthamii, Eucalyptus dunnii* and *Eucalyptus grandis* planted in Uruguay. Resquin, F.; R. M. Navarro-Cerrillo; L. Carrasco-Letelier; C. Rachid-Casnati Biomass and Bioenergy (en evaluación).

Adicionalmente, el candidato ha participado en la publicación de dos artículos científicos en revistas indexadas y aportaciones a congresos científicos:

Artículos:

Bentancor, L., Hernandez, J., del Pino, A., Califra, Á., Resquín, F., & González-Barrios, P. (2019). Evaluation of the biomass production, energy yield and nutrient removal of *Eucalyptus dunni*i Maiden grown in short rotation coppice under two initial planting densities and harvest systems. Biomass and Bioenergy, 122(January), 165–174. https://doi.org/10.1016/j.biombioe.2019.01.019

Lopretti, M. I., Baldyga, N. I., Gonzalez, M., Olazabal, L. B., Torres, M. G., Resquin, F. and Carrasco, L. (2016) 'Biodegradation pretreatment of wood of *E. grandis, E. dunnii,* and *E. benthamii* to work in biorefinery processes', Journal of Renewable Materials, 4(1). doi: 10.7569/JRM.2015.634133.

Aportación a Congresos:

- Seminario Presentación de resultados de investigación en Producción y costos de cultivos para biomasa, así como aspectos de sustentabilidad e impactos socioeconómicos de generación de energías renovables. Uruguay Tipo de participación: Expositor oral Nombre de la institución promotora: INIA - Programa Forestal Palabras Clave: Biomasa forestal Áreas de conocimiento:

Ciencias Agrícolas / Agricultura, Silvicultura y Pesca / Silvicultura / Biomasa forestal Presentación: Producción de biomasa con especies de eucaliptos. http://www.inia.uy/Documentos/Privados/INIA%20Tacuaremb%C3%B3/Biomasa%2029%20octubre%202015 %20Fernando%20Resquin%20Producci%C3%B3n.pdf. Abril 2013.

- Congreso Internacional Argentina Tipo de participación: Poster. Nombre de la institución promotora: INTA Título: Producción de biomasa con especies de Eucalyptus a alta densidad y corta rotación plantado en Uruguay Autores: F. Resquin, C. Rachid, A. Hirigoyen, L. Carrasco, J. Doldan, M. de Martini, M. Lopretti. Setiembre 2013.

- Seminario Presentación de resultados de investigación en producción y combustibles derivados de madera Uruguay Tipo de participación: Expositor oral Nombre de la institución promotora: INIA - Programa Forestal Palabras Clave: Biomasa forestal biocombustibles corta rotación logistica Areas de conocimiento: Ciencias Agrícolas / Agricultura, Silvicultura y Pesca / Silvicultura / Biomasa Forestal Título de la presentación: Productividad de biomasa con Eucalyptus a alta densidad. http://www.inia.uy/estaciones-experimentales/direcciones-regionales/iniatacuaremb%C3%B3/actividad-2013-40. Setiembre 2015

Por todo ello, se autoriza la presentación de la Tesis Doctoral "Producción de biomasa en plantaciones intensivas de Eucalyptus sp. en Uruguay.".

En Córdoba, 26 de ~~Marzo de~~ 2019

Firma del director

Fdo.: Rafael Mª Navarro Cerrillo

Agradecimientos

Los agradecimientos son muchos (tanto que ni por asomo caben en estas breves líneas) y muy sinceros. Muchas personas han colaborado para que ahora yo este escribiendo esto. En mi país: Gustavo Ferreira, Roberto Scoz y Gustavo Brito que me dieron el apoyo imprescindible para el punto de partida. A Cecilia Rachid y Leónidas Carrasco con los que trabajé en conjunto en todas las etapas del proyecto: desde que instalamos los ensayos (allá por el año 2010) hasta que mandamos los artículos a las revistas.

En la Universidad de Córdoba: a Rafael Navarro que desde que esto era solo una idea me orientó y contribuyó para que el trabajo iniciado años atrás culminara de buena manera. A Joaquín Duque por su valiosa contribución con la tesis y en mi aprendizaje de R.

A la Universidad de Córdoba por darme la enorme oportunidad de aprender sobre los temas que más me gustan.

Sin el financiamiento de INIA y la ANII a lo largo de todos estos años y sin el apoyo de la empresa Forestal Oriental de Uruguay esto sin duda no habría sido posible.

A mi madre que siempre me estaba esperando, a mi padre que seguro está contento por esto y a Carolina por el aguante.

No me olvido de mis amigos Pastora y Pedro.

Y por supuesto a “Avellaneda” por los momentos vividos.

A todos, un enorme gracias de nuevo….

Resumen

La producción de biomasa con especies de eucaliptos muestra un alto potencial, teniendo en cuenta los altos niveles de crecimiento que tienen estas especies en los diferentes suelos de prioridad forestal de Uruguay. La biomasa de estas especies (en particular la madera) presentan características interesantes desde el punto de vista tecnológico teniendo en cuenta la densidad básica, la homogeneidad de la composición química, el bajo contenido de azufre, cenizas y nitrógeno y un poder calórico relativamente alto. Estas características determinan que las plantaciones intensivas de estas especies puedan ser una alternativa interesante en sistemas de producción cuyo objetivo sea la obtención de distintos tipos de biocombustibles.

Los cultivos de altas densidades y corta rotación tienen particularidades que merecen especial atención desde el punto de vista productivo, tecnológico y ambiental teniendo en cuenta la falta de información que hay sobre los mismos en los suelos forestales de Uruguay. En función de estas necesidades se instalaron en la primavera de los 2010 dos ensayos a campo en dos localizaciones (Tacuarembó-NE, y Paysandú-SW), con tipos de suelos representativos de los suelos predominantes en las regiones litoral y norte del país. Fueron evaluadas tres especies de eucaliptus (*Eucalyptus benthamii, E. dunnii* y *E. grandis*) establecidas con cuatro densidades de plantación (2220, 3330, 4440 y 6660 árboles por hectárea) en un diseño de parcelas divididas con tres repeticiones.

El Capítulo 1 presenta un contexto general de la matriz energética en Uruguay y la conceptualización de la biomasa forestal y, en particular, de los cultivos energéticos; además de su posible adaptación a las condiciones del país y su potencial como materia prima para la obtención de combustibles. En función de ese contexto se plantean el objetivo general y los específicos los cuales se relacionan directamente con los capítulos de la presente tesis.

En el Capítulo 2 se justifica la elección de las especies de eucaliptos y se analiza la distribución potencial de *E. grandis* y *E. dunnii* en los distintos tipos de suelos de prioridad forestal del país. *E. benthamii* no fue incluida en este primer análisis ya que no se contaban con datos suficientes de inventario por ser una especie de uso relativamente reciente por las empresas productoras de pasta de celulosa. Los resultados permitieron identificar los parámetros de suelo, topografía y clima que mayor asociación muestran con el crecimiento de estas especies y, por tanto, generar una cartografía de las regiones con mayor potencial para el crecimiento de ambas especies. Los modelos de predicción de hábitat ajustados mostraron un grado elevado de precisión, y también permiten visualizar la distribución a futuro de estas especies en función de diferentes escenarios de cambio climático.

El Capítulo 3 analiza la evolución de la sobrevivencia y su relación con las especies y densidades de plantación en los primeros 5 años de crecimiento. La evolución de la sobrevivencia también es analizada en función de las variaciones de la temperatura y precipitaciones ocurridas durante el período de evaluación en ambos sitios, así como de las condiciones de preparación previo e inmediatamente posterior a la plantación. Fueron analizados los efectos de la competencia entre individuos y sus efectos sobre el volumen individual y por hectárea. La evolución de las curvas de crecimiento indica el momento óptimo de cosecha para cada caso.

En el Capítulo 4 se presenta la dinámica de la densidad de la madera a lo largo de los ciclos de cultivo, la cual muestra un comportamiento diferente en ambas localizaciones para las especies y densidades de plantación en las diferentes edades evaluadas. El análisis del peso individual mostró un comportamiento similar al del volumen en cada una de las densidades de plantación. El análisis del efecto de la competencia en las diferentes densidades de plantación se manifiesta de forma similar al del volumen individual determinando diferencias en la productividad por hectárea de las especies en cada uno de los espaciamientos. Con estos resultados es posible identificar las especies y densidades de plantación con una productividad más elevada, y el momento óptimo de cosecha en cada caso. Al mismo tiempo, se observó la relación del espaciamiento y del turno de cosecha. Fueron identificadas las variables que permiten estimar con mayor precisión tanto del volumen como el peso individual para cada localidad, especie y densidad de plantación.

En el capítulo 5 se analizan los siguientes parámetros energéticos: poder calórico superior, densidad de la madera, densidad energética y rendimiento energético por hectárea y por año. Fueron analizados los efectos de la localidad, la edad, la especie y la densidad a partir de los parámetros descritos, a los efectos de identificar la combinación de factores que maximiza la producción de energía por unidad de superficie y de tiempo. A su vez, fueron analizadas las relaciones entre la densidad de la madera y el poder calórico, y el peso relativo de estas en la densidad energética. Finalmente fue estimada la superficie plantada necesaria para abastecer una planta de generación de energía eléctrica de 10 MWh en cada localidad estudiada.

En el Capítulo 6 se evalúan los niveles de producción de biomasa considerando todas las fracciones aéreas del árbol (madera, corteza, ramas y hojas), para cada especie y densidad de plantación. Se estudian los efectos de la competencia entre árboles sobre la proporción del peso de cada fracción con respecto a la biomasa total. Se analizan las concentraciones de nutrientes (P, Ca, Mg, K y N) de las fracciones madera, corteza y hojas en cada especie y densidad de plantación. Los contenidos de nutrientes entre fracciones muestran la relación de proporciones entre las mismas debido a las diferencias en la actividad fisiológica de cada una. El estudio de las concentraciones de nutrientes en cada fracción también permite visualizar la diferente distribución de estos en los diferentes componentes de la biomasa y las implicancias de extracción considerando las fracciones madera versus el árbol entero. La estimación de los kg de nutrientes extraídos para cada especie y densidad de plantación dan una idea clara de la fertilización que sería necesario reponer en el suelo para conseguir la sostenibilidad de este tipo de sistemas de producción. La cantidad de nutriente extraído versus la cantidad de biomasa producida da una idea de la eficiencia con que son utilizados los diferentes nutrientes en cada combinación especie, densidad de plantación y sitio. El balance del stock de cationes en el suelo versus las cantidades de nutrientes extraídos determina el número de rotaciones en los que sería posible mantener los actuales niveles de crecimiento asumiendo turnos de cosecha próximo a los seis años. Esto, a su vez, muestra cuál de los tres cationes evaluados (Ca, Mg y K) se tornarían restrictivos para el crecimiento en el corto y mediano plazo.

En el Capítulo 7 se presenta la discusión general de la tesis y señalando nuevas interrogantes que surgen en este tipo de cultivos energéticos en los turnos siguientes a la primera cosecha teniendo en cuenta las particularidades de estos en esas etapas de crecimiento. Finalmente, en el Capítulo 8 se puntualizan las principales conclusiones obtenidas.

Summary

Production of biomass from eucalyptus species shows a high potential taking into account their high levels of growth in the different forest priority soils in Uruguay. The biomass from these species (particularly wood) presents interesting characteristics from the technological point of view considering basic density, homogeneity of the chemical composition, the low content of sulphur, ash and nitrogen and a relatively high caloric power. These characteristics determine that these species could be an interesting alternative in production systems whose production objective is to obtain different types of biofuels.

High density and short rotation plantations have particularities that need special attention from the productive, technological and environmental points of view, taking into account there is a lack of information on them in Uruguayan forest soils. Based on these needs, two field trials were installed in the spring 2010, at two sites with soil types which were representative of the predominant ones in the coastal and northern regions of the country. Three species of eucalyptus (*Eucalyptus benthamii*, *E. dunnii* and *E. grandis*) were evaluated in four planting densities (2220, 3330, 4440 and 6660 trees per hectare) in a split plot design with three replications.

Chapter 1 presents a general context of the energy matrix in Uruguay and the conceptualization of forest biomass and, in particular, of energy crops as well as their possible adaptation to the country's conditions as well as their potential as raw material for fuels. Depending on this context, the general objective and the specific ones are established, which are directly related to the chapters of this thesis.

In Chapter 2 the choice of eucalyptus species is justified and the distribution potential of *E. grandis* and *E. dunnii* is analysed in the different types of forest priority soils in the country. *E. benthamii* was not included in this first analysis since there was not enough inventory data as it is a relatively recent species used by pulp producers. Results allowed to identify the parameters of soil, topography and climate that show a greater association with their growth and therefore a mapping of regions with greater potential for the growth of both species. The models for adjusted habitat prediction showed a high degree of precision and also allowed to visualize a future distribution of these species depending on different climate change scenarios.

Chapter 3 analyses survival evolution and its relationship with species and planting densities in the first 5 years of growth. The evolution of survival is also analysed according to the variations in temperature and rainfall during the evaluation period in both sites and also from the point of view of soil preparation conditions prior to and immediately after planting. Competition effects between individuals and their effects on individual volume and per hectare were analysed as well. The evolution of the growth curves indicates the optimum harvest time in each case.

In Chapter 4, dynamics of wood density are presented. A different behaviour is shown on both sites for the species and planting densities at the different evaluated ages. The analysis of the individual weight showed a similar behaviour to the volume in each of the planting densities. The analysis of the competition effect on the different densities of plantation manifests in a similar way to the individual volume, determining differences in the species productivity per hectare in each of the spacings. Based on these results it is possible to identify the species and plantation densities with higher productivity levels as well as the optimum harvest time in each case. At the same time, a relationship between spacing and harvest time was observed. The variables that allow to estimate with greater precision both volume and individual weight for each species site and density of plantation were identified.

Chapter 5 discusses the following energy parameters: higher caloric power, wood density, energy density and energy yield per hectare and per year. The effects of site, age, species and density were analysed with each of these parameters in order to identify the combination of factors that maximizes energy production per area and time. In turn, relationships between wood density and caloric power and their relative weight in determining energy density were analysed. Finally, it was estimated the planted area needed to supply a 10 MWh power generation plant for each site.

In Chapter 6, levels of biomass production are evaluated considering all the tree aerial fractions (wood, bark, branches and leaves) for each species as well as plantation density. It has also studied the effects of competition among trees with the proportion of each fraction weight in respect to the total biomass. The nutrient concentrations (P, Ca, Mg, K and N) are analysed in wood, bark and leaf fractions in each species and planting density. The nutrient contents in fractions show the proportion relationships among them due to the differences in the physiological activity of each one. The study of nutrient concentrations in each fraction also allows to visualize the different distribution pattern of these in the different components of the biomass and the extraction implications considering wood versus whole tree fractions. The estimation of kg of nutrients extracted for each species and plantation density gives a clear idea of mineral magnitudes that would be necessary to replenish the soil in order to achieve the sustainability of this type of production system. The amount of nutrient extracted versus the amount of biomass produced provides an idea of the efficiency with which different nutrients are used in each species combination, planting density and site. Balance of cations stock in the soil versus the amounts of extracting nutrients determines the number of rotations in which it would be possible to maintain current growth levels, assuming turns close to six years. This, in turn, shows which of the three evaluated cations (Ca, Mg and K) would become restrictive for growth in the short and medium term.

Chapter 7 presents the general discussion of the thesis and points out new questions that arise in this type of energy crops in the turns following the first harvest, considering their particularities in those stages of growth.

Finally, in Chapter 8 the main conclusions obtained are highlighted.

Tabla de Contenidos

Capítulo 1. Introducción General

Página

Chapter 2. Modelling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

Chapter 3. Allometry, growth and survival of three eucalyptus species (*Eucalyptus benthamii* Maiden & Cambage, *E. dunnii* Maiden and *E. grandis* Hill ex Maiden) in high-density plantations in Uruguay

Chapter 4. Influence of contrasting stocking densities on the dynamics of above-ground biomass and wood density of *Eucalyptus benthamii, Eucalyptus dunnii,* and *Eucalyptus grandis* for bioenergy in Uruguay

Chapter 5. Influence of age and planting density on the energy content of *Eucalyptus benthamii, Eucalyptus dunnii* and *Eucalyptus grandis* planted in Uruguay

Chapter 6. Evaluation of the nutrient content in biomass of Eucalyptus species from short rotation plantations in Uruguay

Capítulo 7. Discusión general

Capítulo 8. Conclusiones generales

Lista de Figuras   Página

Capítulo 1. Introdución general

Capítulo 2. Modeling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

Chapter 3. Allometry, growth and survival of three eucalyptus species (*Eucalyptus benthamii* Maiden & Cambage, *E. dunnii* Maiden and *E. grandis* Hill ex Maiden) in high-density plantations in Uruguay

Chapter 4. Influence of contrasting stocking densities on the dynamics of above-ground biomass and wood density of *Eucalyptus benthamii*, *Eucalyptus dunnii*, and *Eucalyptus grandis* for bioenergy in Uruguay

Chapter 5. Influence of age and planting density on the energy content of *Eucalyptus benthamii*, *Eucalyptus dunnii* and *Eucalyptus grandis* planted in Uruguay

Chapter 6. Evaluation of the nutrient content in biomass of Eucalyptus species from short rotation plantations in Uruguay

Lista de Figuras

Lista de Tablas

Capítulo 1. Introdución general

Página

Capítulo 2. Modeling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

Chapter 3. Allometry, growth and survival of three eucalyptus species (*Eucalyptus benthamii* Maiden & Cambage, *E. dunnii* Maiden and *E. grandis* Hill ex Maiden) in high-density plantations in Uruguay

Chapter 4. Influence of contrasting stocking densities on the dynamics of above-ground biomass and wood density of *Eucalyptus benthamii*, *Eucalyptus dunnii*, and *Eucalyptus grandis* for bioenergy in Uruguay

Chapter 5. Influence of age and planting density on the energy content of *Eucalyptus benthamii*, *Eucalyptus dunnii* and *Eucalyptus grandis* planted in Uruguay

Chapter 6. Evaluation of the nutrient content in biomass of *Eucalyptus* species from short rotation plantations in Uruguay

Capítulo 7. Discusión general

Capítulo 1. Introducción general

“Cuando éramos niños
los viejos tenían como treinta
un charco era un océano
la muerte lisa y llana
no existía.

luego cuando muchachos
los viejos eran gente de cuarenta
un estanque era un océano
la muerte solamente
una palabra

ya cuando nos casamos
los ancianos estaban en los cincuenta
un lago era un océano
la muerte era la muerte
de los otros.

ahora veteranos
ya le dimos alcance a la verdad
el océano es por fin el océano
pero la muerte empieza a ser
la nuestra.”

Mario Benedetti, 1964

Capítulo 1. Introducción general

1. Sector forestal en Uruguay

1.1.Sector energético

En Uruguay, en los últimos años, se ha venido promoviendo la generación de diversas fuentes ¨no tradicionales¨ de energía mediante una serie de leyes y decretos a través de las denominadas fuentes renovables, como son la biomasa forestal y agrícola, la eólica y la fotovoltaica, entre otras. Esta diversificación de la matriz energética procura reducir la participación de los combustibles derivados del petróleo a favor de las energías autóctonas y renovables en particular. A su vez, estos mecanismos procuran fomentar y regular la producción de agrocombustibles al mismo tiempo que generar un estímulo a las inversiones en la generación de nuevas fuentes de energía que se incorporen a la matriz energética actual.

En el corto plazo la meta es alcanzar un 25% de energías renovables en la matriz de abastecimiento eléctrico (Figura 1).

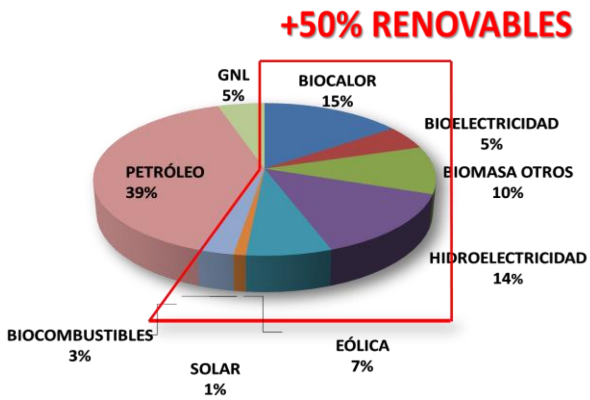


Figura 1. Matriz primaria global en Uruguay para el año 2015. Fuente: MIEM, Dirección General de Energía (2015).

Capítulo 1. Introducción general

A nivel nacional, existen factores que en los últimos años estarían mostrando cierto potencial para el uso de la biomasa como fuente renovable (MIEM - DNI, 2008). Los más importantes a tener cuenta son:

- situación energética regional deficitaria asociada a periodos de déficit de lluvias
- la existencia de módulos de generación adaptados a la industria local.
- buen potencial para el desarrollo de nuevos cultivos.
- marco regulatorio que permite la generación de energía eléctrica a privados.
- el desarrollo de esta cadena se encuentra comprendido dentro de las líneas estratégicas fijadas por el Ministerio de Industria Energía y Minería (MIEM).
- es una fuente descentralizada que promueve la generación de empleo

En este marco, en los últimos años se promovió, mediante procesos de licitación pública, la instalación de plantas generadoras de energía eléctrica a partir de biomasa básicamente de origen forestal, aunque también se incluyó otra fuente de biomasa como la cascara de arroz. Esto se ha traducido en la instalación, recientemente, de varias plantas de generación asociadas a industrias de procesamiento de madera solidas como aserraderos y plantas de tableros contrachapados (Tabla 1).

De este grupo, solamente Fenirol y Liderdat comercializan buena parte de la energía generada con la empresa estatal de generación y transmisión de energía eléctrica (UTE), mientras que el resto tiene un sistema básicamente de autoconsumo de la energía generada. Las dos empresas mencionadas se abastecen de biomasa residual de las operaciones de raleo y tala rasa en montes de eucaliptos y pinos destinados a la producción de madera sólida en las zonas litoral y norte del país. Actualmente está en ejecución una nueva convocatoria por parte de UTE para la licitación de 60 MW a partir de biomasa basado en el hecho de que existe una importante cantidad de residuos generados por las operaciones forestales de cosecha que podrían ser usados con fines energéticos (IICA-PROCISUR. INTA/Argentina, EMBRAPA/Brazil, INIA/Chile, MAG/Paraguay, INIA/Uruguay 2013) (PROBIO, 2015). Este estímulo para el uso de la biomasa forestal radica (además de los efectos sobre la economía nacional), en que es una fuente renovable, que capta gas carbónico de la atmosfera y que almacena carbono orgánico durante la etapa de crecimiento. Esta es una tendencia que ocurre a nivel mundial en la que la participación de la biomasa forestal está ocupando un papel cada vez más importante (Foelkel, 2015).

Tabla 1. Empresas generadoras de energía eléctrica a partir de biomasa. Fuente: MIEM, Dirección Nacional de Energía. 2014

Empresa	Localización	Potencia instalada (MW)	Fuente de Biomasa
Montes del Plata	Colonia	170	licor negro
UPM	Rio Negro	161	licor negro
Subtotal		**331**	
Bioener	Rivera	12	forestal
Weyerhaeuser	Tacuarembó	12	forestal
Fenirol	Tacuarembó	10	forestal y cáscara de arroz
Ponlar	Rivera	7.5	forestal
Liderat	Paysandú	5	forestal
Subtotal		**46,5**	
Alur	Artigas	10	caña de azúcar y sorgo
Galofer	Treinta y Tres	14	cascara de arroz
Otros (menor a 5 MW)		17.6	
Subtotal		**41.6**	
TOTAL		**419**	

1.2 Plantaciones forestales

El sector forestal en Uruguay ha tenido un importante crecimiento a raíz de la implementación de leyes, hacia finales de la década de los años 80, que promovieron la instalación de cultivos forestales con especies del género *Eucalyptus* y *Pinus*, fundamentalmente. Esta promoción se basó (y actualmente se mantienen los mismos criterios) en la definición de suelos denominados de prioridad y/o aptitud forestal (MGAP-DGF, 2016). El primero de los conceptos tiene un origen administrativo mientras que el segundo se refiere a aspectos de la productividad de los distintos tipos de suelos. En su concepción más amplia, los suelos forestales son los de menor productividad desde la perspectiva de un uso agrícola de los mimos. Por tanto, los cultivos forestales se han instalado en aquellos suelos marginales para sistemas más intensivos de producción como la agricultura, lechería, horticultura, etc. A partir de esto, los suelos forestales ocupan una superficie próxima a las 4.400.000 hectáreas; de las cuales, hasta el momento, se han plantado en torno a 1.000.000 de hectáreas (Figura 2) (MGAP, DGF, 2013). Estos suelos están distribuidos en varias regiones del país y tienen diferentes propiedades desde el punto de vista de la composición química, profundidad de los horizontes, textura, topografía, fertilidad, etc.

Los resultados tanto prácticos como empíricos han mostrado que los eucaliptos tienen un alto potencial de crecimiento; adaptándose, en buena forma, a los distintos suelos del país. Como resultado de la investigación en el área de mejoramiento genético se han identificado diversos genotipos de alta productividad de varias especies de *Eucalyptus.* En ese sentido se destacan claramente *Eucalyptus grandis* y *Eucalyptus dunnii* por su velocidad de crecimiento. A nivel experimental se han evaluado varias especies, entre las cuales el *Eucalyptus benthamii* ha mostrado niveles muy altos de crecimiento, lo cual hace pensar que podría tener un buen potencial para la producción de biomasa (Balmelli y Resquin 2001, 2002, 2006ab; Resquin y Balmelli, 2008, 2009ab).

También hay otro grupo de especies que históricamente han mostrado buena adaptación a las condiciones del país y que además se caracterizan por tener una madera de alta densidad lo cual contribuye a la productividad para usos energéticos (Resquin y Balmelli, 2008). Este es el caso de los eucaliptos denominados colorados, que en Uruguay lo integran básicamente *Eucalyptus tereticornis* y *Eucalyptus camaldulensis*. A su vez, estas especies de eucaliptos tienen valores de densidad básica considerada de intermedia a alta (comparada con otras especies), con valores del orden de 0,45 a 0,80 g cm^{-1} (Tuset et al., 2008).

En términos generales, los materiales genéticos de mayor productividad alcanzan valores de IMA comercial de 35 a 40 m^3 ha^{-1} $año^{-1}$, con densidades de plantación de unos 1300 árboles ha^{-1}, y turnos de corta que van desde los 8 a 10 años para celulosa y 12 a 15 años para madera sólida. El manejo silvicultural de este tipo de plantaciones, sumado a la información surgida de la investigación, ha generado datos en cuanto a las características de las curvas de crecimiento de las distintas especies en las diferentes regiones, turnos de cosecha, propiedades de la madera, comportamiento sanitario, etc. Esto, entre otras cosas, ha permitido identificar el potencial de los mejores genotipos en los distintos grupos de suelos desde el punto de vista de la producción de madera por unidad de superficie

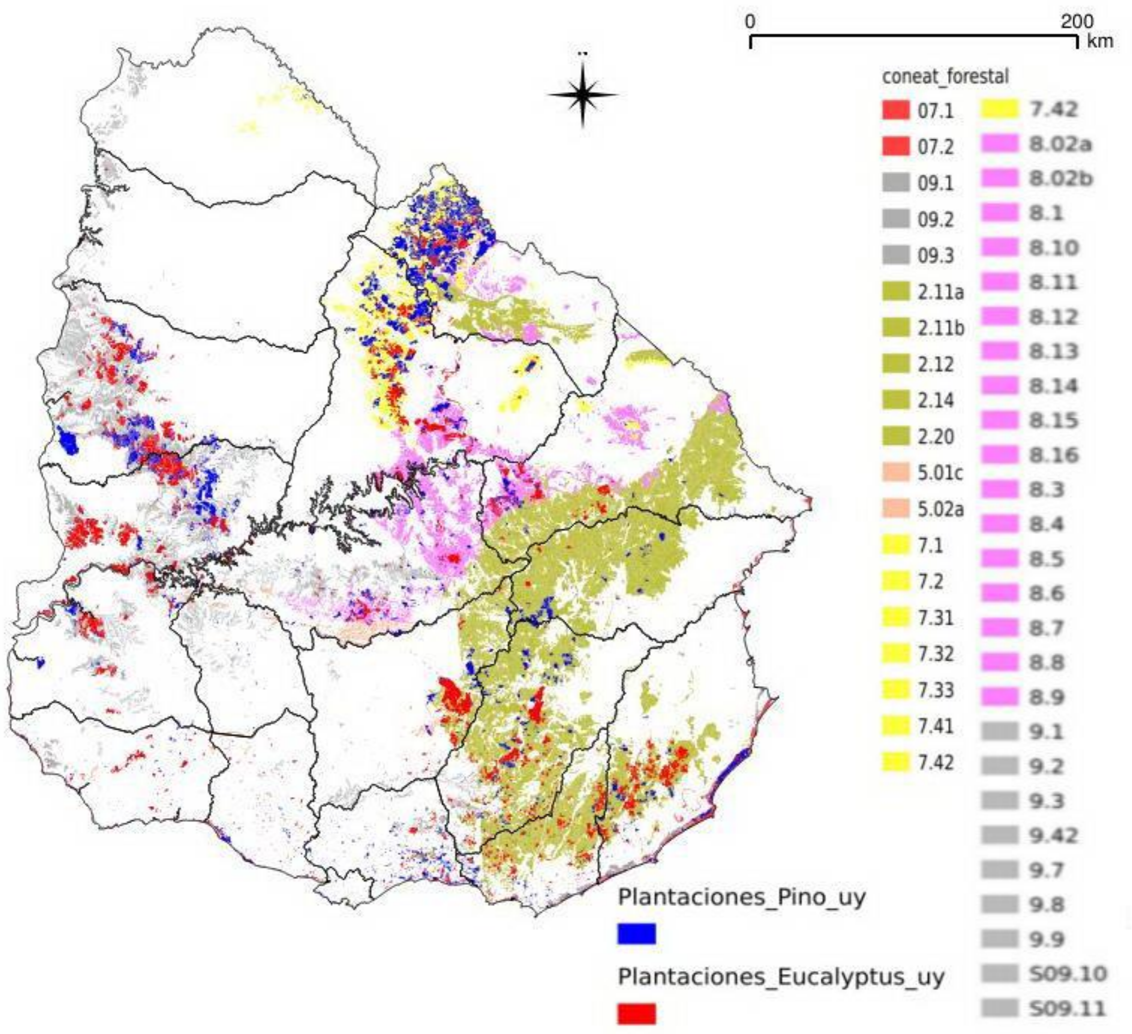


Figura 2. Mapa de suelos de prioridad forestal y denominación de clasificación de grupos CO.NE.A.T.

La combinación de alta velocidad de crecimiento y densidad básica de la madera determina que se puedan producir grandes cantidades de biomasa en plazos relativamente cortos de tiempo.

1.3 Potencial de producción de biomasa

La producción de biomasa tiene la particularidad de integrar al sector forestal, como generador de materias primas, y al sector industrial, como transformador de las mismas en distintos tipos de energía (electricidad y calor o ambas al mismo tiempo). Por otro lado, tiene la ventaja de que la biomasa puede ser transformada en varios tipos de combustibles (líquidos, sólidos y gaseosos), lo que permite cierta flexibilidad al momento de optar por alguna alternativa que se adapte a las condiciones y/o situaciones particulares del momento (Zsuffa et al., 1992; Carrillo, 2004). Otras particularidades de este tipo de plantaciones es que no compiten por tierras de interés agrícola y al mismo tiempo aseguran un secuestro neto de carbono muy superior a otros cultivos agrícolas a través de la biomasa total (parte aérea más raíces enterradas) (Sims et al., 2006).

Debido al surgimiento de otras fuentes de energía eléctrica como la eólica y la fotovoltaica, la generación a partir de biomasa forestal en Uruguay está siendo menos atractiva básicamente por una razón de costos. De todas maneras, la generación de energía a partir de biomasa tiene algunas ventajas comparativas con respecto a las mencionadas, como es el impacto positivo en la generación de puestos directos e indirectos de trabajo producidos por la instalación de este tipo de plantas en el interior del país. Por otro lado, existe un creciente interés por parte de la empresa estatal responsable de la producción y distribución de combustibles (ANCAP) en la exploración de alternativas de producción de combustibles líquidos o gaseosos a partir de distintos tipos de biomasa como los residuos forestales de campo, cultivos energéticos forestales de corta rotación, cultivos intensivos agrícolas, etc. Esto ha permitido la ejecución de proyectos de investigación (entre diferentes instituciones) con la finalidad de identificar las materias primas con mayor potencial desde el punto de vista de su disponibilidad, acceso y características tecnológicas para evaluarlas en diferentes procesos de generación de combustibles básicamente líquidos y gaseosos. La información que surge en los últimos años muestra que existen una serie de procesos denominados por su sigla en inglés BTL (biomasa a Liquido) o BTG (biomasa a gas) que podrían llegar a ser usados a nivel comercial en los próximos años (Swain et al., 2011; Sunde et al., 2011).

Estos proyectos han tenido como objetivo la transformación de madera en gases combustibles, e incluso en productos químicos de mayor valor ("Gas de Síntesis" o hidrógeno), recurriendo para ello a su descomposición térmica en atmósfera pobre en oxígeno (pirólisis y gasificación). La gasificación da lugar a una mezcla de gases de considerable poder calorífico. También dicha mezcla gaseosa, dado su alto contenido en H_2, podría usarse como fuente del mismo, luego de separarlo de los otros componentes gaseosos (CO, CO_2, hidrocarburos, etc.). Otro de los posibles usos de la biomasa forestal es la producción de pellets con destino a la exportación a los países de Europa (AEBIOM, 2008; Hiegl y Janssen, 2009). Este producto tiene un alto precio en el mercado europeo y al mismo tiempo una demanda creciente que supera la capacidad de producción en muchos países ya que es usado tanto para usos domésticos (calefacción de hogares) como industriales (plantas de co-generación). En estas evaluaciones se espera obtener resultados concluyentes respecto a rendimientos másicos y energéticos del proceso y caracterizar los combustibles líquidos obtenidos. En el futuro se podrán ensayar otros tipos de biomasa o de residuos orgánicos, buscando la valorización de la materia prima desde el punto de vista energético u obteniendo productos de alto valor agregado.

2. Cultivos energéticos

2.1 Generalidades

En este contexto, el cultivo de especies forestales con el objetivo de producción de biomasa (plantaciones energéticas) destinada a la obtención de diferentes biocombustibles se muestra como una alternativa interesante. Sin embargo, en términos de cadena agroindustrial presenta algunos aspectos aún no analizados y/o resueltos que sería necesario considerar. Estos aspectos están relacionados con la producción, el impacto ambiental y la valoración económica de los cultivos forestales. Desde el punto de vista productivo es necesario generar y/o adaptar información sobre el potencial de distintas materias primas energéticas en cuanto a los volúmenes potenciales de producción de biocombustibles fundamentalmente sólidos (chips y carbón) y líquidos (etanol y biodiesel).

En relación a aspectos económicos deben realizarse análisis del balance entre el consumo y la producción de energía al final de proceso particular de cada caso. Esto está muy relacionado a factores tales como (San Miguel et al., 2015):

- alto costo de cosecha y transporte asociados a la baja densidad energética por unidad de volumen
- economía de escala (el aumento de la capacidad reduce los costos fijos e incrementa la eficiencia de conversión)

- precio de la madera (chips) que puedan desviar los usos de la misma

Lo relacionado a la temática ambiental tiene que ver con la conservación del recurso suelo en sistemas de producción con altas densidades de árboles por hectárea, con la particularidad que en estos casos es posible reincorporar los restos (ramas, corteza y hojas) al suelo con el consiguiente reciclado de nutrientes (Achat et al., 2015). El uso de la madera para la producción de energía presenta menos problemas de contaminación comparada con los combustibles fósiles debido a su bajo contenido de azufre. Se debe tener en cuenta que cuando la biomasa es quemada el carbono reacciona con el oxígeno produciendo calor, dióxido de carbono y agua. Estos dos últimos compuestos son absorbidos por las plantas produciendo nuevamente biomasa. Por tanto, este proceso tiene un balance neutro del ciclo del CO_2 (Estrada y Meneses, 2004).

Dentro de las principales fuentes de biomasa disponibles, se mencionan:

- Residuos de cultivos agrícolas y forestales (rastrojo de cultivos, ramas y corteza de árboles)
- Residuos de procesamiento industrial (bagazo de caña, cascara de arroz, aserrín y costaneros)
- Cultivos energéticos (pasto elefante, swicht grass, miscantho, sorgo dulce, forestaciones energéticas)
- Licor negro derivado del proceso Kraft de producción de pasta de celulosa

La biomasa de origen forestal posee algunas ventajas importantes entre las cuales se mencionan: la renovabilidad, la productividad por unidad de superficie, la generación de empleo, la independencia de la estacionalidad, y las tecnologías disponibles, entre otras. De todos modos, existen algunos aspectos ambientales que deber ser necesariamente contemplados porque no todo lo que es derivado del proceso de fotosíntesis puede ser considerado como sustentable o ambientalmente amigable (Foelkel, 2015).

Se debe tener en cuenta que el aprovechamiento energético de los denominados residuos, en términos generales, tiene una serie de limitaciones importantes (Müller, 2005):

- Es un material heterogéneo debido a la presencia de fracciones de distintas características (poder calórico, humedad, contenido de cenizas, granulometría) lo que requiere de un proceso de homogeneización.
- Baja densidad energética lo que requiere de mayores costos de extracción y transporte

- Normalmente se encuentran distribuidos en grandes superficies
- Alta tasa de extracción de nutrientes del suelo

Estos aspectos determinan que la silvicultura específica para la producción de biomasa tenga algunas ventajas comparativas que, a priori, permiten superar algunas de las limitantes mencionadas anteriormente. En este sentido, dentro de los principales puntos a favor pueden mencionarse:

- Es posible producir un tipo de biomasa relativamente homogéneo a partir de materiales con cierto grado de mejora genética (semilla o clones)
- La biomasa producida está concentrada en espacios más reducidos, lo que permite lograr una mayor densificación energética.
- La obtención de biomasa no depende de otras actividades previas lo que simplifica las operaciones de logística.

Estos nuevos sistemas silviculturales para la producción de biomasa están siendo evaluados e implementados en algunos países como en Brasil, Australia, Nueva Zelanda, Alemania, Finlandia, fundamentalmente con especies del género *Eucalyptus, Populus, y Salix*. Estos modelos alteran los esquemas silviculturales convencionales, en tanto la densidad de árboles por hectárea, como por el turno de corta del monte. Cabe recordar que en los montes destinados a la producción de celulosa y madera solida normalmente se utilizan densidades comprendidas entre los 1000 a 1500 árboles ha^{-1} y turnos de corta de 10 a 15 años, respectivamente (Pou, 2011). Los sistemas de plantación denominados *adensados* o energéticos tienen como principal objetivo maximizar la producción de biomasa en plazos relativamente cortos. En términos generales este tipo de cultivos se caracterizan por dos aspectos: a) se utilizan densidades superiores a los 2000 árboles ha^{-1} y b) los turnos de cosecha están próximos a los 4 o 5 años, dependiendo de la densidad utilizada. Estos cultivos también tienen la particularidad de que deben poseer una alta capacidad de rebrote por lo que se espera que deban tener unas 3 a 5 rotaciones (Seixas, 2008). De acuerdo a este autor un cultivo energético debe cumplir con, al menos, los siguientes criterios:

- Un mínimo de 80% de sobrevivencia de los árboles plantados
- Una productividad anual mayor a 10-12 toneladas de materia seca por hectárea
- Uniformidad en el tamaño de los arboles

Capítulo 1. Introducción general

Comúnmente los términos *adensados* y energéticos se utilizan como sinónimos, pero en sentido estricto el primero se refiere a cultivos con altas densidades de plantación (como las mencionadas). En este trabajo vamos a entender por cultivo energético un tipo de plantación forestal cuyo diseño tiene como objetivo optimizar la producción y cosecha de material vegetal lignocelulósico que va a ser utilizado con diversos fines, en particular la producción de biomasa con fines energéticos. Estos pueden ser térmicos, para calefacción, usos industriales, o producción de electricidad como producto final o en procesos de conversión que proporcionan, además, otros productos distintos a los energéticos (por ejemplo, la producción de combustible líquido o gaseoso). Otro término que se utiliza para este tipo de sistemas es de cultivos forestales de corta rotación (SRFC de su sigla en inglés: *short rotation forestry coppice*). De la superficie total plantada con este tipo de cultivos a nivel mundial, las especies latifoliadas representan un 60%, mientras que la superficie ocupada con especies del género *Eucalyptus* es del orden del 40% (Seixas, 2008),

El marco de plantación y, por tanto, la cantidad de árboles plantados es una de las herramientas de manejo silvicultural que mayor impacto tienen sobre el comportamiento de un monte ya desde las primeras etapas del cultivo (Gonçalves et al., 2004). La densidad de plantación tiene efectos sobre el grado de competencia entre individuos, lo que en definitiva se traduce en efectos sobre la tasa de crecimiento individual, las características de la copa, la sobrevivencia, la fisiología del árbol, la dinámica de nutrientes, el momento de cosecha y la productividad a turno final.

Durante el desarrollo de un cultivo suceden cambios en las curvas de crecimiento, las cuales, en general, son medidas en términos de incremento corriente anual (ICA o CAP) para expresar el cambio en un periodo de un año y de incremento medio anual (IMA o CAM), que indica el crecimiento medio desde la plantación hasta un momento determinado (Figura 3).

Este patrón de crecimiento para los cultivos forestales se caracteriza por una tasa creciente del incremento corriente en las etapas tempranas hasta alcanzar un máximo, a partir del cual ocurre una progresiva disminución hasta alcanzar un valor de casi cero. El IMA tiene un comportamiento similar, pero en etapas posteriores del ciclo del cultivo. El cruce de ambas curvas corresponde al punto de máxima producción física en el mínimo de tiempo y es el momento que determina la etapa de rotación técnica o momento de cosecha (Barrero et al., 2011).

Capítulo 1. Introducción general

El estudio del crecimiento de una plantación, en la mayoría de los casos, ha puesto énfasis en el crecimiento total del rodal y han dejado de lado los cambios que ocurren en la estructura del mismo. Esto ha tenido como resultado distintos tipos de evaluaciones de respuesta frente a diferentes densidades de plantación y esquemas de raleo, los cuales se han centrado en parámetros del crecimiento individual del árbol (por ejemplo, diámetro a la altura del pecho y área basal). La investigación más reciente ha puesto el foco en entender los cambios en los patrones de crecimiento y, en particular, en la reducción del crecimiento que comienza a ocurrir luego de los primeros años de instalado el cultivo (Harris, 2007). Existen varios factores que están asociados a esta disminución en la tasa de crecimiento, los cuales están relacionados a la competencia entre individuos (Binkley et al., 2002), al aérea foliar, la tasa de respiración/actividad fotosintética, y la disponibilidad de agua y nutrientes (Ryan et al., 2008, Stape et al., 2010).

A diferencia de una plantación convencional, en los cultivos de alta densidad hay una alta productividad inicial, como fue mencionado anteriormente, debido a una mayor tasa de ocupación del sitio, lo que provoca que en un plazo muy breve comiencen a ocurrir cambios en el comportamiento individual de los árboles, debido a un incremento de la competencia entre los mismos. Los efectos de la rápida competencia entre árboles (asociada a las altas densidades) determinan una serie de cambios silviculturales, tanto en el crecimiento como en la estructura de los diferentes componentes del árbol y del rodal. Los resultados reportados en la literatura muestran que con altas densidades se obtienen altos niveles de producción por hectárea, árboles con una alta relación altura/diámetro, árboles de menor tamaño y con copas más reducidas, mayores índices de mortalidad y mayor heterogeneidad en el tamaño de los individuos (Oliveira Neto et al., 2010; Dos Santos, 2011; Díaz Bravo et al., 2012; Machado et al., 2012; Rodriguez et al., 2013; Schneider et al., 2015; Soares et al., 2016; Van Gust et al., 2016; Albaugh et al., 2017). También se reportan importantes niveles de extracción de nutrientes contenidos en las ramas, hojas y corteza para el caso de especies de eucaliptos (Poggiani et al., 1984; Foelkel, 2005; Couto et al., 2009; Bentancor, 2017). Esto último, forma parte de los aspectos que dan lugar a polémica con respecto al uso de este tipo de sistemas de producción de biomasa con especies de eucaliptos con altas tasas de crecimiento.

Un aspecto importante a tener en cuenta es que en estos sistemas de producción se cosecha el árbol entero (fuste y copa), lo que determina que la biomasa resultante este formada por todas las fracciones del árbol. El producto obtenido es una mezcla de las distintas fracciones del árbol, compuesta por la madera, la corteza, las ramas y las hojas, lo que resulta en un material heterogéneo desde el punto de vista de su granulometría, contenido de humedad, composición química y, por lo tanto, en sus propiedades tecnológicas (Knapic et al., 2014). La evaluación de este tipo de cultivos, a diferencia de los denominados convencionales (para madera solida o celulosa), requiere de la cuantificación de las distintas fracciones lo que implica medir o estimar por algún método, el peso por separado de cada componente del árbol. Las propiedades tecnológicas de la biomasa dependen en gran medida del proceso al que sea sometida y del tipo de combustible que se quiera obtener.

En términos energéticos los principales puntos a favor de la biomasa proveniente de *Eucalyptus* de acuerdo con Foelkel, (2005) son:

- Homogeneidad de la composición química (holocelulosa, lignina y extractivos)
- Bajo contenido de azufre, cenizas y nitrógeno
- Poder calórico relativamente alto
- Metodologías sobre los procesos de producción, procesamiento y transporte

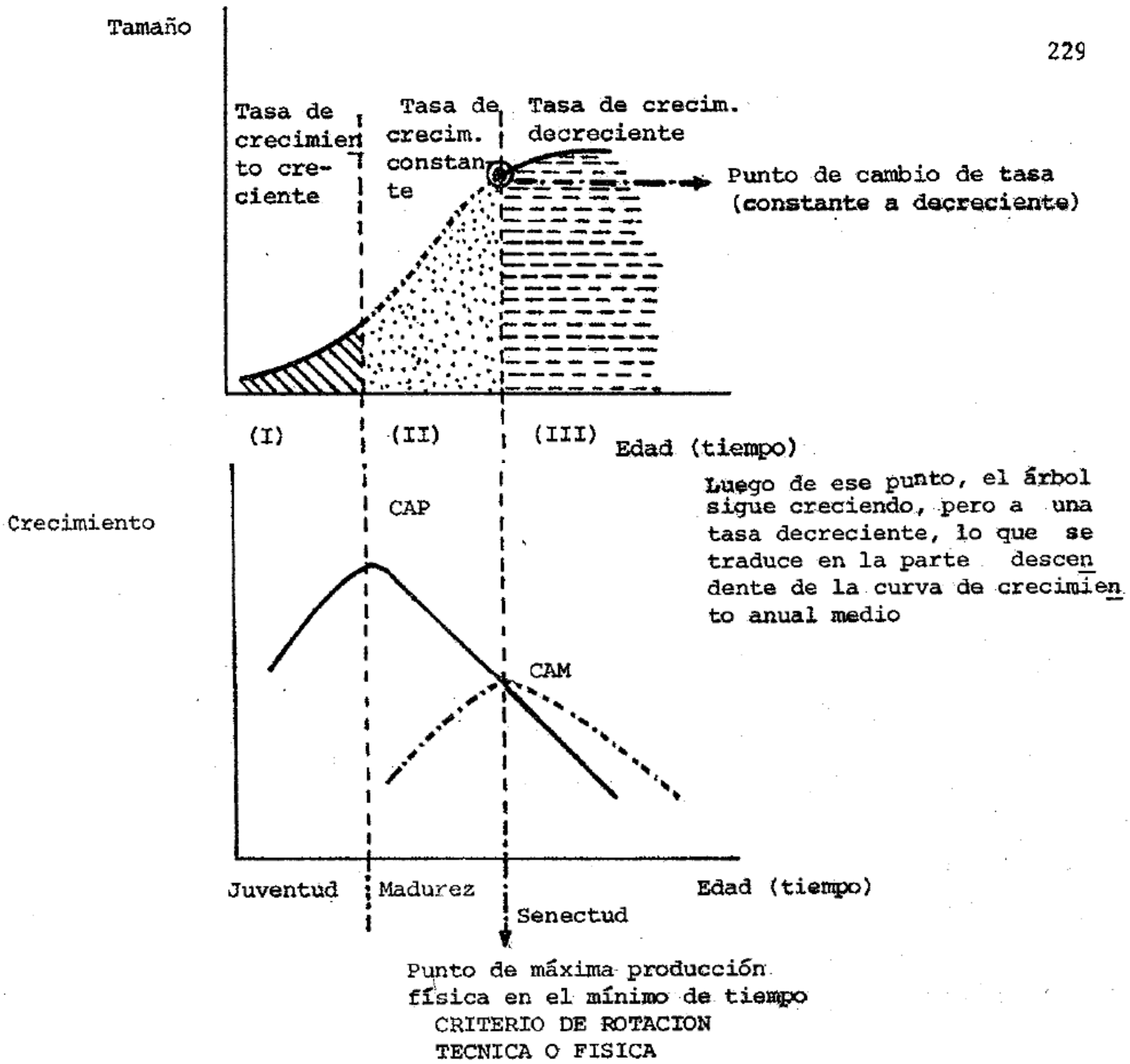


Figura 3. Patrón general de cambios en el CAP e CAM de cultivo forestal a lo largo del tiempo. Fuente: Sorrentino, 1994.

A su vez, la madera de eucalipto posee una elevada adecuación para la combustión, con bajo nivel de emisiones (Scholz y Ellerbrock, 2002) y baja tendencia a la sinterización, lo que repercute en el buen funcionamiento y bajo mantenimiento de los equipos. También se destaca el balance energético muy positivo frente a otros cultivos utilizados con este mismo propósito, en torno a 13 unidades energéticas generada por unidad de energía consumida (Balsari y Airoldi, 2002), llegando incluso a citarse balances que alcanzan valores de 20. De acuerdo a Zanetti, (2008), existen expectativas de que para el etanol celulósico el balance energético alcance una relación de 1:36.

2.2. Aplicación a Uruguay

En función de la experiencia obtenida en Uruguay con varias especies de eucaliptos es posible afirmar que son las de mayor potencial desde el punto de vista de la producción de biomasa y de las características energéticas (densidad de la madera y poder calórico) (Eloy et al., 2015). Esto determina que, en principio, estén inidentificadas las especies que podrían tener el mejor comportamiento en las diferentes zonas forestales del país.

En términos generales, es conocido el efecto que tienen algunos espaciamientos sobre el crecimiento de los eucaliptos en zonas agroecológicas similares a las de Uruguay (Stape et al., 2010). Las especies que mayor potencial muestran para ser usadas en cultivos de corta rotación son *E. grandis, E. dunnii, E. benthamii* y *E. maidenii*, pero es importante tener en cuenta las diferencias en los niveles de productividad que muestran los distintos materiales genéticos que componen estos géneros, y su respuesta en los distintos grupos de suelos (Balmelli y Resquin, 2006). Estas son especies que cuentan, además, con una base genética amplia, ciclos de mejora breves, facilidad para la multiplicación vegetativa, capacidad de rebrotar tras la corta, etc.; características, todas ellas, que las adecuan para esta finalidad productiva. En ese sentido, varios autores reportan niveles de productividad del orden de 15 a 35 toneladas de materia seca por hectárea y por año en primera rotación (Bernardo et al., 1998; Leite et al., 1997; Sims et al., 1999; Leles et al., 2001; Sims et al., 2001; Goulart et al., 2003; Goncalves et al., 2004; Foelkel, 2015).

En Uruguay se han instalado varios ensayos de cultivos energéticos, en donde se pretende estimar la producción de biomasa de diferentes especies de eucaliptos, según distintos diseños de plantación. Resultados preliminares indican que en la zona norte y litoral podrían obtener valores del orden de 25 toneladas por hectárea y año con *E. benthamii* y *E. grandis,* en densidades de 5000 árboles por hectárea (Resquin, 2015). Sin embargo, algunos autores señalan que los mayores espaciamientos tienen algunas ventajas: se obtiene mayor retorno del capital invertido, se facilitan las operaciones mecánicas después de la plantación, y hay una tasa menor de mortalidad y de árboles dominados (Stape, 2006; Hakamada, 2012). De acuerdo a este último autor, la densidad de plantación más rentable para la producción de biomasa es muy similar que para la de celulosa y se encuentra entre 900 y 1600 árboles por hectárea con un turno de 6 a 8 años. Este tipo de análisis tienen en cuenta los altos costos de plantación y de cosecha, asociados a las mayores densidades de plantación.

Al mismo tiempo, existen una serie de interrogantes que deberían ser respondidas y que tienen que ver con algunos aspectos de la sustentabilidad de este tipo de cultivos en particular para los materiales genéticos de alta productividad. Esto es especialmente importante en suelos de bajo aporte de nutrientes o en situaciones de déficit hídrico (Stape, 2006; Hakamada, 2012; Scatolini, 2012; de Paula Lima, 2012). Otro aspecto a tener en cuenta es que el marco de plantación de este tipo de cultivos produce una alta densificación en la línea de plantación, lo cual se contrapone con una distribución uniforme de las plantas que da lugar a un uso menos eficiente del agua y de los nutrientes. En relación al balance de nutrientes, además de una mayor extracción por utilizar toda la biomasa aérea (madera, corteza y copa) se producen cosechas en periodos relativamente cortos (3 a 5 años). Varios estudios con especies de eucaliptos muestran que la cantidad de nutrientes contenidos en la madera juvenil es sustancialmente mayor que en edades más avanzadas, a pesar de que los arboles tienen tamaños de copa reducidos en las primeras etapas del crecimiento (Poggiani, 1980; Poggiani et al., 1983 y 1984; Bentancor, 2017). Esto implicará un aumento sustancial en la necesidad del aporte de nutrientes para mantener la productividad en el largo plazo. Estos autores afirman, por tanto, que desde el punto de vista de la ¨economía de los nutrientes¨ las rotaciones más largas son más convenientes que los ciclos cortos, debido a que en estas últimas ocurre un mayor reciclaje de nutrientes lo cual determina que las masas forestales sean más estables en el largo plazo. En tal sentido, se mencionan algunas alternativas para mitigar estos efectos, como es el uso de materiales genéticos que posean alta eficiencia de producción de biomasa con bajos niveles de nutrientes (Poggiani, 1980); o dejar en campo algunas fracciones como, por ejemplo, la corteza por su alto contenido de Ca y K (Müller, 2005; Andrade et al., 2011). A esos efectos, hay que sumarle los posibles efectos de compactación por el transito sucesivo de equipos de cosecha debido a los cortos turnos de rotación (Scatolini, 2012).

3. Justificación e hipótesis

Resulta evidente la importancia de investigar sobre los aspectos productivos y ambientales de la producción de biomasa para energía a partir de especies de eucaliptos plantados a alta densidad en Uruguay. Este tipo de cultivos pueden llegar a ser una alternativa para la producción de biomasa atendiendo a las necesidades crecientes del país en cuanto a la diversificación de la matriz de generación de energía y, al mismo tiempo, la sustitución de la importación de combustibles de origen fósil. En ese sentido, surge la necesidad de evaluar la viabilidad silvicultural de este tipo de plantaciones, teniendo en cuenta algunos aspectos relevantes como la producción que es posible obtener, así como los costos ambientales en términos de la extracción de nutrientes.

Es conocido el hecho que los diseños (esquemas) silviculturales orientados a la producción de biomasa son sustancialmente diferente a las plantaciones convencionales para la producción de madera solida o celulosa, en el sentido de que los primeros utilizan densidades de plantación muy superiores y turnos de cosecha relativamente más cortos que las plantaciones forestales convencionales. Sobre este tipo de plantaciones energéticas prácticamente no se ha generado información en Uruguay. Actualmente existen algunos ensayos que se están evaluando, pero aún están en las primeras etapas del cultivo. En los últimos años; sin embargo, se ha generado información muy valiosa sobre el potencial energético de cultivos agrícolas, como, por ejemplo, el pasto elefante, *switchgrass,* sorgo dulce, y caña de castilla, entre otros. Es necesario, por lo tanto, ampliar este tipo de investigaciones a los cultivos forestales, ya que los mismos han mostrado un alto potencial de producción en las condiciones del país.

4. Objetivo general

El objetivo general de esta tesis es evaluar el potencial de producción de cultivos energéticos lignocelulósicos con especies de *Eucalyptus* en función de diferentes diseños de plantación en suelos de la zona norte y litoral de Uruguay.

Objetivos específicos

- Predecir el hábitat futuro de *E. grandis* Hill ex Maiden y *E. dunnii* Maiden en los suelos de aptitud forestal de Uruguay bajo diferentes escenarios climáticos futuros.
- Evaluar la sobrevivencia y el potencial de producción de cultivos energéticos de *E. benthamii, E. dunnii* y *E. grandis,* en función de diferentes diseños de plantación, en suelos de aptitud forestal de la zona norte y litoral de Uruguay durante un periodo de 57 meses.
- Determinar la combinación especies/densidad de plantación que maximiza la producción de biomasa del fuste por hectárea durante un periodo de 76 meses.
- Cuantificar el rendimiento energético de cada una de las especies ensayadas en función de la densidad de plantación a lo largo del ciclo del cultivo.

- Cuantificar la extracción de macronutrientes en las fracciones de biomasa del árbol y su distribución en las diferentes fracciones aéreas del árbol a la edad de 76 meses.

En función de los objetivos planteados la memoria se ha estructurado en 5 capítulos, los cuales se describen a continuación:

En el capítulo 1 se analizan los parámetros del sitio que mejor explican el crecimiento de *E. dunnii* y *E. grandis* en los distintos suelos forestales del país. Este análisis permite identificar modelos de predicción de hábitat con un alto grado de precisión y al mismo tiempo visualizar la distribución de ambas especies en función de distintos escenarios de cambio climático. *E. benthamii* no fue incluida en este análisis debido a que no se cuenta con suficiente información de datos de inventario por ser una especie de uso en los últimos años.

En el capítulo 2, se evalúa la sobrevivencia y las curvas de crecimiento de las especies y densidades de plantación en los primeros 5 años de crecimiento en dos suelos representativos de las zonas litoral y norte del país. Con los parámetros obtenidos es posible ajustar modelos de estimación del crecimiento individual y visualizar los efectos de competencia entre individuos en los primeros años del crecimiento. La evolución de las curvas de crecimiento permite identificar los turnos de cosecha y su relación con los diferentes espaciamientos evaluados.

En el capítulo 3 se evalúa la evolución de la densidad de la madera y del peso del fuste individual y por hectárea para cada especie y densidad de plantación en los primeros 76 meses de crecimiento. También se ajustaron modelos de estimación del peso individual en función de parámetros de rápida obtención en inventario de campo. La evolución de estos parámetros permite visualizar las diferencias en el comportamiento en el peso con respecto al volumen en lo largo del ciclo del cultivo.

En el capítulo 4 se estudian los parámetros relacionados con el contenido energético de la madera considerando además el efecto de la edad y del sitio. La evolución del poder calórico y la densidad de la madera condicionan la densidad energética y estos junto con la producción de biomasa determinan los rendimientos de energía por hectárea y por año de las biomasas evaluadas. Los resultados del efecto de la edad y del sitio muestra un comportamiento diferente en las variables analizadas explicadas por las diferentes tasas de mortalidad de ambos experimentos.

En el capítulo 5 se analizan las diferentes fracciones de biomasa analizadas desde el punto de vista del peso por hectárea y del contenido de macronutrientes a los efectos de contemplar la sustentabilidad de estos sistemas de producción en el mediano y largo plazo. A su vez se analiza las alternativas de cosechar el árbol entero vs solo el fuste en relación al balance de nutrientes y su repercusión sobre la disponibilidad de nutrientes de ambos tipos de suelos.

En el capítulo 6 se presenta la discusión general de los resultados obtenidos y las implicancias desde el punto de vista práctico al momento de implementar sistemas de producción de biomasa con especies de eucaliptos a altas densidades de plantación.

En el capítulo 7, se exponen las principales conclusiones obtenidas y perspectivas de investigación a futuro sobre los cultivos energéticos.

5. Referencias

Achat, D. L.; C. Deleuze; G. Landmann; N. Pousse; J. Ranger; L. Augusto. 2015. Quantifying Consequences of Removing Harvesting Residues on Forest Soils and Tree Growth - A Meta-Analysis. Elsevier B.V. Forest Ecology and Management 348: 124–41.

AEBIOM. 2008. A Pellet Road Map for Europe. European Biomass Association. https://www.canadianbiomassmagazine.ca/images/stories/pellet_roadmap_final.pdf

Albaugh. T.J.; R.A. Rubilar; C.A. Maier; E.A. Acuña; R.L. Cook. 2017. Biomass and nutrient mass of Acacia dealbata and Eucalyptus globulus bioenergy plantations. Biomass and Bioenergy 9:162-171.

Andrade, G. d. C.; I. A.. Bognola; A. F. J. Bellote; L. Franciscon; M. J. Waterloo; L. A. Bruijnzeel. 2011. Site Evaluation and Productivity of a 3-Year Old Stand of *Eucalyptus urograndis* in São Paulo, Brazil. Pesquisa Florestal Brasileira 31 (68): 331–46.

Balmelli, G.; F. Resquin. 2002. Evaluación Del Crecimiento de Especies de Eucalyptus En Diferentes Zonas de Prioridad Forestal. Serie Aftercare Forestal INIA - JICA, 14.

Balmelli, G.; F. Resquin; I. Trujillo. 2001.Evaluación de Fuentes de Semilla de Las Principales Especies de Eucalyptus Ln: Seminario de Actualización En Tecnologías Forestales Para Areniscas de Tacuarembó y Rivera. Serie Técnica INIA 123.

Balmelli, G.; F. Resquin. 2006a. Productividad de Diferentes Especies de Eucalyptus Sobre Areniscas de Tacuarembó-Rivera.” Serie Técnica 159. INIA Tacuarembó 159: 305–12.

Balmelli, G.; F. Resquin. 2006b. Productividad de Diferentes Especies de Eucalyptus Sobre Areniscas de Tacuarembó-Rivera. 30 Años de Investigación En Suelos de Areniscas INIA Tacuarembó. Serie Técnica. Montevideo. UY.

Balsari, P.; G. Airoldi. 2002. Valutazione Energetica Ed Economica Di Una Coltivazione

Di Pioppo per La Produzione Di Biomasa. Rivista Di Agronomia 26: 163–69.

Barrero, H.; O. Peraza; D. Álvarez; M. Guera. 2011. Determinación Del Turno de Corta Para Pinus Caribaea Var. Caribaea En La Empresa Forestal Integral Macurije. Floresta e Ambiente 18 (1): 109–15.

Bentancor, L. 2017. Extracción de Nutrientes Por Eucalyptus Dunnii Maiden de 4 Años Con Destino a La Producción de Biomasa Para Energía y Celulosa. Tesis de Maestria. Universidad de la República-Facultad de Agronmía. Montevideo, Uruguay. 114 p.

Bernardo, A.L.; M.G. F. Reis; G. Reis; R.B. Harrison; D. J. Firme. 1998. Effect of Spacing on Growth and Biomass Distribution in *Eucalyptus camaldulensis, E. pellita* and *E. urophylla* Plantations in Southeastern Brazil. Forest Ecology and Management 104: 1–13.

Binkley, D.; J.L. Stape; M.G. Ryan; H. R. Barnard; J. Fownes. 2002. Age-Related Decline in Forest Ecosystem Growth : An Individual- Tree , Stand-Structure Hypothesis. Ecosystems. 5: 58–67.

Carrillo, L. 2004. Energía de Biomasa. Fotosíntesis. Biomasa. Conversión Por Microorganismos. Biogas. Etanol. Biodiesel. Edición de. Jujuy-Argentina. 83 p.

Couto, L.; C.P. Abrahão; A.C.O. Carneiro; G.S. Nogueira; H.G. Leite; L.C. Couto; M.D. Müller; R.C. Santana. 2009. Efeito Do Espaçamento Sobre a Produção de Biomassa Em Florestas Energéticas de Eucalipto. Rede Nacional De Biomassa Para Energia. http://www.cnpf.embrapa.br/pfb/index.php/pfb/article/view/273/232.

de Paula Lima, W. 2012. O Assunto Requer Cuidado Alias Muito Cuidado! Revista Opiniões. http://revistaonline.revistaopinioes.com.br/revistas/flo/71/#page/38.

Díaz Bravo, S.; M. Espinosa; L. Valenzuela; J. Cancino; J.P. Lasserre. 2012. Efecto del raleo en el crecimiento y algunas propiedades de la madera de Eucalyptus nitens en una plantación de 15 años. Maderas. Ciencia y tecnología, 14(3): 373-388.

Eloy, E.; B. O. Caron; D.A. da Silva; V.Q. Souza; R.. Trevisan; Al. Behling; E. F. Elli. 2015. Produtividade Energética de Espécies Florestais Em Plantios de Curta Rotação. Ciência Rural 45 (8): 1424–31.

Estrada, C. A.; A. Z. Meneses. 2004. Gasificación de Biomasa Para Producción de Combustibles de Bajo Poder Calorífico y Su Utilización En Generación de Potencia y Calor. Scientia et Technica 2 (25).

Foelkel, C. 2005. Minerais e Nutrientes Das Árvores Dos Eucaliptos: Aspectos Ambientais, Fisiológicos, Silviculturais e Industriais Acerca Dos Elementos InorgâNicos Presentes Nas Árvores. Eucalyptos Online Book & Newsletter, 133.

Foelkel, C. 2015. Qualidade Da Biomassa Florestal Do Eucalipto Para Fins Energéticos.Eucalyptos Newsletter No 49.

Gonçalves, J.L. de M.; J.L. Stape; J.-P. Laclau; P.Smethurst; J.L. Gava. 2004. Silvicultural Effects on the Productivity and Wood Quality of Eucalypt Plantations. Forest Ecology and Management 193 (1–2): 45–61.

Goulart, M.; C. R. H. Haselein; J. M. Hoppe; J. A. Farias; D. T. Pauleski. 2003. Massa Específica Básica e Massa Seca de Madeira de Eucalyptus Grandis Sob o Efeito Do Espaçamento de Plantio e Da Posição Axial No Tronco. Ciência Florestal 13 (2): 167–75.

Hakamada, R. 2012. Inovação Tecnológica Há Mais de Um Século. Revista Opiniões. http://revistaonline.revistaopinioes.com.br/revistas/flo/71/#page/19.

Harris, F 2007, The effect of competition on stand, tree, and wood growth and structure in subtropical Eucalyptus grandis plantations', PhD thesis, Southern Cross University, Lismore, NSW. 193 p.

Hiegl, W.; R. Janssen. 2009. Development and Promotion of a Transparent European Pellets Market. Creation of an European Real-Time Pellets Atlas. www.pelletsatlas.info.

IICA-PROCISUR; INTA/Argentina; EMBRAPA/Brazil; INIA/Chile; MAG/Paraguay; INIA/Uruguay. 2013. Lignocellulosic Feedstock Catalogue. Final Report. Montevideo, Uruguay. 135 p.

Jesus, H.D.; Eufrade Junior; A. W. Ballarin. 2013. Influência Do Espaçamento Na Densidade Básica Da Madeira Em Sistemas Florestais De Curta Rotação. In 8° Congresso internacional de bioenergia São Paulo – SP – 05 A 07 de Novembro, 5–9.

Knapic, S.; M. Pirralho; J. L. Louzada; H. Pereira. 2014.Early Assessment of Density Features for 19 Eucalyptus Species Using X-Ray Microdensitometry in a Perspective of Potential Biomass Production. Wood Sci Technol 48 (1): 37–49.

Leite, F.P.; N.F. de Barros; R.F. de Novais; L.M.A. Sans; A.S. Fabres. 1997. Crescimento de *Eucalyptus grandis* Em Diferentes Densidades Populacionais. Árvore 21 (3): 313–21.

Leles, P.S.D.S.; G.G.D. Reis; M.D.G.F. Reis; E.J.D. Morais. 2001. Crescimento, Produção e Alocação de Matéria Seca de *Eucalyptus camaldulensis* e *E . pellita* Sob Diferentes Espaçamentos Na Região de Cerrado, MG. Scientia Forestalis 59: 77–87.

Machado, F.De C.; S. Philipe; S. Guerra; N. Ceragioli; G. Oguri. 2012. Influência do espaçamento na produtividade e alocação de biomassa em um plantio de *Eucalyptus* *grandis*. In Congresso Internacional de Bioenergia, 1–6.

MGAP-DGF. 2013. "N." http://www.mgap.gub.uy/portal/page.aspx?2,dgf,dgf-recurso-forestal,O,es,0,.

MGAP. 2016. "No Titl." http://www.mgap.gub.uy/portal/page.aspx?2,dgf,dgf-legislacion,O,es,0,.

MIEM-DNI. 2008. Cadenas Productivas En Energías Renovables Biomasa, Agrocombustibles, Eólica y Solar Térmica Fase I - Análisis de Cadenas y Diagnóstico Preliminar.

Müller. M.D. 2005. Produção de madeira para geração de energia elétrica numa plantação clonal de eucalipto em Itamarandiba, MG. Tese de Doutorado. Universidade Federal de Viçosa. http://www.bibliotecaflorestal.ufv.br/bitstream/handle/123456789/31/129121_c.pdf?sequence=2&isAllowed=y.

Neto, S.N.d.O.; G.G. Reis; M.d.G.F. Reis; H.G. Leite; J. C. L. Neves. 2010. Crescimento e Distribuição Diamétrica de *Eucalyptus camaldulensis* Em Diferentes Espaçamentos e Níveis de Adubação Na Região de Cerrado de Minas Gerais. Floresta 40 (4): 755–62.

Oliveira Neto, S.N.; G.G. dos Reis; M.G.F. Reis; H.G. Leite; J.C.L. Neves. 2010. Crescimento e distribuição diamétrica de Eucalyptus camaldulensis em diferentes espaçamentos e níveis de adubação na região de Cerrado de Minas Gerais. Floresta, 40 (4): 755-762.

Poggiani, F. 1980. Florestas Para Fins Energéticos e Ciclagem de Nutrientes. IPEF - Série Técnica 1 (2): 1–11.

Poggiani, F.; H.T. Couto; W.S. Suiter Filho. 1983. Biomass and Nutrient Estimates in Short Rotation Intensively Cultured Plantation of *Eucalyptus grandis*. Revista Do Ipef 23 (23): 29–36. http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Biomass+and+Nutrient+Estimates+in+Short+Rotation+Intensively+Cultured+Plantation+of+Eucalyptus+grandis#0.

Poggiani, F.; S. Zen; F. S. Mendes; F. Spina-França. 1984. Ciclagem e Exportação de Nutrientes Em Florestas Para Fins Energéticos. Ipef 27: 17–30.

PROBIO. 2015. Mejoramiento En La Calidad de La Información Vinculada Con La Utilización de La Biomasa Forestal. Montevideo, Uruguay. 157 p.

Pou, R. 2011.Caracterización de la forestación en Uruguay. Aspectos técnicos, empresariales del desarrollo forestal a mayo del año 2011. Rosario Pou & Asociados.

14 p. Available at: http://www.uruguayforestal.com/informes/Forestacion%20en%20Uruguay-2011.pdf

Resquin, F. 2015. Producción de Biomasa Con Especies de Eucalipto. http://www.inia.uy/estaciones-experimentales/direcciones-regionales/inia-tacuarembó/jornada-de-biomasa-forestal-2015.

Resquin, F.; G. Balmelli. 2008. Desarrollo de Una Raza Local de *E. teeticornis* de Buen Potencial Productivo Para Las Condiciones Del Uruguay: Inicio de Un Plan de Mejora Genética. INIA Serie Actividades de Difusión 557.

Resquin, F.; G. Balmelli. 2009a. Evaluación de Varias Fuentes de Semilla de *Eucalyptus dunnii* Al Noveno Año. INIA Serie Actividades de Difusión 584.

Resquin, F.; G. Balmelli. 2009b. Mejora Genética En *Eucalyptus grandis*: Productividad y Calidad de Madera. INIA Serie Actividades de Difusión 584.

Rodríguez, A.; J. Cancino; E. Acuña; R. Rubilar, E. Muñoz. 2013. Evaluación del crecimiento de plantaciones dendroenergéticas de *Eucalyptus globulus*, según densidad de plantación y turno de rotacion en suelos contrastantes de la región del Biobío, Chile. Cienc. Investig. For. INFOR Chile, 19 (1); 7-18.

Ryan, M. G.; D. Binkley; J. L. Stape. 2008. Why Don ' t Our Stands Grow Even Faster ? Control of Production and Carbon Cycling in Eucalypt Plantations Why Don ' t Our Stands Grow Even Faster ? Control of Production and Carbon Cycling in Eucalypt Planta. Southern Forests: A Journal of Forest Science 70 (2): 99–104.

San Miguel, G.; B. Corona; D. Ruiz: D. Landholm; R. Laina; E. Tolosana; H. Sixto; I. Cañellas. 2015. Environmental, energy and economic analysis of a biomass supply chain based on a poplar short rotation coppice in Spain. Journal of Cleaner Production, 94: 93–101.

Santos, M D. 2011. Efeito Do Espaçamento de Plantio Na Biomassa Do Fuste de Um Clone Híbrido Interespecífico de *Eucalyptus grandis* e *Eucalyptus urophylla*. Dissertação de Mestrado. Faculdade de Ciências Agronômicas, Universidade Estadual Paulista Botucatu, Brazil. 152 p.

Schneider, P.R.; C.A. Guimarães Finger; P.S. Pigatto Schneider; F.D. Fleig; T.A. da Cunha. 2015. Influência do espaçamento no autodesbaste de povoamento monoclonal de *Eucalyptus saligna* Smith. Ciência Florestal, Santa Maria, 25 (1): 119-126.

Scatolini, F M. 2012. Floresta Adensada: Alguns Aspectos a Considerar. Revista Opiniones. http://revistaonline.revistaopinioes.com.br/revistas/flo/71/#page/25.

Scholz, Vo.; R. Ellerbrock. 2002. The Growth Productivity, and Environmental Impact of the Cultivation of Energy Crops on Sandy Soil in Germany. Biomass and Bioenergy 23 (2): 81–92.

Seixas, F. 2008. Harvesting and Use of Forestry Biomass for Energy Production in the USA. Auburn, Alabama, USA. Southern Research Station USDA Forest Service. 118 p.

Sims, R. E.H.; T. G. Maiava; B. T. Bullock. 2001. Short Rotation Coppice Tree Species Selection for Woody Biomass Production in New Zealand. Biomass and Bioenergy 20 (5): 329–35.

Sims, R.E. H.; A. Hastings; B. Schlamadinger; G. Taylor; P. Smith. 2006. Energy Crops : Current Status and Future Prospects. Global Change Biology 12: 2054–76.

Sims, R.E.H.; Ki. Senelwa; T. Maiava; B.T. Bullock. 1999. *Eucalyptus* Species for Biomass Energy in New Zealand—I: Growth Screening Trials at First Harvest. Biomass and Bioenergy 16 (3): 199–205.

Soares, A.V.; H.G. Leite; A.L. Souza; S.R. Silva; H.M. Lourenço; D.I. Forrester. 2016. Increasing stand structural heterogeneity reduces productivity in Brazilian Eucalyptus monoclonal stands. Forest Ecology and Management 373: 26–32

Sorrentino, A. 1994. Manual teórico - práctico : técnicas e instrumentos de medición forestal. Montevideo: Facultad de Agronomía. 2 v. 312 p.

Stape, J. L.; D. Binkley; M.G. Ryan; S. Fonseca; R.A. Loos, E. N. Takahashi; C. R. Silva; S.R. Silva; R. Hakamada; J.M.A. Ferreira; A.M.N. Lima; J.L. Gava, F.P. Leita; H.B. Andrade; J.M. Alves; G.G.C Silva; M.R. Azevedo. 2010. The Brazil Eucalyptus Potential Productivity Project: Influence of Water, Nutrients and Stand Uniformity on Wood Production. Forest Ecology and Management 259 (9): 1684–1694.

Stape, J.L. 2006. Espaçamento de Plantio. Conceitos e Aplicações. Piracicaba, Brazil. http://www.tume.esalq.usp.br/simp/arquivos/espacamento.pdf.

Sunde, K.; A. Brekke; B. Solberg. 2011. Environmental Impacts and Costs of Woody Biomass-to-Liquid (BTL) Production and Use - A Review. Forest Policy and Economics. Elsevier B.V. 13 (8): 591–602.

Swain, P. K.; L. M. Das; S. N. Naik. 2011. Biomass to Liquid: A Prospective Challenge to Research and Development in 21st Century. Renewable and Sustainable Energy. Elsevier Ltd. Reviews 15 (9): 4917–33.

Tuset, R.; F. Durán; C. Mantero; G. Baillod; A. Aber; S. Böthig; A. Ono. 2008. Manual de Maderas Comerciales, Equipos y Procesos de Utilización; Volumen 2. Edited by

Hemisferio Sur. Montevideo, Uruguay.

Van Gunst, K.J.; P.J. Weisberg; J. Yang; Y. Fan. 2016. Do denser forests have greater risk of tree mortality: A remote sensing analysis of density-dependent forest mortality. Ecology 96(11); 2855-2861

Zanetti, E.A. 2008. Balanço de Carbono. Revista Opiniões. http://revistaonline.revistaopinioes.com.br/revistas/flo/34/#page/32. .

Zsuffa, L.; W. A. Kenney; R. L. Gambles. 1992. Wood Feedstock Qualities for Energy Conversion and the Potential for Their Biological Improvement. Biomass and Bioenergy 2 (1–6): 55–69.

Chapter 2. Modelling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

"…Mentira, mentira, yo quise decirle,
las horas que pasan ya no vuelven más.
Y así mi cariño al tuyo enlazado
es sólo una mueca del viejo pasado
que ya no se puede resucitar.
Callé mi amargura y tuve piedad.
Sus ojos azules, muy grandes se abrieron,
mi pena inaudita pronto comprendió
y con una mueca de mujer vencida
me dijo: "Es la vida". Y no la vi más.

Volvió esa noche, nunca la olvido,
con la mirada triste y sin luz.
Y tuve miedo de aquel espectro
que fue locura en mi juventud.
Se fue en silencio, sin un reproche,
busqué un espejo y me quise mirar.
Había en mi frente tantos inviernos
que también ella tuvo piedad."

Alfredo Le Pera, 1935

Chapter 2. Modeling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

1. Introduction

Eucalypt plantations have a long history in Uruguay, the first introductions from Australia being recorded at the beginning of the 1850s (Brussa, 1994). Commercially, Eucalyptus trees have been planted in different areas of the country since the 1950s, although in the last 25 years the planting rate has increased to 20,000 hectares per year, and today trees of this genus occupy 726,000 ha (MGAP-DGF, 2018). There is still a large area of soils prioritized for forestry by the government that could be planted, according to the current legislation. This tendency could continue, although the increasing restrictions imposed on the sector (e.g. environmental restrictions and limitations of Department governments) may cause a decrease in the rate of planting.

Even though different ecoregions of Uruguay offer a variety of conditions for forest ecosystems (Brazeiro et al., 2012), many of the planted species have enough plasticity to adapt to a wide range of environmental conditions. For this reason, several eucalypt species of commercial interest have been used to evaluate the possible impact of climate change in some regions and, at the same time, their ability to adapt to it (Booth, 2016). According to some authors (Prior and Bowman, 2014; Booth et al., 2015), Eucalyptus species are adequate for studies of climate change adaptability because trees of this genus are planted in a broad range of environments. This indicates that, in general, eucalypts are relatively less affected by climate changes (Hughes et al., 2013). Nevertheless, Anjos and Toledo (2018) mentioned that forest ecosystems are more vulnerable to climate stress than grassland ecosystems, given that the former are less resilient. Worldwide, eucalypt plantations are dominated by nine species, including *Eucalyptus grandis* and *E. dunnii* (Booth, 2013). These are two of the most planted tree species in Uruguay, showing great adaptation to soils with low fertility and moderate dryness (Buckeridge, 2010). Also, according to Booth (2013), eucalypt species have a high ability to adapt to climate changes due to their relatively short harvest cycles, making it faster to identify optimal genotypes for different conditions (Buckeridge, 2010). For the Campos region (Southern Brazil, Uruguay, and the centre of Argentina), the evolution of climate has been studied for the last 70 years: an increase in spring-summer precipitation, a decrease in maximum temperature in summer, an increase in the lowest annual temperature, and a shortening of the frost period have occurred (Giménez et al., 2009; Zaninelli et al., 2018). These authors' predictions indicate that there will be a subtle increase in summer precipitation and an increase in the highest and lowest temperatures throughout the year. These types of changes do not imply a relocation of the species because the eventual climate alterations do not necessarily represent a limit to their distribution (Hughes et al., 2013). Predictions for 2080 for the South of Brazil (among other areas) indicate a decrease in the area planted with *E. grandis* following a reduction of the optimal area for this species, explained by an alteration in the precipitation regime (Garcia et al., 2014) along with an increment in evapotranspiration (Pereira et al., 2018). On the other hand, the expected increment in the CO_2 levels in the atmosphere in the coming decades, with respect to the current one (IPCC, 2013), will also affect the physiological activities and plant growth. According to several studies, this increase will induce acceleration in the growth rates of some species because of a higher photosynthetic rate, provided there is an absence of limiting factors (Rogers et al., 1983; Fearnside, 1999; Kamosky et al., 2005). In general, the physiological response to climate change is known at the individual plant level but not at the plantation level or a similar scale (Chmura et al., 2011), especially with respect to the interaction of multiple factors. Moreover, there is evidence that an increment in the temperature would impact negatively on trees with higher "maintenance costs" (high physiological activity), such as trees with the greatest growth, compared to smaller trees (Larjavaara et al., 2012; Prior and Bowman, 2014).

One way to understand the eventual effect of climate change on the behavior (distribution and/or productivity) of a species is through predictive models of species distribution (Hamman and Wang, 2006). Species distribution models (SDM) are currently used to describe the habitats of species and to make predictions, considering different variables of location and climate (Araújo et al., 2019). These are numeric tools that combine observations of the presence or abundance of the species with environmental estimates

(Elith and Leathwick, 2009). They are useful for predicting, for example, the response of a species to the eventual climate changes that are foreseen in the next few decades. These models offer two types of estimations: i) the probability of occurrence of a species in particular environmental conditions, and ii) the potential of a certain habitat for a particular species (Elith and Franklin, 2013). They use two types of information: primary and secondary. The former consists of the observed characteristics of the studied species, which are generally obtained from databases. The latter comprises information about the environment - climate, topography, aspect, soil, etc. - in the area where the species occurrence is under study (Elith and Franklin, 2013). The first group of variables is usually named as response or dependents, and the second one as independent or environmental indicators (Mateo et al., 2011). According to these authors, the modeling techniques usually employed depend basically on the type of variable to be predicted: dichotomic or continuous. Some algorithms used are based on presence-absence records, like the Generalized Linear Models (GLM), Generalized Additive Models (GAM), and Artificial Neural Networks (ANN); others, such as Bioclim and MaxEnt, consider only the presence (Pliscoff et al., 2011). These algorithms try to identify the environmental conditions that have the deepest association with a species' occurrence. The data used for modeling are stored in a Geographical Information System, in vector or raster format, the latter being the most frequent for environmental variables (Pearson, 2010). One of the inconveniences that arise when applying SDM is that there are a great number of available alternatives, which, in some cases, provide different results; this complicates the choice of the best option for each case (Thuiller et al., 2009). According to these authors, this kind of situation happens when the priority is to predict the distribution of a species as a function of different scenarios of climate change. Another disadvantage may appear when many predictive environmental variables are used, producing an over-adjustment (Breiner et al., 2015). Over-adjustments frequently reduce the applicability of the models to a new set of data (Merow et al., 2014). One way to overcome this problem is by using ensemble methods (or ensemble techniques), to obtain ensemble models with greater precision than the individual counterparts. An example of these techniques is the biomod2 R package (Thuiller et al., 2019), which contains the four most used modeling tools for species' prediction. This model uses a reduced number of predictive variables, compared with simple models, and has been applied to project the distribution of species in different climate change scenarios (Becerra-López et al., 2016).

In this work, we used an ensemble approach (biomod2) (Thuiller et al., 2019) to describe the current and future habitat of *E. grandis* and *E. dunnii* in Uruguay, as a basis to study potential changes in the optimal plantation areas for both species, under different climate scenarios. Description of the potential current and future habitat allows selection of the areas with greater value for commercial plantations - which can assist afforestation plans, including the selection of appropriate genetic stock materials. In this sense, this work is a preliminary step in the development of silvicultural alternatives for short-term plantations intended for biomass production with eucalypt species in Uruguay. For this purpose, five environmental variables were selected, considering their predictive values, and assigned to the selected climate changes to calculate the foreseen future values of the bioclimatic variables used in the species distribution modeling.

Our hypothesis was that the climate change that is forecast for Uruguay and its surrounding region will have some effect on the area planted with eucalypts and/or species productivity. The general objective of this work was to predict the current and future potential habitat of *E. grandis* and *E. dunnii* in soils prioritized for forestry in Uruguay, under different future climate change scenarios. The specific objectives were: i) to identify the environmental variables that show the greatest association with the probability of occurrence of both species, ii) to adjust a prediction model of current and future habitat for the studied species, iii) to identify the regions with the greatest potential for the growth of these species. The results will be important for the selection of future plantation sites and the eucalyptus species to be planted

2. Materials and Methods

2.1 Study area

The forest priority soils cover areas defined as "forest" according to the current legislation. They comprise those territories deemed inappropriate - because of the type of soil, suitability, climate, or location - for other types of exploitation and those classified as such by the relevant authority, as a function of their suitability or for reasons of public use (Califra and Durán, 2010) (Figure 1).

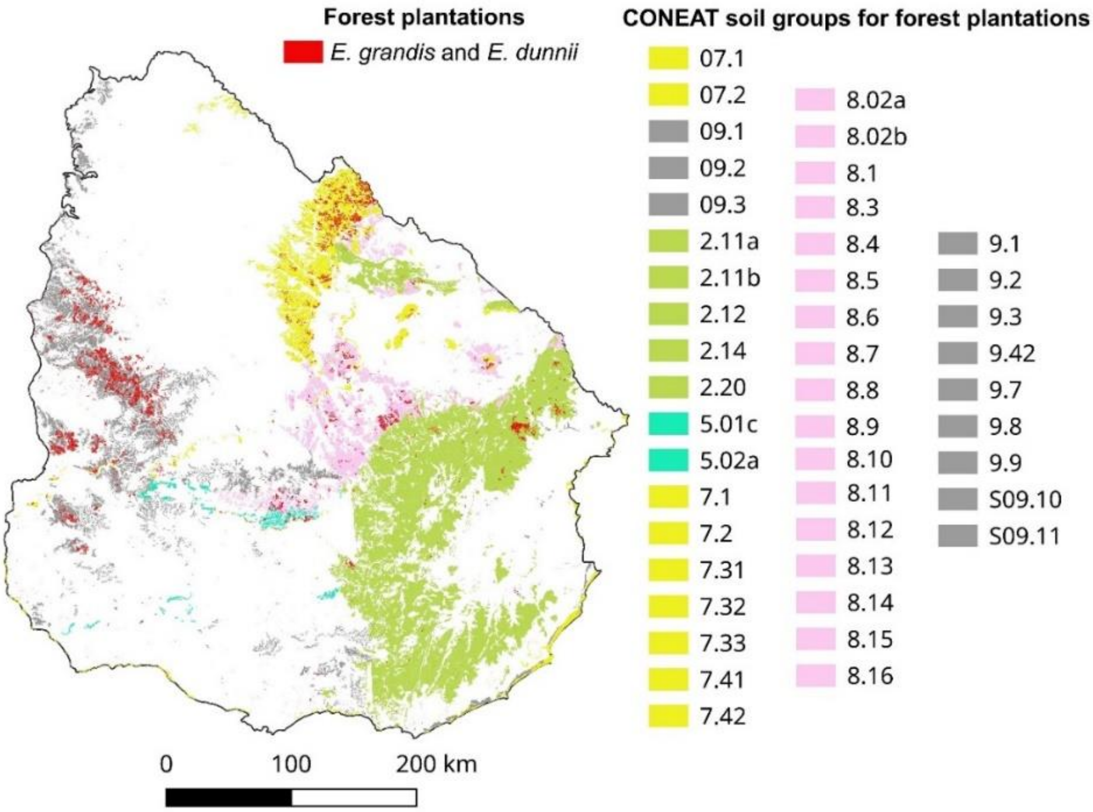


Figure 1. Map of zones prioritized for forestry and planted area with *E. dunnii* and *E. grandis.* According to the National Commission for Agroeconomic Studies of the Land Classification CO.N.E.A.T.), soils correspond to groups 2, 7, 8 and 9 have an adequate soil conditions for forest plantation

The study areas correspond to plantations of *E. grandis* and *E. dunnii* located on soils prioritized for forestry in the northern, western coastal, and south-eastern regions of Uruguay (Table S1, Supplementary material, Figure 2).

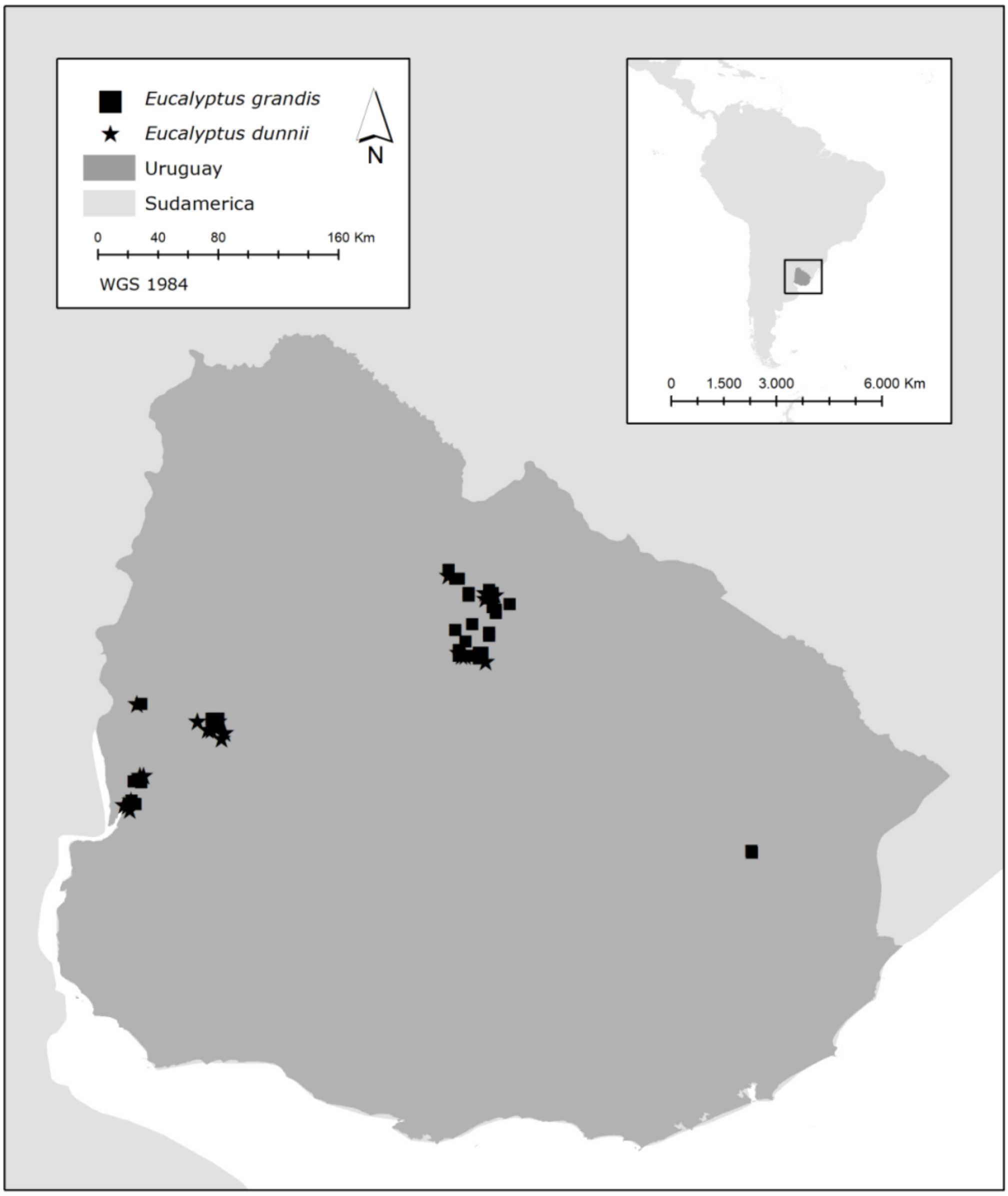


Figure 2. Location of the study areas in Uruguay for the *Eucalyptus dunnii* ( ) and *Eucalyptus grandis* ( ).

Its suitability is associated with the conditions which allow good forest growth: good conditions for root formation, adequate drainage, and low natural fertility. Currently, the total area of these soils is 4.42 million hectares and this land is characterized by having a low or average suitability for arable crops or livestock, according to the national productivity index. This index (C.O.N.E.A.T.) determines the capacity of a soil in terms of meat (ovine and bovine) and wool production per hectare and is expressed as a value relative to the country's average productivity capacity, corresponding to a value of 100. A description of the main characteristics of the forest priority soils is presented in the Supplementary material.

2.2 Source of data and environmental and edaphic variables

The growth data of *E. grandis* and *E. dunnii* correspond to the National Forest Inventory developed by the General Directorate of Forestry (Dirección General Forestal) – MGAP during the years 2010, 2011, 2014, and 2016. In total, 326 plots of *E. grandis* and 128 plots of *E. dunnii*, formed by a variable number of trees, were evaluated: in the first inventory 5041 trees were measured, in the second one 1200 trees, and with the last two, 3561 trees. The plots are rectangular and 200 m2 in area, or circular with a variable size: 113, 314, 616, or 1018 m2. In all cases the diameter at breast height (dbh, cm), considering breast height as 1.30 m, was measured as well as the commercial height (Hf, m), total height (Ht, m), and number of living trees (N, trees ha-1). Each plot was georeferenced through its latitude and longitude.

A total of 19 bioclimatic and 48 monthly climatic variables were selected, either for the current situation or for projections for the years 2050 and 2070. These were obtained from the Worldclim database with a resolution of ~1 km (Table 2). A model of global circulation of the atmosphere (GCM), which provides projections of the carbon dioxide concentration in the atmosphere (Vadillo, 2017) and considers a climate reconstruction (Community Climate System Model, CCSM4), and four representative pathway scenarios (RCP) of different greenhouse concentrations (2.6, 4.5, 6.0, 8.5) were used. The chosen values represent the increase in the heat absorbed by the Earth (for the year 2100) according to the concentration of greenhouse gases in each trajectory, measured in Watts per square meter. Also, we used 20 edaphic and four topographical variables, which were considered as constant for future projections.

2.3 Variables selection

The variable selection was made by eliminating those with high collinearity according to the Variance Inflation Factor (VIF), using a threshold value of 10 (Duque-Lazo et al., 2016). This index was calculated as:

$$VIF=1/(1-R^{\wedge 2}) \quad [1]$$

Where R2 is the coefficient of determination. After the selection of the non-collinear variables, the elimination was made through a stepwise procedure with the Biomod2 package in the R program (R Core Development Team, 2019), in a function considering the importance of each variable, which was determined through simple linear correlations between predictions including all the variables (full model) and the prediction excluding the evaluated variable (reduced model). The prediction of a model including a variable with a reduced contribution is very similar to obtained with that of a reduced model from which that variable is excluded (Duque-Lazo et al., 2016).

Table 1. Environmental data used to predict the occurrence of habitat suitable for *Eucalyptus dunnii* and *E. grandis* in Uruguay. The variables selected to predict the occurrence of both species appear in bold type

Code	Variables	Units
Bioclimatic		
Bio1	Annual Mean Temperature	ºC
Bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	ºC
Bio3	Isothermality (BIO2/BIO7) (* 100)	ºC
Bio4	Temperature Seasonality (standard deviation *100)	
Bio5	Max Temperature of Warmest Month	ºC
Bio6	Min Temperature of Coldest Month	ºC
Bio7	Temperature Annual Range (BIO5-BIO6)	**ºC**
Bio8	Mean Temperature of Wettest Quarter	**ºC**
Bio9	Mean Temperature of Driest Quarter	ºC
Bio10	Mean Temperature of Warmest Quarter	ºC
Bio11	Mean Temperature of Coldest Quarter	ºC
Bio12	Annual Precipitation	mm
Bio13	Precipitation of Wettest Month	**mm**
Bio14	Precipitation of Driest Month	mm
Bio15	Precipitation Seasonality (Coefficient of Variation)	
Bio16	Precipitation of Wettest Quarter	mm
Bio17	Precipitation of Driest Quarter	mm
Bio18	Precipitation of Warmest Quarter	**mm**
Bio19	Precipitation of Coldest Quarter	**mm**
Climatic		
Tmin 1-12	Minimum monthly temperature	ºC
Tmean 1-12	Medium monthly temperature	ºC
Tmax 1-12	Maximum monthly temperature	ºC
Prep 1-12	Monthly precipitation	mm
Edaphic		
Esp.	Depth Horizon A	cm
Ar.	Sand	%
Lim.	Silt	%
Arc.	Clay	%
Ph-water	Acidity	

C	Carbon	%
Mat.org.	Organic matter	%
N	Nitrogen	%
Ca	Calciu,	%
Mg	Magnessium	%
K	Potassium	%
B	Bases	%
Al	Aluminum	meq/100gr
CEC7	CEC ph7	meq/100gr
Vph7	Bases Saturation ph7	%
Na_int.	interchangeable sodium	%
Al_int.	interchangeable aluminium	%
Topographic		
RN 1-12	Monthly solar radiation	Joules/m2
A	Aspect	Degrees
S	Slope	percentage
E	Elevation	m

- Bio1- Bio12: January to December
- Source: http://www.worldclim.org/

2.4 Statistical models

The biomod2 R package assembles the SDM, which include the Generalized Lineal Mode (GLM), Generalized Additive Models (GAM), Classification and Regression Trees (CART), Flexible Determinant Analysis (FDA), Artificial Neuronal Networks (ANN), Multivariate Adaptive Regression Splines (MARS), and Envelope Surface Range (SRE). We used ensemble models calculated using the mean, median, coefficient of variation, confidence interval (inferior and superior), committee averaging (CA), and probability mean weight decay (WD) of the single model prediction. The CA was achieved by a binary (presence/absence) transformation using the threshold of the single model predictions. The threshold is the maximum score of the evaluation metric (“True Skill Statistics”, TSS) for the evaluated dataset. Subsequently, the probability value of each pixel was calculated as the mean of the single pixel predictions. The WD ensemble modeling scaled the individual model predictions according to their accuracy statistic value (AUC) and the sum of all individual models (Duque-Lazo et al., 2018; Kukunda et al., 2018). We made ensemble predictions based on all single models with an AUC > 0.90. Most of the techniques to be applied along with biomod2 require the data of the species` distribution to be in absence/presence form. When using a dataset containing only presence records, it is necessary to generate pseudo-absences randomly (Thuiller et al., 2009).

2.5 Selection and validation of the model

The evaluation and selection of the model correspond to the determination of the predictive capacity based on the quantification of the error and the misclassified data (errors). These errors may be: of commission, which is the classification as an absence of a data point that is present (false negative), and of omission, which is the opposite. The criteria used to determine the predictive capacity of the model were the Kappa coefficient (K), the Area Under the curve (AUC), the ROC (Operational Characteristic of the Receptor), and the coefficient TSS. The first of these was used to estimate the veracity of the maps developed, and the latter was applied to estimate the precision of the model with the presence/pseudo-absence data (Duque-Lazo and Navarro-Cerrillo, 2017). The AUC is the graphical representation of the commission errors on the horizontal axis (presences classified incorrectly, 1-specificity), and the omission errors (real presences which are omitted, sensitivity) are represented on the vertical axis for the whole value range (Allouche et al., 2006). The values obtained vary from 0.5 to 1, where 1 represents a perfect classification (presences and absences) and 0.5 represents a random prediction. According to Thuiller et al. (2005), the adjusted model may be classified as poor (AUC<0.8), satisfactory (0.8<AUC<0.9), good (0.9<AUC<0.95), or very good (0.95<AUC<1). The K index is a qualitative measure of the concordance between the categoric predictors and describes the concordance rate between the observed and predicted values. The values of K vary from +1 to -1, where +1 represents a perfect classification and negative values represent a random adjustment (Cohen, 1960). The TSS compares the number of correct predictions except for those attributed to the random and, in the same way as the K index, considers the omission and commission errors. Its values oscillate between -1 and 1, where 1 indicates a perfect concordance and negative values indicate random behavior (Allouche et al., 2006). This index is defined according to the following expression:

$$TSS = \text{sensitivity} + \text{specificity} - 1 \quad [2]$$

In this case, the chosen threshold of precision was TSS>0.90. The probability values were classified in four categories (25%, 50%, 75%, and 100%) for the present or future occurrence of both species in Uruguay. The probability maps were reclassified to 0 and 1 to calculate the variation in the area occupied in the future, compared to the area currently occupied by the two species, using the same threshold applied to calculate TSS and Kappa.

3. Results

3.1 Variables´selection

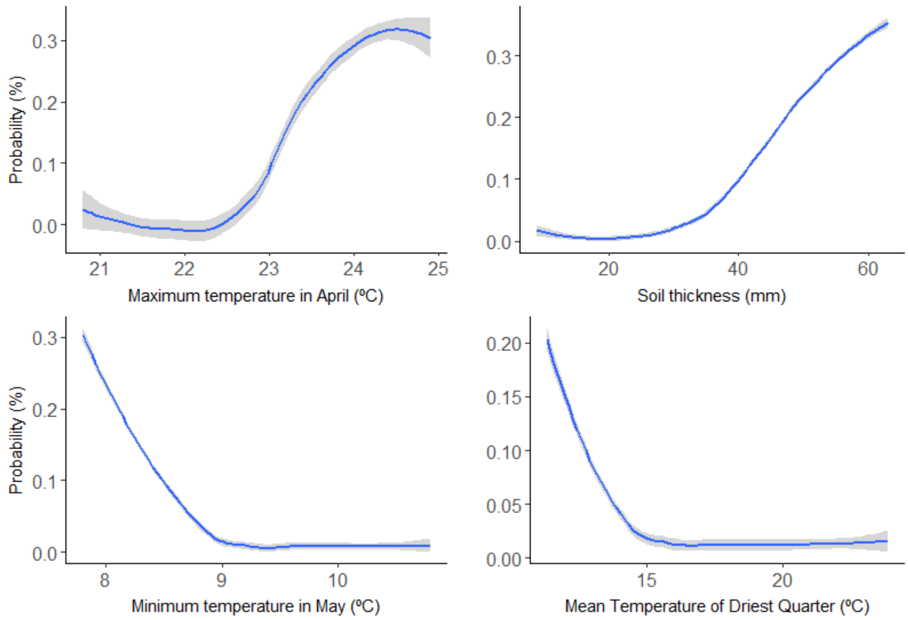
The VIF analysis for each species determined that 27 variables were discarded due to their collinearity. The selected variables were classified by importance (1 being the most important, and 5 the least important), considering the reduction of the standard deviation of the AUC and the improvement of the precision of the model given by the inclusion of each variable. The five variables ranked most highly were chosen (Table 2). The selected variables with greater predictive power for *E. dunnii* included: the depth of the A horizon, the highest and lowest temperatures of April and May, respectively, and the average temperature of the driest month. In the case of *E. grandis*, the most important variables were the % of clay, the depth of the A horizon, the isothermality, the % silt, and the orientation.

Table 2. Importance ranking of independent variables for predicting distribution of *E. dunnii* and *E. grandis*.

E. dunnii				*E. grandis*			
Order	**Variables**	**Importance**	**Probability of selection**	**Order**	**Variables**	**Importance**	**Probability of selection**
1	Depth Hor. A	8.49	1.00	**1**	% Clay	8.20	0.98
2	Temp.max in April	6.96	1.00	**2**	Depth Hor.A	7.06	0.99
3	Temp.min in May	5.12	0.98	**3**	Isotermality	4.11	0.65
4	Bio 9	4.69	0.95	**4**	% Silt	4.10	0.91
				5	Aspect	2.20	0.57

The response curves analysis shows that the probability of occurrence for *E. dunnii* decreases as the temperature of the driest quarter increases and increases in soils where the A horizon is deeper (Figure 2 A). The effect of the temperature of the driest trimester remains constant as it rises above 15 °C, while as the depth of the A horizon increases above 4 cm a constant increase in the probability of occurrence is observed. For *E. grandis*, the probability of occurrence is associated positively with the thickness of the A horizon and the aspect, but negatively with the percentage of clay in the A horizon (Figure 2 B). The probability of presence is highest when the proportion of clay is near 0% and remains constant when it exceeds 25%. Similarly, to *E. dunnii*, an A horizon thickness greater than 4 cm determines an important increase in the probability of occurrence. The orientation has a quadratic effect, with a higher probability of presence in the extremes of the range; the probability is highest for aspects over 300° (northwest). On the other hand, the isothermality shows a polynomic relationship with the probability of occurrence, the probability being highest with levels close to 47.5%. The silt content in the A horizon has an effect very similar to that of the clay content.

A)



B)

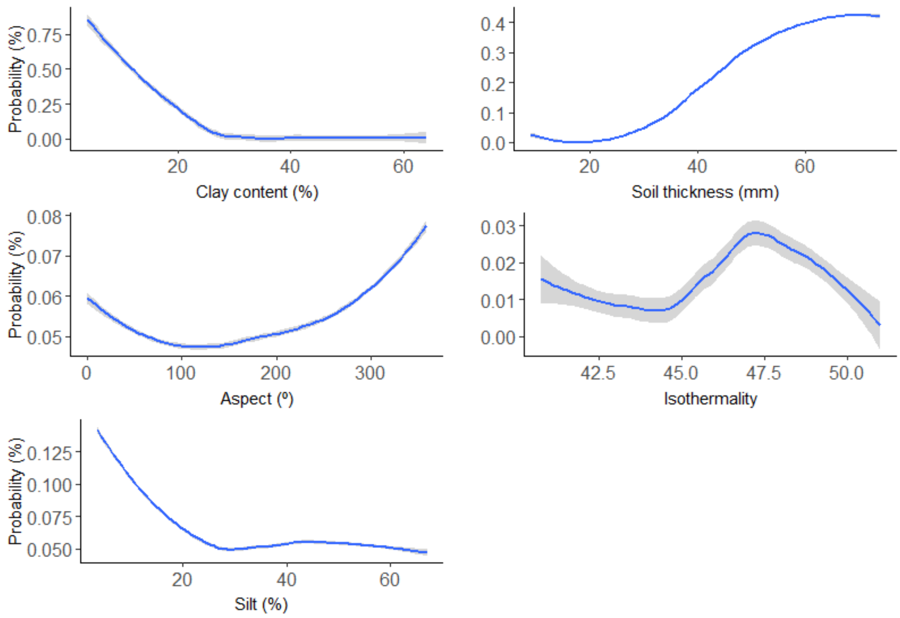
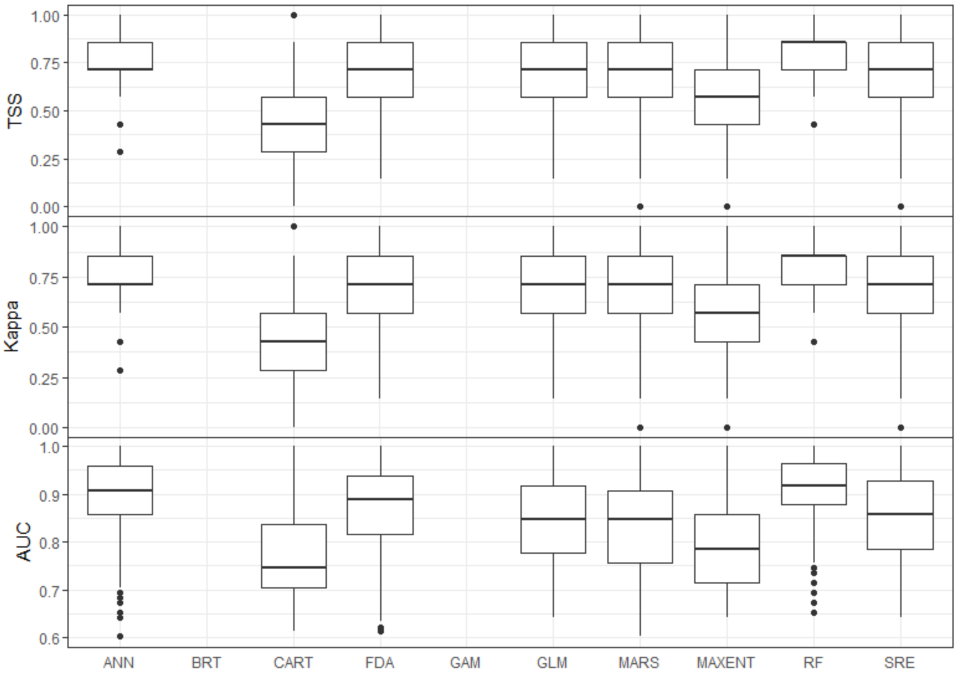


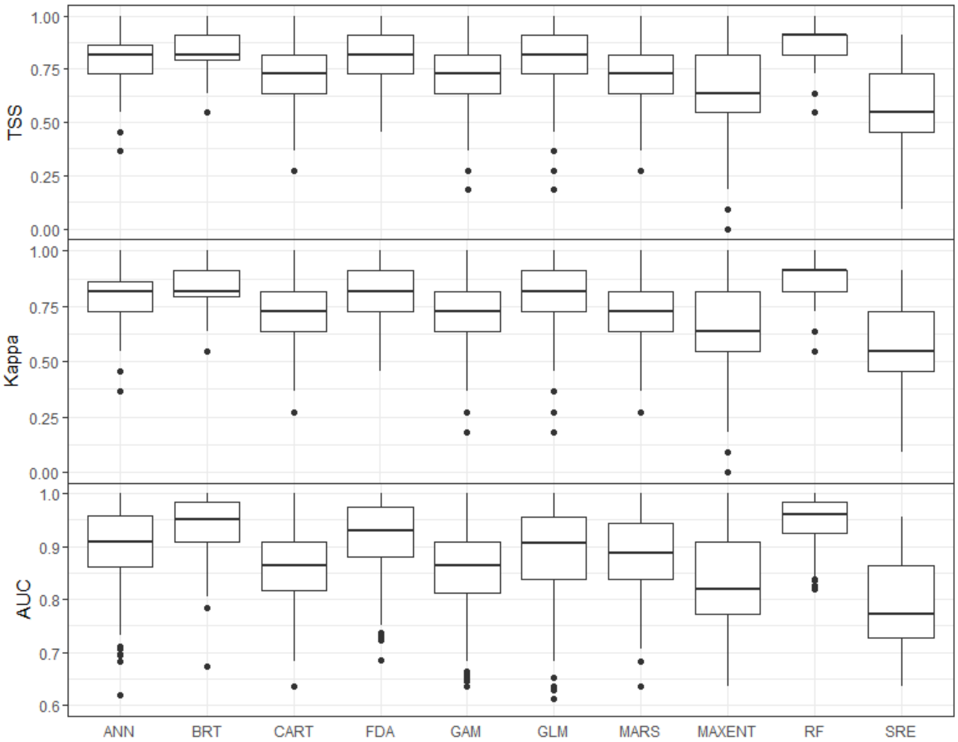
Figure 3. Response curves showing the average probability value of the ensemble model for each explanatory variable, for *E. dunnii* (A) and *E. grandis* (B).

3.2 Model selection and validation

The response curves analysis shows that the probability of occurrence for *E. dunnii* decreases as the temperature of the driest quarter increases and increases in soils where the A horizon is deeper (Figure 2 A). The effect of the temperature of the driest trimester remains constant as it rises above 15 °C, while as the depth of the A horizon increases above 4 cm a constant increase in the probability of occurrence is observed. For *E. grandis*, the probability of occurrence is associated positively with the thickness of the A horizon and the aspect, but negatively with the percentage of clay in the A horizon (Figure 2 B). The probability of presence is highest when the proportion of clay is near 0% and remains constant when it exceeds 25%. Similarly, to *E. dunnii*, an A horizon thickness greater than 4 cm determines an important increase in the probability of occurrence. The orientation has a quadratic effect, with a higher probability of presence in the extremes of the range; the probability is highest for aspects over 300° (northwest). On the other hand, the isothermality shows a polynomic relationship with the probability of occurrence, the probability being highest with levels close to 47.5%. The silt content in the A horizon has an effect very similar to that of the clay content.



A)



B)

Figure 4. Statistic of fit values proved by ten different distribution models for *Eucalyptus dunnii* (A) and *E. grandis* (B) in Uruguay.

Table 3. Statistic of fit values obtained with the ensemble model for predicting habitat for *E. dunnii* (top) and *E. grandis* (bottom) in Uruguay.

Ensemble model	Kappa	TSS	AUC	Threshold	Sensitivity	Specificity
Mean	0.771	0.987	0.980	0.511	1.00	0.987
Confident interval Inferior	0.771	0.891	0.981	0.500	1.00	0.891
Confident interval Superior	0.77	0.887	0.980	0.557	1.00	0.887
Median	0.741	0.887	0.980	0.502	1.00	0.887
Committee averaging	0.801	0.878	0.982	0.500	1.00	0.878
Probability mean weight decay	0.771	0.891	0.981	0.500	1.00	0.887
Ensemble model	**Kappa**	**TSS**	**AUC**	**Threshold**	**Sensitivity**	**Specificity**
Mean	0.807	0.866	0.978	0.651	0.944	0.922
Confident interval Inferior	0.812	0.869	0.979	0.636	0.944	0.922
Confident interval Superior	0.807	0.866	0.978	0.675	0.944	0.922
Median	0.788	0.864	0.975	0.712	0.944	0.919
Committee averaging	0.830	0.867	0.979	0.843	0.917	0.949
Probability mean weight decay	0.807	0.866	0.978	0.500	9.44	0.920

3.3 Current and future habitat projection

The probability maps for the current habitat distribution show greater potential for both species in the northern and western areas (Figure 4). Likewise, the southwest appears to be the area most suitable for *E. grandis*, while for *E. dunnii* the probability of occurrence is greater in the west of the country. In terms of area, *E. grandis* is the species with the highest potential for occurrence in forest priority soils.

The prediction of the future occurrence of both species is shown in Figures 5 and 6. For *E. dunnii*, a drastic reduction in the species' habitat is predicted for the year 2050, with respect to the current situation, whereas for the year 2070 the reduction is less conspicuous. In both cases, the restriction of the occurrence of *E. dunnii* is greater in the scenarios in which greenhouse gases increase (RCP 8.5 vs 2.6). This reduction would reach 100% in the first scenario shown, for all the studied regions. For *E. grandis*, on the other hand, the probability of occurrence for the two-time series does not show great changes for any of the four possible scenarios of temperature increment. These tendencies are shown in Table 6 and Figure S1 (Supplementary material). For *E. dunnii*, a reduction of over 95% in the area of occurrence, even for the scenario of lowest temperature, was predicted by the models CA and WD for 2050. This reduction is almost total for the scenarios with higher greenhouse gas concentrations. The predictions for *E. grandis* show that the probability of occurrence will remain virtually constant for all the evaluated scenarios.

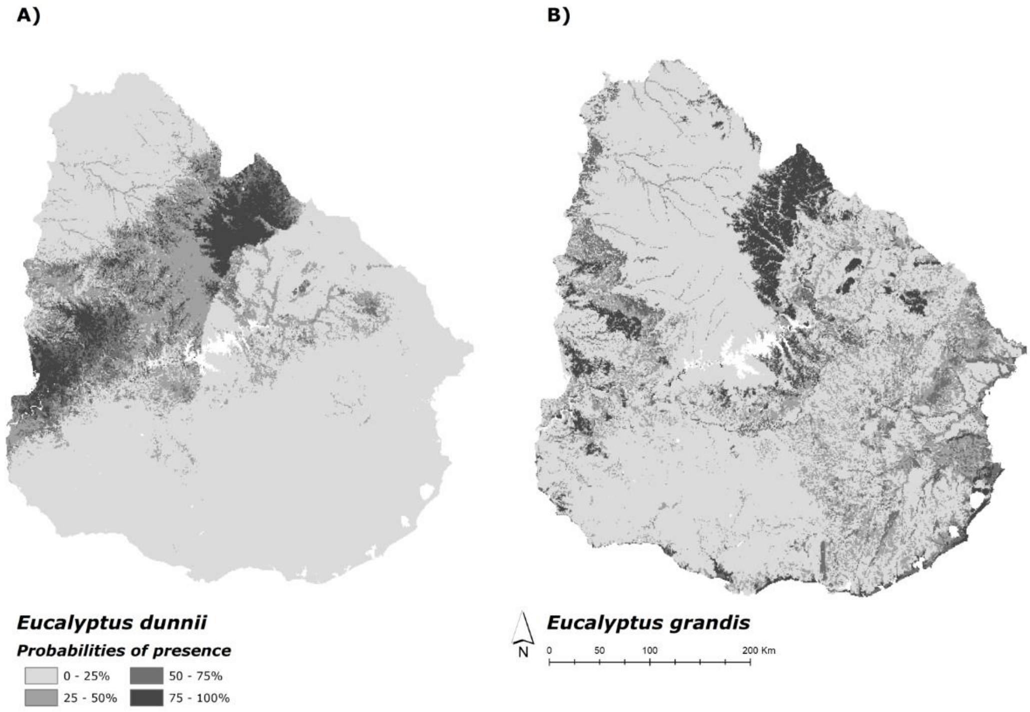


Figure 5. Current probability of occurrence of *Eucalyptus dunnii* (A) and *E. grandis* (B) in Uruguay. The potential distribution was mapped in both cases with the average ensemble model.

Figure 6. Probability of future occurrence of the *Eucalyptus dunnii* obtained with the ensemble model global circulation CCSM4 on the scenarios rcp 26, 45, 60 and 85 for 2050 and 2070

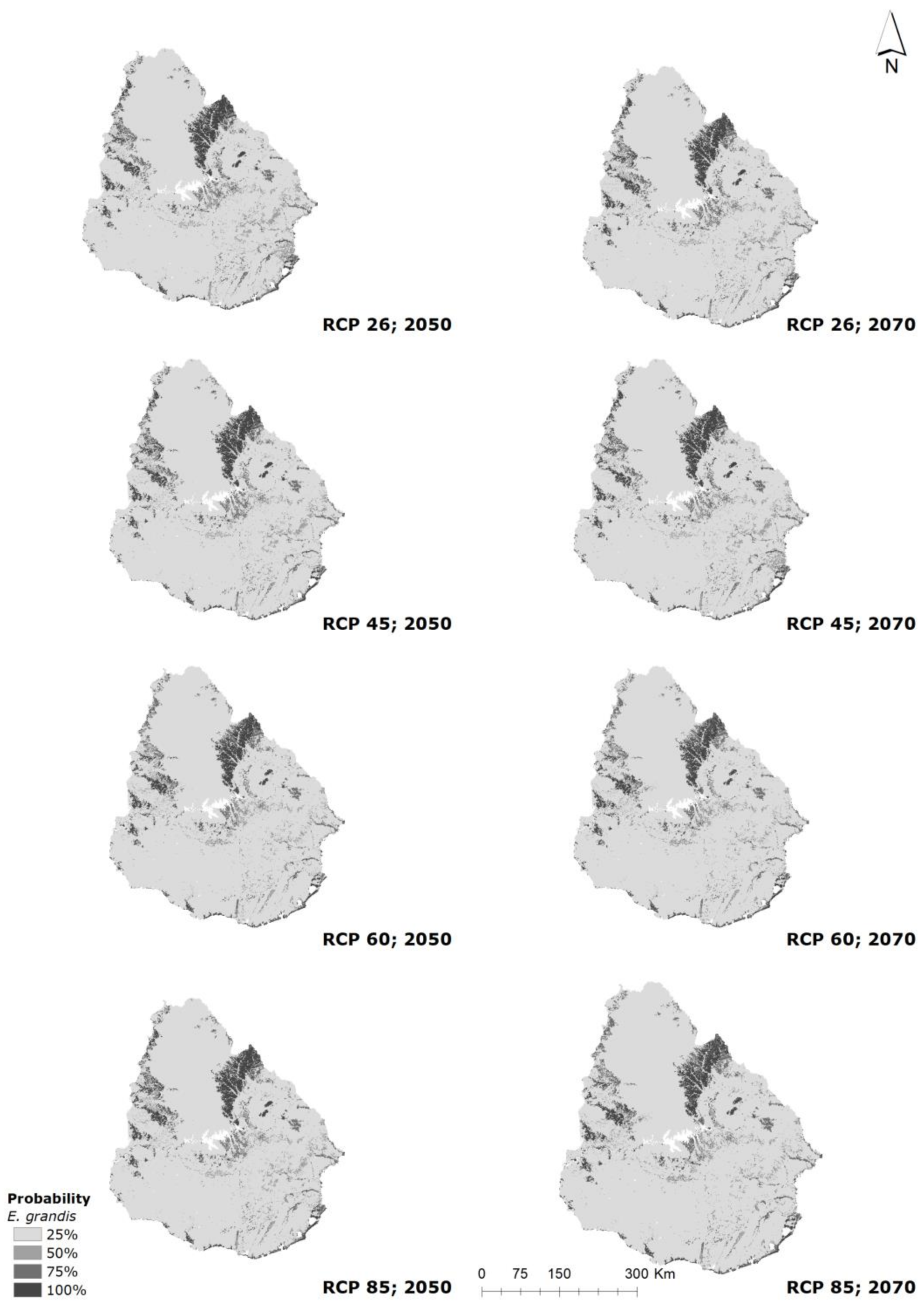


Figure 7. Probability of future occurrence of the *Eucalyptus grandis* obtained with the ensemble model global circulation CCSM4 on the scenarios rcp 2.6, 4.5, 6.0 and 8.5 for 2050 and 2070.

Table 4. Future projection for the total area (ha) and prediction (%) of *Eucalyptus dunni* (A) and *E. grandis* (B) for the different scenarios (rcp 2.6, 4.5, 6.0 and 8.5) applying Global Circulation Model CCSM4.

	Year		Area	%	Area	%
Present	**2000**		28891	100.00	30537	100.00
		rcp	**CA**		**CW**	
Future	**2050**	**26**	1214	4.20	794	2.60
		45	0	0.00	0	0.00
		60	10	0.03	0	0.00
		85	0	0.00	0	0.00
	2070	**26**	1134	3.93	990	3.24
		45	3	0.01	1	0.00
		60	0	0.00	0	0.00
		85	0	0.00	0	0.00

	Year		Area	%	Area	%
Present	**2000**		16070	100	12105	100
		rcp	**CA**		**CW**	
Future	**2050**	**26**	16471	102.50	12107	100.02
		45	16211	100.88	12183	100.64
		60	15518	96.57	11496	94.97
		85	16198	100.80	12285	101.49
	2070	**26**	16121	100.32	11901	98.31
		45	16401	102.06	12129	100.20
		60	15292	95.16	11168	92.26
		85	35	0.22	33	0.27

4. Discussion

4.1 Variable selection and model precision

Species Distribution Models are usually applied to, among other things, the understanding of which variables better explain the occurrence of the targeted species (Phillips et al., 2006; Elith and Franklin, 2013). The number of selected variables for each species must be relatively low because this determines the precision of the obtained models (Varela et al., 2014). According to these authors, the predicted area decreases with the increase in the number of variables, given that the number of conditions an area must provide to be considered optimal increases. The response curves show relationships of different types between the occurrence probability of the species and the most important variables of each site. With each of the selected variables, we obtain zones with wide ranges, between the maximum and minimum probability of occurrence of each species. In this study, both species were found to respond relatively differently according to the variable analyzed. The selected variables for *E. grandis* are related to soil texture and depth (silt, clay, and depth of the A horizon), the orientation, and temperature (isothermality). The values of occurrence increase as a function of the clay content decrease and increase as the depth of the surface horizon increases. With the rest of the variables, very low values of probability were obtained. These soil texture and depth variables are closely related to eucalyptus growth given their major influence on water availability (Bourne et al., 2015; Souza et al., 2017), nutrients availability (Rutherford et al., 2017), and the volume of soil explored by the roots. For Uruguay, similar results have been reported (Rachid, 2016), leading to the conclusion that the available water in the soil is one of the variables that better explain *E. grandis* growth as well as the growth of other eucalypt species (Almeida et al., 2010). Likewise, Escudero et al. (2002) found a negative effect of the clay and silt presence on *E. globulus* growth. Isothermality, which indicates the temperature stability through the year (González de León, 2015), has also been reported as one of the variables explaining the growth of *E. cloeziana* (Lafetá et al., 2018) and *E. grandis* (Song et al., 2016). The positive effect of northwest to northeast aspects on the probability of occurrence could be related to the greater exposure to solar radiation and the higher temperatures to which the planted trees in these orientations are exposed (Kinsey et al., 2008; Weiskittel et al., 2009), although the positive effect of these variables arises from the interaction with variables such as soil moisture, temperature, or slope (Verbyla and Fisher, 1989). The values of the probability of occurrence of *E. dunnii* are, in general, relatively low and of similar magnitude for the selected variables. For this species the thickness of the A horizon was also positively associated with the probability of presence, for similar reasons. The occurrence of this species also depended on the temperature during fall and summer. The positive effect of the temperature during April may be explained by the combined effect of a high relative water content in the soil (with greater precipitation than evapotranspiration) and intermediate temperatures that would promote tree growth. The increase in temperature during summer contributes to greater evapotranspiration, which may cause a deficit in the potentially available water in the soil during this period, although the precipitation has a relatively uniform distribution during the year (Castaño et al., 2011).

In both species, higher values and less variation of the AUC were obtained with ensemble models compared to the use of individual models, which confirms the advantage of using the former to predict the occurrence of species (Araújo and New, 2007; Marmion et al., 2009; Breiner et al., 2015). According to these authors, the techniques used in this analysis, such as biomod2, reduce the uncertainty of the statistical validity of the results. The Random Forest (RF) model showed great precision for both species, with a slightly superior value of 0.95. High levels of precision have been reported previously when using this model (Pliscoff et al., 2011; Duque-Lazo, 2016; Navarro-Cerrillo et al., 2018).

The TSS index has been suggested by some authors as a simple intuitive average for the evaluation of habitat predictions for species when expressed in maps of presence-absence (Allouche et al., 2006). For *E. dunnii* the average values of the TSS index were high for all the evaluated models except MAXENT and CART. The higher TSS index and lower variation of the ensemble model, compared to the individual models, indicate the higher precision of this technique. For *E. grandis*, the RF model had the highest TSS index.

However, the differences in this index were very small with respect to the ensemble model, RF showing greater variation.

Values of TSS above 0.85 (as for the RF model) represent excellent predictive power (Koo et al., 2017). The ensemble models and RF have shown very high capacities for predicting habitat in several species (Koo et al., 2017; Mi et al., 2017; Kukunda et al., 2018). Except for MAXENT and SRE, all the techniques yielded relatively high precision. Shabani et al. (2017) obtained slightly lower values for this index (0.66 and 0.78) when analyzing the habitat prediction of two eucalyptus species. Likewise, the Kappa index has been used frequently in SDM evaluation despite having some disadvantages compared to the AUC and TSS (Allouche et al., 2006), related to its dependence on threshold values as well as prevalence values (the sensitivity vs specificity relationship). The Kappa index values in this work are similar to the TSS index values, for both species. According to the scale used by Quintana et al. (2013), several models in the group analyzed showed good to very good precision in habitat prediction, with the highest values corresponding to the RF model, for both species. This particular model had higher values than the ensemble models. This evaluation scale considers the following categories: <0.20 = poor, 0.21-0.40 = limited, 0.41-0.60 = moderate, 0.61-0.80 = good, and 0.81-1.00 = very good concordance. In general, greater values of this index were obtained for *E. grandis*, with all the evaluated models. The MAXENT model showed the lowest value of this index, for both species. Considering the three statistics assessed, the RF and ensemble models yielded the best habitat prediction, for both eucalyptus species tested.

4.2 Current potential habitat and future projection

Several eucalypt species planted commercially and experimentally have shown very good adaptation to the soil and climatic conditions in Uruguay; that is the case of the two species evaluated in this work (Balmelli and Resquin, 2002; Balmelli and Resquin, 2006). The natural distribution area of *E. dunnii* is relatively small; however, this species has shown high productive potential over a wide range of conditions (Jovanovic et al., 2000), as well as an important genetic variability. It stands out for its relative tolerance of frosts, which makes it optimal for areas that are marginal for other eucalyptus species. It requires deep loamy soils and good drainage, showing moderate tolerance of dryness (Boland et al., 2006). Relevant climatic parameters of the area of its natural distribution are: temperature range from 8 to 29 °C, annual precipitation from 1000 to 1500 mm, and a maximum altitude of 800 m.a.s.l. (FAO, 1981). The map of potential habitat developed for the species in Uruguay shows that the greatest probability of occurrence is in the northern and western areas (Figure 4 A). The areas with the greatest probability of occurrence are associated with the deepest A horizon, with low amounts of clay and silt, corresponding to soils of the North of the country. This kind of soil structure favors the availability of water (even when the rate of evapotranspiration is high, as in the summer), drainage, and a large exploration volume for the roots. The high probability of occurrence is also related to the high average temperatures of the area, which decrease from NW to SE by 4 to 5 °C. This favors growth during periods with greater potential water availability, such as fall (Castaño et al., 2011). Conditions that promote the growth of *E. grandis* combine deep, well drained, loamy to slightly sandy soil and an annual precipitation of 1000-1800 mm, in a temperature range from 8 to 36 °C, the optimum being 26 °C (FAO, 1981; Almeida et al., 2004). This species has low tolerance of frosts and may grow at altitudes close to 900 m.a.s.l., although it has been cultivated successfully at higher levels. The natural distribution of the species (Australia) occupies a large area, with a latitude from 17° to 36° south, and covers different growing conditions. The areas with a greater probability of occurrence in Uruguay, according to our work, are similar to the ones described for *E. dunnii* (Figure 4 B). Soils with the required characteristics are also present, although over a smaller extension, in some central and western areas, and in some reduced areas in the northwest. The soils of southwestern Uruguay show less potential because they are shallower - and therefore have lower water holding capacity and nutrients availability - and have higher silt and clay contents. The relative heterogeneity of the probability of occurrence of this species that is depicted in the map (at a national level) is explained by the high heterogeneity of soils, resulting from the variety of geological parent materials. On the other hand, temperature increases are foreseen for this region, towards ranges more favorable for the growth of this species. The cardinal temperatures of *E. grandis* are reported to be 8, 25, and 36 oC (minimum, optimum, and maximum, respectively), while the average values in Uruguay are 12.9, 17.7, and 22.6 oC, respectively. Therefore, an increase in temperature could have a negative effect on growth by influencing the availability of water, but it is not expected that it will negatively influence the physiology of the species.

The future habitat projection for *E. grandis* shows virtually no area changes in any of the climate change scenarios considered (Figure 6). The stability of the area occupied by this species can be explained by the fact that its presence is closely related to soil characteristics and the topography, and less so to climatic variables such as the temperature. For this reason, the average increase in temperatures projected for this region of 1 to 1.8 °C (Giménez et al., 2009) would not imply changes in the species' area, although effects on its productivity may occur.

The expected temperature increase (particularly in the north) would be accompanied by an increment in precipitation of 2.5 to 7%, which would have a positive effect on tree growth (Chmura et al., 2001). For these authors, the response of forest crops to pests and diseases would change in a climate change scenario (Pinkard et al., 2017), as well as for extreme climatic events (Baesso et al., 2010) or an increase in the CO_2 level in the atmosphere (Almeida et al., 2009). The predicted occurrence of *E. dunnii* shows a large reduction in the suitable area, especially for the scenarios with a greater increase in temperature (RCP: 4.5, 6.0, and 8.5) in the west of the country (Figure 5). This reduction is predicted for the period 2000-2050; afterwards, the area would stay relatively unchanged for all the temperature increase scenarios (Table 6, Figure 7). Although one of the most important variables explaining the occurrence of this species is the thickness of the A horizon, the future presence seems to be heavily influenced by the temperature change. In spite of the forecasted increases in temperature and average annual precipitation, increased variation between periods within years is also forecasted (Giménez et al., 2009). Such studies predict temperature increases during summer (1.2 to 1.8 °C) that will be greater in the period 2020-2050. This increment may explain the decrease in the presence of this species, given the negative effect of this variable on the probability of occurrence (Figure 2). Temperature increases in summer could cause plant water deficiency, given the negative balance between evapotranspiration and precipitation.

5.Conclusions

The results obtained in this work indicate that the growth of *E. grandis* is associated basically with soil parameters, while that of *E. dunnii* shows a greater association with the temperatures of the fall and summer months. The direct relationship of the growth of both species with the depth of the surface horizon of the soil determines the importance of the choice of site with regard to obtaining high levels of growth. From this point of view, the potential of these species is greatest in the northern and coastal soils of the country - which, in general, have a comparatively greater volume of soil to be explored by the roots than the soils of the southeast of the country. With *E. grandis*, the positive effect of the north-northwest orientation on growth, but conditioned by soil conservation practices, must be taken into account. In this work, the ensemble models of habitat prediction emerge as useful tools to identify the most suitable areas for both species, based on the adjustment values obtained. *E. grandis* shows greater plasticity than *E. dunnii* regarding the different agroclimatic conditions of the country. Predictions of the future habitat of both species indicate that *E. grandis* is a species that could be used with certainty in the long term, in a wide variety of sites, whereas with *E. dunnii* there may be areas of higher risk due to the probable climate change.

6.References

Allouche, O.; A. Tsoar; R. Kadmon. 2006. Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS). Journal of Applied Ecology 43 (6): 1223–32.

Chapter 2. Modelling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

Almeida, A.C., J.J. Landsberg; P.J. Sands. 2004. Parameterisation of 3-PG Model for Fast-Growing *Eucalyptus grandis* Plantations. Forest Ecology and Management 193 (1–2): 179–95.

Almeida, A.C.; A. Siggins; T.R. Batista; C. Beadle. 2010. Mapping the Effect of Spatial and Temporal Variation in Climate and Soils on Eucalyptus Plantation Production with 3-PG , a Process-Based Growth Model. Forest Ecology and Management 259: 1730–1740.

Almeida, A.C.; P.J. Sands; J. Bruce; A. W. Siggins; A. Leriche; M. Battaglia; T. R. Batista. 2009. Use of a Spatial Process-Based Model to Quantify Forest Plantation Productivity and Water Use Efficiency under Climate Change Scenarios. In 18th World IMACS / MODSIM Congress, 1816–1822.

Anjos, L.J.S.; P.M.D. Toledo. 2018. Measuring Resilience and Assessing Vulnerability of Terrestrial Ecosystems to Climate Change in South America. PLOS ONE 13 (3): 1–15.

Araújo, M.B.; M. New. 2007. Ensemble Forecasting of Species Distributions. Trends in Ecology and Evolution 22 (1): 42–47.

Araújo, M.B.; R.P. Anderson; A. Márcia Barbosa; C.M. Beale; C.F. Dormann; R. Early; R.A. Garcia; A. Guisan; L. Maiorano; B. Naimi; R.B. O'Hara; N.F. Zimmermann; C. Rahbek. 2019. Standards for distribution models in biodiversity assessments. Science Advances 5, eaat4858: 1-10

Baesso, R.C. E.; A. Ribeiro; M. P. Silva. 2010. Impacto Das Mudanças Climáticas Na Produtividade Do Eucalipto Na Região Norte Do Espírito Santo e Sul Da Bahia. Ciência Florestal 20 (2): 335–344.

Balmelli, G.; F. Resquin. 2002. Evaluación del crecimiento de especies de Eucalyptus en diferentes zonas de prioridad forestal. Tacuarembó, UY: INIA. 20 p. (Serie Aftercare Forestal INIA - JICA, 14). Aftercare del Proyecto de Mejoramiento Genético Forestal en el Uruguay (2000-2002). file:///C:/Users/Iniatest/Downloads/Aftercare-del-Proyecto-de-Mejoramiento-Genetico-Forestal-en-el-Uruguay-2000-2002-Nro.-14%20(3).pdf.

Chapter 2. Modelling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

Balmelli, G.; F. Resquin, F. 2006. Productividad de diferentes especies de Eucalyptus sobre areniscas de Tacuarembó-Rivera, Serie Técnica 159. INIA Tacuarembó, 159, pp. 305-312. http://www.ainfo.inia.uy/digital/bitstream/item/7774/1/ST-159-305-312.pdf.

Becerra-López, JL; U.l. Romero-Méndez; A. Ramírez-Bautista; S. Becerra-López. 2016. Revisión de Las Técnicas Para El Modelado de La Distribución de Las Especies. Review of Techniques for Modelling Species Distribution. Revista Biológico Agropecuaria Tuxpan 5 (7): 1514–1525.

Boland, D.J., M.I.H. Brooker; G.M. Chippendale; N. Hall; B.P.M. Hyland; R.D. Johnston; D.A. Kleinig; J.D. Turner. 1984, Forest trees of Australia, 4th edn, rev. Nelson-C.S.I.R.O., Melbourne.

Booth, T. H. 2013. Eucalypt Plantations and Climate Change. Elsevier B.V. Forest Ecology and Management. 301: 28–34.

Booth, T.H. 2016. Estimating Potential Range and Hence Climatic Adaptability in Selected Tree Species. Elseviwe B.V. Forest Ecology and Management. 366: 175–83.

Booth, T. H.; L. M. Broadhurst; E. Pinkard; S. M. Prober; S. K. Dillon; D. Bush; K. Pinyopusarerk; J. C. Doran; M. Ivkovich; A. G. Young. 2015. Native Forests and Climate Change: Lessons from Eucalypts. Elsevier B.V. Forest Ecology and Management. 34: 18–29.

Bourne, A. E.; A. M. Haigh; D. S. Ellsworth. 2015. Stomatal Sensitivity to Vapour Pressure Deficit Relates to Climate of Origin in Eucalyptus Species. Tree Physiology 35 (3): 266–78.

Brazeiro, A.; D. Panario; A. Soutullo; O. Gutierrez; A. Segura; P. Mai. 2012. Clasificación y delimitación de las eco-regiones de Uruguay. Informe Técnico. Convenio MGAP/PPR – Facultad de Ciencias/Vida Silvestre/ Sociedad Zoológica del Uruguay/CIEDUR. 40p.

Breiner, F.T.; A. Guisan; A. Bergamini; M.P. Nobis. 2015. Overcoming Limitations of Modelling Rare Species by Using Ensembles of Small Models. Methods in Ecology and Evolution 6: 1210–1218.

Chapter 2. Modelling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

Brussa, C. 1994. *Eucalyptus*. Especies de Cultivo Más Frecuente En Uruguay y Regiones de Clima Templado. Montevideo, Uruguay. Ed. Hemisferio Sur. 328 p.

Buckeridge, J. S. 2010. Some Biological Consequences of Environmental Change: A Study Using Barnacles (*Cirripedia: Balanomorpha*) and Gum Trees (*Angiospermae: Myrtaceae*). Integrative Zoology, 5: 122-131.

Califra, H, A. Durán. 2010. 10 Años de Investigación En Producción Forestal. Jornada de Actualización Técnica. Dpto. de Suelos y Aguas. Facultad de Agronomía. Universidad de la República. Montevideo, Uruguay. 65 p.

Castaño, J. P.; A. Ceroni; M. Furest; J. Aunchayna; R. Bidegain, R. 2011. Caracterización agroclimática del Uruguay 1980-2009, Serie Técnica INIA. Montevideo, Uruguay, 193, p. 33. http://www.ainfo.inia.uy/digital/bitstream/item/2538/1/18429021211104157.pdf.

Chmura, D.J.; P.D. Anderson; G. T. Howe; C.A. Harrington; J. E. Halofsky; D.L. Peterson; D. C. Shaw; J. B. St. 2011. Forest Responses to Climate Change in the Northwestern United States: Ecophysiological Foundations for Adaptive. Elsevier B.V. Management. Forest Ecology and Management 261 (7): 1121–1142.

Cohen, J. 1960. A Coefficient of Agreement for Nominal Scales. Educational and Psychological Measurement 20 (1): 37–46.

Duque-Lazo, J. 2013. Transferability of Species Distribution Models. A Case Study of the Fungus *Phytophthora Cinnamomi* in Andalusia and Southwest Australia. M.Sc. ´Thesis. Lund University, Sweden, 101 p.

Duque-Lazo, J.; H. van Gils; T. A. Groen; R. M. Navarro-Cerrillo. 2016. Transferability of Species Distribution Models: The Case of *Phytophthora Cinnamomi* in Southwest Spain and Southwest Australia. Elsevier B.V. Ecological Modelling 320: 62–70.

Duque-Lazo, J.; R.M. Navarro-Cerrillo. 2017. What to save, the host or the pest? The spatial distribution of xylophage insects within the Mediterranean oak woodlands of Southwestern Spain. Forest Ecology and Management. 392: 90-104.

Duque-Lazo, J.; R.M. Navarro-Cerrillo; H. van Gils; T.A. Groen. 2018. Forecasting oak decline caused by *Phytophthora cinnamomi* in Andalusia: Identification of priority areas for intervention. Forest Ecology and Management. 417: 122-136.

Durán, A. 2008. Índice de Productividad CONEAT: Origen de Los Índices, Concepto de Productividad, Nomenclatura y Utilización.

Elith, J.; J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu. Rev. Ecol. Evol. Syst 40: 677–697.

Elith, J.; J. Franklin. 2013. Species Distribution Modelling. In: Editor-in-Chief: Simon, A.L. (Ed.), Encyclopedia of Biodiversity (Second Edition). Academic Press, Waltham: 692-705.

Escudero, R.; J.C. Sganga; L. Sayagués; E. Graf; R. Pedochi; L. Petrini; C. Munka; F. Iirisity; G. Morás. 2002. Análisis de los efectos de algunos factores ambientales sobre la productividad de *Eucalyptus globulus* ssp. *globulus*. ln: INIA Tacuarembó. Programa Nacional de Investigación en Producción Forestal. Seminario Forestal, 27 de junio, INIA Las Brujas, 2002. Mejoramiento Genético, Silvicultura y Sanidad de *Eucalyptus globulus* en la Región Sureste. Tacuarembó (Uruguay): INIA, 2002. p. 48-54 (INIA Serie Actividades de Difusión; 289) Proyecto INIA FPTA 106, página 48. http://www.ainfo.inia.uy/digital/bitstream/item/11130/1/SAD-289P48-542.pdf

FAO. 1981. El Eucalipto en la repoblación Forestal. Colección FAO: Montes. 11. Organización de las Naciones Unidas para la Agricultura y la Alimentación. Roma. 790 p.

Fearnside, P. M. 1999. Plantation Forestry in Brazil: The Potential Impacts of Climatic Change. Biomass and Bioenergy 16: 91–102.

Garcia, L.G.; Si. F. D. B. Ferraz; C. A. Alvares; K.M.P.M. d. B. Ferraz; R.C.V. Higa. 2014. Modelagem Da Aptidão Climática Do *Eucalyptus grandis* Frente Aos Cenários de Mudanças Climáticas No Brasil Modeling Suitable Climate for *Eucalyptus grandis* under Future Climates Scenarios in Brazil. Scientia Forestalis. 42 (104): 503–11.

Giménez, A.; J. P. Castaño; L. Olivera; W. Baethgen. 2009. Cambio climático en Uruguay, posibles impactos y medidas de adaptación en el sector agropecuario Montevideo (Uruguay): INIA, 2009. 56 p. (INIA Serie Técnica; 178). http://www.ainfo.inia.uy/digital/bitstream/item/3014/1/18429071209133815.pdf

González de León, S. 2015. BioInvasiones 1 (2015). Revista de Invasiones Biológicas de América Latina y El Caribe. http://bioinvasiones.org/.

Hamann, A.; T. Wang. 2006. Potential Effects of Climate Change on Ecosystem and Tree Species Distribution in British Columbia. Ecology. 87 (11): 2773–2886.

Hughes, L.; E.M. Cawsey; M. Westoby. 1996. Climatic Range Sizes of Eucalyptus Species in Relation to Future Climate Change. Global Ecology and Biogeography Letters 5: 23–29.

IPCC - The Intergovernmental Panel on Climate Change. 2013. Cambio climático 2013, bases físicas. Resumen para responsables de políticas. Contribución del Grupo de trabajo I al Quinto Informe de Evaluación del Grupo Intergubernamental de Expertos sobre el Cambio Climático. 34 p

Jovanovic, T.; R. Arnold; T. Booth. 2000. Determining the Climatic Suitability of *Eucalyptus dunnii* for Plantations in Australia, China and Central and South America. New Forests. 19 (3): 215–26.

Karnosky, D.F.; K.S. Pregitzer; D.R. Zak; M.E. Kubiske; G.R. Hendrey; D. Weinstein; M. Nosal; J.E. Percy. 2005. Scaling Ozone Responses of Forest Trees to the Ecosystem Level in a Changing Climate. Plant, Cell and Environment. 28: 965–81.

Koo, K. A.; S. U. Park; W. S. Kong; S. Hong; I. Jang; C. Seo. 2017. Potential Climate Change Effects on Tree Distributions in the Korean Peninsula: Understanding Model & Climate Uncertainties. Elsevier B.V. Ecological Modelling 353: 17–27.

Koo, K. A.; S. U. Park; C. Seo. 2017. Effects of Climate Change on the Climatic Niches of Warm-Adapted Evergreen Plants: Expansion or Contraction? Forests 8 (12): 1–26.

Kimsey, M. J.; J. Moore; P. McDaniel. 2008. A Geographically Weighted Regression Analysis of Douglas-Fir Site Index in North Central Idaho. Forest Science 54 (3): 356–66.

Chapter 2. Modelling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

Kukunda, Co.B.; J. Duque-Lazo; E. González-Ferreiro; H. Thaden; C. Kleinn. 2018. Ensemble Classification of Individual Pinus Crowns from Multispectral Satellite Imagery and Airborne LiDAR. Elsevier International Journal of Applied Earth Observation and Geoinformation 65: 12–23.

Lafetá, B.O.; R.C. Santana; T.M.A. Penido; E.L.M. Machado; D.S. Vierira. 2018. Climatic Suitability for *Euaclyptus cloeziana* Cultivation in Four Brazilian States. Floresta 48 (1): 77–86.

Lara, B.D.C. 2017. Determinación de Cambios de Distribución de Especies Por Efectos Del Cambio Climático En El Parque Municipal Natural Campo Alegre y Parque Regional Natural Ucumari En Risaralda Colombia. Tesis de Maestría. Universidad Distrital Francisco Jose de Caldas. 105 p.http://repository.udistrital.edu.co/bitstream/11349/5403/1/LaraBallesterosDiana2017.pdf.

Larjavaara, M.; H. C. Muller-landau. 2012. Temperature Explains Global Variation in Biomass among Humid Old-Growth. Global Ecology and Biogeography 21: 998–1006.

Marmion, M.; M. Parviainen; M. Luoto; R. K. Heikkinen; W. Thuiller. 2009. Evaluation of Consensus Methods in Predictive Species Distribution Modelling. Diversity and Distributions 15 (1): 59–69.

Mateo, R.G.; A.M. Felicísimo; J. Muñoz. 2011. Modelos de Distribución de Especies: Una Revisión Sintética Species Distributions Models : A Synthetic Revision. Revista Chilena de Historia Natural 84: 217–40.

Merow, C.; M.J. Smith; T.C. Edwards; A. Guisan; S.M. McMahon; S. Normand; W. Thuiller; R.O. Wüest; N.E. Zimmermann; J. Elith, J. 2014. What do we gain from simplicity versus complexity in species distribution models? Ecography 37: 1267-1281.

MGAP-DGF. 2018. Bosques Plantados de Eucaliptos Registrados. http://www.mgap.gub.uy/unidad-organizativa/direccion-general-forestal/informacion-tecnica/estadisticas-y-mercados/recurso-forestal.

Mi, C.; F. Huettmann; Y. Guo; X. Han; L. Wen. 2017. Why Choose Random Forest to Predict Rare Species Distribution with Few Samples in Large Undersampled Areas? Three Asian Crane Species Models Provide Supporting Evidence. PeerJ 5, e2849: 122-131.

Molfino, JH. 2012. Características Grupos CO.N.E.A.T. (MGAP). INIA-GRASS.

Navarro-Cerrillo, RM.; J Duque-Lazo; R.D. Manzanedo; R. Sánchez-Salguero; G. Palacios-Rodriguez. 2018. Climate Change May Threaten the Southernmost *Pinus nigra* Subsp. *salzmannii* (Dunal) Franco Populations: An Ensemble Niche-Based Approach. IForest - Biogeosciences and Forestry 11 (3): 396–405.

Pearson, R. 2010. Species' Distribution Modeling for Conservation Educators and Practitioners. Lessons in Conservation 3: 54–89.

Pereira, V. R.; G. C. Blain; A. Maria; H.D. Avila; R. Célia; D. M. Pires; H. S. Pinto. 2018. Impacts of Climate Change on Drought: Changes to Drier Conditions at the Beginning of the Crop Growing Season in Southern Brazil. Agrometeoroly 77 (1): 201–11.

Phillips, S.J.; R.P. Anderson; R.E. Schapire. 2006. Maximum Entropy Modelling of Species Geographic Distributions. Ecological Modelling 190: 231–52.

Pinkard, E.; T. Wardlaw; D. Kriticos; K. Ireland; J. Bruce. 2017. Climate Change and Pest Risk in Temperate Eucalypt and Radiata Pine Plantations: A Review. Australian Forestry: 1–14.

Pliscoff, P.; T. Fuentes_Castillo. 2011. Modelación de La Distribución de Especies y Ecosistemas En El Tiempo y En El Espacio: Una Revisión de Las Nuevas Herramientas y Enfoques Disponibles 1. Revista de Geografía Norte Grande 79: 61–79.

Prior, L.; D. Bowman. 2014. Big Eucalypts Grow More Slowly in a Warm Climate: Evidence of an Interaction between Tree Size and Temperature. Global Change Biology 20: 2793–2799.

Quintana, M.; O. Salomón; R. Guerra; M. Lizarralde De Grosso; A. Fuenzalida. 2013. Phlebotominae of Epidemiological Importance in Cutaneous Leishmaniasis in Northwestern Argentina: Risk Maps and Ecological Niche Models. Medical and Veterinary Entomology 27 (1): 39–48.

R Core Development Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rachid Casnati, A. 2016. Hybrid Mensurational-Physiological Models for *Pinus taeda* and *Eucalyptus grandis* in Uruguay. Ph.D.´ Thesis. New Zealand School of Forestry. University of Canterbury, New Zealand. 220 p.

Rogers, H.H.; G.E. Bingham; J.D. Cure; J.M. Smith; K.A. Surano. 1983. Responses of Selected Plant Species to Elevated Carbon Dioxide in the Field. J.Environ. Qual. 12 (4): 569–74.

Rutherford, S.; S. P. Bonser; P. G. Wilson; M. Rossetto. 2017. Seedling Response to Environmental Variability: The Relationship between Phenotypic Plasticity and Evolutionary History in Closely Related Eucalyptus Species. American Journal of Botany 104 (6): 840–57.

Shabani, F.; L. Kumar; M. Ahmadi. 2017. Climate Modelling Shows Increased Risk to *Eucalyptus sideroxylon* on the Eastern Coast of Australia Compared to *Eucalyptus albens*. Plants 6 (4): 58.

Song, Z.; M. Zhang; F. Li; Q. Weng; C. Zhou; M. Li; J. Li; H. Huang; X. Mo; S. Gan. 2016. Genome Scans for Divergent Selection in Natural Populations of the Widespread Hardwood Species *Eucalyptus grandis* (Myrtaceae) Using Microsatellites. Scientific Reports 6 (October). Nature Publishing Group: 1–13.

Sorrentino, A. 1994. Manual teórico - práctico : técnicas e instrumentos de medición forestal. Montevideo: Facultad de Agronomía. 2 v. 312 p.

Souza, T. S.; M. A. P. Ramalho; B. Marco; D. L. Gabriel; D. Sampaio. 2017. Performance of Eucalyptus Clones According to Environmental Conditions Desempenho de Clones de Eucalipto Em Função de Condições Ambientais. Scientia Forestalis 45 (116): 601–610.

Thuiller, W. 2003. BIOMOD – Optimizing Predictions of Species Distributions and Projecting Potential Future Shift Sunder Global Change. Global Change Biology 9: 1353–1362.

Thuiller, W.; S. Valorel; M.B. Araújo; M. T. Sykes; I. .C. Prentice. 2005. Climate Change Threats to Plant Diversity in Europe. PNAS 102 (23): 8245–8250.

Thuiller, W.; B. Lafourcade; R. Engler; M.B. Araújo. 2009. BIOMOD2a Platform for Ensemble Forecasting of Species Distributions. Ecography 32: 369–373.

Thuiller, W.; D. Georges; R. Engler, R. 2019. biomod2: Ensemble platform for species distribution modeling. In. R package version 3.3.1.

Vadillo, FV. 2017. Modelamiento Espacial Aplicado Al Desarrollo Del Ecoturismo y La Conservación de La Avifauna En La Vertiente Occidental de Perú. Lic. Pontificia Universidad Católica del Perú. Facultad de Letras y Ciencias Humanas.134 p.

Varela, S.; R.G. Mateo; R. García-Valdés; F. Fernández-González. 2014. Macroecología y Ecoinformática: Sesgos, Errores y Predicciones En El Modelado de Distribuciones. Ecosistemas 23 (1): 46–53.

Varela, S.; L.C. Terribile; G. de Oliveira; J.A.F. Diniz-Filho; J. González-Hernández; M.S. Lima-Ribeiro. 2015. EcoClimate vs. Worldclim: Variables Climáticas SIG Para Trabajar En Biogeografía. Ecosistemas 24 (3): 88–92.

Verbyla, D. L.; R. F. Fisher. 1989. Effect of Aspect on Ponderosa Pine Height and Diameter Growth. Forest Ecology and Management 27 (2): 93–98.

Weiskittel, A.; P. Gould; H. Temesgen. 2009. Sources of Variation in the Self-Thinning Boundary Line for Three Species with Varying Levels of Shade Tolerance. Forest Science 55 (1): 84–93.

Zaninelli, P. G.; C. G. Menéndez; M. Falco; N.L. Franca; A. F. Carril. 2018. Future Hydroclimatological Changes in South America Based on an Ensemble of Regional Climate Models. Springer. Climate Dynamics.

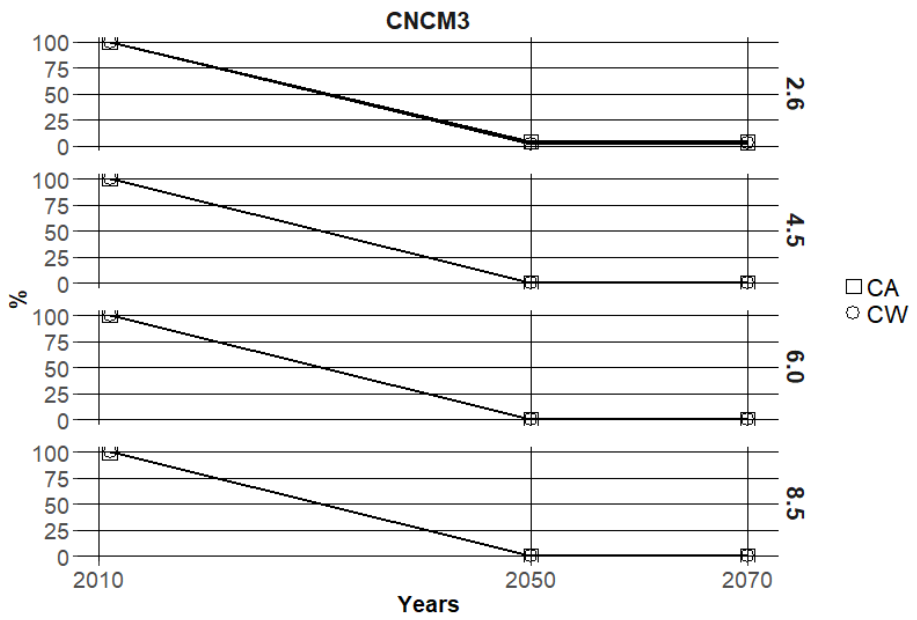
Chapter 2. Modelling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

Supplementary material

Table S1. Planted area (hectares) by department in Uruguay with *Eucalyptus* species. Source: MGAP-DIEA, 2017

Department	***Eucalyptus grandis***	***Eucalyptus dunnii***	**Other *Eucalyptus* species**
Tacuarembó	21.291	2.050	17.539
Rivera	47.853	742	2.786
Lavalleja	2.553	2.954	102.870
Paysandú	45.891	23.682	30.293
Río Negro	47.703	29.962	36.177
Cerro Largo	34.917	2.003	14.189
Rocha	1.030	112	37.811
Maldonado	1.646	927	33.128
Treinta y Tres	6.590	627	13.411
Durazno	20.466	7.755	24.830
Florida	4.132	0	44.984
Soriano	8.971	6.225	19.965
Salto	838	0	0
Artigas	334	0	13
Canelones	4.686	1.071	10.444
San José	753	310	3.583
Colonia	262	0	1.689
Flores	436	2945	453
Montevideo	217	0	1068
Total	**243.711**	**79.520**	**280.303**

A)



B)

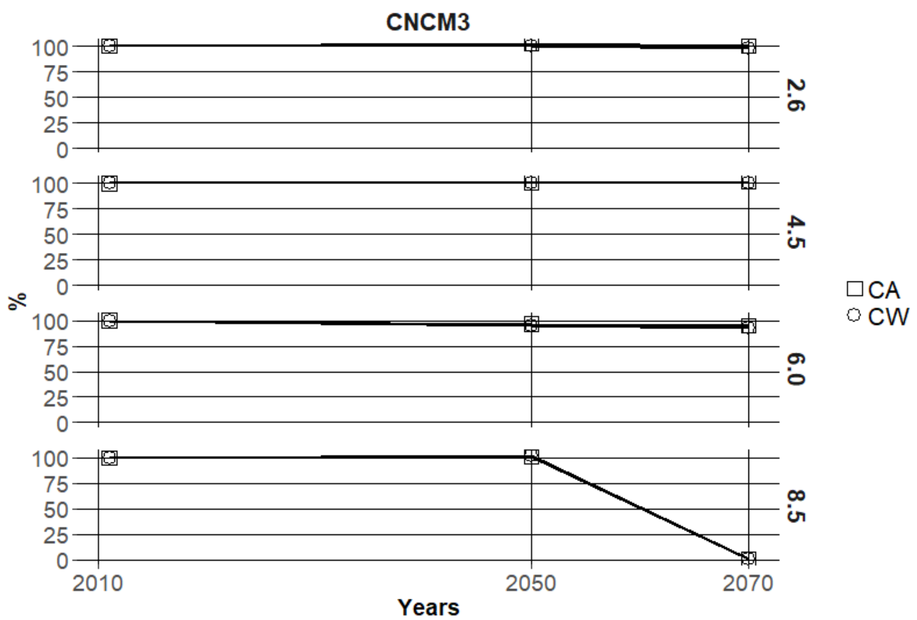


Figure S1. Reduction of occurrence area (%) of *E. dunnii* (A) and *E. grandis* (B) for 2050 and 2070 considering different scenarios (rcp 26, 45, 60 and 85) and the Global Circulation Model CCSM4.

Chapter 2. Modelling current and future potential habitat for plantations of *Eucalyptus grandis* and *Eucalyptus dunnii* in Uruguay

Appendix. Description of the forest soils according to the CO.N.E.A.T. classification

Group of soils CONEAT Nro. 7: They have a value range of this index from 31 to 92 and compound all the soil associations formed by sandstone in Tacuarembó, altered in situ or settled (Durán, 2008). They are in an area of 477,027 hectares and contain the deepest soils and with less natural fertility of the country. They are acid soils, with a very light texture and with toxicity problems thanks to the excess of aluminium. The type of vegetation is of a prairie of a summer type, with very low winter production. There, is possible to develop agricultural activities, but with intensive conservation practices. They represent the 13.3% of the total area of forest priority and are in the north area of the country. The media annual precipitation of the region is 1400-1500 mm; the average annual temperature is 18 °C with a highest and lowest average of 24 °C and 12 °C (Castaño et al., 2011).

Group of soils CONEAT Nro. 2: It has an index range from 9 to 105. It's known for forming associations of superficial and deep soils of median textures (Durán, 2008). The geological material is made of igneous rocks, metamorphic, and effusive acids. The relief is of mountain ranges and hills with outcropping of variable frequency. The type of vegetation is of a summer prairie with a tapestry type denser on the hills and sparse on the mountain ranges, associated to the brush and close by the mount. They have a surface of 1,453.774 hectares, representing 40.7% of the total surface occupied by the forest soils. These types of soils are in a strip from southeast to northeast with an annual average temperature which oscillates from 17 °C to 18 °C, and highest average of 21 °C to 23°C, and a lowest average of 12 °C to 13 °C. The average range of annual precipitations is from 1300 to 1500 mm (Castaño et al., 2011).

Group of soils CONEAT Nro. 9: It has an index range from 31 to 114 and it's compound by average and light texture soils, well defined and heavy soils (Durán, 2008). In general terms, this soils group have the highest relative fertility compared to the previous two soils group and therefore have the highest values of this index on average. They form part of the west littoral region of the country, on a surface of 822.054 hectares, representing 23% total of the forest soils. The average range of annual precipitation is 1200 to 1400 mm, an average temperature through the year from 18 °C to 19 °C, a range of highest average from 22 °C to 25 °C, and a lowest average from 12 °C to 13 °C (Castaño et al., 2011).

Chapter 3. Allometry, growth and survival of three eucalyptus species (*Eucalyptus benthamii* Maiden & Cambage, *E. dunnii* Maiden and *E. grandis* Hill ex Maiden) in high-density plantations in Uruguay

“He andado muchos caminos
he abierto muchas veredas;
he navegado en cien mares
y atracado en cien riberas.

En todas partes he visto
caravanas de tristeza,
soberbios y melancólicos
borrachos de sombra negra.

…Y en todas partes he visto
gentes que danzan o juegan,
cuando pueden, y laboran
sus cuatro palmos de tierra.

Nunca, si llegan a un sitio
preguntan a donde llegan.
Cuando caminan, cabalgan
a lomos de mula vieja.

Y no conocen la prisa
ni aún en los días de fiesta.
Donde hay vino, beben vino,
donde no hay vino, agua fresca.

Son buenas gentes que viven,
laboran, pasan y sueñan,
y en un día como tantos,
descansan bajo la tierra.”

Antonio Machado, 1903

Chapter 3. Allometry, growth and survival of three eucalyptus species (*Eucalyptus benthamii* Maiden & Cambage, *E. dunnii* Maiden and *E. grandis* Hill ex Maiden) in high-density plantations in Uruguay

This chapter has been published in:

Fernando Resquin, Rafael M. Navarro-Cerrillo, Cecilia Rachid-Casnati, Andrés Hirigoyen, Leonidas Carrasco-Letelier, Joaquín Duque-Lazo. Allometry, Growth and Survival of Three Eucalyptus Species (*Eucalyptus benthamii* Maiden and Cambage, *E. dunnii* Maiden and *E. grandis* Hill ex Maiden) in High-Density Plantations in Uruguay. Forests 2018, 9, 745; doi:10.3390/f9120745.

1. Introduction

In the last decade, the use of renewable energy has been a growing trend, worldwide, to reduce fossil fuel use and greenhouse gas emissions (Sixto et al., 2007). Within the renewable energies, plant biomass stands out because it could have a neutral balance of carbon and represent an important source of employment (Estrada and Meneses, 2004). In this framework, Uruguay designed an energy policy to create and promote the use of renewable energy in electric power generation as well as the use of biomass for energy purposes. Additionally, there is a growing impulse for the production of liquid fuels (bioethanol and biodiesel) from national raw materials to mix with the fossil fuels. Degraded, abandoned, and marginal lands are the most important areas for bioenergy production (Gelfand et al., 2013). Eucalyptus species have been shown to respond to high density plantation with enhanced biomass growth.

There are two numerical approaches to the estimation of forest biomass from inventory data: biomass expansion factors (BEFs) and biomass estimation equations (Brown, 2002). Biomass expansion factors are coefficients which allow the conversion of the volume of wood (usually expressed in m^3) of a tree or forest mass as a whole into dry weight of the tree or mass (usually expressed in tonnes). On the other hand, the biomass estimation equations are relationships between the volume and some measured variable on the tree or representing the site conditions (density and productivity). For the use of the data in studies of ecosystem functioning, nutrient cycles and quantification of carbon pools, a separate study of the different fractions of the tree is usually performed (Bravo et al., 2008). Due to the degree of precision, the most-used procedure in the quantification of biomass is the destructive one. By relating the growth and characteristics of the plantation (density, productivity, etc.) to the dry weight of the different fractions, equations can be obtained that quantify the dry matter of the tree and then provide the dry weight of the forest mass. Thus, with the biomass equations for each of the fractions, the amount of dry matter present in the trees of a given forest can be estimated (González García et al., 2013; Razakamanarivo et al., 2012; Winck et al., 2015; Ounban et al., 2016).

In Uruguay, several models of growth simulation have been developed for *E. grandis, E, globulus* and *E. dunnii*, for both solid wood and cellulose production (Methol, 2001; Hirigoyen et al., 2013; Rachid, 2008; Rachid-Casnati, 2014). However, in the light of recent research in the field of biomass use for energy provision, there is interest in having models to estimate aboveground biomass production from *Eucalyptus* spp. energy crops. In this sense, the main objective of this work was to assess the aboveground biomass production of three *Eucalyptus* species (*E. benthamii* Maiden & Cambage, *E. dunnii* Maiden and *E. grandis* Hill ex Maiden), with different planting densities, in soils prioritized for forests of the northern and coastal zones of Uruguay. The specific objectives were i) to evaluate the effect of species and planting density on survival, diameter and height throughout the evaluation period, ii) to fit allometric models for the estimation of volume as a function of easily-measured dasometric variables in the field, iii) to evaluate the effect of species and planting density on volume during the first crop rotation, and iv) to determine the optimum time of harvest for each species/planting density combination.

2. Materials and Methods

2.1. Study area

The experiment was carried out in two different zones: in the north (32º13'30´´S-55º54'40´´W, hereafter Tacuarembó) and west (32º24'05´´S–57º31'02´´W, hereafter Paysandú) (Figure 1). These zones have a temperate subtropical climate, with a mean annual temperature of 18°C (12°C in the coldest month, 24°C in the warmest month). The mean annual rainfall is between 1300 and 1400 mm (Castaño, 2011). According to the National Commission for Agroeconomic Studies of the Land classification (CO.NE.A.T.), soils correspond to group 7.32. Those soils comprise Luvisols and Acrisols: horizon A with 50-60 cm of depth, sandy-loam texture, very-low fertility, high risk of erosion, moderate slopes (3-

4%), weak structure, low organic matter, imperfect drainage and good rooting capacity. The Paysandú soil is classified in CO.NE.A.T. group 9.3 (Uruguayan system of soil aptitude classification), which corresponds to Planosols districts, with low fertility, horizon A with 40 to 50 cm of depth, sandy texture, weak structure, low level of organic matter, slopes of 2-3%, medium to low risk of drought, imperfect drainage, moderately-slow to slow permeability and good rooting ability. A description of soils profiles including a characterization of the main chemical and physical properties were undertaken for both sites 49 months after the trial was installed. Parameters measured were: pH, organic carbon, exchangeable bases (calcium, magnesium, potassium, and sodium), exchangeable acidity (aluminium), and available phosphorus (Bray 1-P) (Tables S1 and S2, Supplementary Material). With this information, soils were classified as fine-loamy, siliceous, Mollic Hapludalf (Bentancor, 2017).

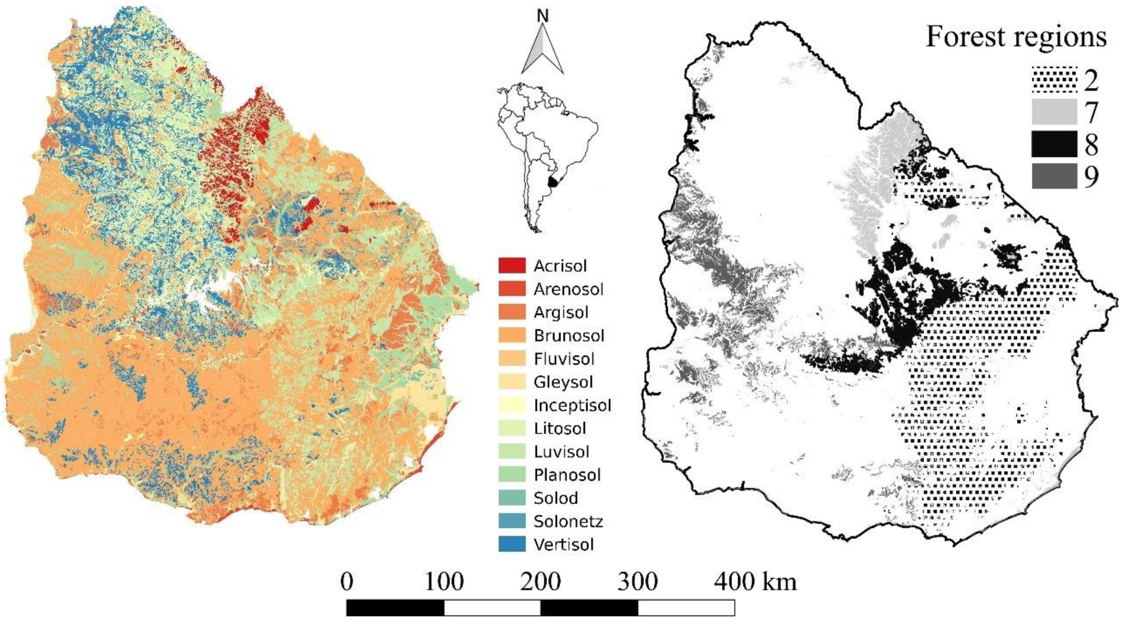


Figure 1.- Soil classification (left) and regions prioritized for forest plantations including trial locations in Paysandú (yellow triangle) and Tacuarembó (red triangle) (right).

2.2. Experimental design

The experiment was designed as a split-plot, with completely-random blocks having three replicates of every treatment at each of the two locations. There were two factors – species (main plot), with three levels, and planting density (subplots), with four levels - and three replicates, forming a total of 12 treatments and 36 plots. The species tested were *Eucalyptus* *benthamii*, *E. dunnii* and *E. grandis*. The planting distances were 3 m x 0.5 m, 3 m x 0.75 m, 3 m x 1 m and 3 m x 1.5 m, corresponding to 6660, 4440, 3330 and 2220 trees per hectare. Plantation densities were chosen based on previous studies which showed high mortality rates when more than 6600 stems are planted per hectare (Rodríguez et al., 3013). The sources of the seeds were Brazil (APS Pinhao-State of Paraná-Brazil) for *E. benthamii*, INIA's (National Institute of Agricultural Research) seed orchard (2^{nd} generation) for *E. grandis* and Undera (Moleton West Coffs Harbor, Australia) for *E. dunnii*. Seedlings were planted on October 13 to 15, 2010 at Tacuarembó and October 27 to November 1, 2010 at Paysandú. The plots used were rectangular, six rows and 25 trees per row. The trees of the four central rows were used for all assessments and the first and the last tree of each row were not measured. The planting area was subsoiled, using a ripper with a single tine, to a depth of more than 60 cm, and soil clods were broken up using a spring harrow and culta-mulcher to provide a more-level surface for planting. Planting and fertilisation were manual. The fertilisation applied 150 kg per hectare of an 18/46/0 (N, P, K) mixture and 180 kg per hectare of a 14/30/12 (N, P, K) mixture plus 6% S, and 0.2% B at Tacuarembó and Paysandú, respectively. This dose was applied at the moment of plantation only. The type and dose of fertilizer was defined by the forestry company where the trials were installed. This responds to expected differences in the chemical properties of both types of soils.

2.3. Sampling and measurements

The total height (H_t, distance between the root collar and the base of the final bud, m) and diameter at breast height (*dbh*, 130 cm above the soil, cm) and the dead trees were measured and recorded at the five inventories: (1) July-October 2011, (2) May-August 2012, (3) January 2013, (4) August-December 2014 and (5) January-July 2015; at both Paysandú and Tacuarembó. The survival in each inventory was calculated as the proportion of living trees in relation to the total planted and expressed as a percentage. The *dbh* was measured with a metric tape, with an accuracy of 0.1 cm, for trees of $dbh \geq 3$ cm in the four central rows of the plot (rows 2 to 5). The H_t (m) was measured with a Vertex IV hypsometer (Haglof, Sweden), in rows 2 to 4. The slenderness coefficient was calculated as the ratio of H_t and *dbh*. This resulted in 39,088 diameter/height observations in a five-year growth period.

Trees of all ages comprised a single dataset to adjust height-diameter equations, using tree number per hectare, for each site, species and planting density as co-variates. For Tacuarembó and Paysandú, equations [1] and [2] were used respectively:

$$H_t = \beta_0 + \beta_1 * dbh + \beta_2 * dbh^{\wedge 2} + \beta_3 * Ln(dbh) + \beta_4 * (1/dbh) + \beta_5 * N + \beta_6 * Ln(N/ha) \quad [1]$$

$$H_t = exp((a + b * Ln(dbh) + c * Ln(dbh^{\wedge 2}) + d * Ln(dbh^{\wedge 3})) \quad [2]$$

Where, H_t is the total height, *dbh* the diameter at breast height, N the number of trees per hectare and $\beta_o, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5$ and β_6 the coefficients of the models (Table S3, Supplementary Material).

In three inventories (2012, 2014 and 2015), a sample of 3 to 5 trees per treatment in each plot was selected for the development of allometric equations representing the diametric classes with the highest relative frequency. The H_t was measured and diameter (including bark) was measured at 0.7 m, 1.3 m and then every meter until 1 cm diameter.

2.4. Volume equation

The individual tree volume (V_i) was calculated based on the diameter measurements at different heights, using equation [3]:

$$V = \pi \frac{1}{3} * l * (\frac{D_1}{2} + \frac{D_2}{2})^2 \quad [3]$$

Equation 3 uses the length (l) and the lower (D_1) and upper (D_2) diameters of each stem section to estimate the volume. Thus, the total volume for each tree was estimated by adding together the volumes of the sections according to Smalian's formulae. With these values, linear (single and multiple) and non-linear (logarithmic) volume equations were adjusted for the site and species according to the *dbh,* total height and number of trees per hectare. For each plot, the volume per hectare was calculated as the product of the average individual tree volume and the number of trees in the plot and expressed as volume with bark per hectare (V_t, $m^3\ ha^{-1}$).

2.5. Optimum time of harvest

Mean annual increment (MAI, $m^3\ ha^{-1}\ year^{-1}$) of volume was computed as the average volume per hectare within a period (MAI = $volume_i / t_i$). The current annual increment (CAI, $m^3\ ha^{-1}\ year^{-1}$) of volume is the growth increase during the current year (CAI=volume t_0 – volume t_i). We estimated the optimum time of harvest when the current annual increment (CAI) equals the mean annual increment (MAI).

2.6. Statistical analysis

The normality of all variables was checked using Shapiro-Wilk's test. Variables without a normal distribution were transformed using the Box and Cox procedure in R. Survival analysis was performed using the Kaplan-Meier non-parametric's test and Log-rank test. The differences in *dbh*, H_t. slenderness, V_i V_t among the densities and species were compared using a two-way analysis of variance (ANOVA) followed by Tukey´s test. Effects of species, plantation density, and interactions were assessed. The effect of species was compared with the interaction between species and blocks, whereas the effects of plantations density and the interaction were compared to the mean squared error (Table 1). The level of significance was set at P<0.05. Results in the tables are shown as means with their standard errors for the untransformed variables. Linear (single and multiple) and non-linear (logarithmic) regressions were carried out to obtain a statistical model to predict the effects of each site and specie on total volume according to the *dbh*, total height and number of trees per hectare. The variables showing the highest correlation coefficient with the volume were used as predictors for each species and site. The polynomial linear models were compared with the standardised error of the residuals, the coefficient of determination (R^2_{ajd}), the root mean square error (RMSE) and the Akaike information criterion (AIC). Relationships between measured and estimated tree volume for each tested specie and site were analyzed. Trees with a height less than 130 cm were omitted. All statistical analyses were performed using R version 3.4.0 (R Development Core Team, 2012). The packages *lmtest*, *reshape*, *ggplot2* and *plyr* were used for ANOVAs test and regression models.

Table 1. Split-plot ANOVA effects

Source	Degrees of freedom
Blocks	B-1
Species	S-1
Error (Blocks*Species)	(B-1)*(S-1)
Planting density	Pd-1
Species*Planting density	(S-1)*(Pd-1)
Error (Blocks*Species*Planting density)	(B-1)*(S-1)*(Pd-1)
Total	(B*S*Pd)-1

Note: B, number of blocks; S, number of Species; Pd, number of Planting densities

3. Results

3.1. Survival

The evolution of survival in both sites according to species and planting density during the evaluation period is shown in Figure 2. Survival between the time of planting and 57 months later averaged 53% in Tacuarembó in contrast to 81% in Paysandú. Between 12 and 8 months and the end of the experiment 57 months later, trees suffered 23% and 10% mortality overall for Tacuarembó and Paysandú respectively. According to the Kaplan-Meier survival curve, significant differences between species and planting densities were observed in both locations ($\chi 2$=49.6 P <0.001 and $\chi 2$=29.1 P <0.001 respectively in Tacuarembó and Paysandú). At Tacuarembó, final tree survival was higher in high density plantations (6660 tree ha^{-1}) for *E. benthamii* (73.3%) and *E. dunnii* (67.3%) compared to *E. grandis* where the highest survival was found at the lowest planting density (64%). Conversely, in Paysandú, the intermediate densities provided the greatest survival for *E. benthamii* (88%), *E. dunnii* (92%).

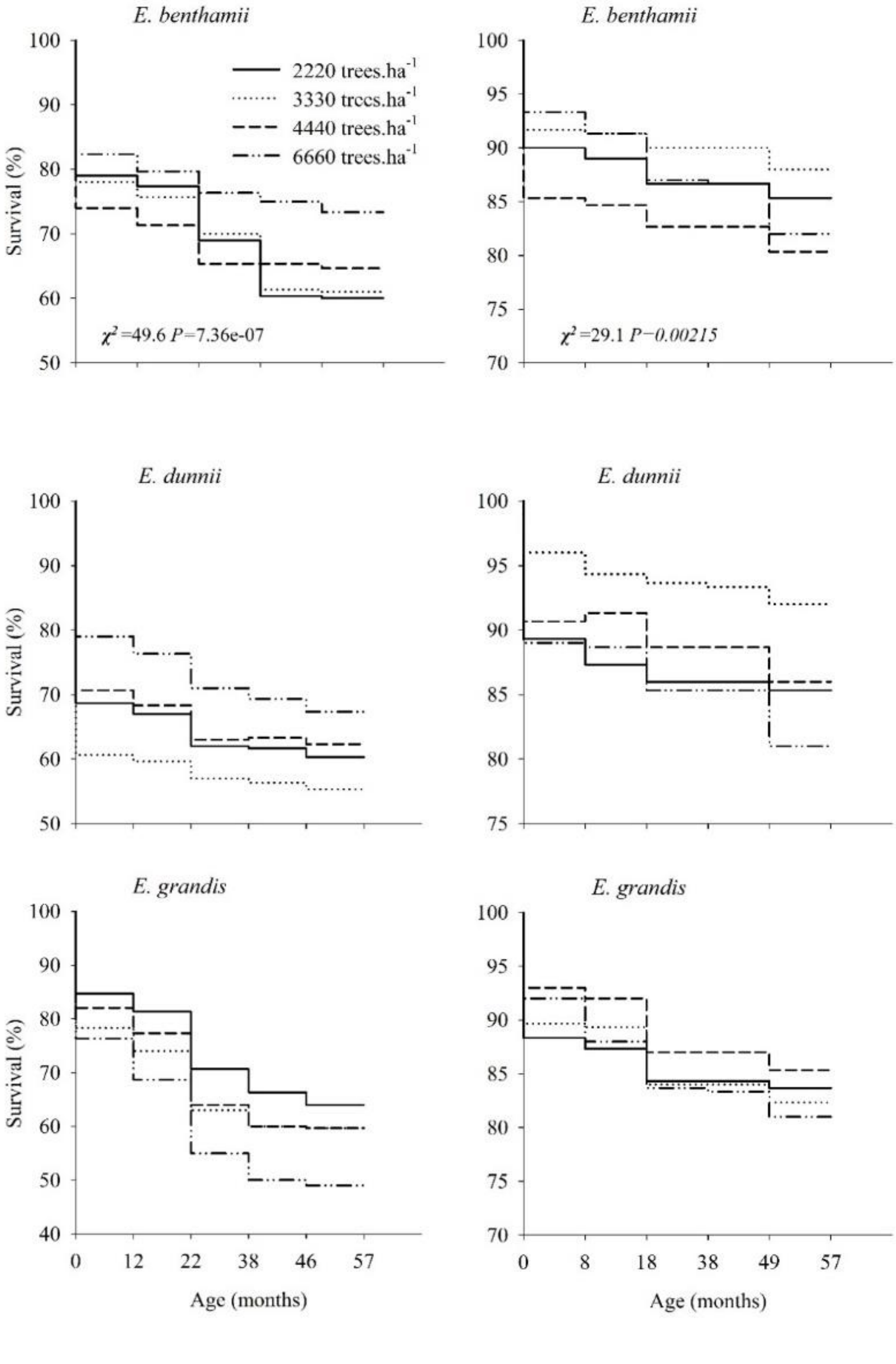


Figure 2. Tree survival for *Eucalyptus* species and stand density tested in Tacuarembó (left) and Paysandú (right) sites (Uruguay).

3.2. Diameter at breast height, total height and slenderness

At both locations, the planting density had a significant effect on all the variables at 57 months (Table 2). ($F_{3,18}$=67.18, $F_{3,18}$=14.78, $F_{3,18}$=19.0, $F_{3,18}$=77.9, $F_{3,18}$=75,65, $F_{3,18}$=8.41 for Tacuarembó and Paysandú respectively).

Table 2. *P* values of two-way ANOVA test for total height (H_t), diameter at breast height (*dbh*), slenderness, tree volume (V_i) and volume per hectare (V_t) in Tacuarembó and Paysandú experiments at 57 months. Bold statistics correspond to significant *P* values ($p < 0.05$).

Effects	Variables	Sites	
		Tacuarembó	**Paysandú**
		p-value	***p-value***
Species	*dbh*	0.642	0.055
	H_t	0.401	0.082
	slenderness	0.363	**0.002**
	V_i	0.913	**0.030**
	V_t	0.353	**0.031**
Density	*dbh*	**<0.001**	**<0.001**
	H_t	**<0.001**	**<0.001**
	slenderness	**<0.001**	**0.001**
	V_i	**<0.001**	**<0.001**
	V_t	**<0.001**	0.071
Species*	*dbh*	0.081	0.916
Density.	H_t	0.636	**<0.001**
	slenderness	0.093	**0.006**
	V_i	0.099	0.170
	V_t	**0.016**	0.102

At Paysandú, on the other hand, the effect of the interaction (Species*Planting Density) was significant for the *H* and slenderness ($F_{6,18}$=6.9, P<0.001, $F6_{,18}$=4.37, P=0.0068). The values of *dbh*, H_t, slenderness, MAI, CAI, V_i and V_t for the distinct species and planting densities 57 months after planting are presented in Table 3. At Tacuarembó, all species showed lower *dbh* and H_t, and higher slenderness with increasing planting density; *E. grandis* had the greatest *dbh* at almost all planting densities while *E. benthamii* and *E. dunnii* had similar value.

Table 3. Average growth values ± S.E. by location, species, and planting density at age 57 months

Sites	species	Planting density (trees ha^{-1})	*Ht* (m)	*dbn* (cm)	Slenderness (*Ht/dbh*)	*Volume* (m^3 tree^{-1})	*Volume* (m^3 ha^{-1})	MAI (m^3 ha^{-1} year^1)	CAI (m^3 ha^{-1} year-^{1})
Tacuarembó	*E. benthamii*	2220	17.5 (0.2)	14.9 (0.9)	1.18 (0.030)	0.17 (0.016)	205.6 (6.0)	43.3 (1.3)	44.2 (6.2)
		3330	15.6 (0.6)	11.9 (0.1)	1.31 (0.043)	0.11 (0.02)	226.4 (25.0)	47.7 (5.3)	48.1 (4.1)
		4440	15.5 (0.8)	11.8 (1.0)	1.31 (0.019)	0.11 (0.02)	327.5 (26.4)	68.9 (5.6)	60.5 (12.4)
		6660	14.1 (0.4)	10.3 (0.9)	1.37 (0.053)	0.09 (0.017)	416.4 (45.1)	87.7 (9.5)	87.2 (22.4)
	E. dunnii	2220	16.2 (0.1)	15.1 (0.3)	1.07 (0.016)	0.17 (0.008)	205.6 (4.3)	43.3 (0.9)	43.7 (6.0)
		3330	16.5 (0.4)	14.2 (0.6)	1.17 (0.151)	0.14 (0.009)	256.2 (6.2)	53.9 (1.3)	43.0 (3.3)
		4440	15.1 (0.5)	11.9 (0.4)	1.26 (0.124)	0.10 (0.009)	267.7 (14.9)	56.4 (3.1)	40.9 (0.9)
		6660	13.7 (0.7)	9.4 (0.3)	1.45 (0.077)	0.07 (0.006)	294.1 (15.2)	61.9 (3.2)	51.9 (12.7)
	E. grandis	2220	16.8 (0.5)	15.6 (0.2)	1.08 (0.061)	0.17 (0.009)	235.6 (17.1)	49.6 (3.6)	54.8 (10.2)
		3330	15.3 (0.6)	13.5 (0.7)	1.14 (0.032)	0.13 (0.007)	243.0 (16.2)	51.2 (3.4)	59.0 (3.3)
		4440	15.8 (1.2)	12.7 (0.3)	1.24 (0.018)	0.12 (0.007)	296.7 (11.2)	62.5 (2.4)	64.9 (9.0)
		6660	13.6 (0.6)	11.2 (0.2)	1.21 (0.013)	0.09 (0.004)	294.7 (14.5)	62.0 (3.0)	47.5 (10.3)
Paysandú	*E. benthamii*	2220	17.6 (0.3)	12.6 (0.3)	1.40 (0.030)	0.13 (0.005)	234.8 (8.4)	49.4 (1.8)	8.9 (16.8)
		3330	14.4 (0.4)	10.8 (0.1)	1.34 (0.043)	0.08 (0.002)	239.7 (18.3)	50.5 (3.8)	54.2 (29.7)
		4440	14.3 (0.4)	9.9 (0.2)	1.44 (0.019)	0.08 (0.003)	269.2 (12.8)	56.7 (2.7)	20.0 (18.6)
		6660	11.9 (0.1)	8.3 (0.4)	1.44 (0.053)	0.05 (0.005)	272.4 (19.3)	57.4 (4.0)	49.7 (17.0)
	E. dunnii	2220	17.4 (0.8)	12.7 (0.3)	1.37 (0.016)	0.14 (0.008)	256.2 (15.7)	53.9 (3.3)	15.7 (8.4)
		3330	17.2 (0.7)	10.4 (0.4)	1.65 (0.151)	0.09 (0.009)	269.7 (24.4)	56.8 (5.1)	16.5 (7.4)
		4440	15.2 (0.5)	9.2 (0.4)	1.65 (0.124)	0.07 (0.007)	245.6 (26.1)	51.7 (5.4)	14.7 (11.9)
		6660	14.7 (0.3)	7.8 (0.2)	1.88 (0.077)	0.05 (0.004)	248.8 (13.4)	52.4 (2.8)	−9.2 (8.3.8)
	E. grandis	2220	16.4 (0.5)	13.8 (0.9)	1.19 (0.061)	0.16 (0.016)	285.6 (27.3)	60.1 (5.7)	34.4 (8.4)
		3330	16.2 (0.4)	12.1 (0.1)	1.34 (0.032)	0.14 (0.006)	366.2 (22.6)	77.1 (4.7)	36.0 (18.7)
		4440	15.0 (0.6)	10.6 (0.6)	1.41 (0.018)	0.11 (0.014)	407.6 (30.8)	85.8 (6.4)	71.2 (6.0)
		6660	13.2 (0.5)	9.3 (0.1)	1.42 (0.013)	0.08 (0.002)	427.9 (14.2)	90.1 (3.0)	35.2 (20.3)

The analysis also highlighted *E. grandis* as the species with the greatest *dbh* at Paysandú, at all planting densities. At Tacuarembó, the reduction in individual growth (diameter) between the extreme densities (2220 vs 6660 trees ha^{-1}) was 38, 31 and 28% for *E. dunnii*, *E. benthamii* and *E. grandis*, respectively. The reduction in height was 15, 19 and 19%, respectively. At Paysandú, these values were somewhat higher, for both diameter (38, 34 and 32%, respectively) and height (16, 32 and 20%, respectively) (Figures 3 and 4).

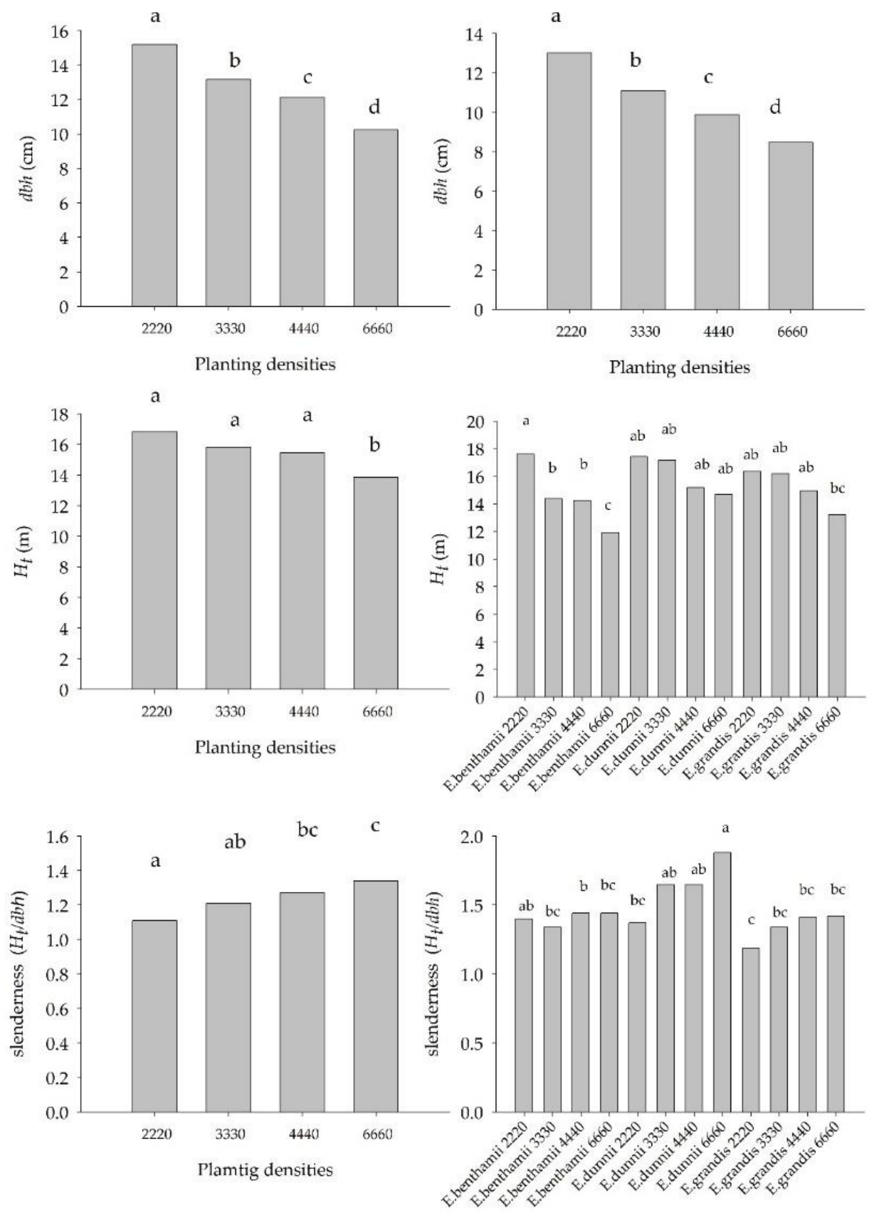


Figure 3. Results of the Tukey test for means comparison for *dbh*, *Ht* and slenderness for Tacuarembó (left) and Paysandú (right) at 57 months. Different letters indicate significant differences with a 5% probability level.

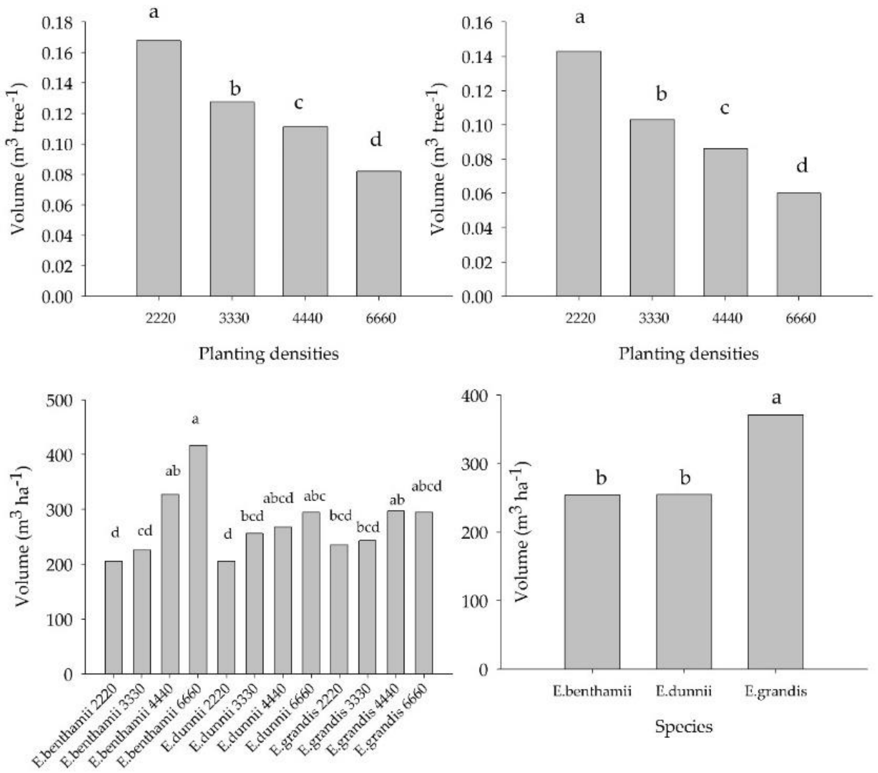


Figure 4. Results of the Tukey test for means comparison of Vi and Vt for the Tacuarembó (left) and Paysandú (right) at 57 months. Different letters indicate significant differences with a 5% probability level.

3.3. Allometric equations and volume

The tree models of volume are included in Table 4, where the best fits for each species and site are shown. The models indicated in bold are those that were selected based on the R^2, RMSE Bias, AIC and measured vs. estimated volume graphs.

The V_i was highly significant at Tacuarembó for the planting density and Paysandú for the species and planting density (Table 2). In Tacuarembó, a significant interaction between the species and planting density was also detected for V_t ($F_{6,18}$=3.65, P=0.016) and at Paysandú a significant effect the specie was detected ($F_{2,4}$=9.25, P=0.031). The maximum values of over bark volume per hectare were obtained with the highest densities (Table 3). At Tacuarembó, *E. benthamii* showed the highest volume at the highest density (416.4 m^3 ha^{-1}) compared to *E. grandis* which had the highest volume (427.8 m^3 ha^{-1}) at Paysandú. At Tacuarembó, the highest volume values were obtained for *E. benthamii* at densities of 4440 and 6660 trees per hectare. This, in turn, could have influenced the differences in growth between the two extremes of density (6660 vs 2220 trees ha^{-1}), as *E. benthamii* showed an increase of 102% between these two densities. By comparison, *E. dunnii* and *E. grandis* exhibited increases in growth of 43 and 25%, respectively. For these two species, growth was greatest at the lowest densities, their values being very similar. At Paysandú, the increase in volume growth at 6660 relative to 2220 trees per hectare was approximately 50% for *E. grandis* and 16% for *E. benthamii*, although the latter was not significant; *E. dunnii* also showed no differences in volume growth between densities, explained by a greater reduction of survival at higher densities.

Table 4. Predictive equations and statistics of fit for individual tree volume (*Vi*) for three species of *Eucalyptus* planted in each studied site. The selected models are in bold.

Site	Species	Models	R^2	RMSE	Bias	AIC	F	p-value
Tacuarembó	*E. benthamii*	**$V_i = \exp((-9.86876-0.29901*Ln(dbh)+1.05411*Ln(dbh^2*H_t))$**	0.99	0.009	0.0001	-362	15150	<0.001
		$V_i=\exp((-9.35966+2.75971*Ln(dbh))$	0.94	0.020	-0.0010	121	5111	<0.001
		$V_i=-0.02471+0.006340*(dbh)+0.00003951*(dbh^2*H_t)*-0.0003778*(dbh^2)$	0.98	0.009	0.0048	-1111	4197	<0.001
	E. dunnii	**$V_i=-0.005625+0.001523*(dbh)+0.00003184*(dbh^2H_t)$**	0.98	0.002	0.0050	-1019	6033	<0.001
		$V_i=\exp((-8.38487+2.38262*Ln(dbh))$	0.95	0.015	0.0004	104	5095	<0.001
		$V_i= \exp((-9.86876-0.29901*Ln(dbh)+1.05411*Ln(dbh^2*H_t))$	0.96	0.013	0.0079	208	7893	<0.001
	E. grandis	**$V_i=-0.01781+0.004755*(dbh)-0.0003141*(dbh^2)+0.00004038*(dbh^2*H_t)$**	0.99	0.007	0.0042	-1159	8847	<0.001
		$V_i=\exp((-9.48276+1.38990*Ln(dbh^2))$	0.96	0.017	0.0001	118	8696	<0.001
		$V_i=\exp((-9.79678+0.12407*Ln(dbh)+0.91076*Ln(dbh^2*H_t))$	0.99	0.008	0.0005	236	31360	<0.001
Paysandú	*E. benthamii*	**$V_i=\exp((-9.711769+0.936637*Ln(dbh^2*H_t))$**	0.99	0.005	0.0002	-441	44070	<0.001
		$V_i=\exp((-8.99697+02.65528*Ln(dbh))$	0.96	0.011	0.0040	-1510	5885	<0.001
		$V_i=\exp((-9.70756+0.01996*Ln(dbh)+0.92976*Ln(dbh^2*H_t))$	0.99	0.005	0.0002	-441	21910	<0.001
	E. dunnii	**$V_i=0.02608-0.009986*(dbh)+0.001309*(dbh^2)$**	0.98	0.009	0.0068	-1093	3177	<0.001
		$V_i=\exp((-9.01150+2.65731*Ln(dbh))$	0.95	0.010	0.0020	116	4011	<0.001
		$V_i=\exp((-9.01550+1.32866*Ln(dbh^2))$	0.96	0.009	0.0016	116	4011	<0.001
	E. grandis	**$V_i=-0.006259+0.002463*(dbh)+0.00004120*(dbh^2*H_t)*-0.000226*(dbh^2)$**	0.99	0.004	0.0026	-1371	22980	<0.001
		$V_i=\exp((-9.25879+2.75792*Ln(dbh))$	0.96	0.015	0.0001	116	6477	<0.001
		$V_i=\exp((-9.79678+0.12407*Ln(dbh)+0.91076*Ln(dbh^2*H_t))$	0.99	0.005	0.0005	233	28120	<0.001

3.4. Optimum time of harvest

The higher planting densities resulted in higher MAI and CAI, excepting for *E. dunnii* in Paysandú, for which values were similar for all plantation densities. (Table 3). At Tacuarembó and in all treatments, CAI values increased until month 40th after which a noticeable reduction in the values of this parameter occurred (Figures 5-7), with a change in the volume growth rate respected to MAI. At Paysandú the values of both parameters showed a similar tendency in the sense that the major decreases in volume growth occurred around 40 months after planting (Figures 8-10). The evolution of MAI was different of that of CAI in the sense that up to 40 months the increase continued until the end of the study period (57-months). At Tacuarembó, in most treatments the CAI was equal to the MAI, and those the optimum time of harvest, in month 46, but at Paysandú, for all species and planting densities, this point occurred around 49 months after planting.

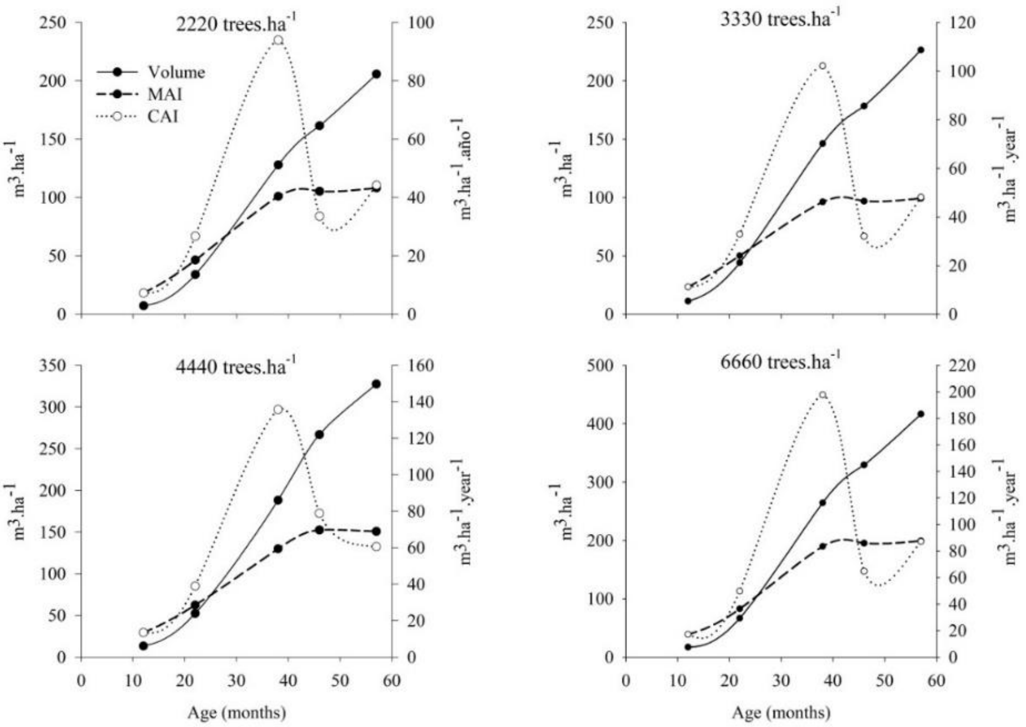


Figure 5. Cumulative growth mean annual increment and current annual increment of volume of *E. benthamii* in Tacuarembó for each stand density.

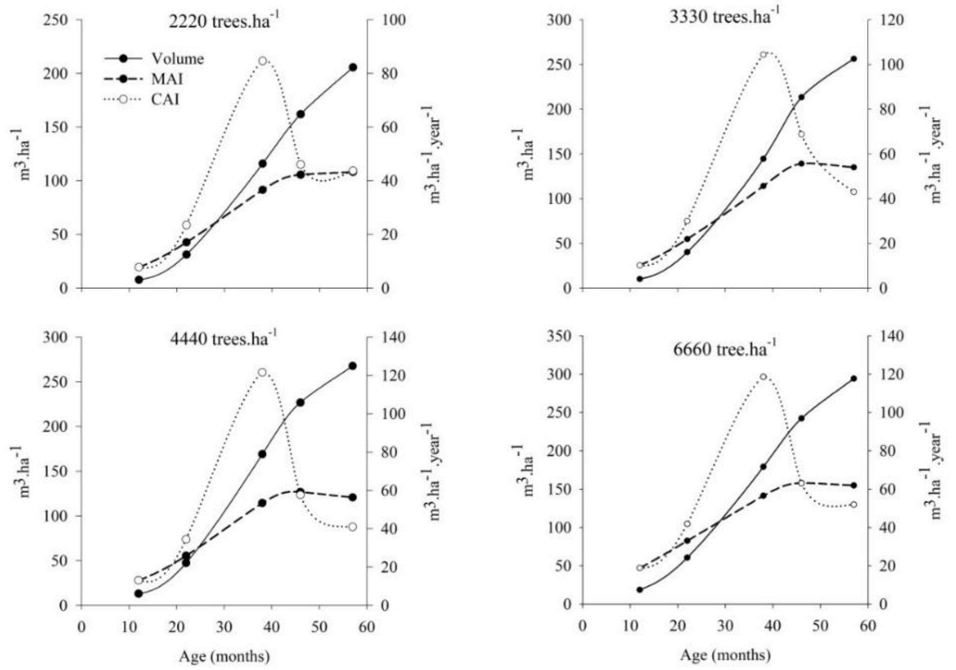


Figure 6. Cumulative growth mean annual increment and current annual increment of volume of *E. dunnii* in Tacuarembó for each stand density.

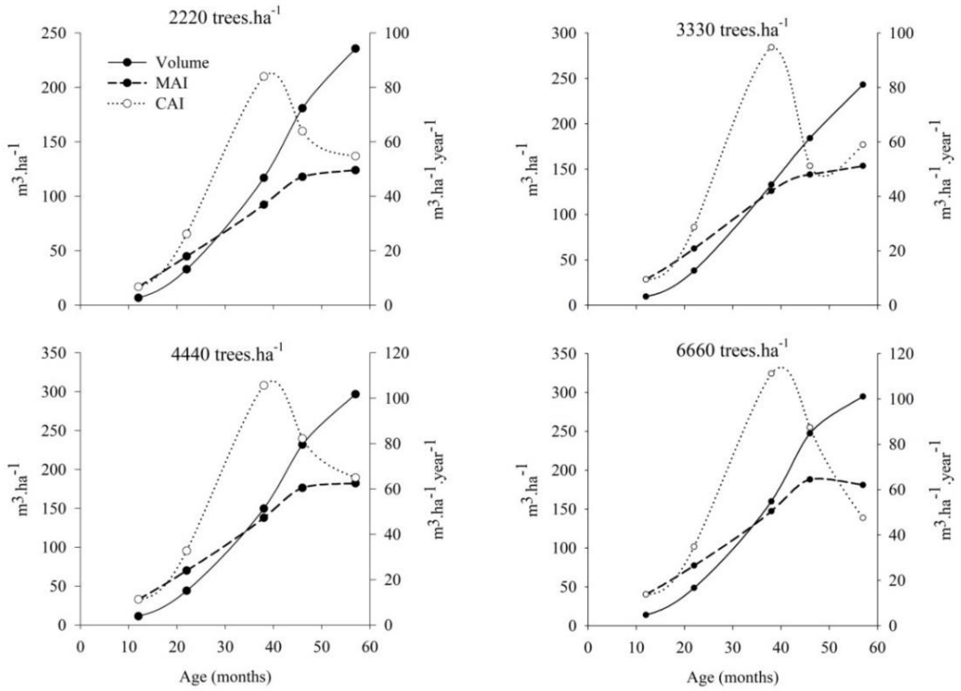


Figure 7. Cumulative growth mean annual increment and current annual increment of volume of *E. grandis* in Tacuarembó for each stand density.

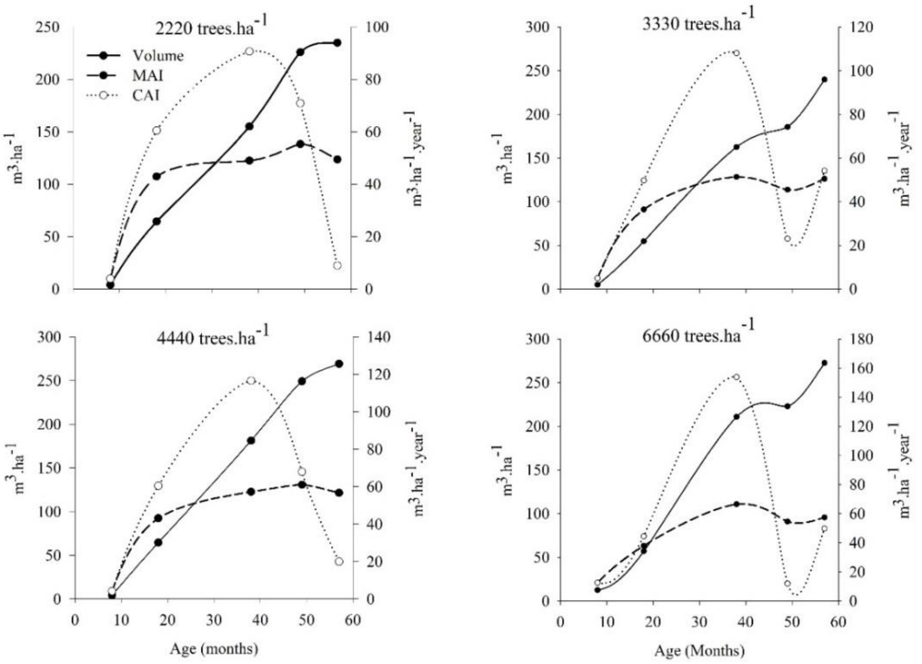


Figure 8. Cumulative growth mean annual increment and current annual increment of volume of *E. benthamii* in Paysandú for each stand density

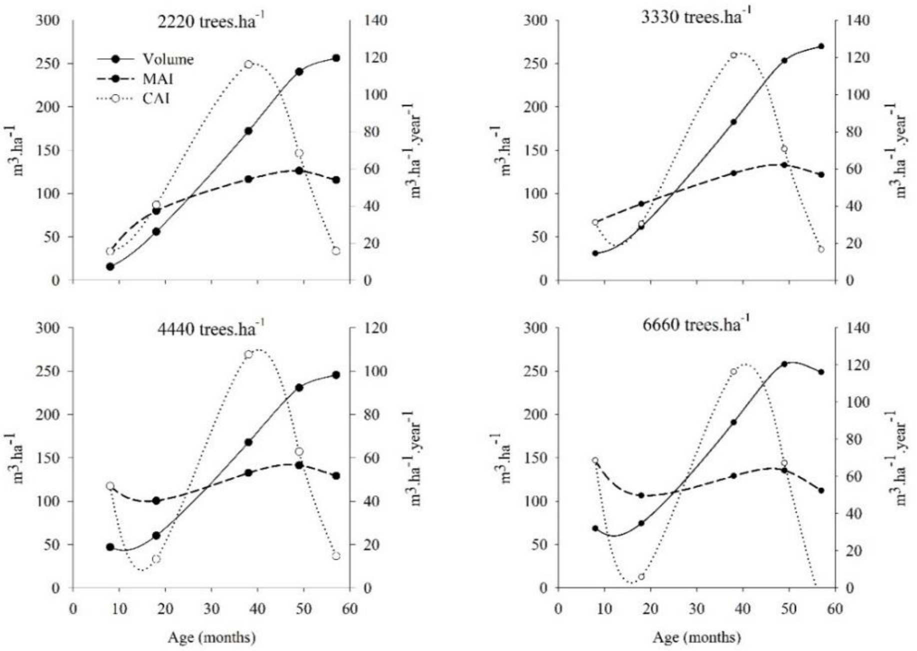


Figure 9. Cumulative growth mean annual increment and current annual increment of volume of *E. dunnii* in Paysandú for each stand density.

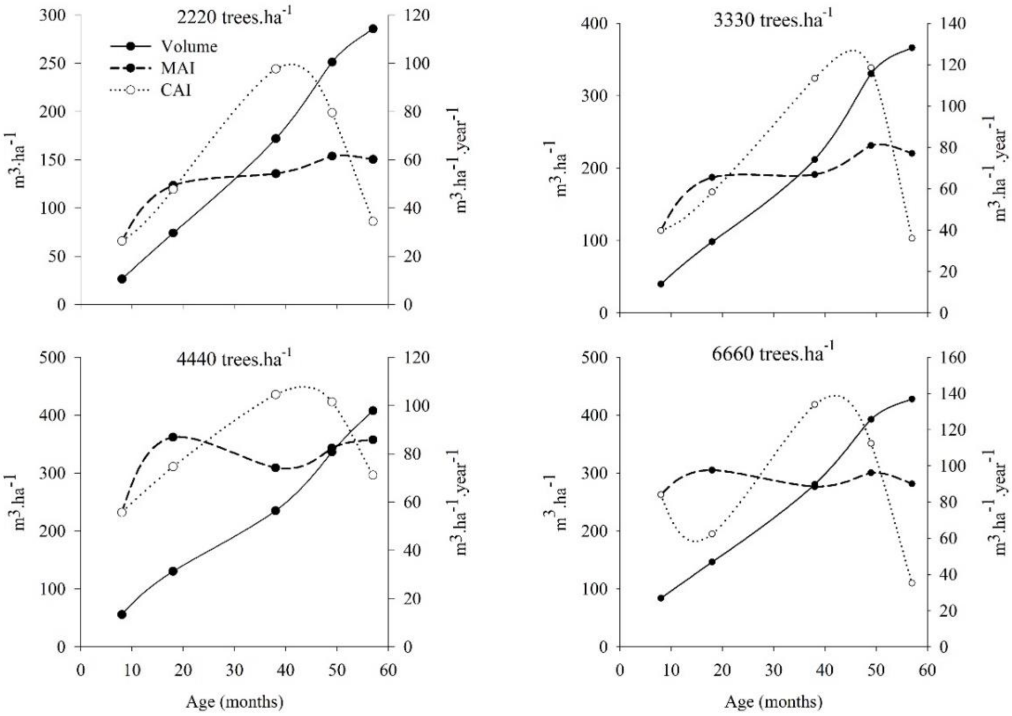


Figure 10. Cumulative growth mean annual increment and current annual increment of volume of *E. grandis* in Paysandú for each stand density.

4. Discussion

4.1. Survival

The results obtained in this work do not confirm the hypothesis that greater competition among trees determines an increase in tree mortality over time (Harris, 2007; Schneider et al., 2015). There is extensive information on competition in relation to planting density and mortality (Larson et al., 2015; Van Gunst et al., 2016); this indicates that the relationship between these two parameters depends on factors such as age, growth rate and soil quality (Schönau and Coetzee, 1989; Dwyer et al., 2010) and in some cases it is not possible to establish an evident relationship between them (Lonsdale, 1990). The mortality results of this work indicate that 57 months after planting severe competition between individuals was not occurring, even at the highest densities (> 6000 trees ha−1). This supports the idea that tree mortality does not depend on planting density (Lintz et al., 1016) and has a random distribution pattern (Puettman et al., 2016) associated with the climate (Gendreau-Berthiaume et al., 2016). At each site, the evolution of survival was similar among the three species, but with important differences among the different planting densities. Similar results were obtained when evaluating high planting densities with clones of *E. globulus* in Chile (Schäfer and Ponce, 2007) and when evaluating *E. camaldulensis* at densities up to 2200 trees per hectare (Akhtar et al., 2008). Those authors indicated that the reduction in the number of live trees, at least in the first years of growth, could be explained by reasons other than competition among individuals. Some authors mention soil fertility, the intensity of silviculture and water availability as the main factors that explain the survival of trees in the early stages of growth (Sale, 2005; Jacobs, 1955). Soil analysis indicated that soils of both sites are appropriate for growth of all three species studied. Likewise, in both sites the quality of soil preparation assured good conditions for seedlings´ growth. In this study, a gradual decline in tree survival over the 57 months after planting was observed in all cases, although at Tacuarembó there was a noticeable reduction in the number of live trees at 12 months and significant mortality at the end of the evaluation period unlike at Paysandú, where survival was relatively high for most treatments. Higher mortatlity rate in Tacuarembó could be explained by weed competition in the initial growth stages in this particular site. The precipitation patterns at the two sites do not explain the differences in tree mortality (Figure S1, Supplementary material). The standardised precipitation index (IPE) of the evaluation period, which measures the excess or deficit of precipitation in relation to the historical average (1980-2010) (INUMET, 2017), shows that there were no significant drought events at either site that could have compromised the survival of the trees (Figure S2, Supplementary material). The average IPE value recorded in the first year at Tacuarembó (-0.6) indicates slightly-dry conditions, but with levels of water availability in the soil that would not be limiting for the growth of these Eucalyptus spp., even in the current situations. In the case of lower planting densities with *E. benthamii* and *E. dunnii*, mortality in the last stages of evaluation may be due to the loss of smaller trees (Akhtar et al., 2006; Bouvet, 1997; Newton and Jolliffe, 1998). *E. grandis* in Tacuarembó however, was the only species for which lower survival rates was related to competition among trees in higher plantation densities (Brand and Magnussen, 1988; von Euler et al., 1992; Tomé et al., 1994).

4.2. Height, diameter and slenderness

For both sites, the H_t and *dbh* values show that the three species had very-similar growth with the exception of *E. grandis* at Paysandú, with a smaller *dbh*. The effect of the planting density on growth was consistent with that reported in the literature (Brand and Magnussen, 1988; von Euler et al., 1992: Tomé et al., 1994; Jacobs 1995; Bouvet 1997; Newton and Jolliffe, 1998; Gonçalves et al. 2004; Sale 2005; de Córdoba et al., 2012; de Jesus et al., 2013): a reduction of growth as density increased was observed in both sites. The reduction in diameter was greater than for height because of the increased competition among trees; the height largely depends on site quality and is affected little by forestry practices (Alcorn et al., 2007; Neto et al., 2010). The higher values of *dbh* recorded for all species at Tacuarembó seem to be related to less competition between individuals, given the lower survival rate recorded at that site. A reduction in *dbh* and *H* between the extreme densities (2220 vs 6660 trees ha^{-1}) was observed for *E. dunnii*, *E. benthamii* and *E. grandis*, respectively. At Paysandú, these differences values were somewhat higher, for both *dbh* and *H*. These differences between sites can probably be explained by the higher survival at Paysandú. The effect of the competition also resulted in a smaller tapering, expressed as a lower conicity of the trees, as shown by the ratio between tree height and *dbh*. For all three species, greater slenderness was obtained when the planting density was increased. This was more evident in Paysandú, probably due to the greater survival rate. Some authors reported increases in the height of eucalyptus species with increased density due to intense competition for light, the trees seeking to maximise the exposed leaf surface area (Patiño-Valera, 1990; Assis et al., 1999). According to several authors, increased competition determines the occurrence of suppressed trees associated to the phenomenon of asymmetric competition (between trees of different size), which determines that smaller trees lose their vigour more quickly than larger trees and become suppressed (Brand and Magnussen, 1988; Forrester et al. 2013). Some authors consider that this asymmetric competition occurs between both aerial parts and roots (Chrstina et al., 2011; Trouvé et al., 2014), and that it is more evident at sites with greater availability of resources (Campoe et al., 2013). This effect is more evident under conditions of more-severe competition (basically for light) associated with more reduced spacing. With wider spacing, there is a high proportion of larger trees, which are more competitive for light and nutrients than trees spaced more closely together (Campoe et al., 2013; Binkley et al., 2013). The efficiency of the different types of trees is the result of the tissue distribution within the different components of the tree (Xue et al., 2011), resulting in larger trees with greater growth of wood than of below-ground tissues (Stape et al., 2010).

4.3. Allometric equations and volume

The relationship between the stem volume values and dbh^2 and $dbh^2 * H$ was assessed using different types of models in agreement with previous studies (Rance et al., 2012; Kuyah et al., 2013; Vega-Nieva, 2015) (Table 3). Among the independent variables evaluated, the planting density did not make a significant contribution to the fitting of the models. The *dbh* and $dbh * H_t$ (or their transformations) are frequently used to predict the weight and volume of trees; although age, density and mean square diameter are variables also used in volume models (Bravo et al., 2008). These results were expected considering the close relationship between stem volume and *dbh* and *H*, although some authors have also obtained models with a high degree of fit using basal area and dominant height as independent variables (Bravo et al., 2008). The R^2 values obtained were high for all the selected models, while REMC and E were very close to zero - which implies that these models have high precision and the results they predict show a very-low deviation from those observed (Segura and Andrade, 2008). The *E. dunnii* and *E. grandis* selected models were those with the lowest values of AIC in both sites. The graphs analysis of measured vs. estimated volume shows that, except with *E. grandis* in Paysandú, the point cloud is aligned along the line x = y, with a slope very close to 1, indicating that the errors of the prediction is very low in all cases as shown by the REMC values (Figure S3, Supplementary material). The *E. grandis* models for Paysandú underestimates the observed values. With the exception of the *E. dunnii* model for Paysandú, the models give higher prediction errors as the volume values increase.

The individual volume followed the same trend as H_t and *dbh* in relation to species and planting density, at both sites (Table 3) (Berger et al., 2002; Pinkard and Neilsen, 2003; Morais, 2006).The evolution of the volume values shows that all species and planting densities had very-similar behaviour, with a relatively-sustained increase in volume up to 57 months. According to (von Euler et al., 1992), volume is a better indicator of individual growth with respect to *dbh*, since under intense competition trees may accumulate significant wood volume in the upper portion of the stems. All three species reached similar growth levels, related to greater individual volumes at lower densities. The reduction of volume (6660 trees ha^{-1} vs 2220 trees ha^{-1}), as a function of increased competition, was greater than those recorded for *dbh* and H_t because it added together the responses of these two parameters. This effect was more important at Paysandú, associated with survival differences. On both sites, *E. dunnii* exhibited the greatest changes in individual growth in relation to tree spacing.

At Tacuarembó the analysis of variance detected a significant effect of the species planting density interaction, indicating a close relationship between these two factors and the volume per hectare. The values of accumulated volume at both sites confirm the hypothesis that overall productivity is increased by raising the planting density (Rodríguez et al., 2013). The highest volume values were obtained for *E. benthamii* at densities of 4440 and 6660 trees per hectare, explained basically by its greater survival at the final assessment. For all the species the growth was lower at the lowest planting densities. This, in turn, could have influenced the differences in growth between the two extremes of density (6660 vs 2220 trees per hectare), as *E. benthamii* showed an increase of 102% between these two spacings. By comparison, *E. dunnii* and *E. grandis* exhibited increases in growth of 43 and 25%, respectively. For these two species, growth was greatest at the highest densities, their values being very similar. At Paysandú, the evolution of the volume values shows that all species and planting densities had very-similar behaviour, with a relatively sustained increase in volume up to 57 months. *E. grandis* had the greatest volume per hectare, while *E. benthamii* and *E. dunnii* reached similarly lower levels. Except for *E. dunnii*, a direct relationship between volume production and planting density was observed at Paysandú. Several studies have reported the effect of density on volume growth for *Eucalyptus* species (Leite et al., 1997; Berger et al., 2002; Akhtar et al., 2008; Gonçalves et al., 2004;). The increase in volume growth at 6660 relative to 2220 trees per hectare was approximately 50% for *E. grandis* and 16% for *E. benthamii*, although the latter was not significant; *E. dunnii* also showed no differences in volume growth between densities, explained by a greater reduction of survival at higher densities. The volume of *E. dunnii* increased until 48 months, decreasing thereafter. These results agree with those reported by several other authors, in the sense that the increase in planting density did not translate into the same increment of productivity per unit area (Gendreau-Berthiaume et al., 2016). In most cases, individual growth decreased when the density increased; as compensation, the population growth increased (Rodríguez et al., 2013). This compensation effect promoted by competition means that increased growth of larger trees exceeds the loss that occurs in smaller trees, resulting in increased productivity per unit area (Akhtar et al., 2008).

4.4. Optimum time of harvest

At Tacuarembó, the curves of the MAI values showed a similar trend, with two differentiated stages: a first stage with increments, lasting until approximately month 48, and then a second stage with a stabilization of values. The behaviour in this latter stage, according to the reports of some authors, is the result of intense competition producing an increase in the proportions of suppressed trees (Balloni, 1980; Rodríguez et al., 2013). At Paysandú, the MAI values showed a variable behaviour with a tendency to decrease towards the end of the evaluation period. The highest MAI values were obtained with *E. benthamii* and *E. grandis* at Tacuarembó and Paysandú, respectively, as a function of the accumulated volume values.

The intersection of the CAI and MAI curves indicate that the maximum production per unit of time was obtained for trees that were close to 48 months-old in most cases, indicating the optimum time of harvest. These results confirm the tendency, cited by several authors, that high densities allow high levels of productivity to be obtained in relatively-short times (Goulart et al., 2003; Sochacki et al., 2007). However, the idea that higher planting densities advance the time of harvest was not supported (Rodríguez et al., 2013); although the results seem to confirm that higher densities give high levels of production in shorter rotations than with lower densities (Chen et al., 2011; Sartório, 2014). According to some authors, the intense competition at higher densities causes a more-proportional use of the environmental resources by the dominant trees, increasing the number of suppressed trees and finally resulting in tree death (Binkley et al., 2002; Cunningham et al., 2010;). In these cases, the mortality of suppressed trees probably reduces the effects of competition among trees, allowing larger and dominant trees to maintain their growth rates at relatively-high levels (Binkley et al., 2002). The higher productivity of the Paysandú soil is related to the greater survival and homogeneity of growth - leading to the low presence of small trees, which are inefficient in the use of light (Binkley et al., 2010; Campoe et al., 2013). Changes in planting densities allow larger trees to maintain high growth rates, which compensate for the low growth of suppressed trees (Berger et al., 2004). It is possible, therefore, that, at least up to 57 months of growth, there were no significant limitations on the availability of water for tree growth, taking into account that the soils of the evaluated sites are classified as very suitable for forestry (MGAP, 1979) and the high level of precipitation that occurred at both sites (INUMET, 2017).

5. Conclusions

The survival of *E. grandis*, *E. benthamii* and *E. dunnii* was not related to planting density, and the highest mortality values occurred, after the first year, in Tacuarembó. At that site, the effects of competition among trees were more evident at the highest planting density for *E. grandis*. At Paysandú, the survival response of all three species survival to changes in density was very similar. In all species, the reduction in *dbh* was more marked than that of H_t, as planting density increased. Tree volume showed the same trend as *dbh* and H_t growth, but with a greater reduction than these at higher densities. At both sites, the total volume values were highest with higher planting densities. Thus, the reduction in individual growth was offset by the increase in the number of trees. At Tacuarembó, the highest production was obtained with *E. benthamii* at 4440 and 6660 trees per hectare. At Paysandú, *E. grandis* was the species with the highest levels of productivity per hectare. With all species and planting densities there was an increase in the accumulated volume during the 57-month study period; however, the growth curves indicate that the maximum production per unit time and, therefore, the optimum harvest time occurred at 48 months. The higher densities did not bring forward the time of harvesting but gave high levels of production in a relatively-short time. Results of this study are relevant for foresters or government agents selecting species for biomass production.The information offered could help on planning crop tree plantations at a regional scale, reducing uncertainty of biomass production estimates, and provide a theoretical basis for the sustainable management of intensive Eucalyptus plantations.

6. References

Akhtar, J.; Z.A. Saqib; R.H. Qureshi; M.A. Haq; M.S. Iqbal; N.E. Marcar. 2008. The effect of spacing on the growth of *Eucalyptus camaldulensis* on salt-affected soils of the Punjab, Pakistan, Canadian Journal of Forestry Research. 38: 2434–2444.

Alcorn, P.J..; P. Pyttel; J. Bauhus; R.G.B. Smith; D. Thomas; R. James; A. Nicotra. 2007. Effects of initial planting density on branch development in 4-year-old plantation grown *Eucalyptus pilularis and Eucalyptus cloeziana* trees, Forest Ecology and Management. 252: 41–51.

Assis, R.; M. Ferreira; E. de Morais; L. Fernandes. 1999. Produção de biomassa de *Eucalyptus urophylla* s.t. blake sob diferentes espaçamentos na região de cerrado de Minas Gerais, Revista Arvore. 23: 151–156.

Balloni, E.A.; J.W. Simoes. 1980. O espaçamento de plantio e suas implicações silviculturais, Série Técnica. Piracicaba: IPEF. 1: 1–16.

Berger, R.; P.R. Schneider; C.A.G. Finger; C.R. Haselein. 2002. Efeito do espaçamento e da aduabação no crescimento de um clone de *Eucalyptus saligna* Smith, Ciência Florestal. 12: 75–87.

Berger, U.; H. Hildenbrandt; V. Grimm. 2004. Age-related decline in forest productivity: modelling the role of neighbourhood cometition, Journal of Ecology. 92: 846–853.

Binkley, D.; J.L. Stape; M.G. Ryan; H.R. Barnard; J. Fownes. 2002. Age-related decline in forest ecosystem growth: An individual-tree, stand-structure hypothesis, Ecosystems. 5: 58–67.

Binkley, D.; J.L. Stape; W.L. Bauerle; M.G. Ryan. 2010. Explaining growth of individual trees: Light interception and efficiency of light use by Eucalyptus at four sites in Brazil, Forest Ecology and Management. 259: 1704–1713.

Binkley, D.; O.C. Campoe; M. Gspaltl; D.I. Forrester. 2013. Light absorption and use efficiency in forests: Why patterns differ for trees and stands, Forest Ecology and Management. 288: 5–13.

Bouvet, J.M. 1997. Effect of spacing on juvenile growth and variability of eucalyptus clones, Canadian Journal of Forest Research. 27: 174–179. file:C:/Users/xwei/Reprints/SortedByLetters/A/BouvetJM spacing on gowth and variability euc.pdf.

Brand, D.G.; S. Magnussen. 1988. Asymmetric, two-sided competition in even-aged monocultures of red pine, Canadian Journal of Forestry Research 18: 901–910.

Bravo, F.; A. Bravo-Oviedo; L. Diaz-Balteiro. 2006. Carbon sequestration in Spanish Mediterranean forests under two management alternatives: a modeling approach, Eur J Forest Res. 127: 225–234.

Brown, S. 2002. Measuring carbon in forests: current status and future challenges, Environmental Pollution. 116: 363–372.

Campoe, O.C. J.L. Stape; T.J. Albaugh; H. Lee Allen; T.R. Fox; R. Rubilar; D. Binkley. 2013. Fertilization and irrigation effects on tree level aboveground net primary production, light interception and light use efficiency in a loblolly pine plantation, Forest Ecology and Management. 288: 43–48.

Campoe, O.C.; J.L. Stape; Y. Nouvellon; J.P. Laclau; W.L. Bauerle; D. Binkley; G. Le Maire. 2013. Stem production, light absorption and light use efficiency between dominant and non-dominant trees of *Eucalyptus grandis* across a productivity gradient in Brazil, Forest Ecology and Management. 288: 14–20.

Castaño,J.P.G.; A. Ceroni; M. Furest; J. Aunchayna. 2011. R. Bidegain, Caracterización agroclimática del Uruguay 1980-2009, Serie Técnica INIA. 193, 33.

Chen, S.; R. Arnold; Z. Li; T. Li; G. Zhou; Z. Wu; Q. Zhou. 2011. Tree and stand growth for clonal *E. urophylla* × grandis across a range of initial stockings in southern China, New Forests. 41: 95–112.

Christina, M.; J.-P. Laclau; J.L.M. Gonçalves; C. Jourdan; Y. Nouvellon; J.-P. Bouillet. 2011. Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests, Ecosphere. 2: 1–10.

Cunningham, S.C.; J.R. Thomson; J. Read; P.J. Baker; R. Mac Nally. 2010. Does stand structure influence susceptibility of eucalypt floodplain forests to dieback?, Austral Ecology. 35: 348–356.

de Córdova Machado, F.; S.P.S. Guerra; N. Ceragioli; G. Oguri; M.S. Denadai. 2012. Influência do espaçamento na produtividade e alocação de biomassa em um plantio de *Eucalyptus grandis*, in: Congresso Internacional de Bioenergia, São Paulo, Brazil, pp. 1–6.

De Jesus, H.: E. Junior; A.W. Ballarin. 2013. Influência Do Espaçamento Na Densidade Básica Da Madeira Em Sistemas Florestais De Curta Rotação, in: 8° Congresso Internacional de Bioenergia São Paulo – SP – 05 A 07 DE NOvembro, 2013: pp. 5–9.

Dwyer, J.M.; R.J. Fensham; R.J. Fairfax; Y.M. Buckley. 2010. Neighbourhood effects influence drought-induced mortality of savanna trees in Australia, Journal of Vegetation Science. 21: 573–585.

Estrada, C.A.; A.Z. Meneses. 2004. Gasificación de biomasa para producción de combustibles de bajo poder calorífico y su utilización en generación de potencia y calor, Scientia et Technica. 2.

Forrester, D.I.; J.C. Wiedemann; R.I. Forrester; T.G. Bake. 2013. Effects of planting density and site quality on mean tree size and total stand growth of *Eucalyptus globulus* plantations, Canandian Journal of Forestry Research 43: 846–851.

Gelfand, I.; R. Sahajpal; X. Zhang; R.C. Izaurralde; K.L. Gross; G.P. Robertson. 2013. Sustainable bioenergy production from marginal lands in the US Midwest, Nature. 493: 514–517.

Gendreau-Berthiaume, B.; S.E. Macdonald; J.J. Stadt. 2016. Extended density-dependent mortality in mature conifer forests: causes and implications for ecosystem management, Ecol Appl. 26: 1486–1502.

Gonçalves, J.L. de M.; J.L. Stape; J.-P. Laclau; P. Smethurst; J.L. Gava. 2004. Silvicultural effects on the productivity and wood quality of eucalypt plantations, Forest Ecology and Management. 193: 45–61.

González García, M.; A. Hevia Cabal; M. Barrio Anta. 2013. Modelo dinámico de crecimiento y producción de biomasa para cultivos energéticos de *Eucalyptus nitens* (Maiden) en el noroeste de España, in: S.E. de C. Forestales (Ed.), 6 to Congreso Forestal Español, Vitoria Gateiz: pp. 2–8. http://secforestales.org/publicaciones/index.php/congresos_forestales/article/viewFile/14333/14176.

Goulart, M.; J.M. Haselein; Clovis Roberto Hoppe; J.A. Farias; D.T. Pauleski. 2003. Massa específica básica e massa seca de madeira de *Eucalyptus grandis* sob o efeito do espaçamento de plantio e da posição axial no tronco, Ciência Florestal. 13: 167–175.

Harris, F. 2007. The effect of competition on stand, tree, and wood growth and structure in subtropical Eucalyptus grandis plantations., Southern Cross University.

Hirigoyen, A.; C. Rachid; F. Varela. 2013. Actualizaciones de herramientas informáticas para la toma de decisiones forestales, Revista INIA. 35: 58–62.

INUMET. Available online:https://www.inumet.gub.uy/clima/estadisticas-climatologicas. (accessed on 01 04 2017). (n.d.).

Jacobs, M.R. 1955. Growth habits of the eucalypts, Forestry and Timber Bureau, Forestry and Timber Bureau, Canberra, New Zeland. http://trove.nla.gov.au/version/28637821 (accessed April 25, 2017).

Kuyah, S.; J. Dietz; C. Muthuri; M. Van Noordwijk; H. Neufeldt. 2013. Allometry and partitioning of above- and below-ground biomass in farmed eucalyptus species dominant in Western Kenyan agricultural landscapes, Biomass and Bioenergy. 1–9.

L. Bentancor, Extracción de nutrientes por *Eucalyptus dunnii* Maiden de 4 años con destino a la producción de biomasa para energía y celulosa. 2017. Universidad de la República. Facultad de Agronomía, Montevideo,Uruguay. 99 pp.

Larson, A.J.; J.A. Lutz; D.C. Donato; J.A. Freund; M.E. Swanson; J. HilleRisLambers; D.G. Sprugel; J.F. Franklin. 2015. Spatial aspects of tree mortality strongly differ between young and old-growth forests, Ecology. 96: 2855–2861.

Leite, F.P.; N.F. de Barros; R.F. de Novais; L.M.A. Sans; A.S. Fabres. 1997. Crescimento de *Eucalyptus grandis* em diferentes densidades populacionais, Revista Árvore. 21: 313–321.

Lintz, H.E.; A.N. Gray; A. Yost, R. Sniezko; C. Woodall; M. Reilly; K. Hutten; M. Elliott. 2016. Quantifying density-independentmortality of temperate tree species, Ecological Indicators. 66: 1–9.

Lonsdale, W.M. 1990. The Self-Thinning Rule: Dead or Alive?, Ecology. 71: 1373–1388.

Rance, S.J.; Mendham, D.S.; D.M. Cameron; T.S. Grove. 2012. An evaluation of the conical approximation as a generic model for estimating stem volume, biomass and nutrient content in young Eucalyptus plantations. New Forest. 43: 109–128.

Methol, R. 2001. Comparisons of approaches to modelling tree taper, stand structure and stand dynamics in forest plantations, New Zealand School of Forestry, University of Canterbury.

MGAP-Dirección de Suelos y Fertilizantes, Carta de Reconocimiento de Suelos del Uruguay. Tomo III. Descripción de las Unidades de Suelos [Charter Soil Survey of Uruguay. Volume III. Description of Units Soil], Dirección de Suelos y Fertilizantes, Ministerio de Agricultura y Pesca, Montevideo, Uruguay, 1979.

Morais, N.D.E.M.. 2006. Eucalipto Clonal Sob Diferentes Espaçamentos , Na Região Noroeste Do Estado De Minas Gerais, Universidade Federal de Lavras, http://repositorio.ufla.br/handle/1/3766.

Neto, S.N. de O.; G.G. Reis; M. das Graças F. Reis; J.C.L. Neves. 2010. Crescimento e Distribuição Diamétrica de *Eucalyptus camaldulensis* em Diferentes Espaçamentos e Níveis de Adubação na Região de Cerrado de Minas Gerais, Floresta. 40: 755–762.

Newton, P.F.; P. Jolliffe. 1998. Assessing processes of intraspecific competition within spatially heterogeneous black spruce stands, Canadian Journal of Forest Research. 28: 259–275.

Ounban,W.; L. Puangchit; S. Diloksumpun. 2016. Development of general biomass allometric equations for *Tectona grandis* Linn.f. and *Eucalyptus camaldulensis* Dehnh. plantations in Thailand, Agriculture and Natural Resources. 50: 48–53.

Patiño-Valera, F. P.Y. Kageyama. 1990. Interaction genotype X spacing in progenies of *Eucalyptus saligna* Smith, IPEF Int. 1: 12–22.

Pinkard, E.A.; W.A. Neilsen. 2003. Crown and stand characteristics of *Eucalyptus nitens* in response to initial spacing: implications for thinning, Forest Ecology and

Management. 172: 215–227.

Puettman, K.; D. Hibbs; D. Hann. 2016. The Dynamics of Mixed Stands of Alnus Rubra and Pseudotsuga Menziesii: Extension of Size--Density Analysis to Species Mixture Author (s): K . J . Puettmann , D . E . Hibbs and D . W . Hann Published by : British Ecological Society Stable URL : http://w, Journal of Ecology. 80: 449–458.

R Core Team. 2012. R: a language and environment for statistical computing.

Rachid, C. 2008. SAG Eucalyptus: un nuevo sistema de apoyo a la gestión de plantaciones de Eucalyptus orientadas a la producción de celulosa, Revista INIA. 15, 35–37.

Rachid-Casnati, C.; E.G. Mason; R. Woollons; F. Resquin. 2014. Volume and taper equations for *P. taeda* (L.) and *E. grandis* (Hill ex. Maiden)., Agrociencia (Montevideo). 18, 47–60.

Razakamanarivo, R.H.; A. Razakavololona; M.-A. Razafindrakoto; G. Vieilledent; A. Albrecht. 2012. Below-ground biomass production and allometric relationships of eucalyptus coppice plantation in the central highlands of Madagascar, Biomass and Bioenergy. 45: 1–10.

Rodríguez, A.; J.Cancino; E.Acuña; R. Rubilar; E.Muñoz. 2013. Evaluación del crecimiento de plantaciones dendroenergéticas de *Eucalyptus globulus*, según densidad de plantación y turno de rotacion en suelos contrastantes de la región del Bio Bio, Chile. Ciencia e Investigación Forestal INFOR Chile. 19 (1): 7-18.

Sale, G. 2005. A comparison of between-tree competition effects in separate stands of a Eucalyptus grandis seedling and a single *Eucalyptus grandis x urophylla* hybrid, University of the Witwatersrand, 2005.

Sartório, I.P.; Avaliação e modelagem do crescimento de florestas energéticas de eucalipto plantadas em diferentes densidades, Universidade Federal do Paraná, 2014.

Schäfer, J.P.R.; E.V. Ponce. 2007. Growth and economic analysis of a Eucalyptus globulus clonal spacing trial in Chile, in: Proceedings Australasian Forest Genetics Conference. Breeding for Wood Quality, Hobart Tasmania., Hobart, Tasmania, Australia, 2007. http://www.

Schneider, P.R.; C.A.G. Finger; P.S.P. Schneider; F.D. Fleig; T.A. da Cunha. 2015. Influência do espaçamento no autodesbaste de povoamento monoclonal de *Eucalyptus saligna* Smith, Ciência Florestal. 25:119–126.

Schönau, A.P.G.; J. Coetzee. 1989. Initial spacing, stand density and thinning in eucalypt plantations, Forest Ecology and Management. 29, 245–266.

Segura, M.: H.J. Andrade 2008. ¿ Cómo construir modelos alométricos de volumen , biomasa o carbono de especies leñosas perennes ? Agroforestería en las Américas 46: 89–96.

Sixto, H.; M.J. Hernández; M. Barrio; J.C.I. Cañellas. 2007. Plantaciones del género Populus para la producción de biomasa con fines energéticos : revision. Investigación Agraria: Sistemas y Recursos Forestales 16 (3): 277–294.

Sochacki, S.J.; R.J. Harper; K.R.J. Smettem. 2007. Estimation of woody biomass production from a short-rotation bio-energy system in semi-arid Australia, Biomass and Bioenergy. 3:, 608–616.

Stape, J.L.; W.L. Bauerle; M.G. Ryan; D. Binkley. 2010. Explaining growth of individual trees : Light interception and efficiency of light use by Eucalyptus at four sites in Brazil. Forest Ecology and Management 259: 1704–1713.

Tomé, M.; J.A. Tomé; M.C. Araújo; J.S. Pereira. 1994. Intraspecific competition in irrigated and fertilized eucalypt plantations, Forest Ecology and Management. 69: 211–218.

Trouvé, R.; J.D. Bontemps: C. Collet; I. Seynave; F. Lebourgeois. 2014. Growth partitioning in forest stands is affected by stand density and summer drought in sessile oak and Douglas-fir, Forest Ecology and Management. 334: 358–368.

Van Gunst, K.J.; P.J. Weisberg; J. Yang; Y. Fan. 2016. Do denser forests have greater risk of tree mortality: A remote sensing analysis of density-dependent forest mortality, Forest Ecology and Management. 359:19–32.

Vega-Nieva, D.J. 2015. Modeling the above and belowground biomass of planted and coppiced *Eucalytpus globulus* stands in NW Spain, Annals of Forest Science. 72(7): 967-980.

von Euler, F.; P. Baradat; B. Lemoine. 1992. Effects of plantation density and spacing on competitive interactions among half-sib families of maritime pine, Canadian Journal of Forestry Research 22: 482–489.

Winck, R.A.; H.E. Fassola; S.R. Barth; E. Crechi; A.E. Keller; D. Videla; C. Zaderenko. 2015. Modelos predictivos de biomasa aérea de *Eucalyptus grandis* para el noreste de Argentina., Ciência Florestal. 25: 595–606.

Xue, L.; L. Pan; R. Zhang; P. bo Xu. 2011. Density effects on the growth of self-thinning *Eucalyptus urophylla* stands, Trees - Structure and Function. 25: 1021–1031.

Supplementary Material

Table S1. Main physical and chemical characteristics of Tacuarembó site soil profile

Horizon	Depth	Clay	Silt	Sand	%OM	pH†		Extractable cations							Base
						H_2O	KCl	Al	Ca	Mg	K	Na	Total Bases	CECe	Sat.
	Cm	--------- g kg^{-1} ---------						------------------- $cmol_c\ kg^{-1}$ -------------------							%
A	46	14,7	24,3	61,0	1,2	4,7	3,8	1,0	2,7	1,0	0,3	0,2	4,2	5,3	79,2
AB	18	18,0	29,6	52,4	1,0	4,6	3,8	1,0	3	1,3	0,3	0,2	4,8	5,8	82,8
Bt	27	35,6	40,1	31,1	0,8	4,8	3,7	0,9	5,3	2,6	0,4	0,4	8,5	10,4	81,7
BC	18	36,4	31,7	32,0	0,8	5,1	4,1	0,7	6,5	3,1	0,3	0,6	10,5	11,2	93,8
C	13	27,5	36,8	35,8	0,8	5,1	4,1	0,6	5,1	2,5	0,3	0,2	8,0	8,6	93,0

Table S2. Main physical and chemical characteristics of Paysandú site soil profile

Horizon	Depth	Clay	Silt	Sand	%OM	pH†		Extractable cations							Base
						H_2O	KCl	Al	Ca	Mg	K	Na	Total Bases	CECe	Sat.
	Cm	--------- g kg^{-1} ---------						------------------- $cmol_c\ kg^{-1}$ -------------------							%
A	43	13,1	27,2	59,7	1,1	4,8	3,7	0,8	2,1	0,8	0,1	0,2	3,2	4,0	80,0
E	24	12,6	25,3	62,1	0,5	4,8	3,7	0,8	1,9	0,8	0,1	0,2	3,0	3,8	79,0
Bt	40	30,3	31,7	38,0	0,6	5,1	4,1	0,6	9,6	3,2	0,4	0,3	13,4	14,1	95,0
BC	26	29,0	36,2	34,8	0,3	5,4	4,2	0,3	11	3,7	0,4	0,4	15,4	15,7	98,1

Note: † pH: soil: solution relation v/v 1:2.5; Extractable Al: extracted by KCl 1M; Extractable bases: extracted by Ammonium Acetate 1M; CECe: effective Cation Exchange Capacity; Base Sat.: (Total Bases/CECe)*100. Source: Bentancor 2017.

Table S3. Coefficients of Height´s models adjusted for each site, specie and planting density

Site	Specie	Planting Density (tres ha^{-1})	Coefficient						
			β_o	β_1	β_2	β_3	β_4	β_5	β_6
Paysandú	*E.benthamii*	2220	3.234334	-2.985321	1.849822	-289698			
Paysandú	*E.benthamii*	3330	1.2556572	0.3211152	-0.0687087				
Paysandú	*E.benthamii*	4440	1.2766285	0.4000407	-0.0839982				
Paysandú	*E.benthamii*	6660	1.0797972	0.3029672	-0.0731201				
Paysandú	*E.dunnii*	2220	3.346361	-3.170208	1.945555	-0.309188			
Paysandú	*E.dunnii*	3330	3.282902	-2.932254	1.858174	-0.305457			
Paysandú	*E.dunnii*	4440	1.5678927	-0.3894695	0.6907860	-0.1353519			
Paysandú	*E.dunnii*	6660	1.5139701	-0.4480516	0.6843423	-0.1212293			
Paysandú	*E.grandis*	2220	2.2718742	-1.3487567	0.9908357	-0.1523363			
Paysandú	*E.grandis*	3330	1.5139701	-0.4480516	0.6843423	-0.1212293			
Paysandú	*E.grandis*	4440	1.7035954	-0.7250901	0.8373629	-0.1485176			
Paysandú	*E.grandis*	6660	2.0387488	-1.3187250	1.1720816	-0.2099997			
Tacuarembó	*E.benthamii*	2220	-82.240729	4.887956	-13.394079	-0.013024	14.372559	-0.103941	
Tacuarembó	*E.benthamii*	3330	4.986	6.145	-0.1408	-17.06	-0.0004142		
Tacuarembó	*E.benthamii*	4440	-64.605383	6.204005	-0.127141	-23.010	-21.620	-0.003980	11.844659
Tacuarembó	*E.benthamii*	6660	-890.7	0.859	-0.02367	12.35	33.72	-0.0242	
Tacuarembó	*E.dunnii*	2220	-225.72014	4.15170	-0.07885	-14.216	-0.03759	39.76994	-11.72844
Tacuarembó	*E.dunnii*	3330	-487.3	3.056	-0.07363	23.73	-0.03981	71.59	
Tacuarembó	*E.dunnii*	4440	22.82362	5.35403	-0.13322	-12.47193	-2.70668		
Tacuarembó	*E.dunnii*	6660	7.5333023	3.676834	-0.0014699	-0.0874711	-6.7473766		
Tacuarembó	*E.grandis*	2220	33.40901	-0.02259	17.92124	61.11832	-9.72528		
Tacuarembó	*E.grandis*	3330	-244.2	1.292	-0.03971	-0.01581	33.01	10.7	
Tacuarembó	*E.grandis*	4440	533.088313	2.019936	-74.919410	0.020226	-0.047956	11.947853	
Tacuarembó	*E.grandis*	6660	226	3.399	-30.04	-0.08268	0.005823	-6.914	

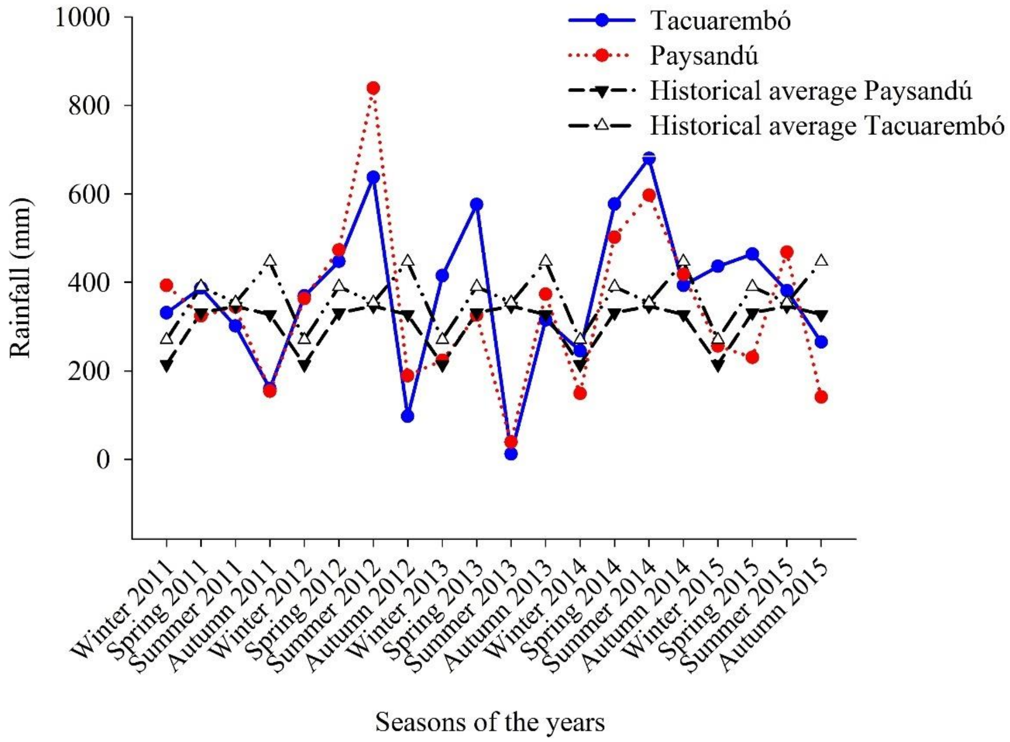


Figure S1. Rainfall regime evolution along the year in the two studied sites

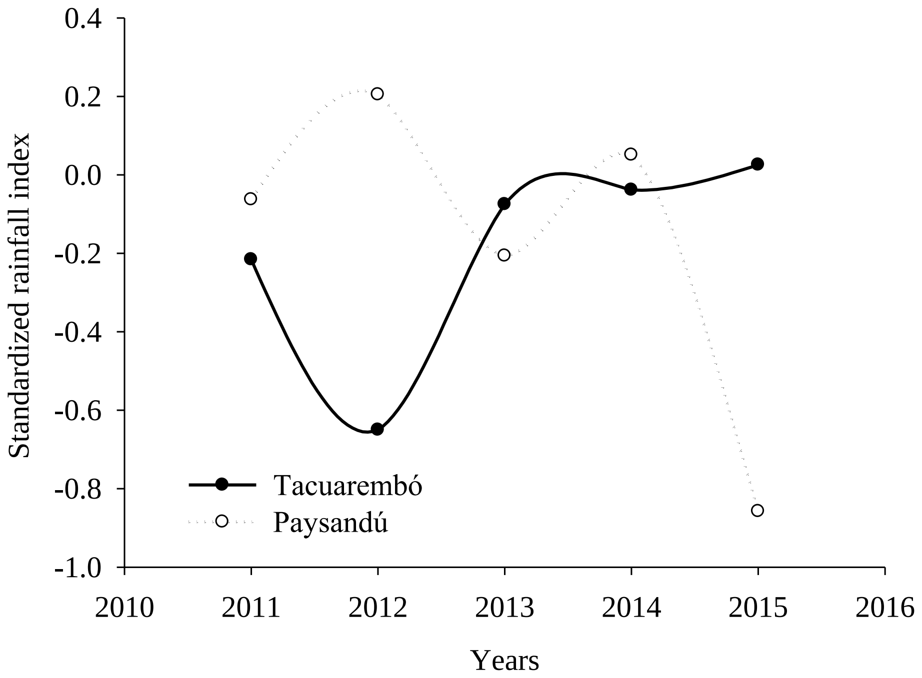


Figure S2. Standardized rainfall index (SRI) evolution in the two sites throughout the evaluation period. Source: www.meterología.com.uy

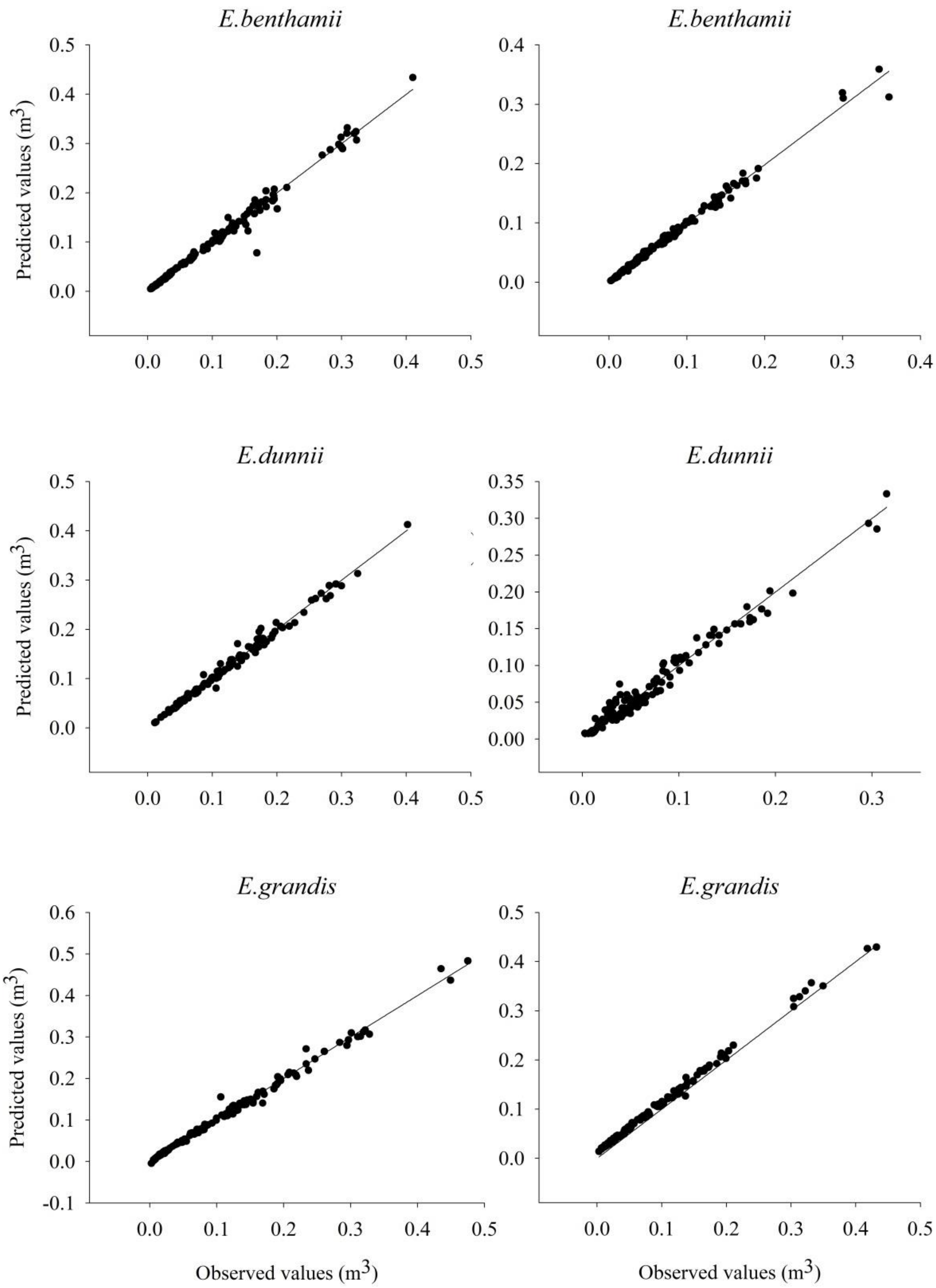


Figure S3. Relations between measured and estimated tree volume for each tested specie in Tacuarembó (left) and Paysandú (right). Line 1: 1

Chapter 4. Influence of contrasting stocking densities on the dynamics of above-ground biomass and wood density of *Eucalyptus benthamii*, *Eucalyptus dunnii*, and *Eucalyptus grandis* for bioenergy in Uruguay

“Si arrastré por este mundo
la vergüenza de haber sido
y el dolor de ya no ser.
Bajo el ala del sombrero,
cuántas veces embozada
una lágrima asomada
yo no pude contener.
Si crucé por los caminos
como un paria que el destino
se empeñó en deshacer.
Si fui flojo, si fui ciego,
sólo quiero que comprendan
el valor que representa
el coraje de querer…”

Alfredo Le Pera, 1934

Chapter 4. Influence of contrasting stocking densities on the dynamics of above-ground biomass and wood density of *Eucalyptus benthamii*, *Eucalyptus dunnii*, and *Eucalyptus grandis* for bioenergy in Uruguay

This chapter has been published in:

Fernando Resquin, Rafael M. Navarro-Cerrillo, Leonidas Carrasco-Letelier, Cecilia Rachid-Casnati. Influence of contrasting stocking densities on the dynamics ofabove-ground biomass and wood density of *Eucalyptus benthamii*, *Eucalyptus dunnii*, and *Eucalyptus grandis* for bioenergy in Uruguay. Forests Ecology and Management 438, (2019), 63-74. https://doi.org/10.1016/j.foreco.2019.02.007

1. Introduction

Since the oil crisis in the 1970s, biomass has become increasingly important in the global energy scenario and there has been a notable transition from direct uses of biomass (i.e. firewood) to the use of transformed biomass (pellets, biofuels). The factors most relevant to its adoption have been the reduction of the costs of utilization and transport (Macedo, 2003), the investigation of more-efficient conversion processes, and the improvement of the management and harvesting of energy crops. In recent decades, global energy consumption has increased and is expected to rise by 36% by 2035, with respect to 2008 (IEA, 2010). Currently, 40% of the world's energy consumption comes from fossil fuels, a value that must be reduced due to its environmental and economic impacts. Therefore, the development of different energy alternatives has been highlighted as an option (Pleguezuelo et al., 2014), and these include the use of lignocellulosic forest materials (Hinchee et al., 2011; Eufrade Junior et al., 2016). The information that has emerged in recent years shows that there are a series of processes called biomass to liquid (BTL) and biomass to gas (BTG) that could be used at a commercial level in the coming years (Bensaid et al., 2012, Yang et al., 2014).

Although in general terms energy crops provide only a small proportion (13.4%) of the total energy produced (Sims et al., 2006), current trends show that their use will increase in the coming decades (IEA, 2010). *Eucalyptus* species have been shown to adapt to a wide range of environments and achieve a relatively-high wood density, which makes them stand out in terms of biomass production (Rockwood et al., 2008). In Brazil, they are cultivated as high-planting-density crops because of their growth rate (Eufrade Junior et al., 2016, Lopes et al., 2017), and their wood is used as a renewable replacement material for coal in the production of "green steel" (Rocha et al., 2016) and to produce different types of biofuel (Senelwa and Sims, 1999; Rockwood et al., 2008; Pérez et al., 2011; Nuberg et al., 2015). There is abundant experimental and empirical evidence that indicates the species, sites, and silvicultural practices that allow high levels of growth in cellulose and solid-wood production systems (Balmelli and Resquin, 2004, 2006). The most-productive eucalypts species are *E. grandis* W. Hill ex Maiden, *E. dunnii* Maiden, *E. benthamii* Maiden & Cambage, *E. maidenii* F. Muell., and *E. globulus* Labill., but interspecific hybrids are also used. The recent appearance of the second-generation biofuels (bioethanol, biodiesel) highlighted short-rotation woody crops (SRWC) systems as a potential source of energy. However, for SRWC production systems there is still a lack of experimental and empirical evidence (species, sites, and silvicultural practices) regarding the performance of species like *E. grandis*, *E. dunnii*, *E. benthamii*, *E. maidenii*, and *E. globulus*, and some interspecific hybrids. These are characterized by their relatively-high wood density (Tuset et al., 2008) and their tolerance of competition (Jacobs, 1955; Tomé and Verwjjst, 1996). For the above-mentioned species, it is necessary to determine their response in an SRWC production system; in particular, the effect of spacing - and thus competition - on the harvest time and wood properties.

Planting density and age at harvest are variables that are related, so that short crop rotations could be achieved with reduced spacing (Harris, 2007) due to the effect of spacing on growth (Sale, 2005; Harris, 2007; Machado et al., 2012). Biomass weight depends on volumetric growth and wood density and is important for the determination of the optimum harvest time, based on the weight per hectare of the stand. For this reason, it is important to follow the increases in biomass production, after the stagnation of the volumetric growth, because an increase in wood density may occur (Souza, 1989; Lopes et al., 2017). The effect of the plantation spacing on eucalypts wood density has been widely studied, and it has been shown that the spacing can have different effects: increases in wood density due to a reduction of the area occupied by each plant (Debell, 2001; Rocha et al., 2016); wood density reduction (Wilkins and Horne, 1991; Malan, 2005; Paulino, 2012); or the absence of wood density changes (Cassidy et al., 2013, Eufrade Junior et al., 2016).

The wood density can also be influenced by the age of the trees (Santana et al., 2012; Resquin et al., 2012) and growth rate changes. This could be important in short crop rotations and high-planting-density crops due to competition between the trees. Malan and Honn (1992) and Malan (2005) determined that a higher growth rate of the diameter - like in crops with more spacing - produced relatively-homogeneous wood; the maximum values of wood density occur in the early stages of growth and when early adult wood is produced, with the consequent increase in wood density and greater homogeneity. Bearing in mind the aforementioned information, it can be assumed as a hypothesis that the production of biomass in eucalypts forest crops with high planting density is conditioned by the species and the spacing. Therefore, it can be expected that the cultivation of different species of eucalypts with different planting densities, and in two different forest soils, would give different levels of production, wood densities, and harvest times. Starting from this hypothesis, the general objective of this work was to test three species of eucalypts (*E. benthamii* Maiden & Cambage, *E. dunnii* Maiden, and *E. grandis* Hill ex Maiden) at different planting densities, to determine which combination had the greatest stem biomass production per hectare during a period of 76 months. To reach these goals we assessed: (i) the effect of the species and the planting density on the wood density, (ii) the fitting of equations to determine the stem biomass for each site and species, using dasometric parameters, and (iii) the biomass production of the eucalypts species, according to the planting density, throughout the crop cycle in the first rotation.

2. Materials and methods

2.1 Study area

The two trials were set up on sites of the Eastern Forestry Company, in the North (hereafter Tacuarembó) and West (hereafter Paysandú) of Uruguay (32º13'30''S and 55º54'40''W and 32º24'05''S and 57º31'02''W, respectively) (Figure S1, Supplementary Material). According to the morphologic description, and the main physical and chemical characteristics (Table S1, Supplementary Material), the soils of the two sites were classified as fine-loamy, siliceous, active, thermic Mollic Hapludalfs (Bentancor, 2017). The climate is temperate subtropical, being temperate and humid without a dry season (Cfa), according to the Köppen-Geiger classification (Kottek et al., 2006). The average annual temperature is 18°C, with average temperatures of 12°C and 24°C for the coldest and warmest months, respectively. The average annual precipitation is between 1300 and 1400 liters m^{-2} (Castaño et al., 2011).

2,2 Experimental design

The plantations studied belong to a split-plot design of randomized complete blocks with two factors - forest species (main plot, three levels: *E. benthamii*, *E. dunnii*, and *E. grandis*) and planting density (subplot, four levels: 2220, 3330, 4440, and 6660 trees ha^{-1}) - and three repetitions (Figure S2, Supplementary Material). This corresponds to a total of 12 treatments and 36 plots, with a total of 3600 trees. The seeds of *E. benthamii* were obtained from APS Pinhão (State of Paraná, Brazil), those of *E. dunnii* from the INIA tree nursery (2nd generation), and those of *E. grandis* from Undera de Moleton (West Coffs Harbor, Australia).

The trees were planted in 2010, on October 13th and 15th at Tacuarembó and between October 27th and November 1st at Paysandú. The plots were composed of six plantation lines with 25 plants of each species in each of them. The planting distances were 3 m x 0.5 m, 3 m x 0.75 m, 3 m x 1 m, and 3 m x 1.5 m, corresponding to the densities of 6660, 4440, 3330, and 2220 trees $hectare^{-1}$, respectively. Each site had a trial of three blocks (36 plots). The soil was prepared to a depth of 40 cm with a subsoiler and then a harrow was used twice, to a depth of 30 cm The planting was carried out manually and an initial fertilization of 150 kg ha^{-1} of 18/46/0 (N, P, K), at Tacuarembó, and of 180 kg ha^{-1} of 14/30/12 (N, P, K), at Paysandú, was applied, plus 6% S, 0.2% B, and 0.3% Zn. The average areas of the plots were 706, 468, 350, and 234 m^2, and the areas evaluated were 470, 314, 234, and 156 m^2, for the densities of 2220, 3330, 4440, and 6660 trees $hectare^{-1}$, respectively. The plot surface area was calculated as the product of the length and the width, both measured using a tape measure. The area of each planting density by species combination was determined as the average of the three replications.

2.3. Sampling of trees and measurements

Six sets of measurements were carried out: in the periods July-October 2011, May-August 2012, January 2013, August-December 2014, January-July 2015, and March-October 2016. The evaluations were carried out in the four central rows (2 to 5) of each block, to avoid the edge effect. In each of the treatments we evaluated the tree survival, the diameter at breast height (*dbh*, cm, at 130 cm height), and the total height of the trees (*H*, m), which was measured with a Vertex IV hypsometer (Haglof, Sweden) in rows 2 and 4. The total height was considered as the distance between the root collar and the base of the terminal bud of the tree. The height of the rest of the trees was estimated from fitted equations, according to the *dbh*. The trees measured were those with a *dbh* greater than 3 cm. In the forest inventories of the years 2012, 2014, 2015, and 2016, three to five trees were selected per block (species x planting density), corresponding to the diametric classes of highest relative frequency. For these, the *H* and *dbh* were measured, together with the diameter at 1-m intervals downwards from the dbh, until a diameter of 1 cm, including bark, was reached. The tree samples (with bark) were weighed on an industrial balance (Model HY10.32.HRP; Radwag Balances, Poland) with a precision of 1 g. At the tree base and at heights corresponding to 50 and 75% of the total height, two 2-cm-thick discs were extracted, which were weighed fresh (with bark) in the field. One of the discs was dried to a constant weight at 103°C, to estimate the dry matter content (W_i, kg). This value was used to estimate the weighted average mass of each tree, considering the surface area.

2.4 Wood density

The wood density (*Db*, g cm^{-3}) was determined for forest inventory samples of years 2012, 2015, and 2016. The second disc extracted from each tree was kept in water until its complete saturation. The volume of water displaced was recorded and then the dry matter was determined by drying to constant weight at 103 ± 2 °C. The *Db* of each tree was estimated using the following formula (Santos, 2011) [1]:

$$Db = (Ab_0 Db_0 + Ab_{50} Db_{50} + Ab_{75} Db_{75}) \;/\; (Ab_0 + Ab_{50} + Ab_{75}) \qquad [1]$$

Where *Db* is the weighted wood density, and Db_0, Db_{50}, and Db_{75} are the densities and Ab_0, Ab_{50}, and Ab_{75} the areas for the heights 0, 50, and 75% of total height, respectively.

2.5 Individual biomass functions

Data from 2592 destructively sampled trees (864 per species) were pooled to develop individual biomass equations, based on the assumption that trees of the same species exhibit similarities in growth form (Fatemi et al., 2011) and that the allometry of stem biomass for trees growing under similar conditions does not differ significantly within the same genus (Senelwa and Sims, 1998). The data were checked for errors prior to analysis and were screened for outliers using scatter plots; the latter also revealed the relationship between the biomass and predictor variables (Quinn and Keough, 2002). To estimate weight per hectare (W_t), the option used was an individual stem weight (W_i) model. Linear (single and multiple) and non-linear (logarithmic) regressions were carried out to predict the *Wi* as a function of the *dbh*, total height, and number of trees per hectare (González García et al. 2013). The variables showing the highest correlation coefficients with the *Wi* were used as predictors for each species and site. Thus, the predictive variables *dbh, H*, and *dbh*H* from years 2012, 2014, 2015, and 2016 were used to obtain allometric coefficients for biomass equations in such a way that it was possible to make a fast estimation of the biomass stock and to project growth by means of the variables of the inventory (Ferrere et al. 2008). The average individual tree biomass of each plot multiplied by the number of trees was used to estimate the biomass per hectare of each species-by-planting density combination.

2.6. Mean annual increment

The mean annual increment (MAI) of W_t was estimated as the average annual increase in volume of individual trees up to the specified point in time, based on the temporal sequence for five periods (MAI = weight increment/t_0 - t_i).

2.7 Statistical analysis

Prior to the analysis of variance (ANOVA) of the variable's survival, *Db, Wi*, and *Wt*, the normality of their residues was checked through the normal Q-Q graph and Shapiro-Wilk test. If the data did not satisfy the assumptions of homoscedasticity and normality, the

Box and Cox procedure was used. The results in the tables are the means with their standard errors for the untransformed variables. The differences in survival, *Db*, *Wi*, and *Wt* among the planting densities and species were compared using a two-way ANOVA followed by a *post hoc* Tukey test. The species, planting density, and interaction effects were analyzed. The year effect for the *Db* was also analyzed. The level of significance was set at $P<0.05$. The polynomial linear W_i models were compared using the standardized error of the residuals (Shapiro-Wilk test), the coefficient of determination (R^2_{adj}), the root mean square error (RMSE), and the autocorrelation (Breusch-Pagan test). The homoscedasticity was evaluated using graphs of the residues as a function of the estimated values, Q-Q graphs, and the Breusch-Pagan test. All regression equations presented here had homoscedastic residual plots. The coefficient of determination (R^2_{adj}) was used to assess the model fit for the equations, to reflect both the number of independent variables in the equation and the sample size. We performed all analyses using R software version 3.4.0. The packages lmtest, reshape, ggplot2, and plyr were used for the ANOVAs and regression models.

3. Results

3.1. Survival

The survival, at both locations, was similar for the distinct planting densities (Table 1). The survival rates at Tacuarembó were clearly lower than at Paysandú, with values between 30 and 60% for all species in the last inventory at the former site, where mortality started at the beginning of the trial (months 12-22). The highest tree survival rates were recorded at Paysandú, with values between 70 and 90% at 76 months for all species and densities (Table 1). In all cases, no relationship was found between tree mortality and planting density and survival values were highest for *E. benthamii* and *E. dunnii*. The ANOVA of the survival, at both locations, detected significant differences among species in the last assessment (Tables 2 and 3).

Table 1. Survival evolution (% ± S.E) for *Eucalyptus benthamii*, *E. dunnii* and *E. grandis* short crop rotation at Tacuarembó and Paysandú.

		Sites											
		Tacuarembó						**Paysandú**					
		Age (months)											
Species	**Planting density (trees ha^{-1})**	**12**	**22**	**38**	**46**	**57**	**75**	**8**	**18**	**38**	**49**	**57**	**76**
E. benthamii	2220	79 (3.2)	77 (3.3)	69 (4.0)	60 (4.1)	60 (3.8)	60 (2.7)	90 (0.6)	89 (0.6)	87 (0.3)	87 (0.3)	85 (1.7)	84 (1.5)
	3330	78 (7.2)	76 (6.6)	70 (7.0)	61 (14.9)	61 (14.8)	52 (11.6)	92 (3.9)	91 (4.3)	90 (4.4)	90 (4.4)	88 (5.2)	87 (4.4)
	4440	74 (9.0)	71 (8.7)	65 (10.1)	65 (9.5)	65 (9.0)	55 (4.9)	85 (2.3)	85 (2.7)	83 (3.3)	83 (3.3)	80 (2.8)	80 (2.8)
	6660	82 (5.7)	80 (4.8)	76 (5.7)	75 (5.0)	73 (4.3)	61 (3.5)	93 (3.2)	91 (3.0)	87 (2.9)	87 (2.6)	82 (2.3)	80 (3.9)
E. dunnii	2220	69 (3.0)	67 (3.5)	62 (4.7)	62 (4.5)	60 (3.8)	57 (4.9)	89 (1.3)	87 (1.8)	86 (1.2)	86 (1.2)	85 (0.9)	85 (0.9)
	3330	61 (7.2)	60 (6.4)	57 (5.7)	56 (5.2)	55 (4.7)	53 (7.3)	96 (0.6)	94 (1.7)	94 (1.9)	93 (1.8)	92 (1.5)	92 (1.8)
	4440	71 (4.9)	68 (4.4)	63 (5.5)	63 (5.5)	62 (5.8)	59 (6.2)	91 (3.0)	91 (3.0)	89 (2.3)	89 (2.3)	86 (1.7)	86 (1.7)
	6660	79 (4.9)	76 (4.6)	71 (3.2)	69 (4.4)	67 (5.0)	62 (3.8)	89 (3.5)	89 (3.2)	85(2.8)	85 (2.8)	81 (3.0)	81 (3.0)
E. grandis	2220	85 (2.6)	81 (3.4)	71 (2.6)	66 (2.0)	64 (2.0)	54 (3.5)	88 (0.9)	87 (0.9)	84 (1.8)	84 (1.8)	84 (1.5)	78 (1.0)
	3330	78 (11.6)	74 (10.6)	63 (8.1)	60 (7.0)	60 (7.0)	47 (4.4)	90 (1.9)	89 (2.2)	84 (1.5)	84 (1.5)	82 (1.5)	73 (2.0)
	4440	82 (4.0)	77 (2.2)	64 (1.0)	60 (1.7)	60 (2.0)	47 (4.5)	93 (2.5)	92 (2.5)	87 (2.9)	87 (2.9)	85 (3.8)	76 (3.4)
	6660	76 (6.4)	69 (5.2)	55 (2.5)	50 (2.9)	49 (2.6)	34 (4.7)	92 (1.7)	88 (1.7)	84 (1.9)	83 (1.8)	81 (1.7)	74 (1.5)

Table 2. Results of two-way ANOVA for survival of *Eucalyptus benthamii*, *E. dunnii* and *E. grandis* short crop rotation at Tacuarembó and Paysandú.

Tacuarembó												
Effects	**Age (Months)**											
	12		**22**		**38**		**46**		**57**		**75**	
	F	***P***	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***
Species	3.13	0.06	2.45	0.10	2.07	0.14	0.95	0.39	1.08	0.35	**5.74**	**0.009**
Density	0.64	0.59	0.57	0.63	0.42	0.73	0,37	0.77	0.28	0.83	0.66	0.58
Sp.*Dens.	0.69	0.65	1.01	0.43	1.32	0.28	1.19	0.34	1.10	0.38	1.27	0.304

Paysandú												
Effects	**Age (Months)**											
	8		**18**		**38**		**49**		**57**		**76**	
	F	***P***	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***
Species	0.31	0.73	0.36	0.70	2.18	0.13	2.25	0.12	1.43	0.25	**18.7**	**$1.24e^{-05}$**
Density	1.13	0.35	1.18	0.33	1.56	0.22	1.60	0.21	2.84	0.05	2.74	0.065
Sp.*Dens.	1.79	0.14	1.32	0.28	1.31	0.29	1.27	0.30	1.23	0.32	1.34	0.276

Table 3. Survival values (%) for *Eucalyptus benthamii*, *E. dunnii* and *E. grandis* short crop rotation at Tacuarembó (75 months) and Paysandú (76 months). Different letters indicate significant post-hoc differences between the planting density and species at alpha = 0.05 based on a Tukey HSD test.

Sites	**Species**			**Planting density (trees ha^{-1})**			
	E. benthamii	***E. dunnii***	***E. grandis***	**2220**	**3330**	**4440**	**6660**
Tacuarembó	56.8 a	57.4 a	45.6 b	56.6 a	50.3 a	53.8 a	52.3 a
Paysandú	82.8 a	86.0 a	75.2 b	82.6 a	83.9 a	80.7 a	78.2 a

3.2 Wood density

At Tacuarembó, the wood densities of *E. benthamii* and *E. dunnii* remained unchanged in the first three forest inventories and for the different planting densities, while *E. grandis* showed a slight reduction in *Db* with the increase in age (Table 4). At Paysandú, the wood density rose for all planting densities between months 57 and 76, reaching values of 9% and 28%, at 6660 and 2220 trees hectare^{-1}, respectively; with an average increase of 21%, 16%, and 12% for *E. grandis*. *E, dunnii*, and *E. benthamii*, respectively. Although an increase was registered with the highest planting densities, it was not detected by the ANOVA. At both sites, *E. dunnii* and *E. benthamii* had the highest values of *Db*, although the values obtained at Tacuarembó were significantly lower than at Paysandú, where the highest *Db* values were obtained with the lowest planting densities (Table 5). In the last inventory at Tacuarembó, a very-significant effect of the species on *Db* was observed, but there was no effect of planting density. In contrast, at Paysandú the effects of both the species and the planting density were highly significant (Table 6).

Table 4. Mean *Db* (g cm^{-3}) ± (SE) for *Eucalyptus benthamii*, *E. dunnii* and *E. grandis* short crop rotation at Tacuarembó and Paysandú. Different letters indicate significant post-hoc differences between ages (within the planting density) at alpha = 0.05 based on a Tukey test.

		Sites					
		Tacuarembó			Paysandú		
		Age (Months)					
Species	**Planting density (trees ha^{-1})**	**22**	**57**	**74**	**18**	**57**	**76**
E.benthamii	2220	0.406 (0.01) a	0.409 (0.01) a	0.410 (0.01) a	0.422 (0.03) b	0.445 (0.01) ab	0.520 (0.01) a
	3330	0.400 (0.01) a	0.415 (0.01) a	0.413 (0.01) a	0.413 (0.03) b	0.447 (0.01) ab	0.509 (0.01) a
	4440	0.412 (0.01) a	0.405 (0.01) a	0.409 (0.01) a	0.427 (0.02) a	0.441 (0.01) a	0.467 (0.01) a
	6660	0.411 (0.01) a	0.423 (0.01) a	0.420 (0.01) a	0.429 (0.03) a	0.443 (0.01) a	0.487 (0.01) a
E.dunnii	2220	0.435 (0.01) a	0.445 (0.01) a	0.420 (0.01) a	0.475 (0.03) b	0.458 (0.01) b	0.610 (0.01) a
	3330	0.454 (0.01) a	0.428 (0.01) a	0.442 (0.01) a	0.464 (0.03) a	0.458 (0.01) a	0.522 (0.01) a
	4440	0.443 (0.01) a	0.417 (0.01) a	0.429 (0.01) a	0.461 (0.03) a	0.466 (0.01) a	0.510 (0.01) a
	6660	0.438 (0.01) a	0.417 (0.01) a	0.434 (0.01) a	0.456 (0.02) a	0.475 (0.01) a	0.513 (0.01) a
E. grandis	2220	0.410 (0.01) a	0.368 (0.01) b	0.376 (0.01) b	0.432 (0.03) a	0.379 (0.01) b	0.503 (0.02) a
	3330	0.395 (0.01) a	0.368 (0.01) a	0.381 (0.01) a	0.406 (0.03) b	0.389 (0.01) b	0.480 (0.01) a
	4440	0.395 (0.01) a	0.365 (0.01) b	0.369 (0.01) ab	0.373 (0.03) b	0.379 (0.01) b	0.446 (0.01) a
	6660	0.390 (0.01) a	0.345 (0.01) b	0.378 (0.01) ab	0.399 (0.02) a	0.366 (0.01) a	0.402 (0.02) a

Table 5. Results of two-way ANOVA for *Db* of *Eucalyptus benthamii*, *E. dunnii* and *E. grandis* short crop rotation at Tacuarembó and Paysandú at three temporal inventories. All significant results are indicated in bold.

	Sites											
	Tacuarembó						Paysandú					
	Age (Months)											
	22		57		74		18		57		76	
	F	*p-value*	*F*	*p-value*	*F*	*p-value*	*F*	*p-value*	*F*	*p-value*	*F*	*p-value*
Species	**52.90**	**<0.001**	**51.50**	**<0.001**	**32.09**	**<0.001**	**55.2**	**<0.001**	**117.9**	**<0.001**	**8.91**	**<0.001**
Planting Density	0.22	0.882	1.15	0.331	0.82	0.481	**3.80**	**0.011**	0.12	0.947	**5.00**	**0.03**
Species * Planting Density	1.90	0.084	2.26	0.47	0.24	0.961	3.05	0.07	1.05	0.397	0.75	0.607

Table 6. Mean *Db* ± (S.E.) by site for *Eucalyptus benthamii*, *E. dunnii* and *E. grandis* short crop rotation at Tacuarembó (75 months) and Paysandú (76 months). Different letters indicate significant post-hoc differences between the planting density (lower case) and species (capital letter) at alpha = 0.05 based on a Tukey HSD test.

Species	Planting density (trees ha^{-1})	Sites: Tacuarembó	Sites: Paysandú
		-------------------*Db* (g cm^{-3})------------------	
E.benthamii	2220	0.410 (0.01) B a	0.520 (0.01) A a
	3330	0.413 (0.01) B a	0.509 (0.01) A ab
	4440	0.409 (0.01) B a	0.467 (0.01) A b
	6660	0.420 (0.01) B a	0.487 (0.01) A b
E. dunnii	2220	0.420 (0.01) A a	0.610 (0.01) A a
	3330	0.442 (0.01) A a	0.522 (0.01) A ab
	4440	0.429 (0.01) A a	0.510 (0.01) A b
	6660	0.434 (0.01) A a	0.513 (0.01) A b
E. grandis	2220	0.376 (0.01) C a	0.503 (0.02) B a
	3330	0.381 (0.01) C a	0.480 (0.01) B ab
	4440	0.369 (0.01) C a	0.446 (0.01) B b
	6660	0.378 (0.01) C a	0.402 (0.02) B b

3.3 Tree biomass equations

The models that related ln(W_i) to the predictor variables ln(*dbh*) and ln(*H*), or to potential and quadratic combinations of these two variables, are presented in Tables S2 and S3 (Supplementary material). Of these, at Tacuarembó the models which used *dbh* and *H* as predictors showed the best fit, as indicated by the root mean square error (RMSE) and the coefficient of determination ($R^2_{\text{adj}} > 0.97$). However, at Paysandú the best models involved ln(dbh^2*H), closely followed by ln(*dbh*) and ln(*H*) ($R^2_{\text{adj}} > 0.97$). Comparative plots of predicted against observed data are shown in Figures S3 and S4 (Supplementary Material). Consistent with the results in Tables S4 and S5, the agreement between predicted and observed values was very high for all the models. An examination of these general equations also indicated a marked stability of the residuals, with a low level of systematic under- or over-estimation (Figures S3 and S4)

3.4 Species and planting density effects on the biomass

The highest and lowest W_i corresponded, in all species, to the lowest and highest planting densities, respectively (Table 7). In addition, the W_i at Tacuarembó was higher than at Paysandú due to the lower survival at Tacuarembó (see Table 3). At Tacuarembó, the highest W_i corresponded, in all species, to the lowest planting densities. *Eucalyptus. dunnii* was the species with the highest individual biomass at Tacuarembó (111.7 kg) and Paysandú (100.8 kg) at the lowest planting density, although the W_i for all species at Tacuarembó was higher than at Paysandú (Table 7). At Paysandú, *E. grandis* showed the highest average value of W_i (74.1 kg tree^{-1}), while *E. benthamii* and *E. dunnii* had the lowest values, which were similar (55.4 and 63.3 kg tree^{-1}, respectively) (Table 7).

Table 7. Mean *Wi* and *Wt* ± S.E. by site for *Eucalyptus benthamii*, *E. dunnii* and *E. grandis* short crop rotation at Tacuarembó (75 months) and Paysandú (76 months). Different letters indicate significant post-hoc differences between the planting density (lower case) and species (capital letter) at alpha = 0.05 based on a Tukey HSD test. Different bold letters indicate differences due to the interaction species and planting densities.

		Sites			
		Tacuarembó		Paysandú	
Species	**Planting density (trees ha^{-1})**	***Wi* (kg)**	***Wt* (Mg)**	***Wi* (kg)**	***Wt* (Mg)**
E. benthamii	2220	83.5 (1.2) **ab**	104.2 (4.9) **d**	90.0 (16.8) B a	166.1 (27.9) **ab**
	3330	68.2 (5.5) **ab**	110.1 (19.9) **d**	64.7 (3.4) B b	185.6 (4.5) **ab**
	4440	74.9 (8.9) **ab**	172.6 (3.4) **abcd**	35.2 (1.2) B c	124.8 (5.7) **b**
	6660	55.9 (6.9) **b**	212.6 (18.2) **a**	33.6 (3.3) B d	174.9 (8.0) **ab**
E. dunnii	2220	111.7 (12.0) **a**	130.3 (5.6) **bcd**	100.8 (5.0) AB a	187.7 (10.9) **ab**
	3330	90.7 (7.8) **ab**	153.3 (8.3) **abcd**	62.1 (3.9) AB b	188.6 (9.1) **ab**
	4440	63.2 (2.6) **b**	155.8 (11.6) **abcd**	53.0 (4.5) AB c	198.5 (17.3) **ab**
	6660	48.3 (1.1) **b**	186.5 (6.7) ab	37.1 (3.1) AB d	198.1 (8.7) **ab**
E. grandis	2220	97.3 (6.2) **ab**	111.2 (11.1) **cd**	93.9 (5.6) A a	159.3 (8.8) **b**
	3330	85.0 (3.5) **ab**	124.3 (9.1) **bcd**	97.9 (2.4) A b	233.0 (12.0) **a**
	4440	92.8 (17.8) **ab**	184.5 (25.4) **abc**	58.1 (6.6) A c	195.1 (11.3) **ab**
	6660	68.7 (7.9) **ab**	150.1 (3.3) **abcd**	46.1 (3.0) A d	224.1 (9.9) **a**

At Tacuarembó, significant effects of the planting density and the planting density*species interaction on W_i were found (Table 8). At Paysandú the W_i differed significantly among species and planting densities (Table 8), but there was no significant interaction between the two factors. Regarding the W_t, at both sites the planting density and the interaction showed a statistically significant effect (Table 8). *Eucalyptus benthamii* was the species with the highest *Wt* at Tacuarembó (212.6 Mg ha^{-1}) while at Paysandú it was *E. grandis* (224.1 Mg ha^{-1}), at the highest planting density. At Tacuarembó, there was a close relationship between the number of live trees and productivity per hectare. At Paysandú, no relationship between planting density and productivity per hectare was observed for *E. benthamii* or *E. dunnii* (Table 8).

Table 8. Result of two-way ANOVA of individual and total weight for *Eucalyptus benthamii*, *E. dunnii* and *E. grandis* short crop rotation at Tacuarembó (75 months) and Paysandú (76 months).

	Sites							
	Tacuarembó				**Paysandú**			
	Wi		***Wt***		***Wi***		***Wt***	
	F	***p-value***	***F***	***p-value***	***F***	***p-value***	***F***	***p-value***
Species	1.77	0.281	4.64	0.091	**8.42**	**0.037**	5.52	0.071
Planting density	**15.18**	**<0.0001**	**15.91**	**<0.001**	**64.94**	**<0.0001**	**7.84**	**0.002**
Specie * Density	**3.37**	**0.020**	**2.75**	**0.044**	2.57	0.056	**4.14**	**0.009**

3.5 MAI evolution

At both sites, the W_i and *Wt* increased over time and with planting density for the species studied (Figures 1, 2, and 3). The MAI increased with time for all species and planting densities. At Tacuarembó, the MAI values were mostly stabilized as some treatments showed an increasing trend, although at a lower rate, e.g. *E. dunnii* 6660, *E. grandis* 4440 and 6660 trees ha^{-1}. 57 months after planting.

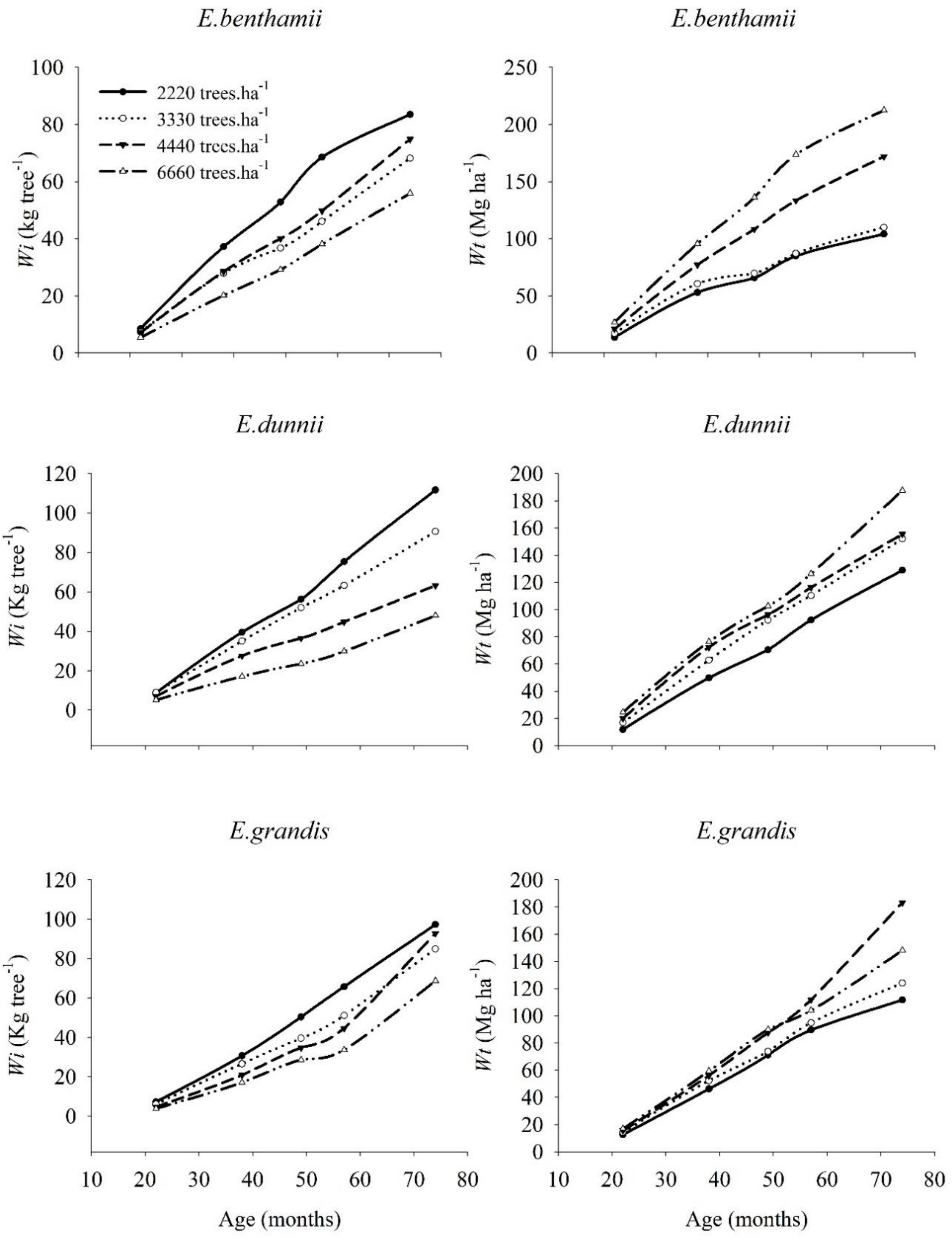


Figure 1. Evolutions of biomass per hectare (*Wt*) and tree (*Wi*) for the species of *Eucalyptus* and planting density at Tacuarembó (Uruguay).

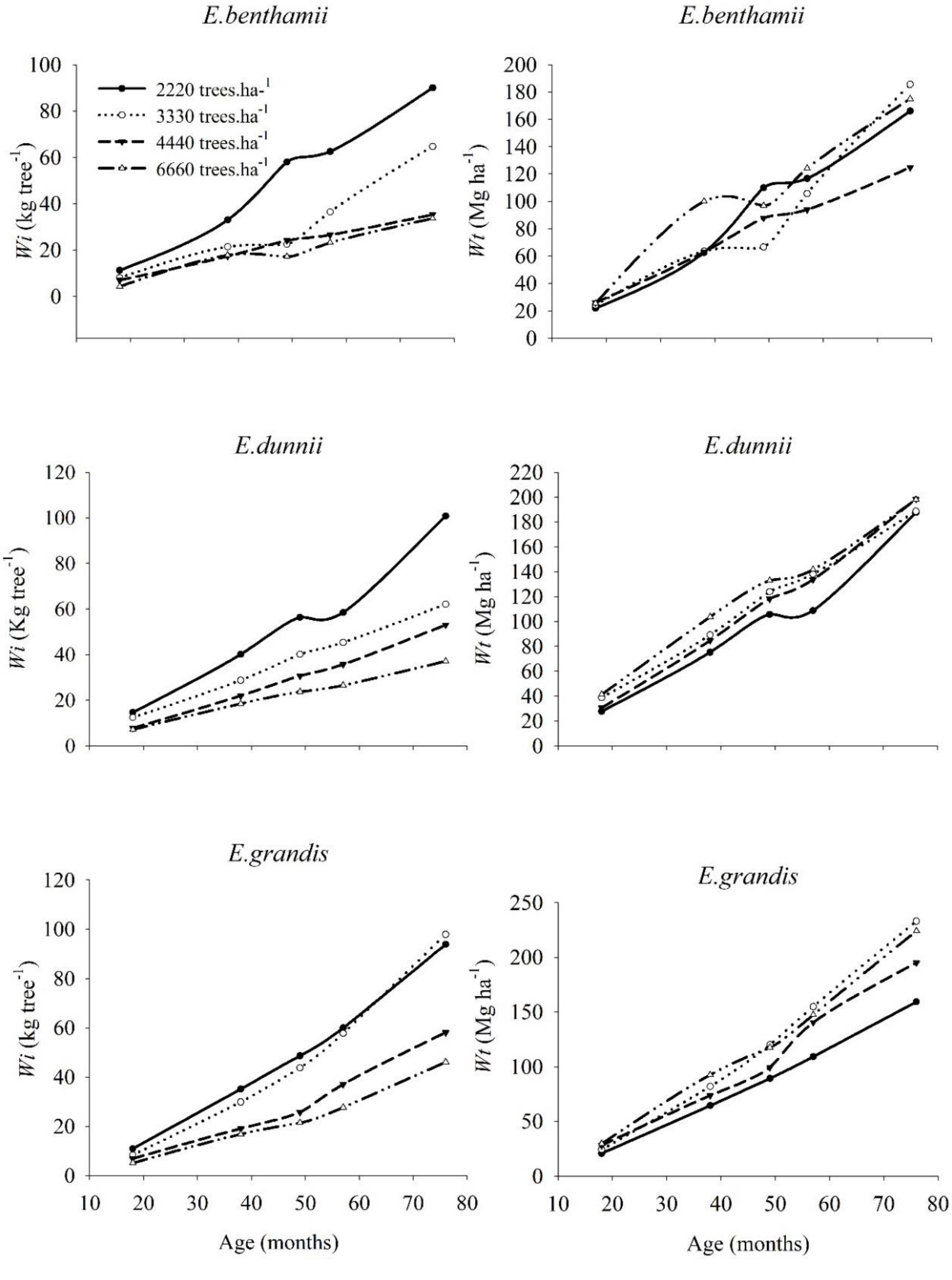


Figure 2. Evolutions of biomass per hectare (*Wt*) and tree (*Wi*) for the species of *Eucalyptus* and planting density at Paysandú (Uruguay).

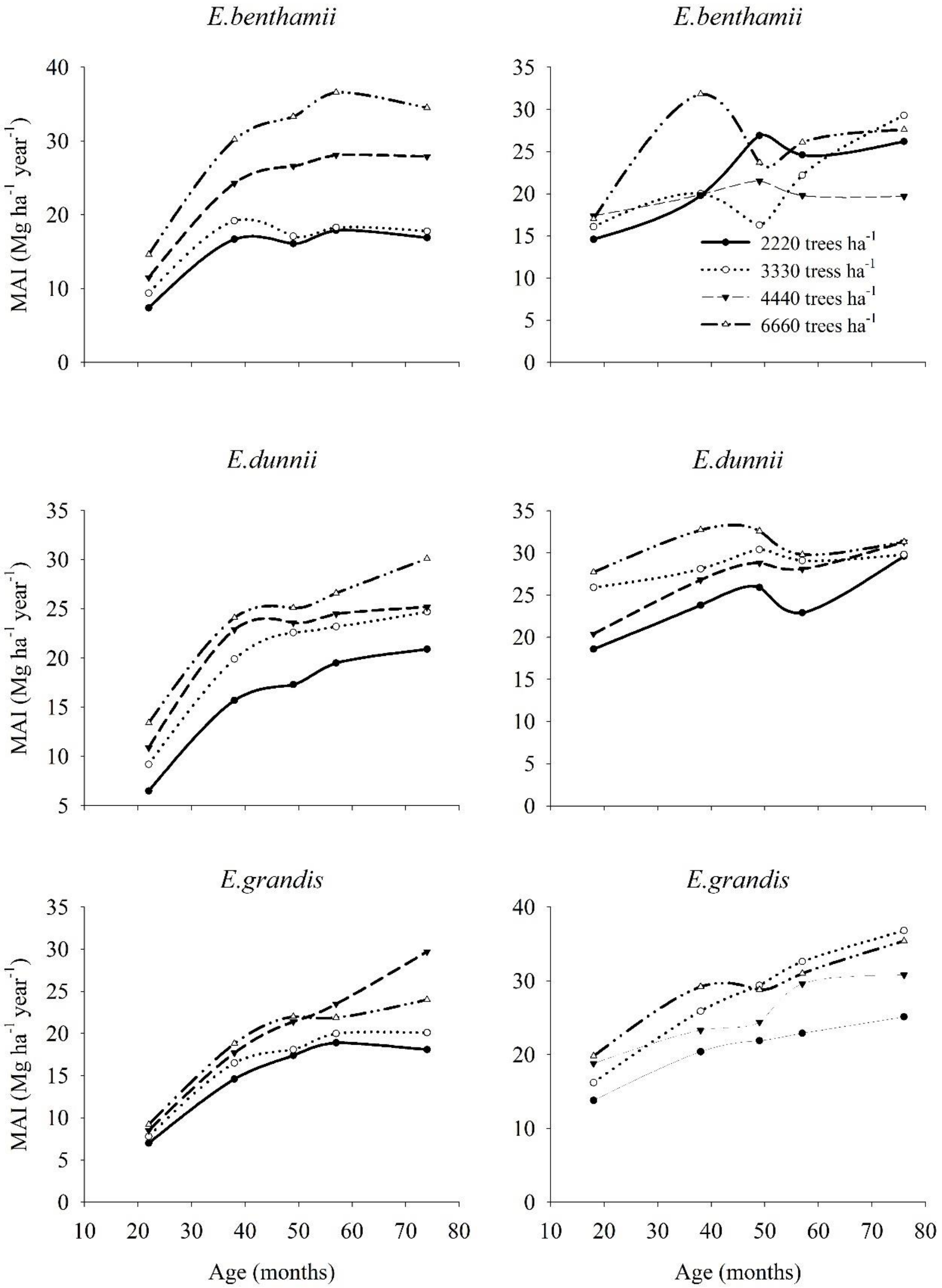


Figure 3. Mean annual increment (MAI) evolution of *Wt* for the species and planting density at Tacuarembó (left) and Paysandú (right) sites.

4. Discussion

In this study, we developed, for three eucalypt species, site-specific tree above-ground biomass equations and assessed the effect of species and planting density on wood density and overall biomass after six years. Although the results differ between the two sites evaluated, our research confirms the hypothesis that the species and planting density affect the wood density and productivity levels. However, the hypothesis that the species and planting density influence the harvest time is not verified. The reduction of rotation length at the Tacuarembó site could be explained by the decrease in survival. These short-crop-rotation eucalypt plantations in Uruguay showed large variations in biomass with increasing planting density, in particular at Tacuarembó. The biomass production showed significant variation among species and in relation to planting density: *E. grandis* was the most productive species at Tacuarembó, at 6660 trees ha^{-1}, while *E. dunnii* was the most productive at Paysandú, at a lower planting density (4440 trees ha^{-1}). The three species included in this analysis account for most of the current and potential biomass plantations in Uruguay (Balmelli and Resquin, 2006). The results obtained indicate that it is possible to obtain high levels of wood productivity in a relatively short time, even with planting densities that are not very high. However, it is essential to guarantee good conditions that permit proper establishment of the crop and, in consequence, obtain high levels of productivity throughout the rotation.

4.1 Survival

The effect of competition between trees and their survival (Dickel et al., 2010, Van Gunst et al., 2016) could not be verified in the first 76 months of growth. Perhaps this was due to the tolerance of competition shown by *Eucalyptus* species (Jacobs 1995, Tomé and Verwjjst 1996) and/or because these processes did not develop in the evaluation period (Sale 2005, Xue et al., 2011). The lowest survival values in the last forest inventory, at both sites, were for *E. grandis*, which showed greater susceptibility to competition among individuals than the other species studied (Table 2) (Schönau and Coetzee, 1989). The survival values were higher at Paysandú throughout the period studied, since at Tacuarembó the survival rate declined from the beginning of the experiment. In all cases, the tree mortality rate did not show any relationship with the planting density (Table 2). The higher mortality rate at Tacuarembó could be explained by greater weed competition in the initial growth phase than at Paysandú. Also, at Paysandú the soil preparation prior to planting was better than at Tacuarembó. This probably led to a higher occurrence of suppressed trees which had a high mortality rate over time (Binkley et al. 2010; Cunningham et al. 2010). The rainfall regime of the two sites shows that between the first and second year, a higher rainfall level occurred in Paysandú compared to Tacuarembó, although in both cases they were higher than the historical average levels. This in addition to the good weed control could have contributed to maintaining the high levels of survival in Paysandú in the early stages of growth (Figure S5, Supplementary material). The values obtained at the Tacuarembó site show the importance of adequate soil preparation in terms of weed control and good contact between the soil and the roots of the seedlings.

4.2 Wood density

Eucalyptus dunnii and *E. benthamii* had the highest values of *Db*, at both sites. This agrees with the low *Db* values found previously for *E. grandis*, relative to other eucalypts species (Backman and García de Leon, 2003). At Paysandú, higher wood densities were obtained in the trees with greater growth (lower planting density) (Lopes et al., 2017). Cassidy et al. (2013) indicated that larger trees have uniformity of *Db* from the pith to the bark. Malan and Hoon (1992) determined that *E. grandis* growing in low-density plantations began to produce adult wood earlier than when growing at high planting density. The adult wood of eucalypts is characterized by having larger fibers and thicker walls than juvenile wood, features which are closely related to the increase in *Db* (Carrillo et al., 2015). Larson et al. (2001) found that a denser plantation gave rise to trees with a high height/diameter ratio and an important proportion of juvenile wood. Thus, the apical growth is linked to the production of initial wood formed by fibers with thinner walls and with a higher proportion of vessels. The spacing of trees, through the competition for light between individuals, can also influence the capacity for production of photoassimilates and therefore of cellulose - which is stored in the walls of the fibers (De Souza et al., 2008), contributing to an increase in the *Db*. Kojima et al. (2009) found that the diameter growth of *E. grandis* did not affect the xylem density; according to Zobel and Jett (1995), this is common in species with diffuse porosity, like eucalypts species.

The situation described above for the planting density at Paysandú was not observed for any of the planting densities studied at Tacuarembó, which agrees with previous reports (Debell, 2001). In relation to the environmental factors that could explain these differences, the temperature has been found to have a direct effect on the anatomy of the wood and therefore on its density (Thomas et al., 2004, 2007). According to these authors, at higher temperatures there is a reduction of the lumen diameter of vessels and fibers and the wall thickness increases in *E. grandis*. In *E. tereticornis* it was established that the same changes are due to a reduction in water conductivity per unit area of xylem as the ambient temperature increases. It should be noted that the average temperature at Paysandú was 2°C higher than that recorded at Tacuarembó in the period 2010-2016 (Figure S6, Supplementary Material, INUMET, 2017).

At Tacuarembó, there were practically no changes in *Db* with the increase in age or with the different spacings, in any of the forest inventories. The lower growth, in general, at this site could be associated with the majority presence of the juvenile wood shaft throughout the growth period. A similar trend was reported by Castro et al. (2016), who evaluated changes in the *Db* in clones of eucalypts species from seven years of age and indicated the distinct effects of age on materials of differing genetic origin. On the other hand, at Paysandú, the *Db* increased with the tree age, particularly at the lower planting densities, although the ANOVA only showed a significant effect in *E. grandis*. The changes registered with the increase in age could be due to the transition from juvenile to adult wood that occurs in these stages of tree growth (Pelozzi et al., 2012). The proportion occupied by juvenile wood is highly variable, depending on the position in the stem, the genetic material, and the growth rate, but occupies a radius of about 5 to 8 cm around the pith (Calonego et al., 2005). This change in the properties of the wood is explained by alterations in the characteristics of the constituent's elements of the xylem that happen over time, such as an increase in the thickness of the walls of the fibers and a reduced frequency of occurrence of the vessel elements (Sette Junior et al. 2012). According to Latorraca (2000), the growth in young trees spaced widely apart occurs in conditions of low competition for sunlight; thus, the photosynthetic rate is high, and the initial logs are denser than in trees growing more closely together.

4.3 Tree biomass equations

Fitting of the models was performed for each site, species, and planting density. In almost all cases, the models of best fit were linear ones of the type: $\mathrm{Ln}W_i = \beta o + \beta 1 * \mathrm{Ln}\ (X)$, where βo and β1 are the regression coefficients and Ln (X) is the natural logarithm of the independent variable (i.e. *dbh*, *H*, or $dbh^2 * H$). These parameters were used to estimate the individual tree biomass because they are directly related to the stem size (Picard et al., 2012). The number of trees per hectare and the age did not make a significant contribution to the improvement of the *Wi* estimations (Winck et al., 2015). The models fitted in this study explain at least 97% (R^2_{adj}) of the variation observed in *Wi*, with errors and bias

(*RMSE* and ε) very close to zero in most cases (Tables S2 and S3, Supplementary material). In all models, there was very good agreement between the predicted and observed values represented on linear scales (Figures S3 and S4, Supplementary material).

4.4 Biomass of the species and planting density

At Tacuarembó, the W_i depended on the combined effect of the species and planting density. The greatest W_i values were reached with the lowest planting densities, in a similar way for the three species: the *Wi* reduction for the three species was 40% (97.5 vs 57.6 kg tree^{-1}) as the planting density rose from low to high (2220 vs. 6660 trees ha^{-1}). Ribeiro et al. (2017) found that an increase in the spacing raised the growth of the trees and the frequency of the dominant trees, without altering the *Db*. For this reason, there may be greater similarity of *Wi* among the three species studied here, due to the scalability found in the *Db*, and the differences in weight could be attributable to changes in the volume. The *Wt* was highest at the highest densities, but with more-marked differences among planting densities (Table 9). The differences in the W_i among the distinct spacings had a smaller effect on the *Wt* and this was compensated to a greater degree by the increase in the number of trees. The poorer performance of *Wi* and *Wt* at this site is explained by the low tree survival rate recorded at the end. The difference in productivity between the highest and lowest planting densities was 59% (183 vs 115 Mg ha^{-1} at 6660 and 2220 trees ha^{-1}, respectively). The average *Wt* values of the three species were very similar.

At Paysandú, *E. grandis* was the species that had, on average, the highest *Wi* value while *E. benthamii* and *E. dunnii* had lower, very similar values. The value recorded for *E. grandis* is explained by the individual growth, since the *Db* of this species was the lowest of the three species and it had lower average survival and less competition between individuals compared to *E. benthamii* and *E. dunnii*. The average *Wi* reduction for the three species, as the planting density rose from 2220 to 6660 trees ha^{-1}, was 59% (94.9 vs 38.9 kg tree^{-1}, respectively). The reduction in average W_i as the planting density increased was similar to that reported by Hakamada et al. (2017) for eucalypts species and was similar for all three species studied in this work. A similar relationship was found between the number of live trees (5137 vs 1802 trees ha^{-1}), the ratio of the average *Wi* (94.9 vs. 38.9 kg tree^{-1}), and the individual volume (0.140 vs 0.059 m^3 tree^{-1}, data not included), indicating a close relationship among these parameters. Similar results were obtained by Leles et al. (2001) for 52-month-old *E. camaldulensis* and *E. pellita* trees grown at densities of 2220 and 3330 trees ha^{-1}. The *Wt* at Paysandú was similar among the planting densities. This indicates that it would be possible to obtain high yields with low planting densities, which would be an economic advantage and would mean lower soil nutrient extraction (Bentancor, 2017). The *Wt* response to the changes in spacing was lower than that of the volume per tree. This could be explained by the reduction in the *Db* of the wood at the closer spacing (Table 4). Considering all three species, when the planting density increased from 2220 to 6660 trees ha^{-1} the *Wt* increased by approximately 16% (171 vs. 199 Mg ha^{-1}, respectively). The *Wt* results reported here agree with the higher productivity found previously at high planting densities (Rocha, 2011), since the number of trees has a greater effect than the possible alterations in the *Db* (Malan, 2005).

The MAI values registered at Tacuarembó shows that the three species behaved differently. *Eucalyptus benthamii* showed an increase until month 57, and thence a stagnation for all planting densities, whereas *E. dunnii* and *E. grandis* showed an ever-increasing rate of increase until that time and thence a lesser rate of increase for most of the planting densities. This behavior after month 57 can be explained by the progressive reduction in the number of live trees. On average, the MAI values were highest for *E. benthamii* and *E. dunnii* (24.3 and 25.3 Mg ha^{-1} year^{-1}, respectively). The MAI values at Paysandú, in general, show increasing increases, with similar values for *E. benthamii* and *E. dunnii* towards the end of the evaluation (Figure 3). This indicates that at this site the harvest time had not been reached at 76 months, which could be explained by the high level of survival (on average, 84%). The highest average values of MAI were obtained, in decreasing order, with *E. grandis*, *E. dunnii*, and *E. benthamii* (32, 31, and 25 Mg ha^{-1} year^{-1}). In all cases, the weight differences among species for *Wi* and *Wt* increased with the tree age. The standardized rainfall index (SRI) of the evaluation period, which measures the excess or deficit of rainfall in relation to the historical average (1980–2010), shows that there were no significant drought or excessive rainfall events at either site that could have compromised the growth of the trees (Figure S7, Supplementary material). Values of 0.49 to -0.49 indicate a normal situation with respect to the historical average. Values of 0.49 to 0.99 and -0.49 to -0.99 indicate slightly wet and slightly dry conditions, respectively (INUMET, 2017). In 2015, there is a marked difference between both sites with respect to this index. The low value of this index registered in Paysandú (-0.86) associated with a rainfall level below the historical average (Figure S5, Supplementary material) could explain the reduction in the growth rate observed in all species and planting densities (Figure 3). The higher levels of survival achieved in this site could also have contributed to the aforementioned reduction.

5. Conclusions

For the three species tested, survival was not affected by the planting density until the trees had reached the age of 76 months, at both sites. The differences between sites can be explained by the type of soil preparation, and also by the rainfall regime in the early growth stages in both cases. With adequate tillage prior to planting it is possible to obtain, regardless of the density of the plantation, high survival values, which are the key to high levels of productivity. The increase in the number of trees did not affect the productivity to the same extent. According to the values of MAI, the plantations at Paysandú had not reached the optimum harvest time 76 months after planting. On the other hand, at Tacuarembó the MAI stagnation after about 57 months indicates that the harvest time had arrived. Our results could also be of interest for regions with climate and soil conditions like those of these experiments, such as the eastern coast of Argentina and southern Brazil. The eucalyptus species evaluated in this experiment have shown a very good adaptation on these areas, although the particularities of each plantation site can have important effects on certain variables such as wood density and therefore on the final productivity.

6.References

Backman, M. E., García de León, J. 2003. Correlations of pulp and paper properties at an early age and full, In Tecnicelpa (ed.) EUCEPA Conference: sustainable development for the pulp and paper industry. Lisbon-Portugal, pp. 108-112.

Balmelli, G., Resquin, F. 2004. Evaluación del crecimiento de especies de *Eucalyptus* en diferentes zonas de prioridad forestal, Serie Aftercare Forestal INIA - JICA, 14, p. 20. http://www.ainfo.inia.uy/digital/bitstream/item/4330/1/Aftercare-del-Proyecto-de-Mejoramiento-Genetico-Forestal-en-el-Uruguay-2000-2002-Nro.-14.pdf. Accessed May 28th, 2018.

Balmelli, G., Resquin, F. 2006. Productividad de diferentes especies de *Eucalyptus* sobre areniscas de Tacuarembó-Rivera, Serie Técnica 159. INIA Tacuarembó, 159, pp. 305-312. http://www.ainfo.inia.uy/digital/bitstream/item/7774/1/ST-159-305-312.pdf. Accessed April 20th, 2018.

Bensaid, S., Conti, R., Fino, D., 2012. Direct liquefaction of ligno-cellulosic residues for liquid fuel production. Fuel 94, 324-332. https://doi.org/10.1016/j.fuel.2011.11.053

Bentancor, L. 2017. Extracción de nutrientes por *Eucalyptus dunnii* Maiden de 4 años con destino a la producción de biomasa para energía y celulosa. Master's Thesis, Universidad de la República, Montevideo, Uruguay, pp. 99.

Binkley, D., Stape, J.L., Ryan, M.G., Barnard, H.R., Fownes, J., 2002. Age-related Decline in Forest Ecosystem Growth: An Individual-Tree, Stand-Structure Hypothesis. Ecosystems 5: 58-67.

Calonego, F. W., Severo, E. T. D. Assi, P. P. 2005. Mensuração do comprimento das fibras para a determinação da madeira juvenil em *Eucalyptus citriodora*, Scientia Forestalis, 68: 113-121.

Carrillo, I., Aguayo, M.G., Valenzuela, S., Mendonça, R.T., Elissetche, J.P., 2015. Variations in wood anatomy and fiber biometry of *Eucalyptus globulus* genotypes with different wood density. Wood research 60: 1-10.

Cassidy, M., Palmer, G., Smith, R.G.B., 2013. The effect of wide initial spacing on wood properties in plantation grown *Eucalyptus pilularis*. New Forests 44: 919-936.

Castaño, J. P., Ceroni, A., Furest, M., Aunchayna, J,.Bidegain, R. 2011. Caracterización agroclimática del Uruguay 1980-2009, Serie Técnica INIA. Montevideo, Uruguay, 193, p. 33. http://www.ainfo.inia.uy/digital/bitstream/item/2538/1/18429021211104157.pdf. Accessed January 18th, 2018.

Castro, A.F.N.M., Castro, R.V.O., Carneiro, A. de C.O., Santos, R.C. dos, Carvalho, A.M.M.L., Trugilho, P.F., Melo, I.C.N.A. de, Castro, A.F.N.M., Castro, R.V.O., Carneiro, A. de C.O., Santos, R.C. dos, Carvalho, A.M.M.L., Trugilho, P.F., Melo, I.C.N.A. de, 2016. Correlations between age, wood quality and charcoal quality of *Eucalyptus* clones. Revista Árvore 40: 551-560.

Cunningham, S.C., Thomson, J.R., Read, J., Baker, P.J., Nally, R.M., 2010. Does stand structure influence susceptibility of eucalypt floodplain forests to dieback? Austral Ecology 35: 348-356.

DeBell, D.S., Keyes, C.R., Gartner, B.L., 2001. Wood density of *Eucalyptus saligna* grown in Hawaiian plantations: effects of silvicultural practices and relation to growth rate. Australian Forestry 64: 106-110.

Dickel, M., Kotze, H., Gadow, K. von, Zucchini, W., 2010. Growth and Survival of *Eucalyptus grandis* - a study based on modelling lifetime distributions. Mathematical and Computational Forestry & Natural-Resource Sciences (MCFNS) 2 (2): 86-96 (11). http://mcfns.net/index.php/Journal/article/view/MCFNS.2-86. Accessed March 20th, 2018.

Eufrade Junior, H.J., Melo, R.X. de, Sartori, M.M.P., Guerra, S.P.S., Ballarin, A.W., 2016. Sustainable use of eucalypt biomass grown on short rotation coppice for bioenergy. Biomass and Bioenergy 90: 15-21.

Fatemi, F.R., Yanai, R.D., Hamburg, S.P., Vadeboncoeur, M.A., Arthur, M.A., Briggs, R.D., Levine, C.R., 2011. Allometric equations for young northern hardwoods: the importance of age-specific equations for estimating aboveground biomass. Canadian Journal of Forestry Research 41: 881-891.

Ferrere, P., Lupi, A.M., Boca, R., Nakama, V., Alfieri, A., 2008. Biomasa en plantaciones de *Eucalyptus viminalis* Labill. de la provincia de Buenos Aires, Argentina. Ciência Florestal 18: 291-305.

González-García, M., Hevia-Cabal, A., Barrio-Anta, M. 2013. Modelo dinámico de crecimiento y producción de biomasa para cultivos energéticos de *Eucalyptus nitens* (Maiden) en el noroeste de España, in Forestales, S. E. de C. (ed.) 6 to Congreso Forestal Español. Vitoria Gateiz, pp. 2-8. http://secforestales.org/publicaciones/index.php/congresos_forestales/article/view/14333. Accessed May 28th, 2018.

Hakamada, R., Hubbard, R.M., Ferraz, S., Stape, J.L., Lemos, C., 2017. Biomass production and potential water stress increase with planting density in four highly productive clonal *Eucalyptus* genotypes. Southern Forests: A Journal of Forest Science. 79(3): 251-257.

Harris, F. 2007. The effect of competition on stand, tree, and wood growth and structure in subtropical *Eucalyptus grandis* plantations, PhD thesis, Southern Cross University, Lismore, NSW. 193 p. https://epubs.scu.edu.au/theses/125/. Accessed December 28th, 2017.

Hinchee, M., Rottmann, W., Mullinax, L., Zhang, C., Chang, S., Cunningham, M., Pearson, L., Nehra, N., 2009. Short-rotation woody crops for bioenergy and biofuels applications. In Vitro Cell Dev Biol Plant 45: 619-629.

IEA [International Energy Agency] (2010). World Energy Outlook 2010. https://www.iea.org/newsroom/news/2010/november/world-energy-outlook-2010.html. Accessed December 28th, 2017.

INUMET. Estadísticas climatológicas. https://www.inumet.gub.uy/clima/estadisticas-climatologicas. Accessed July 28th, 2018.

Jacobs, M. R. 1955. Growth habits of the eucalypts. Forestry and Timber Bureau, Canberra, 262 pp.

Kojima, M., Yamaji, F.M., Yamamoto, H., Yoshida, M., Nakai, T., 2009. Effects of the lateral growth rate on wood quality parameters of *Eucalyptus grandis* from different latitudes in Brazil and Argentina. Traditional forest-related knowledge in Asia. Forest Ecology and Management 257: 2175-2181.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World Map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15: 259-263.

Larson, P.R., Kretschmann, D.E., Clark, A.I., Isebrands, J.G., 2001. Formation and properties of juvenile wood in southern pines: a synopsis. Gen. Tech. Rep. FPL-GTR-129. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory. 42 p. 129.

Latorraca, J. de F., Albuquerque, C. de, 2000. Efeito do rápido crescimento sobre as propriedades da madeira. Floresta e Ambiente 7: 279-291.

Leles, P. S. D. S., Reis, G. G. D., Reis, M. D. G. F., Morais, E. J. D. 2001. Crescimento, produção e alocação de matéria seca de *Eucalyptus camaldulensis* e *E. pellita* sob diferentes espaçamentos na região de Cerrado, MG., Scientia Forestalis 59: 77-87.

Lopes, E.D., de Laia, M.L., dos Santos, A.S., Soares, G.M., Leite, R.W.P., de Souza Martins, N., 2017. Influência do espaçamento de plantio na produção energética de clones de *Corymbia* e *Eucalyptus.* Floresta 47: 95-104.

Macedo, I.C., 2003. Estado da arte e tendências tecnológicas para energia. Relatório Técnico. Centro de Gestão e Estudos Estratégico Ciência. Ciência, Tecnologia e Inovação. http://finep.gov.br/images/a-finep/fontes-de-orcamento/fundos-setoriais/ct-energ/estado-da-arte-e-tendencias-tecnologicas-para-energia.pdf. Accessed December 28th, 2017.

Machado, F. D. C., Philipe, S., Guerra, S., Ceragioli, N., Oguri, G. 2012. Influência do espaçamento na produtividade e alocação de biomassa em um plantio de *Eucalyptus grandis,* in Congresso Internacional de Bioenergia, pp. 1-6. http://biomassaworld.com.br/artigos-tecnicos/influencia-do-espacamento-na-produtividade-e-alocacao-de-biomassa-em-um-plantio-de-eucalyptus-grandis/. Accessed July 15th, 2018.

Malan, F.S., 2005. The effect of planting density on the wood quality of South African-grown *Eucalyptus grandis.* Southern African Forestry Journal 205: 31-37.

Malan, F., Hoon, M., 1992. Effect of initial spacing and thinning on some wood properties of *Eucalyptus grandis.* South African Forestry Journal 163: 13-20.

Nuberg, I.K., Gunn, B., Tavune, M., Sumareke, A., Kravchuk, O., 2015. Evaluation of short-rotation coppicing fuelwood production systems for Papua New Guinea. Biomass and Bioenergy 78: 126-139.

Quinn, G.P., Keough, M.J. 2002. Experimental design and data analysis for biologists. Cambridge University Press

Paulino, E. J. 2012. Influência do espaçamento e da idade na produção de biomassa e na rotação econômica em plantios de eucalipto. Master's Thesis, Universidade Federal Dos Vales Do Jequitinhonha e Mucuri. Diamantina, MG. Brazil. 60 p. http://acervo.ufvjm.edu.br:8080/jspui/handle/1/492. Accessed March 28th, 2018.

Pelozzi, M.M.A., Severo, E.T.D., Calonego, F.W., Rodrigues, P.L.M., 2012. Propriedades físicas dos lenhos juvenil e adulto de *Pinus elliottii* Engelm var. elliottii e de *Eucalyptus grandis* Hill ex Maiden. Ciência Florestal 22: 305-313.

Pérez, S., Renedo, C.J., Ortiz, A., Mañana, M., Delgado, F., Tejedor, C., 2011. Energetic density of different forest species of energy crops in Cantabria (Spain). Biomass and Bioenergy, 'Biofuels and Bioenergy: Challenges and Opportunities' Proceedings of a joint workshop of IEA Bioenergy Tasks 29, 31 and 39, August 2006, Vancouver, British Columbia, Canada 35: 4657-4664.

Picard, N., Saint-André, L., Henry, M., 2012. Manual de construcción de ecuaciones alométricas para estimar el volumen y la biomasa de los árboles: del trabajo de campo a la predicción. http://agris.fao.org/agris-search/search.do?recordID=XF2013001501. Accessed August 20th, 2017.

Resquin, F., Fariña, I., Rachid, C., Rava, A., Doldán, J., 2012. Influencia de la edad de corte en el pulpeo de *Eucalyptus globulus* plantado en Uruguay. Agrociencia Uruguay 16, 27-38. http://www.scielo.edu.uy/scielo.php?pid=S2301-15482012000200004&script=sci_arttext Accessed December 28th, 2016.

Rocha, M.F.V., Vital, B.R., Carneiro, A.C.O., Carvalho, A.M.M.L., Cardoso, M.T., Hein, P.R.G., 2016. Effects of plant spacing on the physical, chemical and energy properties of *Eucalyptus* wood and bark. Journal of Tropical Forest Science 28: 243-248.

Rocha, M. F. V. 2011. Influência do espaçamento e da idade na produtividade e propriedades da madeira de *Eucalyptus grandis* x *Eucalyptus camaldulensis* para energia. Master's Thesis, Universidade Federal de Vicosa, MG - Brasil. 86 p.

Rockwood, D.L., Rudie, A.W., Ralph, S.A., Zhu, J.Y., Winandy, J.E., 2008. Energy Product Options for *Eucalyptus* Species Grown as Short Rotation Woody Crops. International Journal of Molecular Sciences 9: 1361-1378.

Pleguezuelo, C.R.R., Zuazo, V.H.D., Bielders, C., Bocanegra, J.A.J., PereaTorres, F., Martínez, J.R.F., 2014. Bioenergy farming using woody crops. A review. Agron. Sustain. Dev. 35: 95-119.

Sale, G. 2005. A comparison of between-tree competition effects in separate stands of a *Eucalyptus grandis* seedling and a single *Eucalyptus grandis* x *urophylla* hybrid clone. Master's Thesis, University of the Witwatersrand, Johannesburg. 162 p. Available at: http://wiredspace.wits.ac.za/bitstream/handle/10539/1725/Giovanni thesis.pdf?sequence=1&isAllowed=y

Santana, W.M.S., Calegario, N., Arantes, M.D.C., Trugilho, P.F., 2012. Effect of age and diameter class on the properties of wood from clonal Eucalyptus. CERNE 18: 1-8.

Santos, M. D. 2011. Efeito do espaçamento de plantio na biomassa do fuste de um clone híbrido interespecífico de *Eucalyptus grandis* e *Eucalyptus urophylla*. Master's Thesis, Faculdade de Ciências Agronômicas, Universidade Estadual Paulista, São Paulo-Brazil. 152 p.

Ribeiro, M.D. dos S.B., Jorge, L.A.B., Mischan, M.M., Santos, A.L. dos, Ballarin, A.W., 2017. Avaliação da produção de biomassa do fuste de um clone híbrido de eucalipto sob diferentes espaçamentos. Ciência Florestal 27: 31-45.

Schönau, A.P.G., Coetzee, J., 1989. Initial spacing, stand density and thinning in eucalypt plantations. Forest Ecology and Management 29: 245-266.

Senelwa, K., Sims, R.E.H., 1998. Tree biomass equations for short rotation eucalypts grown in New Zealand. Biomass and Bioenergy 13: 133-140.

Senelwa, K., Sims, R.E.H., 1999. Fuel characteristics of short rotation forest biomass. Biomass and Bioenergy 17: 127-140.

Sette Jr, C.R., Oliveira, I.R. de, Tomazello Filho, M., Yamaji, F.M., Laclau, J.P., 2012. Efeito da idade e posição de amostragem na densidade e características anatômicas da madeira de *Eucalytus grandis*. Revista Árvore 36: 1183-1190.

Sims, R.E.H., Hastings, A., Schlamadinger, B., Taylor, G., Smith, P., 2006. Energy crops: current status and future prospects. Global Change Biology 12: 2054-2076.

Souza, R. N. 1989. Efeito de dois espaçamentos na produção em peso e volume de *Eucalyptus grandis* (W. Hill ex Maiden). Master's Thesis, Universidade Federal de Viçosa, MG-Brazil. 102 p.

Souza de, A., Gaspar, M., Tiné, M., Buckeridge, M. 2008. Ajustando os botões: como as plantas lidam com o aumento do CO2 atmosférico?, in Buckridge, M. (ed.) Biologia & Mudanças Climáticas no Brasil: 101-113.

Thomas, D.S., Montagu, K.D., Conroy, J.P., 2004. Changes in wood density of *Eucalyptus camaldulensis* due to temperature-the physiological link between water viscosity and wood anatomy. Forest Ecology and Management 193: 157-165.

Thomas, D.S., Montagu, K.D., Conroy, J.P., 2007. Temperature effects on wood anatomy, wood density, photosynthesis and biomass partitioning of *Eucalyptus grandis* seedlings. Tree Physiol 27: 251-260.

Tomé, M., Verwijst, T., 1996. Modelling competition in short rotation forests. Biomass and Bioenergy, 11: 177-187.

Tuset, R., Durán, F., Mantero, C., Baillod, G., Aber, A., Böthig, S., Ono, A. 2008. Manual de maderas comerciales, equipos y procesos de utilización; volumen 2. Edited by H. Sur. Montevideo, Uruguay.

Van Gunst, K.J., Weisberg, P.J., Yang, J., Fan, Y., 2016. Do denser forests have greater risk of tree mortality: A remote sensing analysis of density-dependent forest mortality. Forest Ecology and Management, 359: 19-32.

Wilkins, A.P., Horne, R., 1991. Wood-density variation of young plantation-grown *Eucalyptus grandis* in response to silvicultural treatments. Forest Ecology and Management 40: 39-50.

Winck, R.A., Fassola, H.E., Barth, S.R., Crechi, E.H., Keller, A.E., Videla, D., Zaderenko, C., 2015. Modelos predictivos de biomasa aérea de *Eucalyptus grandis* para el noreste de Argentina. Ciência Florestal 25: 595-606.

Xue, L., Pan, L., Zhang, R., Xu, P., 2011. Density effects on the growth of self-thinning *Eucalyptus urophylla* stands. Trees 25: 1021-1031.

Yang, Y., Brammer, J.G., Mahmood, A.S.N., Hornung, A., 2014. Intermediate pyrolysis of biomass energy pellets for producing sustainable liquid, gaseous and solid fuels. Bioresource Technology 169: 794-799.

Zobel, B. J., Jett, J. B. 1995. Genetics of Wood Production. Edited by T.E. Timmel. Syracuse: Springer-Verlag.

Supplementary material

Table S1.- Main physical and chemical characteristics at Tacuarembó and Paysandú soil profiles

Tacuarembó															
Horizon	**Depth**	**Clay**	**Silt**	**Sand**	**%OM**	**pH†**		**Extractable cations**							**Base**
						H_2O	**KCl**	**Al**	**Ca**	**Mg**	**K**	**Na**	**Total Bases**	**CECe**	**Sat.**
	cm	--------- g kg^{-1} ---------						------------------- $cmol_c$ kg^{-1} -------------------							%
A	46	14,7	24,3	61,0	1,2	4,7	3,8	1,0	2,7	1,0	0,3	0,2	4,2	5,3	79,2
AB	18	18,0	29,6	52,4	1,0	4,6	3,8	1,0	3	1,3	0,3	0,2	4,8	5,8	82,8
Bt	27	35,6	40,1	31,1	0,8	4,8	3,7	0,9	5,3	2,6	0,4	0,4	8,5	10,4	81,7
BC	18	36,4	31,7	32,0	0,8	5,1	4,1	0,7	6,5	3,1	0,3	0,6	10,5	11,2	93,8
C	13	27,5	36,8	35,8	0,8	5,1	4,1	0,6	5,1	2,5	0,3	0,2	8,0	8,6	93,0

Paysandú															
Horizon	**Depth**	**Clay**	**Silt**	**Sand**	**%OM**	**pH†**		**Extractable cations**							**Base**
						H_2O	**KCl**	**Al**	**Ca**	**Mg**	**K**	**Na**	**Total Bases**	**CECe**	**Sat.**
	cm	--------- g kg^{-1} ---------						------------------- $cmol_c$ kg^{-1} -------------------							%
A	43	13,1	27,2	59,7	1,1	4,8	3,7	0,8	2,1	0,8	0,1	0,2	3,2	4,0	80,0
E	24	12,6	25,3	62,1	0,5	4,8	3,7	0,8	1,9	0,8	0,1	0,2	3,0	3,8	79,0
Bt	40	30,3	31,7	38,0	0,6	5,1	4,1	0,6	9,6	3,2	0,4	0,3	13,4	14,1	95,0
BC	26	29,0	36,2	34,8	0,3	5,4	4,2	0,3	11	3,7	0,4	0,4	15,4	15,7	98,1

Note: † pH: soil: solution relation v/v 1:2.5; Extractable Al: extracted by KCl 1M; Extractable bases: extracted by Ammonium Acetate 1M;

CECe: effective Cation Exchange Capacity; Base Sat.: (Total Bases/CECe)*100. Source: Bentancor 2017.

Table S2. Adjustment of logarithmic curve fit to Wi versus diameter at breast height (*dbh*) and height (*H*) for three species of Eucalyptus for short crop rotation at Tacuarembó. Regressions are for single-stemmed live trees with dbh greater than 3 cm.

Species	Planting Density (tres ha^{-1})		N	R_{adj}^2	*RMSE*	*Bias*	*F*	*p-value*
E. benthamii	2220	LnW_i=-3.85133+Ln (dbh) *1.60521+1.25189*Ln (H)	43	0.993	0.0803	0.062	3243	< 2.2e-16
	3330	LnW_i=-4.06731+Ln (dbh) *1.69936+1.24073*Ln (H)	43	0.995	0.0692	0.0548	4484	< 2.2e-16
	4440	LnW_i=-4.0288+Ln (dbh) *1.7815+1.1578*Ln (H)	43	0.984	0.135	0.0644	1292	< 2.2e-16
	6660	LnW_i=-3.9741+Ln (dbh) *1.819+1.1045*Ln (H)	43	0.991	0.103	0.0802	2483	< 2.2e-16
E. dunnii	2220	LnW_i=-3.7866+Ln (dbh) *1.8857+0.993*Ln (H)	43	0.982	0.133	0.0921	1178	< 2.2e-16
	3330	LnW_i=-3.54786+Ln (dbh) *1.9381+0.85291*Ln (H)	43	0.993	0.0789	0.0589	3266	< 2.2e-16
	4440	LnW_i=-3.55077+Ln (dbh) *1.76874+1.00589*Ln (H)	43	0.994	0.0747	0.0589	3821	< 2.2e-16
E. grandis	6660	LnW_i=-3.57269+0.93233*$Ln(dbh^2*H)$	43	0.991	0.0965	0.0740	4775	< 2.2e-16
	2220	LnW_i=-3.75887+Ln (dbh) *2.06563+0.75153*Ln (H)	43	0.996	0.0674	0.0573	5640	< 2.2e-16
	3330	LnW_i=-3.8246+Ln (dbh) *1.9724+0.8727*Ln (H)	43	0.985	0.137	0.091	1332	< 2.2e-16
	4440	LnW_i=-3.9033+Ln (dbh) *1.5665+1.2751*Ln (H)	43	0.988	0.123	0.085	1596	< 2.2e-16
	6660	LnW_i=-3.7438+Ln (dbh) *1.9417+0.8522*Ln (H)	43	0.988	0.133	0.0869	1679	< 2.2e-16

Table S3. Adjustment of logarithmic curve fit to Wi versus diameter at breast height (*dbh*) and height (*H*) for three species of Eucalyptus for short crop rotation at Paysandú. Regressions are for single-stemmed live trees with dbh greater than 3 cm.

Species	Planting density (trees ha^{-1})	Models	N	R_{adj}^2	*RMSE*	*Bias*	*F*	*p-value*
E. benthamii	2220	LnW_i=-3.689+1.46708*$Ln(dbh^2)$	43	0.970	0.163	0.133	1349	< 2.2e-16
	3330	W_i=12.2676836-1.5621963*(dbh)+0.022479*(dbh^2*H) - 0.4340308*(H)	43	0.992	3.887	0.0576	908.2	< 2.2e-16
	4440	LnW_i=-2.87299+34.88771*$Ln(dbh)$+0.04097*$Ln(dbh^3)$ - 16.65596*$Ln(dbh^2$*$H)$ +17.37619*$Ln(H)$	42	0.985	0.111	0.0847	688.4	< 2.2e-16
	6660	LnW_i=-3.80372+0.9709*$Ln(dbh^2$*$H)$	42	0.987	0.1206	0.0927	3173	< 2.2e-16
E. dunnii	2220	LnW_i=-4.3231+0.2293*$Ln(dbh)$+0.9755*$Ln(dbh^2$*$H)$	43	0.973	0.1509	0.123	741.1	< 2.2e-16
	3330	LnW_i=-3.8112+0.2207*$Ln(dbh)$+0.9119*$Ln(dbh^2$*$H)$	43	0.982	0.117	0.0874	1133	< 2.2e-16
	4440	LnW_i=-3.85522+0.49256*$Ln(dbh)$+0.83519*$Ln(dbh^2$*$H)$	43	0.988	0.0935	0.0700	1745	< 2.2e-16
	6660	LnW_i=-3.7724+0.9784*$Ln(dbh^2$*$H)$	43	0.984	0.130	0.0984	2660	< 2.2e-16
E. grandis	2220	LnW_i=-3.5873+0.4278*$Ln(dbh)$+0.7862*$Ln(dbh^2$*$H)$	43	0.986	0.113	0.0902	1470	< 2.2e-16
	3330	LnW_i=-4.3098+2.1701*$Ln(dbh)$+0.9201*$Ln(H)$	42	0.984	0.127	0.105	1310	< 2.2e-16
	4440	LnW_i=-4.19476+0.99516*$Ln(dbh2$*$H)$	42	0.984	0.124	0.0974	2626	< 2.2e-16
	6660	LnW_i=-3.6865+0.7172*$Ln(dbh)$+0.7057*$Ln(dbh^2$*$H)$	43	0.986	0.116	0.093	1451	< 2.2e-16

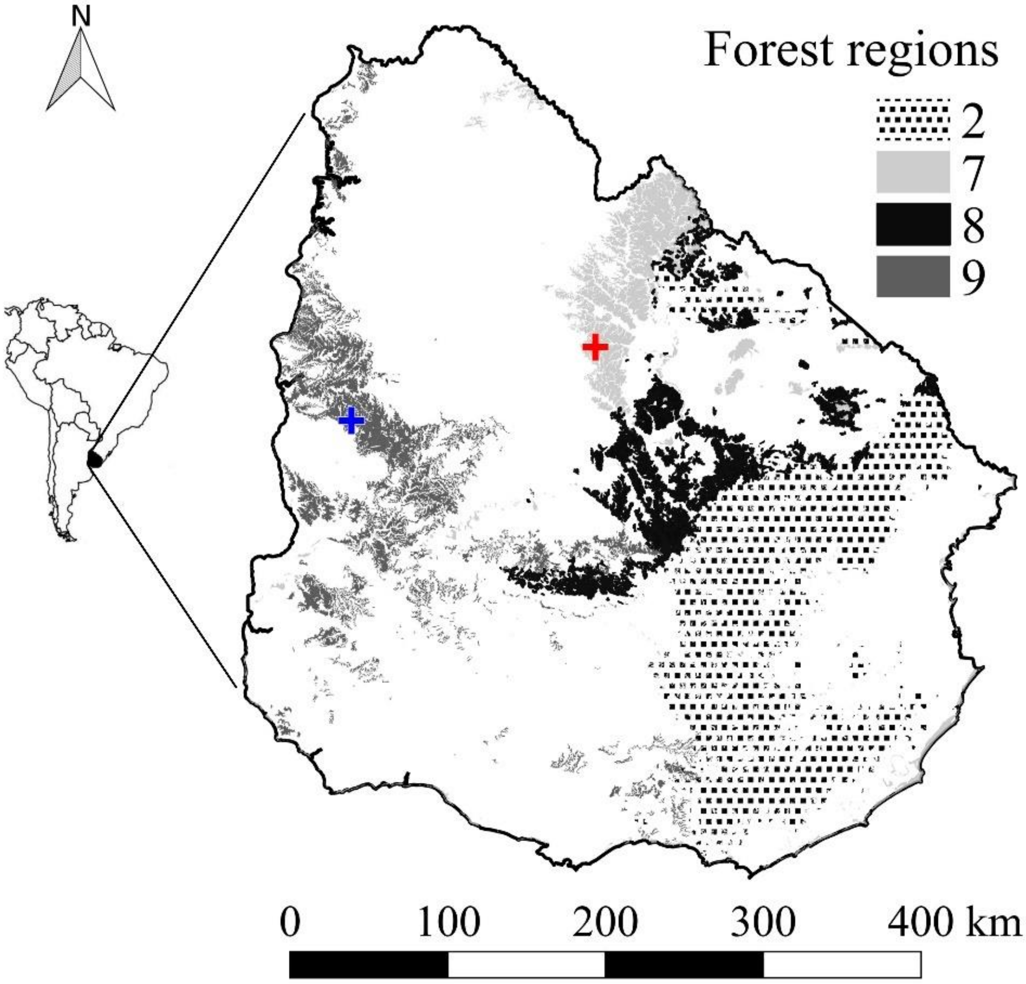


Figure S1. Regions prioritized for forest plantations (Forests regions) including trial locations at Tacuarembó (red plus sign) and Paysandú (blue plus sign). According to the National Commission for Agroeconomic Studies of the Land Classification (CO.N.E.A.T.), soils correspond to groups 2, 7, 8 and 9 have an adequate soil fertility for forest plantation.

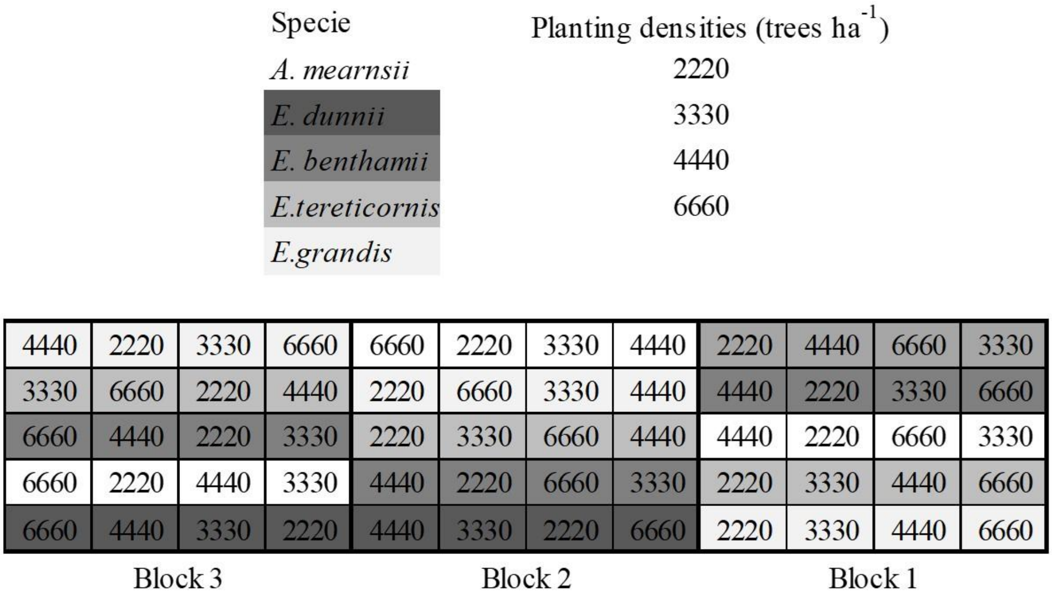


Figure S2. Diagram of experimental design

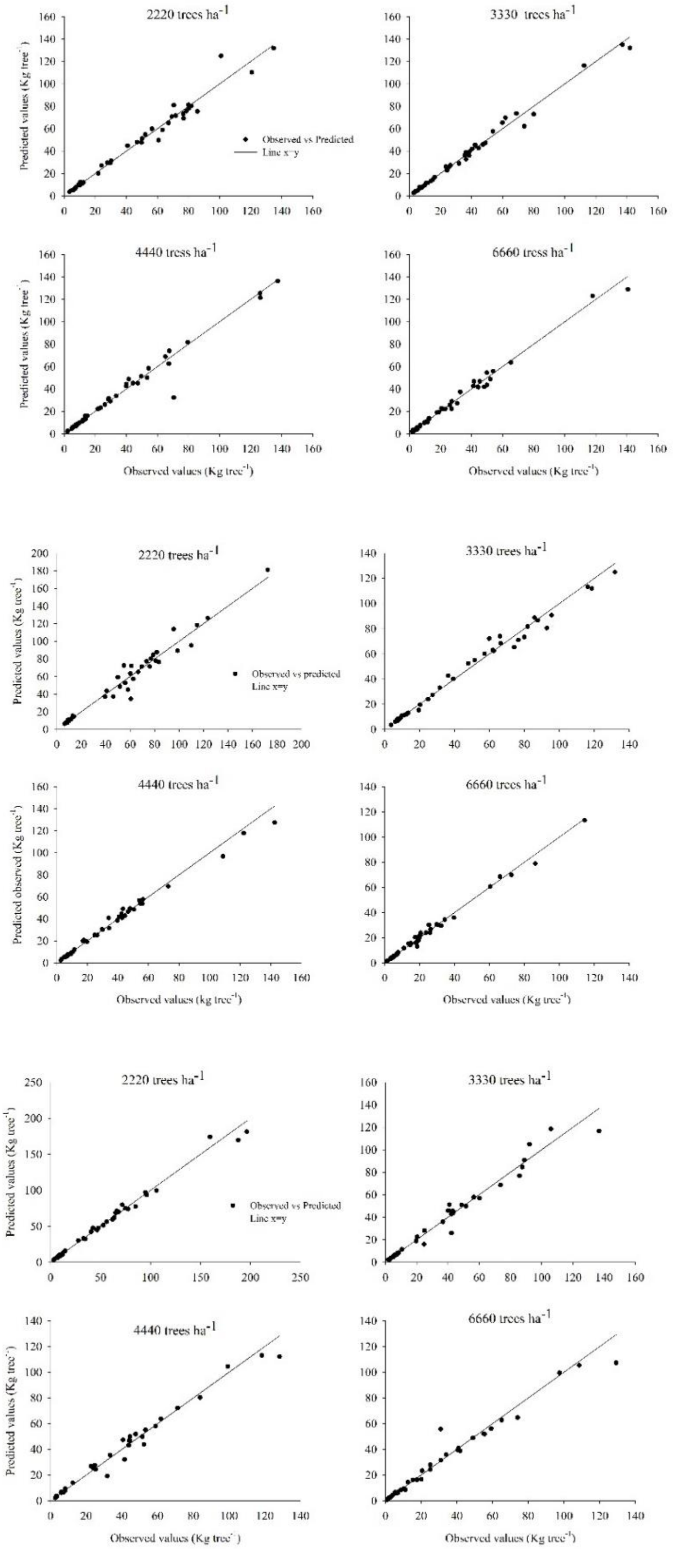


Figure S3.- Bivariate relationships between observed and predicted tree biomass of *E. benthamii* (top), *E. dunnii* (medium) and *E. grandis* (bottom) in Tacuarembó. In all figures linear 1:1 line has been fitted.

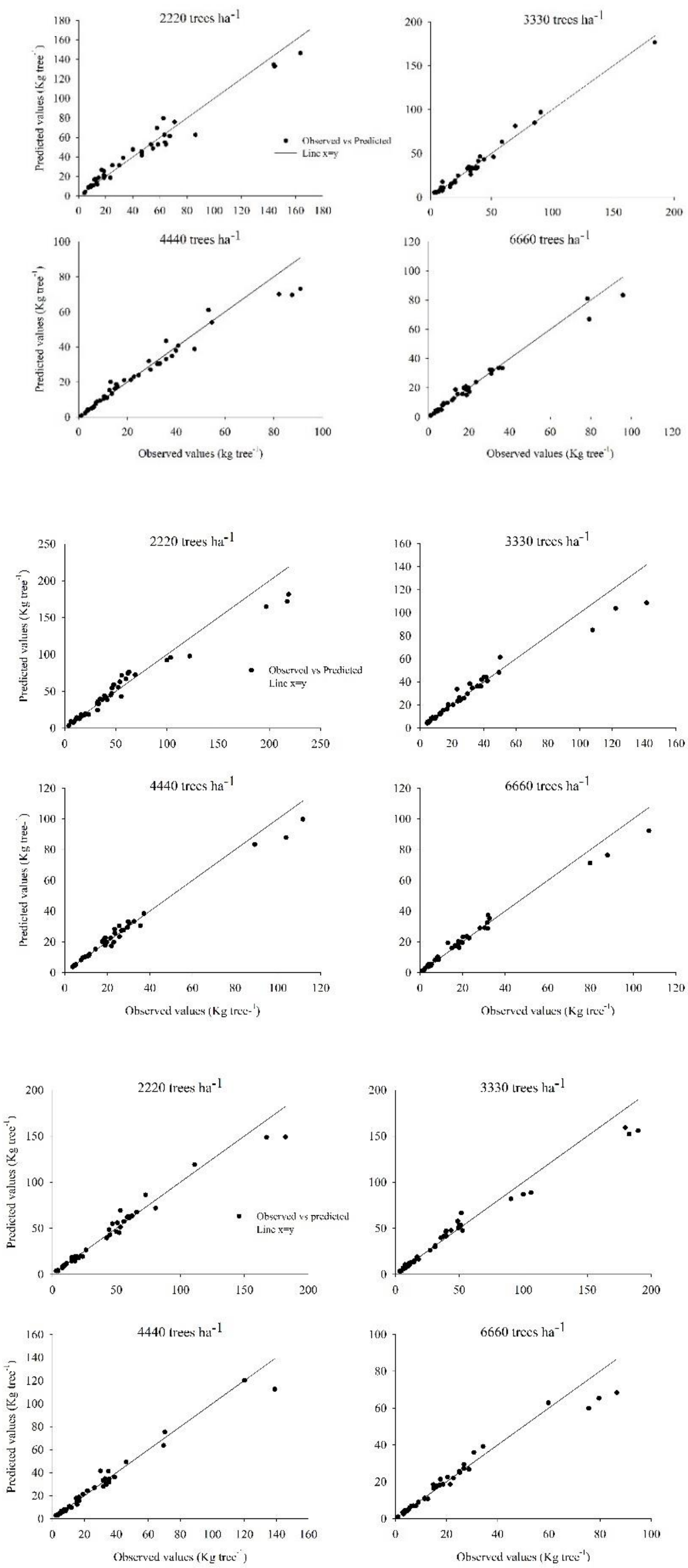


Figure S4.- Bivariate relationships between observed and predicted tree biomass of *E. benthamii* (top), *E. dunnii* (medium) and *E. grandis* (bottom) in Paysandú. In all figures linear 1:1 line has been fitted.

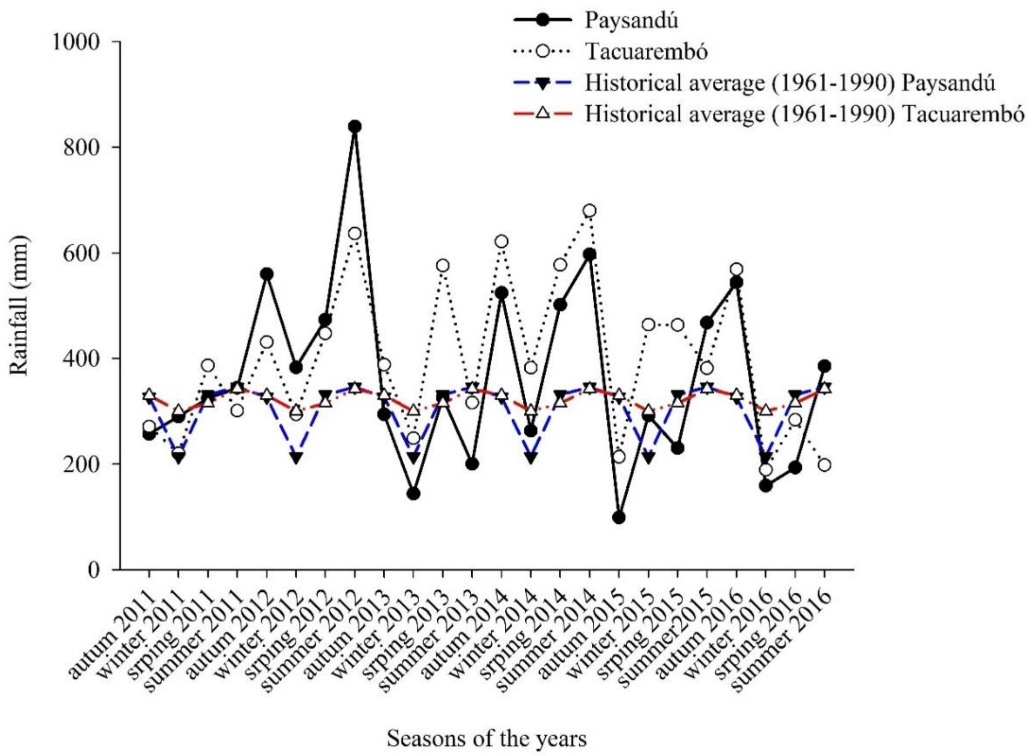


Figure S5. Rainfall regime evolution along the seasons of the years in the both sites. Source: INUMET, 2017.

Chapter 4. Influence of contrasting stocking densities on the dynamics of above-ground biomass and wood density of *Eucalyptus benthamii*, *Eucalyptus dunnii*, and *Eucalyptus grandis* for bioenergy in Uruguay

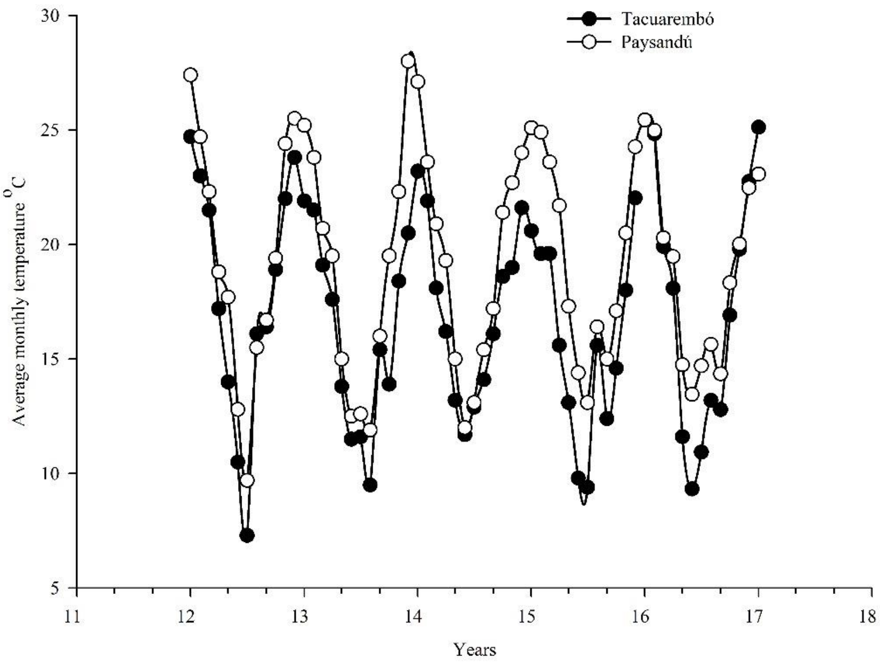


Figure S6. Evolution of the average monthly temperature in the both sites for the period 2011-2017. Source: INUMET, 2017

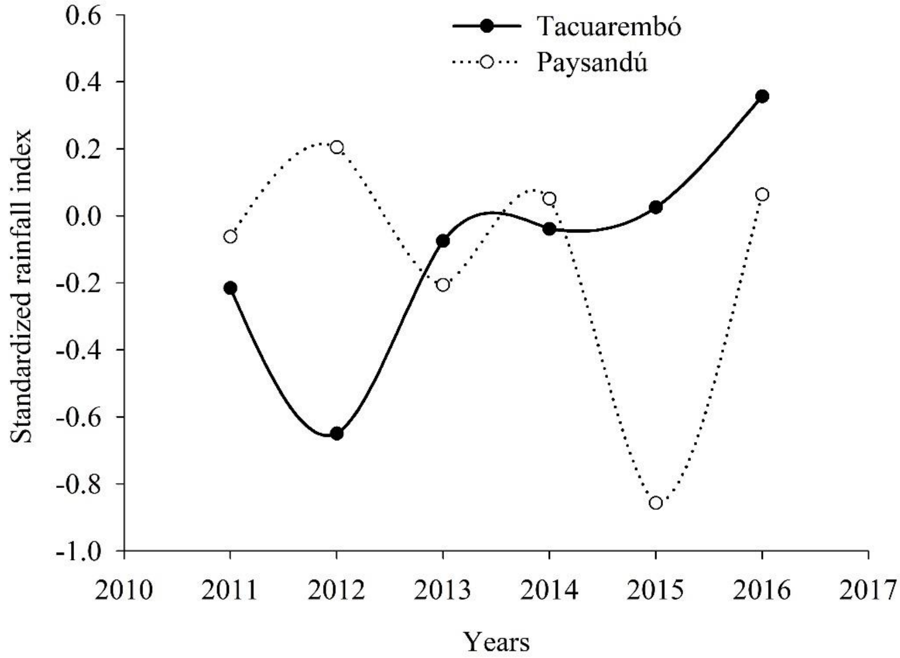


Figure S7. Standardized rainfall index evolution in the both sites. Source: INUMET, 2017.

Chapter 5. Influence of age and planting density on the energy content of *Eucalyptus benthamii, Eucalyptus dunnii* and *Eucalyptus grandis* planted in Uruguay

“Fueron, hace mucho, las románticas proletarias del amor. La noche les puso nombre con seducción de insulto: paicas, locas, milongas, percantas o grelas. Era frecuente verlas al alba desayunando un chocolate con churros en la confitería ¨Vesubio¨ de la calle Corrientes: terminaban a esa hora de trabajar en el ¨Chantecler¨, en el ¨Marabú¨ o en el ¨Tibidabo¨. Con un arranque loco de Madame Bovary de Barracas al Sur, se jugaron la vida a los tangos. Alguna se enamoró de aquel bandoneonista y, por amor, ganó; para otras, la derrota fue mucha: terminaron atendiendo el guardarropa de damas de esos mismos cabarets. Acaso se marcharon todas juntas, un día, como si fueran una pequeña y extinguida raza con ojeras…”

Horacio Ferrer, 1967

Chapter 5. Influence of age and planting density on the energy content of *Eucalyptus benthamii*, *Eucalyptus dunnii* and *Eucalyptus grandis* planted in Uruguay

1. Introduction

The plantations of different forest species in short rotation forestry (SRF) system, and in particular the eucalyptus, both experimentally and commercially, have shown a high potential for biomass production and power generation in several countries (Rodrigues et al., 2010; Carmona et al., 2015; Eloy et al., 2015; Magnano et al., 2016). This has been a response to the attempt to reduce the use of fossil fuels and CO_2 emissions taking into account that it is a renewable raw material, with low emissions (of S_2O and N_2O), and with an almost neutral balance of CO_2. In addition will be a strong increase of energy demand at the future (Berndes et al., 2003). This type of biomass has basically had as its final destination the generation of electrical and thermal energy (Repic et al., 2008), although efforts have been made in recent years to obtain ethanol (López et al., 2010; Hinchee et al., 2011,) and other types of liquid fuels (Swain et al., 2011) and gaseous (Hanaoka et al., 2005).

Forest biomass has generated interest because it has a number of advantages, such as the flexibility of the moment of harvest, the possibility of obtaining several crops, and the option of producing different types of fuels. However, there are doubts regarding the role that biomass will play in the energy market, due to the possible interaction it would have with the soils dedicated to food production, the possible environmental impacts on biodiversity and the conservation of natural resources. natural resources (Berndes et al., 2003). However, several of the forest species used for these purposes adapt well to marginal soils for agriculture (Johnson et al., 2007; Njakou Djomo et al., 2013) and the small spacing used to obtain high yields in relatively short periods (Guerra et al., 2014; Hakamada. 2017). This implies that these production systems are applicable to a wide range of soil and climate conditions, although this determines that the characteristics of the biomass obtained is influenced by the local conditions of each case and by the intensity of the handling used (Nonhebel, 2002; Pérez et al., 2011, Njakou Djomo et al., 2013). To achieve a high degree of adoption of energy crops as a general rule, the following requirements should be met: a) maximize the production of biomass per unit area; b) to be sustainable with low energy costs; and, c) maximize the amount of fuel obtained per unit of biomass, that is to say to get a high conversion efficiency (Johnson et al., 2007). Some authors emphasize this last aspect in the sense of selecting biomasses with low cost of pre-treatment, which allows to obtain high energy yields, which is closely related to the chemical composition of it (Sannigrahi et al., 2010).

In terms of energy efficiency, because the chips obtained from this type of crops have a low energy density, has been frequent the transformation of this type of biomass into fuels such as pellets, briquettes (Eufrade Junior et al., 2016) and even coal (Walter et al., 2006; Briseño-Uribe et al., 2015; Rodrigues et al., 2010). Of the most relevant aspects of the biomass to be considered for the combustion processes are the heating value and the wood density. These two factors determine the energy efficiency, which, in turn, are closely linked to parameters of the chemical composition of the wood, such as lignin, extractive, cellulose, hemicelluloses and minerals (Quirino et al., 2005; Dias Júnior et al., 2015). The heating value is an indicator of the energy content which is transformed into heat by the combustion process (Erol and Ku, 2010). The thermomechanical processes most frequently used to transform biomass are direct combustion, gasification and pyrolysis where the option choosed depends largely on the properties of the raw material (Rocha et al., 2015). For some fuels such as coal, wood characteristics such as low ash content and high levels of lignin and wood density (Trugilho, 2009).

The energy density expressed as the amount of energy generated per unit area (GJ ha^{-1}) depends on the growth, the wood density and the heat value; which in turn are strongly dependent on variables such as species, age and spacing. Although many fast-growing species have been used for energy-saving purposes such as willow and poplar (Villanueva et al., 2011; Kacik et al., 2012), eucalyptus trees stand out due to the ability to adapt to different types of environments and by its high energy productivity (Gonzalez et al., 2011). This productivity is based on high levels of growth added to wood density (medium to high) and heating value. Other characteristics such as: the low content of ash, sulphur and nitrogen homogeneity of chemical composition and fast drying of wood (Foelkel, 2015). Woods with high densities have higher performance at boiler with direct burning and with higher gasification efficiency and low transport costs. Although the heating value per unit of weight is very similar for forest species, those with high wood density have higher heating value per unit volume (Pereira et al., 2000). One of the properties of eucalyptus is that its anatomical and chemical structure undergoes important changes in the first years of growth (Pérez et al., 2011) being the radial variation the most important (Malan, 1995). Wood formed in the early stages is called juvenile wood, and is characterized by its low density, high lignin content and smaller fibers. When become older these tendencies begin to revert in relatively short periods (Vital et al., 1987; Carneiro et al., 2014; Protásio et al., 2014). The effects of age on some energy properties of wood are consistent in that they are accompanied by a decrease in ash and lignin content (Trugilho et al., 1996; Soares et al., 2015) and an increase in density with the passage of time. The heating value depends to a great extent on parameters such as lignin, extractives and ashes (Kumar et al., 2011) but does not always show a definite tendency based on age (Lemenih and Bekele 2004; Kumar et al., 2010). The effects of spacing are more evident on the individual and per hectare growth rate through the modification of competition processes by factors such as light, water and nutrients; Not so about the properties of the wood, registering very different effects (Senelwa and Simms, 1999; Moulin et al., 2015) although the trend indicates that with the wider spacing a biomass with better energy properties is obtained (Zanuncio et al., 2014; Rocha et al., 2016). In short rotation systems (SRC) are observed the combined effects of reduced spacing and short harvest rotations, which determines a type of biomass that is not always suitable for some processes, such as the production of coal (Rocha et al., 2016). These two silvicultural parameters are intimately related, so that plantations with smaller spacing require shorter cycles because the effects of competition between individuals begin to manifest early, determining a stagnation of growth in advance (Acuña et al., 2018). In general terms, it is observed that with longer crop shifts and higher planting densities, the highest energy yields per unit area are obtained (Guerra et al., 2014; Eloy et al., 2016).

Therefore, the results obtained in short-term energy crops depend to a large extent on the site conditions and the used production system, in such a way that it is necessary to identify the conditions that optimize the production of energy based on factors such as the species and density of plantation. From this hypothesis, the main goal of this work was to test three species of eucalyptus (*E. benthamii* Maiden & Cambage, *E. dunnii* Maiden and *E. grandis* Hill ex Maiden), at different planting densities to determine which combination maximizes the energy production per hectare during a period of 76 months. For this, the following specific objectives were established: (a) to know the effects of the species, age and spacing on the energy properties of wood; (b) quantify the energy yield of each species and plantation density along the cycle of the culture; (c) Identify the optimum moment of harvest in each case; and (d) determine the relationships between the wood density and energy density of the biomass. The results will allow to analyse the evolution of yield energy and therefore determine the optimum harvest moment that maximizes the energy obtained per unit area per year.

2. Materials and methods

2.1. Study area

At November and October of 2010 were settled two short-rotation plantation trials at Departments of Tacuarembó and Paysandú (S32º13'30" and W55º54'40" and S32º24'05" and W57º31'02", respectively) (Fig. 1). The soils of the Tacuarembó site (CONEAT group 7.32) are of the Luvisoles and Ochric Acrisols type and those of the Paysandú site (CONEAT group 9.3) are of the Planosoles and Districs Ochric Argisols type (MGAP, 1976) . The climate corresponds to the temperate subtropical type, with an average annual temperature of 18ºC, and average temperatures of 12ºC and 24ºC for the coldest and warmest month, respectively. The average annual precipitation range is between 1300 and 1400 mm (Castaño et al., 2011).

2.2. Experimental design

The experiment has a factorial design of plots divided into random blocks. The factors are the species (three levels) and the density of plantation (four levels). The species used were *E. benthamii*, *E. dunnii* and *E. grandis* at planting densities of 2220, 3330, 4440 and 6660 trees ha $^{-1}$. Table 1 describes the main characteristics of the tests. The origin of the seed was Brazil (APS Pinhao-State of Paraná-Brazil) for *Eucalyptus benthamii*, the seed orchard of the INIA (2nd generation) for *Eucalyptus grandis* and Undera (Moleton West Coffs Harbor, Australia) for *Eucalyptus dunnii.* The plot is rectangular and consists of 6 rows of 25 plants each one evaluating the 4 central rows.

Table 1. Experimental design and trials main characteristics in Tacuarembó and Paysandú departments (Uruguay)

Sites	Date of planting	Spacing	Surface plot (m2)	Fertilization	Tillage
Paysandú	November 2010	3 mx 1.5 m	688	180 kg ha^{-1} of 14/30/12 (N, P, K) plus 6% S, 0.2% B and 0.3% Zn	Two successive applications of an eccentric harrow 30 cm deep plus a ridder
		3 mx 1.0 m	456		
		3 mx 0.75 m	341		
		3 mx 0. 5 m	228		
Tacuarembó	October 2010	3 mx 1.5 m	724	150 kg ha-^{1} of 18/46/0 (N, P, K)	Subsoiling 40 cm deep and the subsequent step of an eccentric harrow
		3 mx 1.0 m	481		
		3 mx 0.75 m	360		
		3 mx 0. 5 m	239		

2.3. Sampling of trees and measurements

The inventories were made on the following dates: May-August 2012, August-December 2014, July-January 2015 and October-March 2016. In the 4 central rows of the plot was measured the diameter at breast height (*dbh*, cm, at 130 cm height with a diametric tape with an accuracy of 0.1 cm) of all trees (rows 2 to 5); and in rows 2 and 4, the total height of all the trees (*h,* m) with a Vertex IV hypsometer (Haglof., Sweden). The height of the rest of the trees was estimated from equations adjusted according to the normal diameter (Annex II, height-diameter adjustment equation). The trees were measured with a *dbh* greater than 3 cm. In each of the inventories, 3 to 5 trees of each one of the plots were harvested (species x density), whose diameters represented the diametric classes with the highest relative frequency. Once they were cutted *h*, *dbh* , and the diameter at the base (to 0.7 meters, *db,* cm) were measured, and from there every meter up to a height corresponding to a diameter with 1 cm bark. The sampled trees were weighed with bark on the Radwag scale with a precision of 1 g. From the bottom (neck), and at a height corresponding to 50 and 75% of the total height, several 2 cm thick discs were extracted, one of which was weighted with bark in the field. That same disk was dried in a stove until constant weight at 103 ± 2 ° C and with these values was estimated the percentage of dry matter of each disk. With the value of each disc, the weighted average of each tree was estimated taking into account the surface of the them.

2.4 Wood density

With the samples of the discs extracted from each tree in the inventories of 2012, 2015 and 2016, the basic density of the wood was determined. Immediately after sampling, the samples were kept in closed nylon bags (to minimize moisture loss) and then immersed in water for several days to achieve complete saturation. The volume of each sample was measured by water displacement and then dried in an oven at 103 ± 2ºC until constant weight. To estimate the density of each tree (*Db* g cm^{-3}) the following formula was used (Santos, 2011) [equation 1]:

$$Db_{pond} = \frac{A_B Db_B + A_{50} Db_{50} + A_{75} Db_{75}}{A_B + A_{50} + A_{75}} \qquad [1]$$

Where *Db* is the weighted basic density, D_B, D_{50} and D_{75} are the density values and A_B, A_{50}, A_{75} the cross-sectional areas for heights 0, 50 and 75% respectively. The amount of biomass was calculated as the product of the volume per hectare and the average basic density of each plot.

2.5. Weight functions

With the dry weight data of the trees removed, the normal diameter and the height of the inventories of the years 2012, 2014, 2015 and 2016 were adjusted 7 equations of weight for each species, density of plantation and site. From these equations, one was selected for each of these situations as a function of the values of R^2_{ajd}, bias, mean square of the error, normality, homoscedasticity and intercorrelation error. These three assumptions were verified with the Shapiro-Wilk, Breusch-Pagan and Durbin-Watson statistical tests, respectively. With the estimated weights, the average weight of the stem of each plot was obtained, whose value multiplied by the number of trees was used to estimate the weight per hectare (Mg ha^{-1}) of each species-by-planting density combination.

2.6. Higher heating value, energy density and energy yield

After drying each disc in a stove with ventilation and forced circulation at a temperature of 60°C, it was milled in a mill RETSCH model SR 200 until reaching a particle size of 40-60 mesh. With the samples taken from the trees removed from each plot in the inventories of the years 2012, 2015 and 2016, a sample composed of a weighted tree was formed according to the surface of each disk of the different heights sampled. The determination of the higher heating value (*Pc*, J g^{-1}) was carried out according to the procedure PEC.FORES.017 based on the standards DIN 519001: 2000 and 51900-2: 2003.

The energy density (*De*, Mj m^{-3}) was estimated (after conversion of units) as the product of the wood density due to the higher heating value of the same for the inventories in the years 2012, 2015 and 2016.

The energy yield per hectare (*Re*, MWh ha^{-1}) was estimated (after conversion of units from Mj to MWh) as the product of the averages of the parcel of biomass productivity per hectare for the higher heating value. With this value divided by each of the ages of all inventories, the increase in energy yield per hectare and per year was estimated (IMA*Re*, MWh ha^{-1} $year^{-1}$).

2.7. Statistical analysis

The analysis of the data was carried out according to a factorial model of plots divided into random blocks [2]:

$$Y_{ijk} = \mu + \beta_j + \tau_i + \gamma_k + \tau\gamma_{ik} + \varepsilon_{ijk}$$

Where Y ijk is the variable measured in species i, density k, in block j; μ is the general average of all observations, τ_i is the effect i of the species, fixed effect; γ_k is the effect k of the density, fixed effect; β_j is the effect j of the block; τ_γ ik is the interaction species and density, fixed effect; and ε_{ijk},is the experimental error associated with each observation, independent and with a normal distribution of mean 0 and variance □^{2}. The statistical analysis began with the verification of normality and homogeneity of variances by the Shapiro-Wilk and Brown-Forsythe tests, respectively. When the variables were not normal, the Box and Cox transformations were used, through the boxcoxfit functions to obtain the lambda and bcPower values to calculate the new variable. The assumption of randomness was verified because the allocation of the factors species and density of plantation (once the species was assigned) was carried out by lot at both sites. The analysis of the years and sites effects was performed with the nonparametric test of Kruskal-Wallis since it was not possible to verify the assumptions of normality and homogeneity of variances. The effect of the species factor was contrasted with the error defined as the interaction of this with the block while the effects of the plantation density and interaction factors were contrasted with the mean squared error. The analysis of the variables higher heating value, wood density, energy density, energy yield per hectare and per year for each site separately in the last inventory was made using the F test of the analysis of variance. The comparisons between *posteriori* means of the F test and the nonparametric test were performed with the Tukey and Dunn test, respectively. The level of significance was established at a value of $p < 0.05$. The analyses were carried out with software R version 2.14.1 (R Development Core Team, 2011) and Statistix10.

3. Results

3.1 Wood density and energy content

The results of the analysis of variance of the variables *Db*, *Pc*, *De*, *Re* and IMA*Re* for the two sites in the last of the inventories carried out are presented in Table 2. In Paysandú, it was detected that the interaction effect species density was significant for the *De*, *Re* and IMA*Re* (*P*=0.0467; *P*=0.066 and *P*=0.0066, respectively). The *Pc* was significantly affected only by the plantation density (*P*=0.02) and the *Db* was significantly affected by the species and planting density (*P*=0.014; *P*<0.0001). In Tacuarembó, the interaction had a significant effect only for the variables *Re* and IMA*Re* (*P*=0.0425; *P*=0.0424, respectively). The *Db* and *De* were significantly affected by the species (*P*=0.0003; *P*<0.0001). No significant effects of the species, planting density and interaction on higher heating value were detected.

Table 2. Variance analysis result of *Db*, *Pc*, *De*, *Re* and IMA*Re* of the last inventory in Paysandú and Tacuarembó sites (Uruguay).

	Sites																			
	Paysandú										**Tacuarembó**									
Effects	***Pc*** ($J g^{-1}$)		***Db*** ($g cm^{3-1}$)		***De*** ($Mj m^{3-1}$)		***Re*** ($MWh ha^{-1}$)		**IMA*Re*** ($MWh ha^{-1}$)		***Pc*** ($J g^{-1}$)		***Db*** ($g cm^{3-1}$)		***De*** ($Mj m^{3-1}$)		***Re*** ($MWh ha^{-1}$)		**IMA*Re*** ($MWh ha^{-1}$)	
	F	***p-value***	***F***	***p-value***	***F***	***p-value***	***F***	***p-value***	***F***	***p-value***	***F***	***p-value***	***F***	***p-value***	***F***	***p-value***	***F***	***p-value***	***F***	***p-value***
Species	0.41	0.689	**14.8**	**0.014**	**22.13**	**0.0069**	**7.38**	**0.0455**	**7.38**	**0.0455**	6.63	0.053	**106.8**	**0.0003**	**66.4**	**<0.0001**	3.35	0.1396	3.38	0.138
Planting density	**4.2**	**0.02**	**15.2**	**<0.0001**	**12.2**	**0.0001**	**8.82**	**0.0008**	**8.81**	**0.0008**	1.01	0.41	0.73	0.549	0.78	<0.521	**16.43**	**<0.0001**	**16.45**	**<0.0001**
Species * Planting density	0.48	0.816	2.3	0.083	**2.72**	**0.0467**	**4.4**	**0.0066**	**4.40**	**0.0066**	2.67	0.05	0.22	0.966	0.16	0.984	**2.79**	**0.0425**	**2.79**	**0.0424**

The values of *Pc*, *Db*, *De*, *Re* and IMA*Re* for the species and planting densities of the last inventory in Paysandú are presented in Table 3. The contrast of means indicated that the highest values of *Pc* were obtained with the highest planting densities for the three species. The *De* values reflected a greater parity between the different species and planting densities because the higher values of *Db* were registered by the lower planting densities and, therefore, reducing the differences observed with the *Pc*.

Table 3. Results of contrasts of means ± (standard error) between species and planting densities for *Pc*, *Db*, *De*, *Re* and IMA*Re* of the last inventory in Paysandú site

Species	Planting density (trees ha^{-1})	*Pc* (J g^{-1})	*Db* (g cm^{-3})	*De* (Mj m^{-3})	Wood production (Mg ha^{-1})	*Re* (MWh ha^{-1})	IMA*Re* (MWh ha^{-1} año^{-1})
E. benthamii	2220	19449 (35.4) A b	0.520 (0.006) AB a	10107 (115.0) **b**	159.9 (27.9)	863 (149.3) **a**	136 (23.6) **a**
	3330	19678 (209.0) A ab	0.509 (0.035) AB b	10011 (634.3) **b**	185.6 (4.5)	1014 (15.8) **a**	160 (2.5) **a**
	4440	19838 (286.3) A a	0.467 (0.006) AB bc	9266 (28.5) **b**	124.7 (5.7)	688 (40.8) **b**	109 (6.4) **b**
	6660	19858 (111.5) A ab	0.487 (0.010) AB c	9663 (174.1) **b**	175.2 (8.0)	966 (40.3) **a**	153 (6.4) **a**
E. dunnii	2220	19467 (204.6) A b	0.610 (0.024) A a	11876 (407.7) **a**	187.7 (10.9)	1014 (48.8) **a**	160 (7.7) **a**
	3330	19707 (92.8) A ab	0.522 (0.005) A b	10281 (133.9) **b**	188.6 (9.1)	1032 (47.8) **a**	163 (7.5) **a**
	4440	19789 (182.9) A a	0.510 (0.0016) A bc	10089 (240.6) **b**	198.7 (17.3)	1092 (91.2) **a**	172 (14.4) **a**
	6660	19710 (190.9) A ab	0.513 (0.014) A c	10104 (204.5) **b**	197.5 (8.7)	1082 (55.2) **a**	171 (8.7) **a**
E. grandis	2220	19445 (337.9) A b	0.503 (0.007) B a	9790 (240.0) **b**	159.2 (8.8)	859 (39.2) **a**	136 (6.2) **b**
	3330	20043 (168.0) A ab	0.480 (0.007) B b	9624 (111.4) **b**	233.0 (12.0)	1296 (55.6) **a**	205 (8.8) **a**
	4440	20100 (98.6) A a	0.446 (0.029) B bc	8968 (563.1) **b**	195.2 (11.3)	1090 (65.8) **a**	172 (10.4) **a**
	6660	19793 (150.3) A ab	0.402 (0.006) B c	7950 (126.7) **c**	224.1 (9.9)	1232 (48.1) **a**	194 (7.6) **a**

Mean values followed by the different lower case and upper-case letter indicate significant differences between planting densities and species, respectively, by means of the Tukey test with a probability of 5%. Different bold letters indicate differences due to the interaction species and planting densities.

The same parameters for the Tacuarembó site are presented in Table 4. The contrasts of means of *De* showed that the highest values correspond to the species *E. benthamii* and *E. dunnii*, which were associated with the highest values of *Db* since the values of *Pc* were very high. similar in the three species evaluated. The *Re* in this site was also associated with the productivity of biomass per hectare, so that the highest levels were reached with the highest planting densities.

Table 4. Results of contrasts of means ± (standard error) between species and planting densities for *Pc*, *Db*, *De*, *Re* and IMA*Re* of the last inventory at the Tacuarembó site

Species	**Planting density (árboles ha^{-1})**	***Pc* (J g^{-1})**	***Db* (g cm^{-3})**	***De* (Mj m^{-3})**	**Wood production (Mg ha^{-1})**	***Re* (MWh ha^{-1})**	**IMA*Re* (MWh ha^{-1} año^{-1})**
E. benthamii	2220	19785 (20.0) A a	0.410 (0.004) B a	8120 (91.1) B a	104.1 (4.9)	572 (26.6) **c**	91.6 (4.3) **c**
	3330	19952 (55.9) A a	0.413 (0.007) B a	8241 (119.3) B a	110.9 (19.9)	614 (109.0) **c**	98.2 (17.4) **c**
	4440	20119 (102.5) A a	0.409 (0.007) B a	8227 (176.4) B a	172.6 (3.4)	965 (19.9) **abc**	154.4 (3.2) **abc**
	6660	19862 (46.0) A a	0.420 (0.012) B a	8332 (221.9) B a	212.6 (18.2)	1172 (97.8) **a**	187.6 (15.7) **a**
E. dunnii	2220	19892 (83.8) A a	0.420 (0.022) A a	8355 (418.8) A a	130.3 (5.6)	720 (33.6) **bc**	115.2 (5.4) **bc**
	3330	19746 (86.3) A a	0.442 (0.003) A a	8728 (31.0) A a	153.3 (8.3)	841 (46.6) **abc**	134.5 (7.5) **abc**
	4440	19768 (177.4) A a	0.429 (0.012) A a	8474 (162.5) A a	155.8 (11.6)	855 (56.2) **abc**	136.7 (9.0) **abc**
	6660	19704 (110.4) A a	0.434 (0.006) A a	8551 (147.5) A a	186.7 (6.7)	1021 (31.1) **ab**	163.4 (5.0) **ab**
E. grandis	2220	19925 (47.8) A a	0.376 (0.006) C a	7486 (129.8) C a	111.2 (11.1)	616 (63.0) **c**	98.5 (10.1) **c**
	3330	20019 (113.7) A a	0.381 (0.011) C a	7617 (216.4) C a	124.3 (9.1)	691 (46.8) **bc**	110.5 (7.5) **bc**
	4440	20034 (18.7) A a	0.369 (0.004) C a	7401 (67.3) C a	184.2 (25.4)	1025 (142.5) **ab**	164.1 (22.8) **ab**
	6660	20160 (150.8) A a	0.378 (0.013) C a	7620 (238.8) C a	150.2 (3.1)	841 (11.4) **abc**	134.5 (1.8) **abc**

Mean values followed by the different lower case and upper-case letter indicate significant differences between planting densities and species, respectively, by means of the Tukey test with a probability of 5%. Different bold letters indicate differences due to the interaction species and planting densities.

3.2 Energy content evolution

The results of the nonparametric analysis of the parameters mentioned in each of the inventories in each site are presented in Table 5. In Paysandú, significant differences were detected between inventories for all the variables analysed, showing that age has an evident effect on the energy properties of wood ($P<0.0001$; $P<0.0001$; $P<0.0001$; $P<0.0001$; $P<0.0001$). However, on Tacuarembó, the age factor modified only the *Pc* and, obviously, the *Re* and IMA*Re*, which depended on the growth as mentioned above ($P<0.0001$; $P<0.0001$; $P<0.0001$). In Paysandú, the contrast of means showed that there were significant differences between the different evaluation ages for all the variables analysed (Table 6).

Table 5. Results of the nonparametric test of the effect of age in each of the sites for *Pc*, *Db*, *De*, *Re* and IMA*Re*

Sites	***Pc*** **(J g^{-1})**		***Db*** **(g cm^{3-})**		***De*** **(Mj m^{-3})**		***Re*** **(MWh ha^{-1})**		**IMA*Re*** **(MWh ha^{-1} year^{-1})**	
	H	*p-value*	*H*	*p-value*	*H*	*p-value*	*H*	*p-value*	*H*	*p-value*
Paysandú	**25.9**	**<0.0001**	**41.5**	**<0.0001**	**46.3**	**<0.0001**	**116.2**	**<0.0001**	**54.6**	**<0.0001**
Tacuarembó	**77.1**	**<0.0001**	2.7	0.263	2.03	0.363	**109.1**	**<0.0001**	**79.6**	**<0.0001**

Table 6. Results of comparison of means ± (standard error) of effect of age in each site for *Pc*, *Db*, *De*, *Re*, IMA*Re*.

Sites	**Months**	***Pc*** **(J g^{-1})**	***Db*** **(g cm^{3-})**	**De (Mj m^{-3})**	***Re*** **(MWh ha^{-1})**	**IMA*Re*** **(MWh ha^{-1} year^{-1})**
Paysandú	18	19665 (17.6) a	0.430 (0.01) b	8451 (105.5) b	154.4 (5.9) c	102.9 (3.9) b
	49	19518 (23.9) b			572.8 (18.7) b	140.3 (4.6) a
	57	19748 (38.9) a	0.429 (0.01) b	8462 (124.5) b	690.4 (21.4) b	145.4 (4.5) a
	76	19740 (57.1) a	0.497 (0.01) a	9810 (166.0) a	1019.0 (31.0) a	160.9 (4.9) a
Tacuarembó	22	19745 (16.3) b	0.416 (0.004) a	8208 (75.9) a	96.9 (4.4) c	52.8 (2.4) b
	46	19437 (37.0) c			481.1 (20.3) b	125.5 (5.3) a
	57	19859 (36.3) ab	0.400 (0.006) a	7954 (120.7) a	612.2 (25.6) b	128.9 (5.4) a
	75	19914 (33.4) a	0.406 (0.005) a	8096 (86.9) a	827.7 (35.0) a	132.4 (5.6) a

Mean values followed with the different letter indicate significant differences between ages for each site, using the Dunn test with a 5% probability.

The *Pc*, *Db* and, therefore, the energy densities experienced a significant increase with the increase in age, particularly in the last evaluation (76 months). The *Re* followed a similar trend to changes in biomass production, showing an accumulated increase with age up to 76 months, while the IMA*Re* showed relatively stable increases from month 49. At Tacuarembó, the *Db* and *De* remained unchanged in the face of increasing age, while at the same time increasing the *Pc* and *Re*; the latter for the reasons already mentioned. With the IMA*Re*, a behaviour similar to that of Paysandú occurred from month 46 (Table 6). The results of the nonparametric analysis and contrasts of means of the parameters mentioned between sites for each of the inventories are presented in Table 7 and 8. In each of the inventories, higher values of *Db* and *De* were obtained at Paysandú, while that an inverse behaviour of the *Pc* occurs. The IMA*Re* was greater in Paysandú in all the inventories due to the higher productivity achieved in this site. The nonparametric analysis detected significant differences between sites for all variables evaluated in all cases except for the *Pc* in the third inventory. The simple linear correlation coefficients between the *Db* and the *Pc* considering all the ages were negative in both sites (Table 9). The coefficients of partial correlation of the *Db* and the *Pc* with the *De* were very similar for both variables.

Table 7. Results of the nonparametric test the effect of the site on each of the inventories.

Months	***Pc*** **($J\ g^{-1}$)**		***Db*** **($g\ cm^{3-}$)**		***De*** **($Mj\ m^{-3}$)**		***Re*** **($MWh\ ha^{-1}$)**		**IMA*Re*** **($MWh\ ha^{-1}\ year^{-1}$)**	
	H	*p-value*	*H*	*p-value*	*H*	*p-value*	*H*	*p-value*	*H*	*p-value*
18-22	**9.4**	**0.0022**	**4.70**	**<0.030**	**4.2**	**0.042**	**35.9**	**<0.0001**	**49.8**	**<0.0001**
46-49	1.4	0.246					**11.5**	**0.0007**	**5.5**	**0.0186**
57	**4.5**	**0.033**	**8.7**	**0.0032**	**7.4**	**0.0066**	**7.5**	**0.0062**	**7.5**	**0.0062**
75-76	**5.2**	**0.022**	**39.9**	**<0.0001**	**39.1**	**<0.0001**	**15.6**	**0.0001**	**14.5**	**0.0001**

Table 8. Results of comparison of means ± (standard error) for *Pc, Db, De, Re*, IMA*Re* of each site in each of the different inventories.

Months	Sites	*Pc* (J g^{-1})	*Db* (g cm^{-3})	*De* (Mj m^{-3})	*Re* (MWh ha^{-1})	IMA*Re* (MWh ha^{-1} year^{-1})
18-22	Paysandú	19665 (17.6) b	0.430 (0.01) a	8451 (105.5) a	154.4 (5.9) a	102.9 (3.9) a
	Tacuarembó	19745 (16.3) a	0.416 (0.004) b	8208 (75,9) b	96.9 (4.4) b	52.8 (2.4) b
46-49	Paysandú	19518 (23.9) a			572.8 (18.7) a	140.3 (4.6) a
	Tacuarembó	19437 (37.0) a			481.1 (20.3) b	125.5 (5.3) b
57	Paysandú	19748 (38.9) b	0.429 (0.01) a	8462 (124.5) a	690.4 (21.4) a	145.4 (4.5) a
	Tacuarembó	19859 (36.3) a	0.400 (0.006) b	7954 (120.7) b	612.2 (25.6) b	128.9 (5.4) b
75-76	Paysandú	19740 (57.1) b	0.497 (0.01) a	9810 (166.0) a	1019.0 (31.0) a	160.9 (4.9) a
	Tacuarembó	19914 (33.4) a	0.406 (0.005) b	8096 (86.9) b	827.7 (35.0) b	132.4 (13.24) b

Mean values followed with different letter indicate significant differences between sites for each of the inventories through the Dunn test with a probability of 5%.

Table 9. Simple and partial correlation coefficients of the variables *Db, Pc* and *De*

Sitios	Partial correlation *DePc.Db*		Partial correlación *DeDb.Pc*		Simple correlación *Pc.Db*	
	r	*p-value*	*r*	*p-value*	*r*	*p-value*
Paysandú	0.988	<0.0001	0.999	<0.0001	-0.355	0.0002
Tacuarembó	0.996	<0.0001	0.999	<0.0001	-0.323	0.0006

The evolution of *Pc* in Paysandú showed that in all cases there was a certain variation of the values that did not respond to a defined pattern, in particular for the different planting densities (Figure 1). On the other hand, in the three species there was an increase in the dispersion in the different spacing with the increase in age, at the same time as a significant increase in the mean values. Tacuarembó showed a very similar trend, with slightly higher mean values than the previous site and a significant increase with increasing age. In both cases, there was a slight decrease in the values in the second inventory.

The *De* recorded at Paysandú followed the trend observed with the increase in *Pc* and wood density at 76 months (Figure 2). Until month 57, the average values of species and densities of plantation remained relatively stable. In the three species, it was observed that in the last inventory the highest values were obtained with the lowest planting densities, basically explained by the higher values of *Db* obtained with the greater spacing. The stability of the *Db* values registered at Tacuarembó determined that the energy density remains unchanged in the face of changes in age and in different planting densities.

The value of *Re* increased with age in both sites, basically due to the increase in accumulated productivity achieved over time (Figure 3). In Paysandú, with *E. dunnii* and *E. grandis,* a clear association between the planting density and the amount of energy per hectare contained in the wood was observed, which responded to the higher productivity of wood registered with lowest spacing. With *E. benthamii*, it was not observed a definite relationship between productivity and planting density, which was reflected in the energy content of the different spacing. Tacuarembó showed a closer relationship with all three species between the *Re* and the planting density, so that in almost all cases the highest energy yields were obtained with the highest planting densities.

The evolution of IMA*Re* in Paysandú increased with increasing age (Figure 4), except with *E. grandis*, the largest increases were associated with the lowest spacing. In Tacuarembó, a different behaviour was observed for each of the species. With *E. benthamii*, an increase in the energy content per hectare was recorded with all planting densities up to month 57, at which point a slight decrease occurred until month 75. With *E. dunnii*, an evident change of the curves of the energy content occurred in month 46, but with slightly increases in all densities until the end of the studied period. With *E. grandis*, there was also a turning change in month 46 with all planting densities, except with 6660 trees per hectare. As of this moment, the densities of 3330 and 2220 trees per hectare remained without major changes or with a slight reduction, respectively.

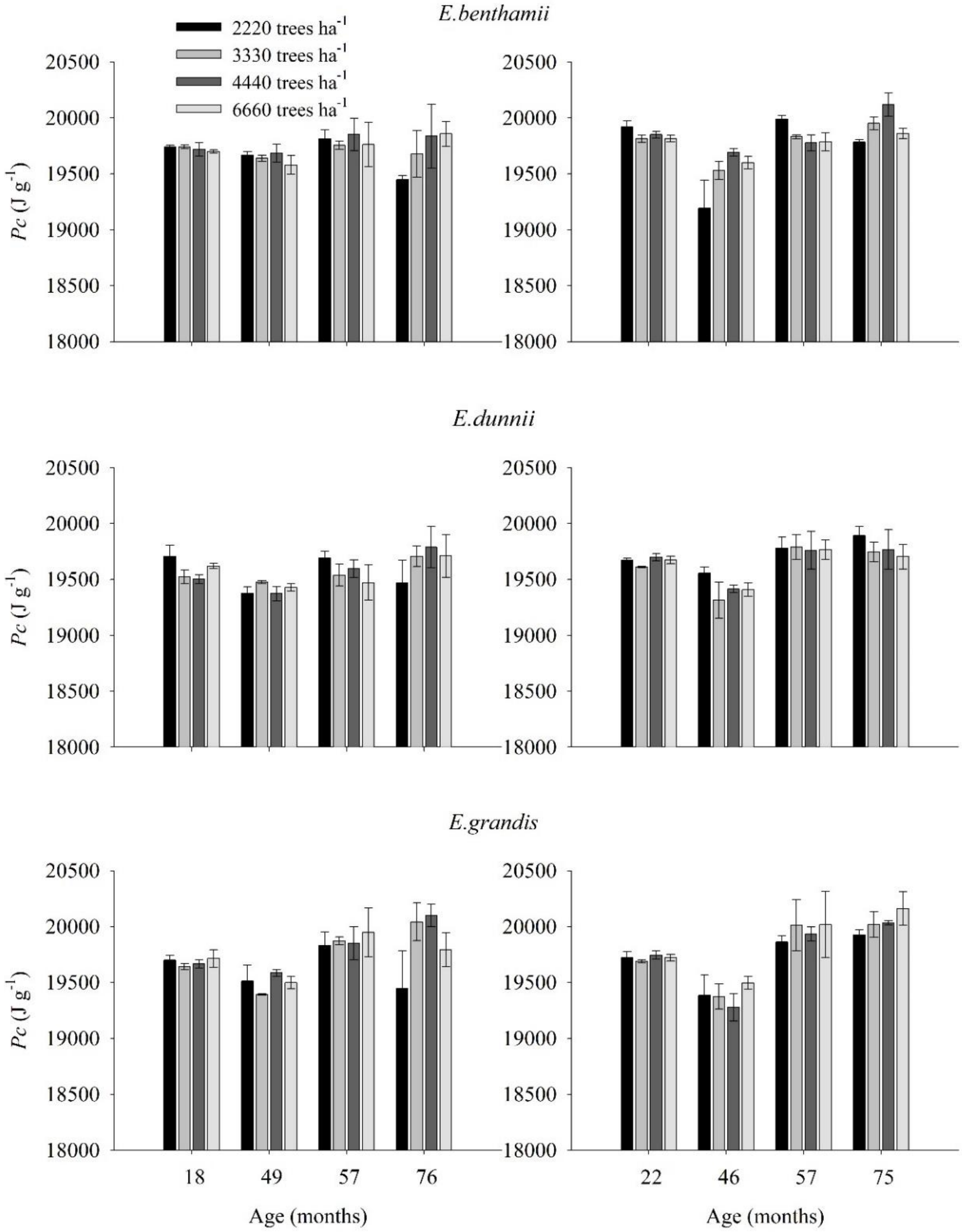


Figure 1. Evolution of the *Pc* ± (standard error) for each species and density of plantation in the Paysandú (left) and Tacuarembó (right).

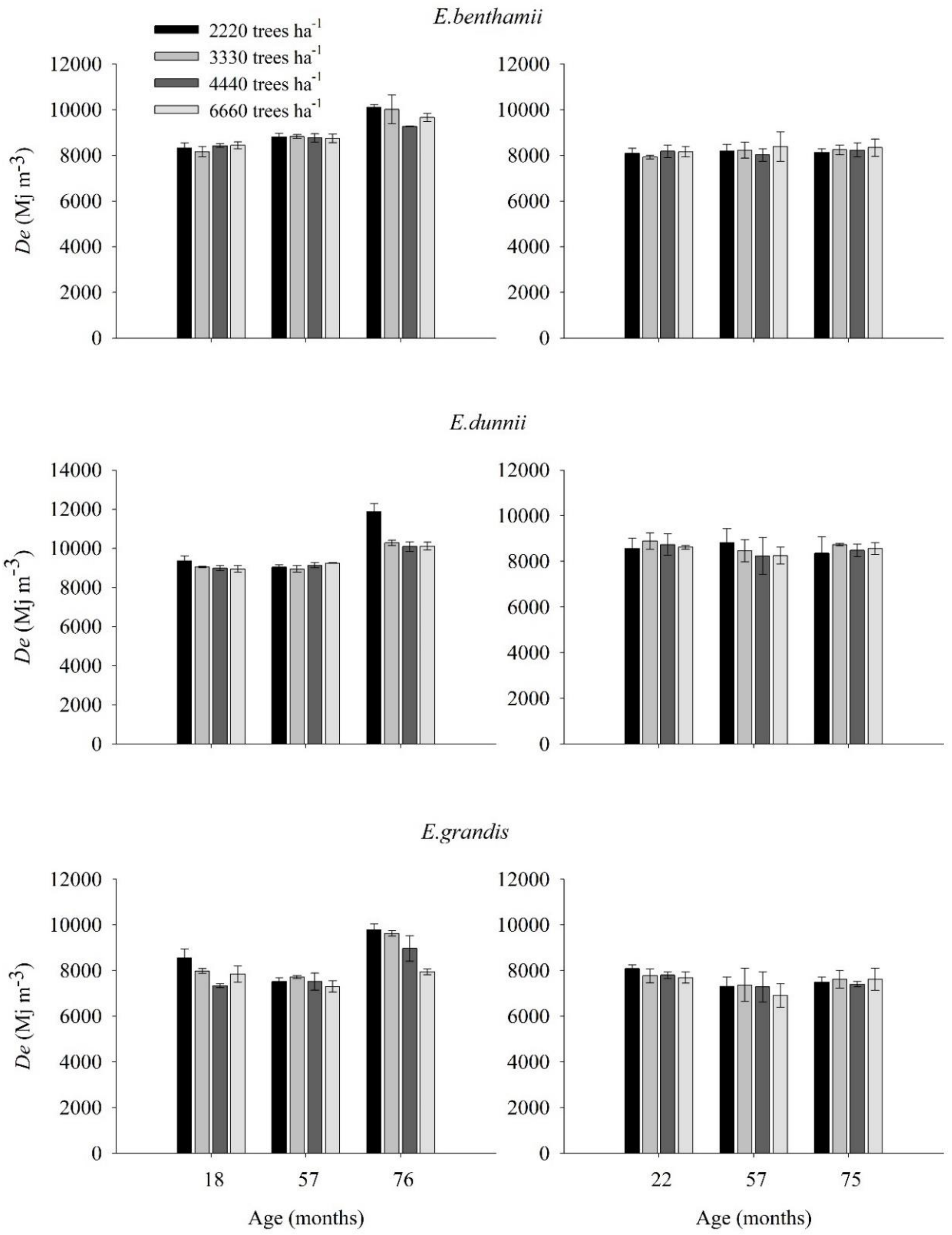


Figure 2. Evolution of *De* ± (standard error) for each species and planting density at Paysandú (left) and Tacuarembó (right).

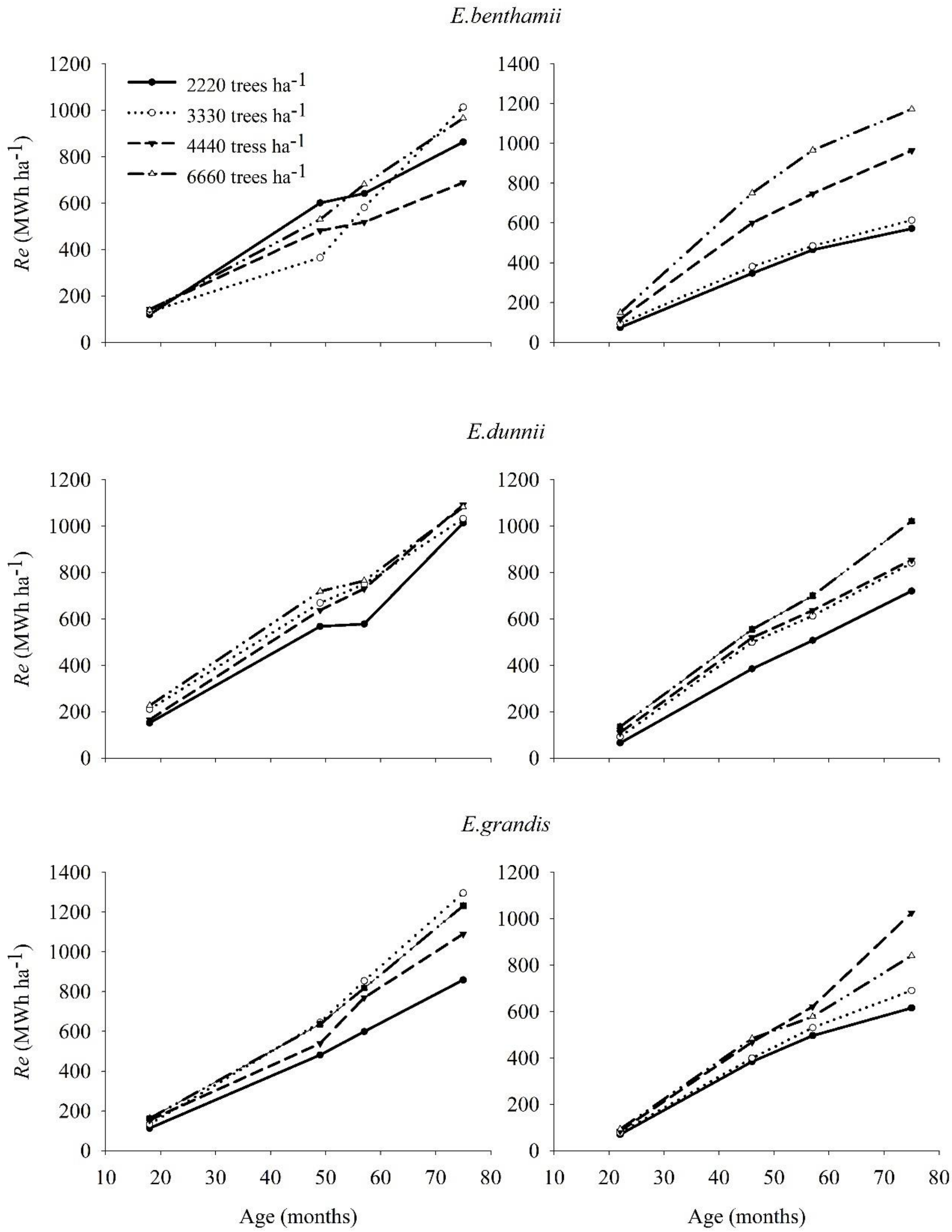


Figure 3. Evolution of *Re* of each species and density of plantation in Paysandú (left) and Tacuarembó (right).

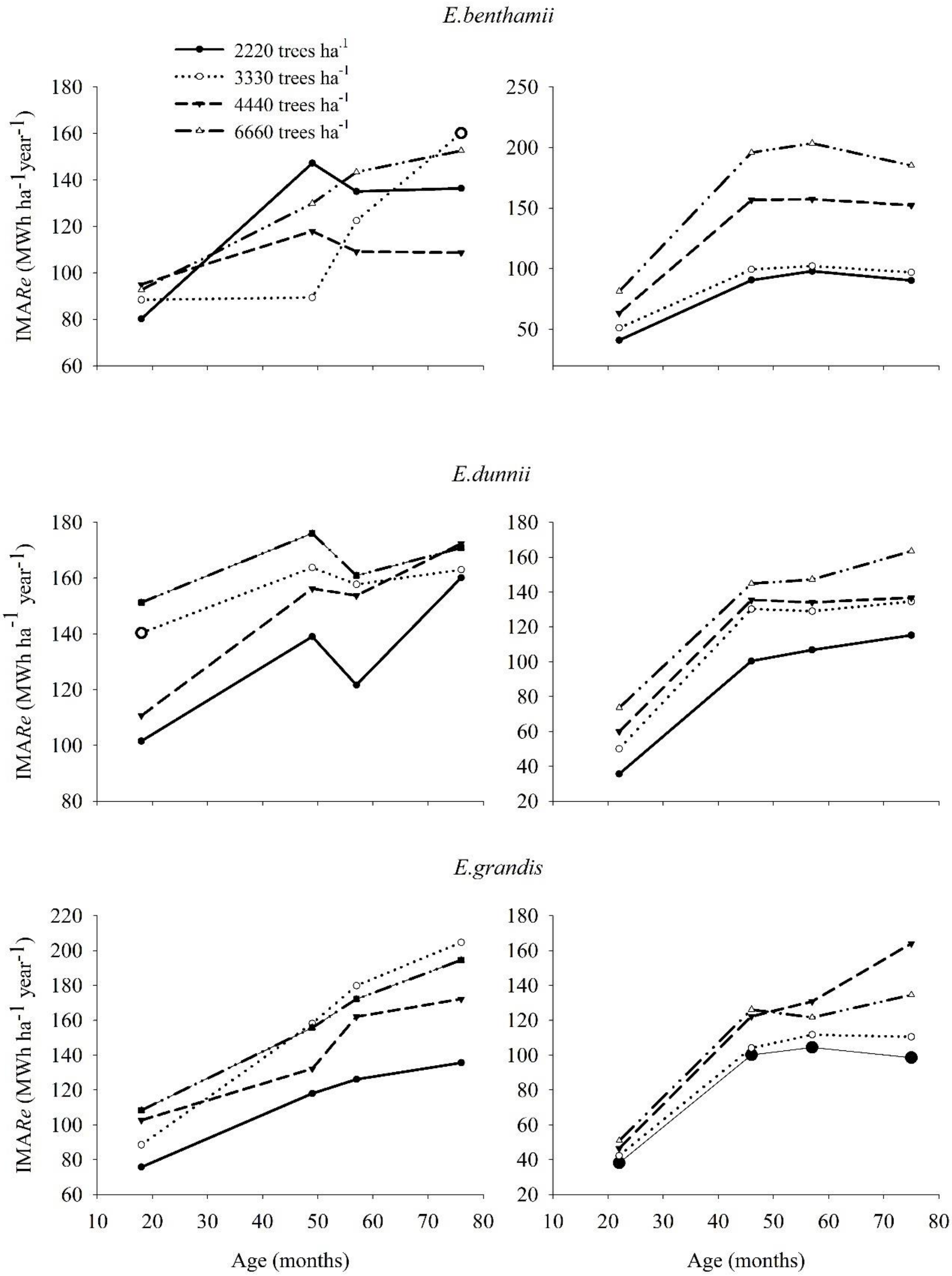


Figure 4. Evolution of IMA*Re* for each species and planting density at Paysandú (left) and Tacuarembó (right).

4. Discussion

The results obtained in this work confirm the hypothesis that the species, planting density, site and age affect the energy parameters of wood. The changes produced by these factors are of very different origins and have different types of effects on the energy contents. The evaluated species have anatomical and growth characteristics that determine differences in both the *De* and the Re. The first of the variables is associated with differences in the fibers dimensions which are directly linked to the amount of wood per unit volume (Mimms et al., 1993) and the *Re* is closely linked to the growth levels of each one as previously verified. Planting density is undoubtedly the factor that has the greatest impact on the energy levels obtained since it is directly related to the productivity of biomass per unit area, which in turn depends on the age of the crop. These parameters together determine the optimum harvest time because they condition the effects of competition between trees. The site, although it is assumed according to previous studies (Balmelli and Resquin, 2002), that influences the growth of eucalyptus species in this case was associated with differences in the conditions prior to and immediately after the trial installation. (Chapter 1). Finally, age intervenes in changes that occur in the physical and chemical properties of wood which cause alterations in both the Db and the Pc of the wood.

4.1 Higher heating value

The analysis of variance indicates that in the Paysandú site the planting density is the only one of the factors that at the age of 76 months has a significant effect on the *Pc* of the wood. The values obtained show that the lowest spacing are those that have the highest values of this variable. According to the literature, it could be explained by a higher lignin content, which in turn would be related to a higher proportion of juvenile wood in trees of reduced diameter (Oliveira, 1997; Calonego et al., 2005, Oliveira). The average *Pc* of the different species of eucalyptus are very similar to each other, which agrees with that obtained by several authors (Senelwa and Simms, 1999; Pérez et al., 2008; Pérez et al., 2014) that determine that this variable has a relatively small range of variation among the different types of wood. According to Guerra et al., (2014); Wionzek, (2014); Eloy et al., (2016) and Eufrade Junior et al., (2018), *Pc* is a variable little affected by silvicultural treatments and depends largely on aspects of chemical composition such as lignin, extractives and ash (Demirbas, 2004; Santana, 2009; Santos et al., 2016). The syringyl/guaiacyl relation is also cited as a parameter positively associated with the increase in age and with the *Pc* of eucalyptus wood (Santos, 2010, Castro et al., 2015). Results obtained by Carvalho, (1998) with a hybrid of eucalyptus, they show an increase in the content of lignin and extractives with the increase in age in eucalyptus plantations between 4 and 9 years, although they have also obtained results with different tendencies (Trugilho et al., 1996).

In Paysandú, an increase of only 2% (400 J g^{-1}) of Pc is observed for the densities of 6660 and 4440 trees per hectare compared to the density of 2220 trees ha^{-1}. For practical purposes, a relevant difference is considered above 1250 J g^{-1} (Brand, 2010). Although there are certain oscillations of this parameter in different ages, a significant increase is observed over time. Different results were reported by Lemenih and Bekele (2004) obtaining a negative relationship between age and the *Pc* of different eucalyptus species. Works related to the subject show that the reduction that occurs in the ash content with the increase in age would be the factor that would be explaining this behaviour (Trugilho et al., 1996; Kumar et al., 2010; Soares et al., 2015).

In the Tacuarembó site, the *Pc* is the same for all species and planting densities, but a behaviour similar to the previous site is observed in the sense that an increase occurs with age, particularly from month 57. Rocha et al., (2016), evaluating the effects of distances from 1.5 to 9 m^{-2} in eucalyptus clones, they also did not detect effects of distancing on the *Pc* of the wood, although there was a positive relationship with the lignin content. In the different inventories, it is obtained that, on average, in Paysandú the Pc is higher than in Tacuarembó. Among the possible causes that could explain these differences is an indirect effect that could cause the *Db,* which is associated with lower ash contents (Soares et al., 2014). The minerals that are part of the ash fraction are an inert material that ultimately contributes to a lower energy content per unit of weight (Hansted et al., 2018).

4.2 Wood density

In Paysandú, the analysis of the data from the last inventory indicates that *E. benthamii* and *E. dunnii* were the species with the highest values of *Db*. This confirms the results obtained in previous tests with this type of species (Backman and García de Leon, 2003).

This is in some way explained by the fact that the genetic materials of these two species are commercially used for their cellulose production skills. The results obtained show an inverse relationship between the *Db* and the planting density. The effects of spacing on the *Db* have been evaluated by several authors and, in general, are associated with changes in the anatomy of wood depending on different growth rates. The causes that explain this type of behaviour are associated to a greater uniformity of the Db and a greater proportion of adult wood in the feet of greater diameters (Malan and Hoon, 1992; Cassidy et al., 2013), at the same time as a greater proportion of juvenile wood in trees growing under conditions of high competition (Larson et al., 2001).

In Tacuarembó, on the other hand, this behaviour was not observed, resulting in the density values of the wood remaining unchanged in the different species, planting densities and ages. The differences between the mean values of both sites, which was observed in each of the inventories, has been determined in previous studies (Resquin et al., 2007) but the possible causes explaining these results have not been identified.

4.3 Energy density

The *De* values of Paysandú were explained by the increase registered in the values of *Db* and the *Pc*. This indicates that the increase in the age of the trees determines a higher energy content per unit of weight, and in particular of volume. Similar results were reported by several authors (Santana, 2009; Soares et al., 2014; Soares et al., 2015; Eloy et al., 2016), evaluating eucalyptus species in short rotation systems. According to these authors, increases in energy content are mainly associated with the changes that occur in the *Db*, since the *Pc* is little affected by the growth of the first years. Bearing in mind that forest biomass combustion equipment has a certain capacity, as long as a raw material with a higher energy content per unit volume is used, the lower the fuel requirement and, therefore, the greater the efficiency of the process. Both the *Db* and the *Pc* also have an influence on economic aspects such as transportation, management and storage (Rocha et al., 2015). With higher *Db* values, it is possible to obtain a better energy performance in direct burning or in transformation processes, since a greater mass per unit volume can be converted into energy (Santos et al., 2013). The evolution in the different inventories showed a significant increase in *De* starting from month 57 associated with changes in the *Db*. At Tacuarembó, the *De* followed the same trend as the *Db*, so that the highest values were reached by *E. dunnii* and *E. bemthamii,* regardless of planting density. The values remained unchanged at different ages, which can be explained by the stability of the *Db* despite the increase registered in the *Pc* in the first years of growth. For these reasons, in Paysandú, higher *De* values were obtained in the different inventories. In both sites, a simple negative correlation was obtained, although of low magnitude, between the *Db* and the *Pc* considering all the ages evaluated (r = -0.36, r = -0.32, for Paysandú and Tacuarembó, respectively The results reported in the literature show that the relationship between both variables with eucalyptus species is very diverse, with positive values (Jesus et al., 2017), negative as in the present study (Soares et al., 2014; Wu et al., 2017) or neutral (de Lima et al., 2011; Días Júnior et al., 2016; Brun et al., 2018).These differences could be attributed to the multiple factors that explain the *Pc*. The greater relation of the *Db* with the *De* compared with the Pc (detected with the values of the partial correlations) is linked with the reduced effect that silvicultural parameters (such as age, spacing, etc.) have on this latest. The analysis of the partial correlations between the De with the *Pc* and the *Db* shows that in both places the latter is the one that has a greater relative weight on the energy content per unit volume.

4.4 Energy yield

The analysis of the *Re* in the last inventory shows that in both sites the result obtained depends on the interaction of the species and the density of plantation. At Tacuarembó, the levels of *Re* correspond directly to biomass productivity, since the *Pc* is practically the same for all species and all planting densities. Therefore, the highest levels of *Re* were obtained with the highest planting densities. These levels of *Re* were within expected with these species and planting densities under similar conditions of latitude, soil and climate (Müller, 2005; Magalhães et al., 2017; Ferreira et al., 2017). Considering the average values of each planting density, it was observed that the fact of doubling or tripling the number of trees per hectare yield an increase of 1.5 to 1.6, respectively, in the productivity of energy. From this point of view, the progressive increases in the number of trees resulted in greater energy production, but in an increasingly less efficient way. This trend has also been observed by several authors, showing that the relationship between the energy obtained and the planting density is little dependent on growth conditions (Guerra et al., 2014; Eufrade Junior et al., 2016). The cumulative values of average *Re* for the species and planting densities were increasing until the 75th month of growth in energy productivity. The cumulative values of average energy yield for the species and planting densities were increasing until the 75th month of growth. *E. dunnii* and *E. grandis* present a very similar tendency with increasing age, with increasing values throughout the period. In the case of *E. benthamii*, however, a certain reduction in the growth rate of this parameter was observed in all planting densities. This could be associated with the increase in mortality that occurred in the last stages of crop development. The values of the energy obtained per hectare and per year followed the same trend as the one mentioned above, in the sense that the highest values were reached with the lowest spacing in a similar way for all species. On average, species and planting densities registered decreasing increases as of month 46 of age. The values of *E. dunnii* and *E. grandis,* in general, showed a significant reduction in growth, while in *E. benthamii* an evident stagnation observed from the mentioned age. This would be an indicator that, to maximize energy production per unit of time, the harvest shift would be close to four years and that it is conditioned by the evolution of biomass productivity (Balloni et al., 1980; Souza, 1989; Lopes et al., 2017).

In Paysandú, a less defined relation was obtained between energy productivity and initial plantation density compared to Tacuarembó. The analysis of the data showed an important similarity between all species and planting densities, and a close relationship with biomass productivity. As in Paysandú, the average accumulated energy yield for species and planting densities was increasing up to the age of 76 months. *E. dunnii* and *E. grandis* reached average values very similar to each other with a positive relationship between energy productivity and the number of trees, particularly for the second species. In the case of *E. benthamii*, a certain independence was observed between the referred parameters. The evolution of the yield per hectare and per year of *E. dunnii* and *E. grandis* presented increasing values (although with oscillations) up to month 75, while with *E. benthamii* some stabilization of the values was observed close to month 57. These results determined that the harvest rotations were reached with more age than in the previous site, which is explained by the increasing productivity of biomass and, to a lesser extent, by the *Db* and the *Pc*. These reasons are what determine the differences in productivity between both sites throughout the range of ages evaluated.

Taking into account the levels of energy productivity obtained in the two sites, it is possible to estimate the area to be afforested to supply a small electric power generation plant, such as 10 MW. With the results obtained in the first rotation in the two sites, the estimates of the plantation surface requirements are presented in Table 10. For this, it is assumed that these plants have a conversion efficiency of the order of 20-25% (Nuñez-Regueira et al., 2003; Pérez et al., 2014), that wood is used with 35% humidity and that it has a *Pc* of 11 Mj/kg (Francescato et al., 2008). The mean values of the species studied are presented at two contrasting plant densities (2220 and 6660 trees ha^{-1}). The results obtained show that, in spite of the important differences in energy production obtained at the sites, the fact of using different harvest times (depending on the IMA*Re* values) determines that the surface requirements to be afforested be relatively similar.

Table 10. Estimates of planted area required to supply a 10MWh plant.

Sites	**Productivity Wet biomass ($Mg\ ha^{-1}\ yr^{-1}$)**	**Planting density (Trees ha^{-1})**	***Pc* ($Mj\ kg^{-1}$)**	***Re* ($MWh\ ha^{-1}$)**	**Rotation (years)**	**Plant requirements ($MWh\ year^{-1}$)**	**Plantation (ha)**
Paysandú	40-47	2220-6660	11	794-935	6	235,000	1775-1510
Tacuarembó	28-44	2220-6660	11	541-862	4	235,000	1740-1090

5. Conclusions

The *Pc* is one of the variables least affected by the species, planting density, age and site. However, in general there was observed an increase in this variable, although it was not very relevant to practical effects, in the first years of growth of the crop and also with the reduction of the spacing in Paysandú. Also, in this site, an increase of the *Db* was observed as the wood matures in the first years of growth and in the wider spacing. In both sites, the highest *Db* density values were registered with *E. dunnii* and *E. benthamii*. The *De* at Paysandú was very similar for all tested conditions and was increasing until the end of the evaluation period. On the contrary, in Tacuarembó, the values were affected only by the species type. The accumulated *Re* increased with age, as a result of the evolution in biomass productivity. Tacuarembó showed a close positive relationship between this parameter and the planting density, an aspect that was not detected at Paysandú. The proportion of energy produced on average is decreasing as the spacing is reduced. The evolution of IMA*Re* was different for each species and site. On Paysandú, *E. dunnii* and *E. grandis* increased increasingly until month 75, while *E. benthamii* showed significant variations. In Tacuarembó, there was a noticeable reduction in the rate of increase from month 46 on all species and planting densities. Paysandú had a higher *Re* in all the inventories due to the higher productivity of biomass. Despite this, the surface requirements for the supply of an electric power generation plant were similar for the two sites and associated with planting density. The *Db* and the *Pc* were negatively related and have a very similar relative weight on the result of the energy density per unit volume.

6.References

Acuña, E.; R. Rubilar; J. Cancino; T.J. Albaugh; C.A. Maier. 2018. Economic assessment of Eucalyptus globulus short rotation energy crops under contrasting silvicultural intensities on marginal agricultural land. Land Use Policy. 76: 329–337.

Backman, M.E.; J. García de León. 2003. Correlations of pulp and paper properties at an early age and full, in: Tecnicelpa (Ed.), EUCEPA Conference: Sustainable Development for the Pulp and Paper Industry, Lisbon-Portugal, pp. 108–112.

Balloni, E.A.; J.W. Simões. 1980. O espaçamento de plantio e suas implicações silviculturais, IPEF - Série Técnica. 1: 1–16.

Balmelli, G.; F. Resquin. 2002. Evaluación del crecimiento de especies de *Eucalyptus* en diferentes zonas de prioridad forestal. Tacuarembó, UY: INIA. 20 p. (Serie Aftercare Forestal INIA - JICA, 14). Aftercare del Proyecto de Mejoramiento Genético Forestal en el Uruguay (2000-2002). file:///C:/Users/Iniatest/Downloads/Aftercare-del-Proyecto-de-Mejoramiento-Genetico-Forestal-en-el-Uruguay-2000-2002-Nro.-14%20(3).pdf

Berndes, G.; M. Hoogwijk; R. Van Den Broek. 2003. The contribution of biomass in the future global energy supply: a review of 17 studies. Biomass and Bioenergy 25: 1–28.

Brand, M.A. 2010. Energia de biomassa florestal. Río de Janeiro. Interciencia. 131 p.

Briseño-Uribe, K.C.; A. Carrillo-Parra; V. Bustamante; H. González-Rodríguez; R. Foroughbachk. 2015. Firewood Production, Yield and Quality of Charcoal From

Eucalyptus camaldulensis and *E. microtheca* Planted in the Semiarid Land of Northeast Mexico, 5075 (2015).

Brun, E.; A. Bersh; F. Pereira; D. Silva; Y. de Barba; J. Dorini Junior. 2018. Caracterização energética da madeira de três materiais genéticos de Eucalyptus sp., Floresta. 48: 87–92.

Calonego, F.W.; E.T.D. Severo; P.P. Assi. 2005. Mensuração do comprimento das fibras para a determinação da madeira juvenil em *Eucalyptus citriodora*, Scientia Forestalis. 68: 113–121.

Carneiro, A. de C.O.; A.F.N.M. Castro; R.V.O. Castro; R.C. dos Santos; L.P. Ferreira; R.A.P. Damásio; B.R. Vital. 2014. Potencial energético da madeira de Eucalyptus sp. em função da idade e de diferentes materiais genéticos, Árvore. 38: 375–381.

Carvalho, H.; R. Oliveira; J. Gomide; J. Colodette. 1998. Efeito da idade de corte da madeira e de variáveis de refino nas propriedades da celulose kraft branqueada de eucalipto, in: ABTCP (Ed.), Congresso Anual de Celulose e ABTCP 31, São Paulo, Brazil, p. 16.

Cassidy, M.; G. Palmer; R.G.B. Smith. 2013. The effect of wide initial spacing on wood properties in plantation grown *Eucalyptus pilularis*. New Forests. 44: 919–936.

Castaño, J.P.G.; A. Ceroni; M. Furest; J. Aunchayna; R. Bidegain. 2011. Caracterización agroclimática del Uruguay 1980-2009 Montevideo (UY): INIA. 34 p. (INIA Serie Técnica; 193. http://www.ainfo.inia.uy/digital/bitstream/item/2538/1/18429021211104157.pdf

Castro, A.F.N.M.; R.V.O. Castro; A.D.C. Oliveira; R.C. dos Santos; A.M.M.L. Carvalho; I. C. N. A. de Melo; P.F. Trugilho. 2015. Correlations between age, wood quality and charcoal quality of eucalyptus clones, Árvore. 40: 551–560.

De Lima, E.A.; H. Damin; O.J. Lavoranti. 2011. Caracterização dendroenergética de árvores de *Eucalyptus benthamii*. Pesquisa Florestal Brasileira. 31, 65, 9–17.

Demirbas, A. 2004. Combustion characteristics of different biomass fuels. Progress in Energy and Combustion Science. 30: 219–230.

Dias Júnior, F.A.; A.M. de Andrade; V.W. Soares; D.S. Costa Junior; D.H.A. Alves Ferreira; P.S. dos Santos Leles. 2015. Potencial energético de sete materiais genéticos de Eucalyptus cultivados no Estado do Rio de Janeiro. Energetic potential of seven

Eucalyptus genetic materials planted in Rio de Janeiro State, Scientia Forestalis. 43: 833–843.

DIN 51900-1, Determining the Gross Calorific Value of Solid and Liquid Fuels Using the Bomb Calorimeter, and Calculation of Net Calorific Value, Deutsches Institut für Normung, Berlin, 2000.

DIN 51900-2, Determining the Gross Calorific Value of Solid and Liquid Fuels Using the Isoperibol or Static-Jacket Calorimeter, and Calculation of Net Calorific Value, Deutsches Institut für Normung, Berlin, 2003.

Eloy, E.; B.O. Caron; A. Behling; E.F. Elli. 2015. Produtividade energética de espécies florestais em plantios de curta rotação, Ciência Rural. 45: 1424–1431.

Eloy, E.; D.A. Da Silva; D. Schmidt; R. Trevisan; B.O. Caron; E. Elli. 2016. Effect of planting age and spacing on energy properties of *Eucalyptus grandis* W. Hill Ex Maiden1, Árvore. 40: 749–758.

Erol, M.; S. Ku. 2010. Calorific value estimation of biomass from their proximate analyses data. Renewable Energy 35: 170–173.

Eufrade Junior, H.; R.X. De Melo; M.M. Pereira Sartori; S.P. Guerra; A.W. Ballarin. 2016. Sustainable use of eucalypt biomass grown on short rotation coppice for bioenergy, Biomass and Bioenergy. 90: 15–21.

Eufrade-Junior, H. de J.; S.P.S. Guerra; C.A. Sansígolo; A.W. Ballarin. 2018. Management of Eucalyptus short-rotation coppice and its outcome on fuel quality. Renewable Energy, 121: 309–314.

Ferreira, M.C.; R. Cavalcante; R. Vinícius; O. Castro; E.D.L. Costa; A.S. Pimenta. 2017. Biomass and energy production at short rotation eucalyptus clonal plantations deployed in Rio Grande do Norte. Árvore, 41: 1-7.

Foelkel, C. 2015. Qualidade da Biomassa Florestal do Eucalipto para Fins Energéticos, Eucalyptus Newsletter No 49: 78–107.

Francescato, V.; E. Antonini; L. Bergomi. 2008. Manual de combustibles de mdera, AVEBIOM, Gráficas Germinal, S.C.L, Valladolid, España, 2008. www.avebiom.org.

Gonzalez, R.; T. Treasure; J. Wright; D. Saloni; R. Phillips; R. Abt; H. Jameel. 2011. Exploring the potential of Eucalyptus for energy production in the Southern United States: Financial analysis of delivered biomass. Part I, Biomass and Bioenergy. 35: 755–766.

Guerra, S.P.S.; E.A. Garcia; K.P. Lanças; M.A. Rezende; R. Spinelli. 2014. Heating value of eucalypt wood grown on SRC for energy production, Fuel. 137: 360–363.

Hakamada, R.; R.M. Hubbard; S. Ferraz; J.L. Stape; C. Lemos. 2017. Biomass production and potential water stress increase with planting density in four highly productive clonal Eucalyptus genotypes. Southern Forests: A Journal of Forest Science. 2620: 1–7.

Hanaoka, T.; S. Inoue; S. Uno; T. Ogi; T. Minowa. 2005. Effect of woody biomass components on air-steam gasification, Biomass and Bioenergy. 28: 69–76.

Hansted, A.; T. Aguiar; G. Tami; V. Eliodoro; H. Yamamoto; F. Minoru. 2018. Industrial Crops & Products Use of a lignocellulosic residue as solid fuel: The effect of ash content in the energy potential, Industrial Crops & Products. 116: 209–214.

Hinchee, M.; W. Rottmann; L. Mullinax; C. Zhang; S. Chang; M. Cunningham; L. Pearson; N. Nehra. 2009. Short-rotation woody crops for bioenergy and biofuels applications. In Vitro Cell.Dev.Biol.—Plant 45: 619–629.

Jesus, M.S.; L.J. Costa; J.C. Ferreira; F.P. De Freitas; L.C. Santos; M. F. V. Rocha. 2017. Caracterização energética de diferentes espécies de eucalyptus, Floresta. 47: 11–16.

Johnson, J.M.; M.D. Coleman; R. Gesch; A. Jaradat; R. Mitchell; D. Reicosky. 2007 Biomass-Bioenergy Crops in the United States: A Changing Paradigm. The Americas Journal of Plant Science and Biotechnology. 1: 1–28.

Kačík, F.; J. Ďurkovič; D. Kačíková. 2012. Chemical profiles of wood components of poplar clones for their energy utilization. Energies. 5 : 5243–5256.

Kumar, R.; K.K. Pandey; N. Chandrashekar; S. Mohan. 2011. Study of age and height wise variability on calorific value and other fuel properties of Eucalyptus hybrid, *Acacia auriculaeformis* and *Casuarina equisetifolia.* Biomass and Bioenergy. 35: 1339–1344.

Kumar,R.; K.K. Pandey; N. Chandrashekar; S. Mohan. 2010. Effect of tree-age on calorific value and other fuel properties of Eucalyptus hybrid, Journal of Forestry Research. 21: 514–516.

Larson, P.R.; D.E. Kretschmann; A.C. Iii; J.G. Isebrands. 2001. Formation and Properties of Juvenile Wood in Southern Pines A Synopsis, Rhinelander, Wisconsin.

Lemenih, M.; T. Bekele. 2004. Efect of age on caloric value and some mechanical properties of three Eucalyptus species grown in Ethiopia, Biomass and Bioenergy 27: 223–232.

Lopes, E.D.; M.L. de Laia; A.S. dos Santos; G.M. Soares; R.W. Pinto Leite; N.D.S. Martins. 2017. Influência do espaçamento de plantio na produção energética de clones de Corymbia e Eucalyptus, Floresta. 47:1-95.

López, F.; J.C. García: A. Pérez; J.M.Feria; M. Zamudio; G. Garrote. 2010. Chemical and Energetic Characterization of Species with a High-Biomass Production: Fractionation of Their Components. Enviromental Progress & Sustainable Energy. 29: 499–509.

Magalhães, M.; A. Carneiro; B.R. Vital; M.M. De Souza; L.D.F. Fialho. 2017. Estimates of mass and energy of different genetic material Eucalyptus, Árvore. 41: 1–8.

Magnago, L.M.; M.D.C. Arantes; G.B. Vidaurre; J.C. Moulin; P.F. Trugilho. 2016. Energy Estimate and Carbon Stock in Short-Rotation Eucalyptus Stands, Cerne. 22: 527–534.

Malan, F.S. 1995. *Eucalyptus* improvement for lumber production, in: CSIR (Ed.), Seminário internacional de utilização da madeira de eucalipto para serraria, Pretoria, South Africa, 1995: pp. 1–19.

Malan, F.S.; M. Hoon. 1992. Effect of initial spacing and thinning on some wood properties of *Eucalyptus grandis*, South African Forestry Journal. 163: 13–20.

MGAP. 1976. Carta de reconocimiento de suelos del Uruguay a escala 1/1000.000 y clasificación de suelos del Uruguay, Montevideo, Uruguay, 1976.

Mimms, A.; M.J. Kocurek; J.A. Pyiatte; E.E. Wright. 1993. Kraft Pulping. A Compilation of Notes. TAPPI, Atlanta, GA, USA. 181 p.

Moulin, J.C.; M.D.C. Arantes; G.B. Vidaurre; J.B. Paes; A.C.O. Carneiro. 2015. Efeito do espaçamento, da idade e da irrigação nos componentes químicos da madeira de Eucalipto. Árvore 39 (1): 199–208.

Müller, M.D. 2005. Produção de madeira para geração de energia elétrica numa plantação clonal de eucalipto em Itamarandiba, MG. Tese de Doutorado. Universidad Federal de Viçosa, Viçosa, MG, Brasil. 108 p.

Njakou Djomo, S.N.; O. El Kasmioui; T. De Groote; L.S. Broeckx; M.S. Verlinden; G. Berhongaray; R. Fichot; D. Zona; S.Y. Dillen; J.S. King; I.A. Janssens; R. Ceulemans. 2013. Energy and climate benefits of bioelectricity from low-input short rotation woody crops on agricultural land over a two-year rotation, Applied Energy. 111: 862–870.

Nonhebel, S. 2002. Energy yields in intensive and extensive biomass production systems, Biomass and Bioenergy. 22: 159–167.

Nuñez-Regueira, L.; J. Proupín-Castañeras; J. Rodrıguez-Añon. 2004. Energy evaluation of forest residues originated from shrub species in Galicia, Bioresource Technology. 91: 215–221.

Oliveira. J. 1997. Caracterização da madeira de eucalipto para a construção civil. Tese de Doutorado. Escola Politécnica de São Carlos. Universidade de São Paulo. Brasil. 414 p.

Pérez, S.; C.J. Renedo; A. Ortiz; F. Delgado; I. Fernández. 20414. Energy potential of native shrub species in northern Spain, Renewable Energy. 62: 79–83.

Pérez, S.; C.J. Renedo; A. Ortiz; M. Man. 2008. Energy potential of waste from 10 forest species in the North of Spain (Cantabria), 99: 6339–6345.

Pérez, S.; C.J. Renedo; A. Ortiz; M. Mañana; F. Delgado; C. Tejedor. 2011. Energetic density of different forest species of energy crops in Cantabria. Biomass and Bioenergy 35 (11): 4657-4664.

Pereira, J.C.D.; J.A. Sturion; A.R. Higa; R.C.V. Higa; J.Y. Shimizu. 2000. Características da madeira de algumas espécies de eucalipto plantadas no Brasil. Embrapa Florestas 38: 2-113.

Protásio, T.D.P.; T.A. Neves; A.A. Dos Reis; P.F. Trugilho. 2014. Effect of age and clone on the quality of Eucalyptus spp. wood aiming, Ciência Florestal. 24: 465–477.

Quirino, W.F.; A.T. Do Vale; A.P.A. De Andrade; V.L.S. Abreu; A.C.D.S. Azevedo. 2005. Poder Calorífico Da Madeira E De Materiais Ligno-Celulósicos, Revista Da Madeira. 89: 100–106.

R Core Team. 2012. R: a language and environment for statistical computing. Viena, Austria: R Foundation for Statistical Computing. URL http://CRAN.R-project.org/doc/Rnews/

Repic, B.S.; D. V Daki; M.J. Paprika; R. V Mladenovi; A.M. Eri. 2008. Soya straw bales combustion in high-efficient boiler. Thermal Science. 12: 51–60.

Resquin, F.; J.D. Mello: I. Fariña; J. Mieres; L. Assandri. 2007 Caracterización de la celulosa de especies del género *Eucalyptus* plantadas en Uruguay Montevideo

(Uruguay): INIA. 84 p (INIA Serie Técnica; 152). http://www.ainfo.inia.uy/digital/bitstream/item/2897/1/18429160709160425.pdf

Rocha, E.P.A.; B.F. Gomes; E. Sermyagina; M. Cardoso; J.L. Colodette. 2015. An Analysis of Brazilian Biomass Focusing on Thermochemical Conversion for Energy Production. Energy and Fuels.1–39. Downloaded from http://pubs.acs.org on November 2, 2015.

Rocha, P.R.G.H.; B.R. Vital; A.C.O. Carneiro; A.M.M.L Carvalho; M.T. Cardoso. 2016. Effects of plant spacing on the physical, chemical and energy properties of Eucalyptus wood and bark. Journal of Tropical Forest Science. 28: 243–248.

Rodrigues, A.; J. Bordado; M. Mateus. 2010. An evaluation of SRCS as a potential carbon neutral source of biomass for energy. International Journal of Energy, Environment and Economics. 23 (4-5): 479-544.

Sannigrahi, P.; A.J. Ragauskas; G.A. Tuskan. 2010. Poplar as a feedstock for biofuels: A review of compositional characteristics. Biofuels, Bioprod, Bioref. 4:209–226.

Santana, W.M.S. 2009. Crescimento, produção e propriedades da madeira de um clone de *Eucalyptus grandis* e *E. urophylla* com enfoque energético. Dissertação de Mestrado. Universidade Federal de Lavras, Lavras, MG, Brasil. 105 p.

Santos, D. 2010. Parâmetros de qualidade da madeira e do carvão vegetal de clones de eucalipto. Tese de Doutorado. Universidade Federal de Lavras, Lavras, MG, Brasil. 175 p.

Santos, M.D. 2011. Efeito do espaçamento de plantio na biomassa do fuste de um clone híbrido interespecífico de *Eucalyptus grandis* e *Eucalyptus urophylla*, Dissertação de Mestrado. Faculdade de Ciências Agronômicas, Universidade Estadual Paulista. São Paulo, Brasil. 152 p.

Santos, D.R.C.; A.C.O. Carneiro; A.S. Pimenta; R.V.O. Castro; I.V. Marinho; P.F. Trugilho; I.C.N. Alves; A.F.N.M. Castro. 2013. Potencial energético da madeira de espécies oriundas de plano de manejo florestal no estado do Rio Grande do Norte. Ciência Florestal 23 (2): 491–502.

Santos. R.; A. Carneiro; B.R. Vital; R. Castro; G. Vidaurre; P. F. Trugilho; A. Castro. 2016. Influência das propriedades químicas e da relação siringil/guaiacil da madeira de eucalipto na produção de carvão vegetal, Ciência Florestal. 26: 657–669.

Senelwa, K.; R.E.H. Sims. 1999. Fuel characteristics of short rotation forest biomass, Biomass and Bioenergy. 17: 127–140.

Soares, V.C.; M.L. Bianchi; P.F. Trugilho; A. Júnior; J. Höfler. 2014. Correlações entre as propriedades da madeira e do carvão vegetal de híbridos de eucalipto, Árvore. 38: 543–549.

Soares, V.C.; M.L. Bianchi; P.F. Trugilho; J. Höfler; A.J. Pereira. 2015. Análise das propriedades da madeira e do carvão vegetal de híbridos de eucalipto em três idades, Cerne. 2: 191–197.

Souza, R.1989. Efeito de dois espaçamentos na produção em peso e volume de *Eucalyptus grandis* (W. Hill ex Maiden). Dissertação de Mestrado. Universidade Federal de Viçosa. Vicosa, MG, Brasil. 102 p.

Swain, P.K.; L.M. Das; S.N. Naik. 2011. Biomass to liquid: A prospective challenge to research and development in 21st century. Renewable and Sustainable Energy Reviews. 15: 4917–4933.

Trugilho, P.F. 2009. Densidade básica e estimativa de massa seca e de lignina na madeira em espécies de Eucalyptus, Ciênc. Agrotec. 33: 1228–1239.

Trugilho, P.F.; L.J. Tarcício; L.M. Mendes. 1996. Influência da idade nas características físico-químicas e anatômicas da madeira de *Eucalyptus saligna*, Cerne. 2: 94–111.

Villanueva, M.; J. Proupín; J.A. Rodríguez-Añón; L. Fraga-Grueiro; J. Salgado; N. Barros. 2011. Energetic characterization of forest biomass by calorimetry and thermal analysis. Journal of Thermal Analysis and Calorimetry. 104: 61–67.

Vital, B.R.; R.M. Della Lucia. 1987. Efeito do espaçamento na produção em peso e na qualidade da madeira de *Eucalyptus grandis* e *Eucalyptus urophylla* aos 52 meses de idade, Árvore. 11: 132–145.

Walter, A.; P. Dolzan; E. Piacente. 2006. Biomass Energy and Bioenergy Trade: Historic Developments in Brazil and Current Opportunities. Country Report: Brazil – Task 40 – Sustainable Bio-energy Trade; securing Supply and Demand Final Version. Unicamp, Campinas – Brazil. 36 p.

Wionzek, F. 2014. Influência do espaçamento nas propriedades energéticas e biomassa de *Eucalyptus benthamii* Maiden et Cambage. Dissertação de Mestrado. Universidade Estadual do Centro-Oeste, PR, Brasil. 76 p.

Wu, S.; Y. Zhu; J. Xu; Z. Lu; G. Chen; P. Song; W. Guo; Y. Zhu; J. Xu; Z. Lu; G. Chen; P. Song; W.G. Genetic; S. Wu; Y. Zhu; J. Xu; Z. Lu; G. Chen; P. Song; W. Guo. 2017. Genetic variation and genetic gain for energy production, growth traits and wood properties in Eucalyptus hybrid clones in China. Australian Forestry. 80: 57–65.

Zanuncio, J.A.V; A.G. Carvalho; P. F. Trugiho; T.C. Monteiro. 2014. Extractive and energetic properties of wood and charcoal, Árvore. 38: 369–374.

Chapter 6. Evaluation of the nutrient content in biomass of Eucalyptus species from short rotation plantations in Uruguay

“…..Fueye, no andés goteando tristezas,
fueye, que tu rezongo me apena.
Vamos, no hay que perder la cabeza.
Vamos, si ya sabemos muy bien
que no hay que hacer,
que ya se fue de nuestro lao,
y que a los dos nos ha tirao
en el rincón de los recuerdos muertos.
Fueye, no andes goteando amargura.
Vamos, que hay que saber olvidar.”

Homero Manzi, 1942

Chapter 6. Evaluation of the nutrient content in biomass of Eucalyptus species from short rotation plantations in Uruguay

1. Introduction

The use of forest biomass as raw material to obtain different types of fuels has generated many expectative about the substitution of fossil fuels. This has been based on the fact that some species have a high production potential (Bouvet et al., 2013), have interesting technological properties for different industrial processes and that it was a renewable resource. It was important to point out that the concept of afforestation as a renewable natural resource were valid as long as the principles of conservation was taken into account (Poggiani, 1980). There has also been interest in the use of crop residues with an energy destination in relation to aspects of processing, transportation, pre-treatment and conversion technologies (Meullemiestre, 2014, Salvador et al., 2016). At the same time, there were some pressure on natural resources to increase the production of biomass per unit area (Bouillet et al., 2008, Dovey, 2009). The intensification of forest production has occurred through the shortening of the rotation length, the use of high productivity genetic material and the application of silvicultural techniques that maximize their growth (Ericsson, 1994). This implies a great challenge in terms of the long-term sustainability of the different forest production systems taking into account that in general large-scale eucalyptus plantations was produced in soils with agriculture suitability (low fertility, high risk of physical degradation) (Silva et al., 1983; Poggiani et al., 1983). This were the type of soil that predominates in the Campos biome (previously called Pampa) that occupies the regions of southern Brazil, northern Uruguay and Northeast of Argentina (Pallarés et al., 2005, Corrêa et al., 2013). In this type of soil, the return of nutrients to the soil through the deposition of mulch and the decomposition of crop residues (Ludvichak et al., 2016) was of greater importance since they were characterized by low nutrient retention associated with a high hydraulic conductivity which translates into a greater capacity to lose them by leaching (Silva et al., 2013). The amounts of nutrients required by forest systems depend on the species, the growth rate, the age of the trees (Grove 1996), the site conditions (Santana et al., 2000; Turner and Lambert, 2008) and the density of plantation (Leite et al., 2011). Of these factors, planting density had the lowest effect on the nutrient concentrations of eucalyptus species with populations of 500 to 6000 trees per hectare (Leite et al., 1998, Leite et al., 2011, Bentancor et al., 2019).

During the first stages of tree growth, the nutrient supply comes from the soil, but as the crown closes, nutrient requirements was covered to a large extent by the biochemist that occurs inside the plant (Ericsson, 1994). Some authors also report differences in the requirements and efficiency of use between different genetic materials even within the same species and in similar growth conditions (Silva et al., 1983, Wang et al., 1991, Leite et al., 2011). According to Camargo et al., (2004) it was difficult to identify genetic materials that show a high efficiency in the use of all the essential nutrients. On the other hand, high efficiency was not necessarily associated with high productivity (Santana et al., 2002). Efficiency can be determined in several ways, but one of the most frequent were by the ratio of biomass produced per unit of nutrient absorbed in the different aerial fractions of the tree (Safou-Matondo et al., 2005). Taking into account that these indices was calculated as the inverse of the concentration they must be interpreted carefully (Barrow, 1978) because they depend on factors such as the assimilated partition, growth rate, among others (Loneragan, 1968). This index was useful when identifying genotypes with low relative accumulation of nutrients which can be more sustainable in the long term (Turner and Lambert, 2014). However, these authors conclude that the highest levels of efficiency were obtained with low values of nutrient availability and in older stands in which productivity remains relatively stable over time. Another relevant aspect related to the content and distribution of nutrients in the fractions of the tree were the spacing and age of the same (Bellote et al., 1980). Short rotation forest systems (SRF) determine a very different use of nutrients and water compared to traditional production systems (Albaugh et al., 2017). The shortening of the cycle due to the greater competition between individuals that occurs in these systems determines changes in the requirements of those resources (Binkley et al., 2010). These changes were partly explained by the increase in population (Leles et al., 2001), which in turn has implications for the proportions of each of the tree fractions (Binkley et al., 2002). In the systems of short rotation (short rotation forestry, SFR) there were a high ratio of the components of the crown compared with the stem which determines a high extraction of nutrients (Laclau et al., 2000). The harvesting of this type of stands often involves the use of the whole tree with the consequent removal of tree's fractions with a high content of nutrients such as the bark and leaves (Merino et al., 2005) due to the high physiological activity of the tissues that compose it. This becomes more important with species such as eucalyptus that do not lose leaves unlike willow and poplar species (Achat et al., 2015). As time goes by, there were an increase in the timber proportion of the tree compared with leaves and branches (Dovey, 2012). In turn, this determines that an increase in efficiency in the use of nutrients occurs because the stem has a lower concentration than the bark and the crown (Santana et al., 2008; Turner and Lambert, 2008). At the same time the increase in age causes the translocation within the shaft due to the process of transformation of the sapwood into heartwood (Bouillet et al., 2008). All these changes imply a redistribution of the biomass of the different tree's fractions of the tree that have different implications in terms of the extraction of nutrients (Salvador et al., 2016). This distribution of tree biomass was closely related to the distribution of nutrients, which depends on the functions of each one (Viera et al., 2013). There was a broad consensus that the concentration gradient of nutrients in eucalyptus species has the following decreasing order: leave> bark> branches> wood (Wise and Pitman, 1981, Schumacher and Poggiani, 1993, Sochacki et al., 2012; Viera et al., 2013). Estimates made with high planting densities and at ages of 3 years show that the summed weight of the leaves and bark per hectare was 15-30% of the total tree biomass (Bernardo et al., 1998; Schumacher et al., 2011; Sochacki et al., 2012; Andrade et al., 2013; Caron et al., 2015). The quantities of nutrients exported was closely linked to growth, so that with some species of eucalyptus it was expected that high levels of extraction will occur (Merino et al., 2005). Therefore, the use of tree's fractions such as leaves, and bark could cause in the long term an imbalance of nutrients with the consequent loss of soil fertility and yield of the following rotations. Based on the above, the hypotheses proposed was that the eucalyptus and plantation density species evaluated in this work do not affect the concentration of nutrients of the different biomass tree's fractions, but the export of nutrients per unit area in short crop turns. The objectives were: i) quantify the content and extraction of major nutrients in the biomass fractions of the tree at the age of 76 months, ii) determine the distribution of major nutrients in the different aerial fractions of the tree, iii) determine the corresponding conversion efficiencies in that length of rotation.

2. Materials and Methods

2.1 Area of study

In the months of October and November 2010 two trials were installed in the Northern and Noth Western soils for forest plantation at Uruguay. The coordinates of the two sites are: 32° 24'17.53 "S; 57°25'32.73" W and 32°11'58.84"S; 55°54'12.22" W respectively. The climate of the region corresponds to the temperate subtropical type (Castaño et al., 2014) but in the sites of the trials during the evaluation period there has been a different temperature and rainfall regime. The average monthly temperature of the Paysandú region was 19.2 °C with a range of 28 to 9.7 °C while on the Tacuarembó region the monthly average was 17.1 °C with a range of 25.8 to 7.3 °C (INUMET, 2018). The average annual precipitation values for the evaluation period were 1297 and 1430 mm in Paysandú and Tacuarembó, respectively. The soils of the Tacuarembó site were of the Luvisoles and Ochric Acrisols type, and those of the Paysandú site was of the planooles and dístricos ochric argisols type (MGAP, 1976).

2.2 Experimental design

The design of both experiments was of plots divided into randomized complete block design with 3 repetitions. The factors were the species (main effect) and density of plantation (secondary effect) each with 3 and 4 levels, respectively. The studied species was: *Eucalyptus benthamii*, *E. dunnii* and *E. grandis* and planting densities: 2220, 3330, 4440 and 6660 trees per hectare. The origin of the seed was Brazil (APS Pinhao-State of Paraná-Brazil) for *Eucalyptus benthamii*, the seed orchard of INIA for *E. grandis* and Undera (Moleton West Coffs Harbor, Australia) for *E. dunnii*. The distance between rows was 3 m and the distance between plants were: 1.5, 1, 0.75 and 0.5 m. The plot consists of 6 rows of 25 plants each of which the 4 central rows were evaluated to avoid the edge effect.

2.3. Sampling of trees and measurements

In the inventory of the year 2016 in each of the plots were added three trees of the diametric classes of greater relative weight trying to identify trees with a value of normal diameter (*db*h, cm) lower, middle and higher within it. Once removed, the green weight of the stem, bark and leaves was measured. From the basal portion of the stem, at 50 and

75% of the commercial height discs of 2 cm thickness were extracted to which the weight of the wood and bark was determined separately. With both weights, the proportion of each was estimated to estimate the green weight of the stem and bark. The green weight of each tree for those two fractions was estimated as the weighted average by the surface of the extracted samples. From the total of the leaves, a sample of approximately 200 grams was extracted from the zone corresponding to the average height of the crown at which the green weight was measured. The dry weights of the tree's fractions were recorded after drying (oven with forced ventilation, Thermo Scientific brand; USA) at 60°C up to constant weight; for the estimation of percentage of dry matter. The dry weight of each individual tree fraction was estimated as the product of the green weight by the respective percentage of dry matter. Of the three trees that were felled, the one that had a value of dn closer to the plot average and that visually had a representative crown size of the tree was selected for the analysis of nutrient content. The replicates of the three fractions of this tree were milled (mill RETSCH, model SR 200, USA) until reaching a particle size of 40-60 mesh to determine the nutrient content.

2.4 Soil sampling

In both sites, at the age of 49 months after the test was installed, a soil characterization was made up to the C horizon. Morphological descriptions were made (Appendices 1 and 2, Supplementary material) and samples from all the horizons were taken for the realization of chemical analysis. Stock calculations of interchangeable nutrients were made taking into account the apparent density of each horizon. The chemical analyzes carried out were: pH, organic carbon, exchangeable bases (calcium, magnesium potassium and sodium), exchangeable acidity (aluminum) and available phosphorus (Bray 1-P) (Tables S1, Supplementary Material). Based on this characterization the soils of the two sites were defined as fine-loamy, siliceous, active, thermic Mollic Hapludalf (Bentancor et al., 2019).

2.5 Laboratory analysis

The determination of the N content was made by dry combustion at 900 °C and detection of the N_2 emitted by the sample by heat conductivity, with LECO TruSpec NC ® autoanalyzer equipment, according to Wright and Bailey (2001). The P content was carried out by means of wet digestion in acidic medium with assistance of heat and subsequent determination of the extracted P by means of absorbance (810 nm) of the reduced molybdophosphate complex (Da Silva, 2009). The contents of Ca^{+2}, K^{+} and Mg^{+2}, were quantified by calcination of the sample (500 °C) and solubilization of the ashes in HCl. The contents in the extract were measured by atomic emission with ICP-AES equipment (Benton et al., 1985).

2.6 Weight of the tree's fractions and nutrients

The weight per hectare of each of the tree's fractions was estimated as the product of the individual weight by the equivalent number of trees per hectare of each plot. The weight of each major nutrient per hectare correspond to the multiplication of each tree's fractions mass per hectare with the corresponding major nutrient content.

2.7 Nutrient use efficiency

The utilization efficiency index of each nutrient (UE) was estimated according to Turner and Lambert, (2014) as the quotient between the sum of the dry weight of the tree's fractions (wood, branches and leaves) and the weight of the nutrient content in the tree's fractions referred to.

2.8 Statistical analysis

The analysis of the data was made according to the following model:

$$Y_{ijk}=\mu + \tau_i + \gamma_k + \tau_{\gamma ik} + \beta_j + \varepsilon_{ijk}$$

Where Y_{ijk} were the variable measured in the plot for species i, density k, in block j; μ were the general average of all observations, τi were the effect i of the species, (fixed effect); γ_{k} were the effect k of the density, (fixed effect); β_j were the effect j of the block; $\tau_{\gamma ik}$ were the interaction species and density, (fixed effect); and ε_{ijk}, were the experimental error associated to each observation, independent and with a normal distribution of mean 0 and variance σ^2.

The model used to analyze the site effect was the following:

$$Y_{ij}=\mu + \beta_j + \tau_i + \varepsilon_{ij}$$

Where Yijk were the variable measured in the plot for site i, in block j; μ were the general average of all observations, τi were the effect i of the site (fixed effect); $\beta_{j\ were}$ the effect j of the block; and ε_{ij}, were the experimental error associated with each observation, independent and with a normal distribution of mean 0 and variance σ^2. The variables analyzed were: concentration of nutrients, weight of tree's fractions and nutrients per hectare and UE. Previous analysis of variance was checked for normality and homogeneity of variance using the Shapiro-Wilk and Brown-Forsythe tests, respectively. When these assumptions were not verified, the Box and Cox transformation was used. The assumption of randomness was verified since the allocation of the species (main) factors and density of plantation (secondary) was carried out by lot in both cases. The effect of the species factor was contrasted with the interaction of this with the block and the effects of the plantation density and interaction factors were contrasted with the mean squared error. The analysis of the site effect on the UE of the Mg^{+2} and N was performed with the Kruskal-Wallis test since it was not possible to check the assumption of homogeneity of variances of the error between both tests. The comparisons between means posteriori of the F test and the nonparametric test were performed with the Tukey and Dunn test, respectively. The level of significance was established at a value of $p < 0.05$. The analyzes were performed with the software Statistix 10 and R version 2.14.1 (R Development Core Team, 2012).

3. Results

3.1 Total biomass and tree's fractions

The values of dry matter per hectare of the different fractions of the tree of the species and planting densities of both sites was presented in Table 1. At the Tacuarembó site, the analysis of variance detects differences between planting densities of the wood (P=0.004), bark (P=0.0032) and total biomass (P=0.044). The effect of the species was also significant for the bark (P=0.0031) and the total biomass (P=0.044). The interaction species and planting density was not significant for any of the four variables analyzed. The contrasts of means determine that the highest weights of wood, bark and total biomass was obtained with the highest planting densities. In turn, *E. benthamii* and *E. dunnii* was the species that reach the highest values of bark and total biomass. At Paysandú site the analysis of variance identifies significant differences for the species interaction and density of plantation for the bark (P=0.037) and the total biomass (P=0.045). According to the contrast of means, the highest weight values are obtained with *E. benthamii* and *E. dunni* at the plantation density of 6660 trees ha^{-1}. The proportion of the wood, bark, branches and leaves fractions in relation to the total biomass for each site, species and density of plantation were presented in Figure 1. At Tacuarembó site, it was obtained that the proportions of the weight per hectare of the wood and leaves fractions was the same for all the species and planting densities (Table S2, Supplementary material). The proportion of the bark were affected by the species (P=0.023) and that of branches by the density of plantation (P=0.047). *E. dunnii* and *E. grandis* was the species that have the highest and lowest proportion of bark, (12.5 and 11.9% respectively), at the same time that there was an inverse relationship between the proportion of branches and spacing. At Paysandú site the proportions of the weight of the wood, leaves and branch fractions were very similar for the species and planting densities (Table S3, Supplementary material). The proportion of bark were affected significantly by the species (P=0.0051) indicating that also in this case *E. grandis* were the species with the lowest value of this variable (10%).

Chapter 6. Evaluation of the nutrient content in biomass of Eucalyptus species from short rotation plantations in Uruguay

Table 1. Biomass of wood, bark, branches and leaves ± (E.S.) of the species and planting densities of both sites.

Sites	Species	Planting density (trees ha^{-1})	Wood	Bark	Leavs	Branch	Total
			(Mg ha^{-1})				
Tacuarembó	*E. benthamii*	2220	93.9 (7.3) A c	15.4 (1.3) A c	4.4 (0.8) A a	12.3 (2.9) A a	125.9 (8.2) A a
		3330	110.9 (32.2) A bc	16.9 (4.5) A bc	4.5 (0.9) A a	8.2 (1.4) A a	140.4 (37.9) A a
		4440	144.7 (8.5) A ab	22.6 (1.8) A ab	7.4 (1.7) A a	14.1 (1.4) A a	188.8 (8.2) A b
		6660	187.6 (11.5) A a	27.8 (1.1) A a	7.7 (2.2) A a	14.6 (3.6) A a	237.8 (17.9) A b
	E. dunnii	2220	96.6 (8.5) A c	15.7 (0.9) A c	4.7 (0.4) A a	11.9 (1.4) A a	128.8 (10.7) A a
		3330	120.6 (6.2) A bc	19.1 (1.7) A bc	5.2 (0.2) A a	11.9 (1.4 A a	156.8 (6.8) A a
		4440	145.0 (22.1) A ab	23.4 (3.2) A ab	6.6 (0.9) A a	17.3 (4.2) A a	192.3 (30.4) A b
		6660	168.9 (41.4) A a	28.2 (6.3) A a	7.1 (2.2) A a	14.3 (2.6) A a	218.6 (51.9) A b
	E. grandis	2220	103.6 (12.7) A c	13.9 (1.3) B c	5.0 (0.4) A a	13.6 (0.8) A a	136.1 (14.3) A a
		3330	95.5 (8.2) A bc	13.4 (0.8) B bc	5.8 (0.4) A a	12.1 (0.5) A a	126.7 (8.4) A a
		4440	116.4 (12.1) A ab	14.9 (1.5) B ab	5.8 (0.7) A a	13.1 (1.1) A a	150.3 (14.9) A b
		6660	120.9 (2.1) A a	16.8 (0.9) B a	6.3 (0.9) A a	12.9 (0.2) A a	157.0 (0.6) A b
Paysandú	*E. benthamii*	2220	129.6 (8.4) A a	21.1 (0.4) ab	5.7 (0.8) A a	11.5 (1.5) A a	167.9 (8.2) A a
		3330	140.6 (37.1) A a	23.3 (5.7) ab	5.4 (1.9) A a	9.4 (3.0) A a	178.6 (47.8) A a
		4440	103.9 (3.8) A a	17.4 (1.0) bc	4.2 (0.6) A a	9.5 (1.8) A a	135.1 (5.5) A a
		6660	172.1 (9.1) A a	30.3 (3.0) a	7.9 (1.2) A a	11.6 (2.1) A a	222.1 (13.9) A a
	E. dunnii	2220	148.7 (7.6) A a	22.4 (1.4) ab	6.9 (0.3) A a	13.2 (2.1) A a	191.2 (9.8) A a
		3330	117.4 (10.8) A a	17.6 (0.6) bc	5.1 (0.5) A a	8.9 (1.1) A a	149.1 (12.9) A a
		4440	123.7 (9.5) A a	20.2 (2.1) abc	5.6 (0.2) A a	8.4 (0.6) A a	157.9 (10.6) A a
		6660	166.7 (21.8) A a	28.7 (3.6) a	18.2 (7.9) A a	21.7 (7.1) A a	235.3 (21.3) A a
	E. grandis	2220	123.9 (7.8) A a	14.2 (0.6) c	4.7 (0.2) A a	10.4 (1.1) A a	153.3 (7.7) A a
		3330	163.2 (9.6) A a	22.9 (1.7) ab	12.1 (4.2) A a	14.1 (1.7) A a	212.3 (6.0) A a
		4440	164.8 (34.5) A a	19.8 (4.8) bc	6.9 (2.1) A a	14.1 (3.9) A a	205.6 (45.2) A b
		6660	123.0 (7.1) A a	16.8 (0.6) bc	6.4 (0.9) A a	17.2 (8.1) A a	163.5 (8.6) A b

Different capital letters indicate significant differences between species and different lowercase letters indicate significant differences by means of the Tukey a posteriori test of the ANOVA for each site with a probability level of 5%.

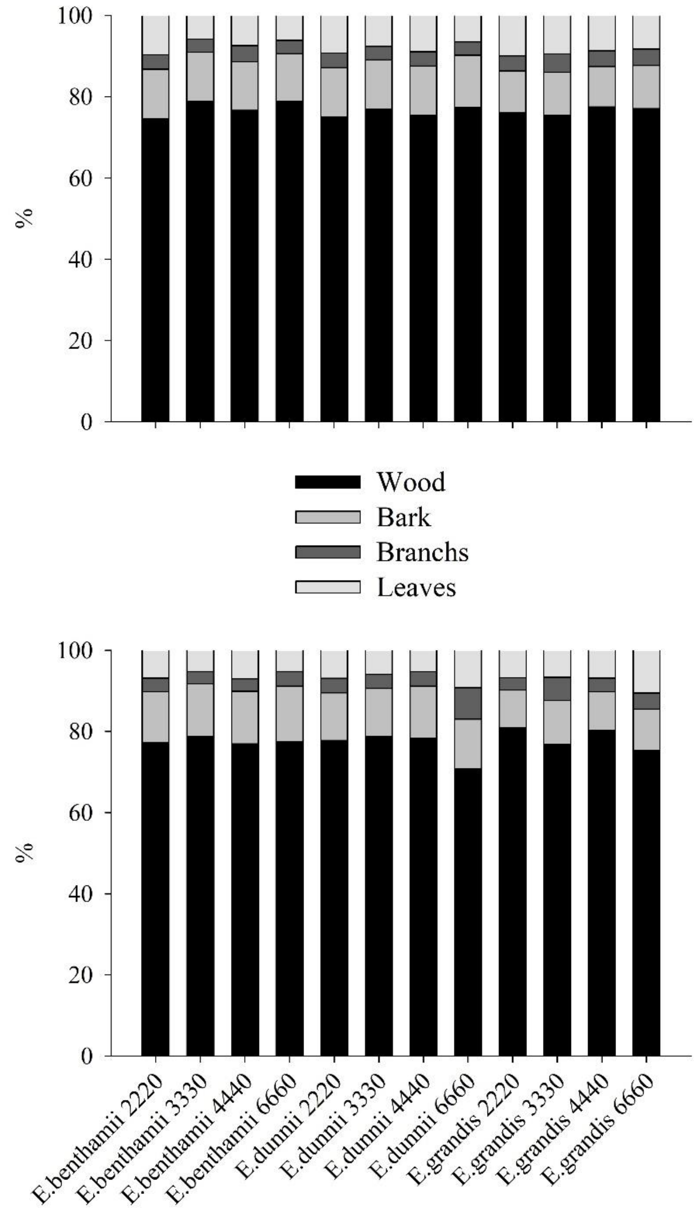


Figure 1. Relative proportion of weight (%) of dry matter per hectare of each fraction in the Tacuarembó (superior) and Paysandú (lower) sites.

3.2 Extraction of nutrients by different tree fractions

The contents of each nutrient per fraction for each species, planting density and site was presented in Tables S4 to S9 (Supplementary Material). At Tacuarembó site it was observed that the effect of planting density was not significant for any of the nutrients in the three fractions evaluated. In contrast, the effect of the species were significant for the P in wood (P=0.0035), bark (P=0.049) and leaves (P=0.032); Ca^{+2} in wood (P=0.017); the Mg^{+2} in wood (P<0.0001) and leaves (P=0.0005), K^{+} in wood (P=0.0019) and N in wood (P=0.033). At Paysandú site the plantation density has the same behavior as in the previous case. The effect of the species was significant for Ca^{+2} in wood (P=0.049), Mg^{+2} in wood (P<0.0001) and leaves (P=0.033). The results of the average contents of each nutrient in fractions of the species and planting densities; Analysis of variance and post hoc comparison of means was presented in Tables S10 and S11 (Supplementary Material). At Tacuarembó site the effect of the species were significant for P (P=0.0085), Mg^{+2} (P=0.0013), K^{+} (P=0.0019) and N (P=0.0034) in the bark; Mg^{+2} (P=0.0263) in leaves; P (P=0.0014), Ca^{+2} (P=0.0299), Mg^{+2} (P=0.0054) and N (P=0.0088) in wood. The effects of planting density were significant for P (P=0.01136) and Mg^{+2} (P=0.0158) in the bark, Mg^{+2} (P=0.037) in leaves; P (P=0.0014), K^{+} (P=0.0029) and N (P=0.0038) in wood. In the nutrients of the fractions that was affected by the species, it was observed that *E. grandis* has the lowest values except for Mg^{+2} in the leaves. In cases where a significant effect of planting density was detected, it was observed that the amounts of nutrients extracted was directly related to the density of plantation. This tendency occurs in all cases except for Ca^{+2} and Mg^{+2} in wood although this was only detected by the analysis of variance in those mentioned above. The interaction species by planting density was not significant in any of the cases. At Paysandú site, the effect of the species was significant for P (P=0.0392) in the bark and Ca^{+2} (P=0.0349) in the leaves. *E. grandis* were the species with the values of the mentioned nutrients. The density of plantation had a significant effect with P (P=0.0147) in bark and Mg^{+2} (P=0.0448) in leaves. The interaction species and density of plantation had a significant effect with Ca^{+2} (P=0.0007) and N (P=0.0085) in the bark; P (P=0.0144) in wood.

The total contents of each nutrient considering the three fractions of biomass together for the two sites was presented in Tables 2 and 3. On the site of Tacuarembó the analysis of variance states that the effect of planting density were significant for P (P=0.030), Mg^{+2}

(*P*=0.033), K^+ (*P*=0.012) and N (*P*=0.016) while the effect of the species were significant for P (*P*=0.0002), Mg^{+2} (*P*=0.0035) and N (*P*=0.037).

Table 2. Extraction of nutrients ± (E.S) in the three fractions added at Tacuarembó site at the age of 74 months. Note: Different capital letters indicate significant differences between species and different lowercase letters indicate significant differences by means of the Tukey a posteriori test of the ANOVA with a probability level of 5%.

Especie	Planting density (trees ha^{-1})	P	Ca	Mg	K	N
		(Mg ha^{-1})				
E. benthamii	2220	49.4 (9.2) A b	321.9 (34.4) A a	56.5 (4.5) B b	479.9 (111.2) A c	293.6 (14.2) A b
	3330	49.3 (11.0)A b	398.4 (127.1) A a	76.2 (23.2) B b	546.7 (109.5) A bc	352.6 (25.7) A ab
	4440	63.2 (7.3) A ab	570.4 (115.1) A a	104.8 (4.4) B ab	779.2 (74.0) A ab	500.1 (15.8) A a
	6660	85.9 (18.1)A a	627.0 (52.2) A a	120.7 (13.1)B a	804.2 (71.8) A a	625.5 (48.7) A a
E. dunnii	2220	28.8 (3.2) B b	455.7 (88.7) A a	131.7 (10.0)A b	555.9 (42.5) A c	307.5 (13.0) A b
	3330	35.4 (2.7) B b	608.5 (135.0) A a	142.9 (6.3) A b	605.9 (48.1) A bc	339.3 (14.7) A ab
	4440	41.4 (4.4) B ab	536.2 (14.7) A a	197.7 (35.4)A ab	676.4 (98.2) A ab	447.2 (18.6) A a
	6660	57.9 (11.7)B a	941.5 (166.7) A a	295.3 (38.9)A a	830.7 (157.3) A a	481.1 (97.9) A a
E. grandis	2220	31.3 (5.7) C b	455.7 (6.8) A A a	131.7 (2.0) C b	507.4 (76.4) A c	268.7 (9.9) B b
	3330	23.8 (0.7) C b	608.5 (51.5) A a	142.9 (7.3) C b	511.4 (15.4) A bc	276.1 (4.5) B ab
	4440	31.6 (2.9) C ab	536.2 (70.3) A a	197.7 (7.2) C ab	593.7 (56.4) A ab	340.4 (22.2) B a
	6660	30.8 (4.2) C a	368.7 (15.3) A a	295.3 (8.7) C a	649.9 (93.4) A a	317.3 (19.4) B a

Table 3. Extraction of nutrients ± (E.S) in the three fractions added in the site of Paysandú at the age of 75 months. Note: Different capital letters indicate significant differences between species and different lowercase letters indicate significant differences by means of the Tukey a posteriori test of the ANOVA with a probability level of 5%.

Species	Planting density (trees ha^{-1})	P	Ca	Mg	K	N
		(Mg ha^{-1})				
E. benthamii	2220	52.6 (3.7) ab	530.9 (3.4) ab	84.5 (7.3) B a	388.8 (12.9) A ab	343.0 (13.2) A b
	3330	46.7 (12.2) ab	646.7 (157.6) ab	83.0 (22.2) B a	408.4 (192.9) A ab	364.4 (82.9) A ab
	4440	36.7 (7.4) ab	432.1 (15.5) b	61.7 (6.3) B a	338.6 (25.1) A b	262.7 (45.4) A b
	6660	58.6 (6.1) a	840.0 (151.4) a	101.5 (17.1) B a	532.7 (92.3) A a	447.5 (57.7) A a
E. dunnii	2220	34.9 (1.0) ab	711.9 (53.6) ab	165.7 (5.3) A a	513.0 (27.6) A ab	301.6 (22.9) A b
	3330	34.3 (3.5) ab	628.7 (45.5) ab	153.5 (5.7) A a	367.5 (42.1) A ab	308.5 (37.5) A ab
	4440	33.6 (0.9) ab	651.8 (68.9) ab	140.0 (5.2) A a	372.7 (43.5) A b	299.5 (14.4) A b
	6660	59.9 (9.2) a	1126.0 (197.6) a	228.2 (32.4) A a	677.7 (175.9) A a	585.3 (121.7)A a
E. grandis	2220	23.1 (1.9) b	522.1 (38.4) ab	64.8 (2.8) B a	250.3 (91.8) A ab	239.1 (6.4) A b
	3330	38.6 (3.3) ab	771.3 (98.2) ab	120.3 (20.6) B a	480.6 (158.3) A ab	455.6 (71.5) A ab
	4440	35.4 (7.3) ab	710.2 (141.2) ab	94.8 (26.1) B a	396.4 (122.0) A b	358.8 (88.6) A b
	6660	32.4 (1.2) ab	574.7 (85.0) ab	80.0 (9.7) B a	351.0 (51.8) A a	297.1 (37.9) A a

Except for Ca^{+2} it was observed that for the rest of the nutrients there were a positive relationship between the extraction of nutrients and the density of plantation. For P, Mg^{+2}

and N it was obtained that *E. grandis* were the species that has the lowest contents. At Paysandú site the analysis of variance detects a significant effect of the interaction species and planting density for P (*P*=0.025) and Ca^{+2} (*P*=0.039) at the same time that a significant effect of the species for Mg^{+2} (*P*=0.0038) and planting density for K^{+} (*P*=0.0216) and N (*P*=0.037). In this site *E. dunnii* were the species with the highest Mg^{+2} content. The proportion of accumulated weight of each nutrient in each of the fractions in both sites (wood, bark and leaves) were presented in Figures 2 and 3. The analysis of variance at Tacuarembó site detects that there was significant differences between species in the proportions of Mg^{+2} (*P*=0.0381), K^{+} (*P*=0.0301) and Ca^{+2} (*P*=0.0487) in the bark, Mg^{+2} in the leaves (*P*=0.0044) and wood (*P*=0.0425), P in leaves (*P*=0.0073) and N in leaves (*P*=0.0031) and wood (*P*=0.016). The contrasts of means indicate that the lower contents of N and Mg^{+2} in wood and Ca^{+2}, Mg^{+2}, K^{+} and N in wood was obtained with *E. grandis* while the lower contents of P and Mg^{+2} in leaves was in *E. benthamii* (Tables S12 to S14, Supplementary material). At Paysandú site a significant effect of the species on the Mg^{+2} content in the bark were observed (*P*=0.0028), leaves (*P*=0.0012) and wood (*P*=0.0085), of the leaves P (*P*=0.0048) and N in the bark (*P*=0.0045). The interaction had a significant effect for the Ca^{+2} in the bark (*P*=0.0231) and wood (*P*=0.0033), the K in wood (*P*=0.0371) and N in bark (*P*=0.0085). The effect of planting density was only significant for the N in wood (*P*=0.0496). The contrasts of means show in *E. grandis* low Mg^{+2} values in wood and bark and N in cortex while *E. benthamii* showed the low values of P and Mg^{+2} in leaves (Tables S15 to S17, Supplementary material). In both sites there were a significant accumulation of P and K^{+} in wood with average levels of 56%, Ca^{+2} and Mg^{+2} in bark with mean values of 57% and 43%, respectively and N in sheet with 33% levels. The proportion of P and K^{+} in wood were low at Paysandú site (54 vs 59%, 49 vs 64%, respectively) despite the high yield obtained in this site. The proportion of Mg^{+2} in bark on average were high at Tacuarembó site (46 vs 40%).

With the soil availability data of K, Ca and Mg (Table S1, Supplementary material) and the levels of extraction of these nutrients, the number of rotatios necessary to absorb all those nutrients by harvesting the wood plus bark or full tree for the species and densities of plantation ages 75 and 76 months in both sites were estimated (Table 4). Since the nutrient analysis of the branches is not available, the data at 46 months age were used (Bentancor et al., 2019).

Table 4. Number of rotations to absorb the total available K, Ca and Mg with two biomass harvest system at Tacuarembó and Paysandú with harvest ages of 75 and 76 months, respectively.

			Site					
			Tacuarembó			Paysandú		
Species	Planting density (trees ha^{-1})	Component	Nutrients					
			K	Ca	Mg	K	Ca	Mg
E. benthamii	2220	Wood + bark	14	47	40	5	49	97
		Full tree	10	36	34	3	39	76
	3330	Wood + bark	12	40	59	4	39	100
		Full tree	9	33	47	3	35	79
	4440	Wood + bark	9	28	44	8	58	131
		Full tree	6	24	34	5	49	96
	6660	Wood + bark	7	25	37	4	30	81
		Full tree	5	22	30	2	26	61
E. dunnii	2220	Wood + bark	10	35	32	4	36	46
		Full tree	8	30	28	3	31	41
	3330	Wood + bark	10	26	30	5	42	51
		Full tree	7	22	26	3	35	45
	4440	Wood + bark	9	20	22	4	40	57
		Full tree	6	18	19	3	34	47
	6660	Wood + bark	9	13	14	3	26	40
		Full tree	6	12	13	2	19	28
E. grandis	2220	Wood + bark	13	41	101	5	48	142
		Full tree	9	32	59	3	41	98
	3330	Wood + bark	13	37	103	3	35	86
		Full tree	9	29	62	2	28	28
	4440	Wood + bark	11	35	81	4	36	147
		Full tree	7	30	51	3	30	63
	6660	Wood + bark	11	49	84	4	46	119
		Full tree	7	38	53	3	36	69

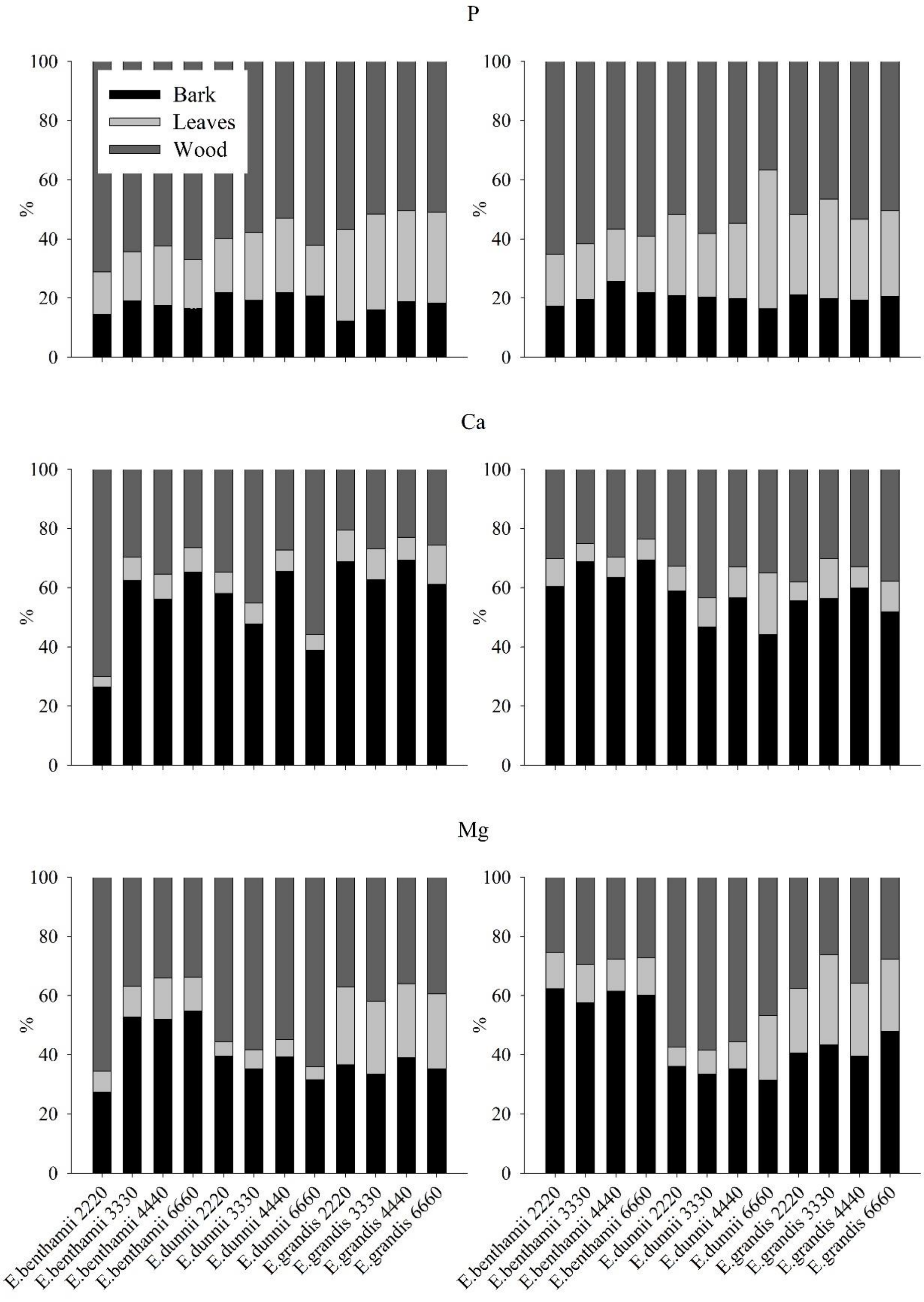


Figure 2. Relative proportion of weight per hectare (%) of P, Ca+2 and Mg of the wood, leafs and bark fractions of the species and planting densities in the Tacuarembó (left) and Paysandú (right) sites at the age of 74 and 76 months, respectively.

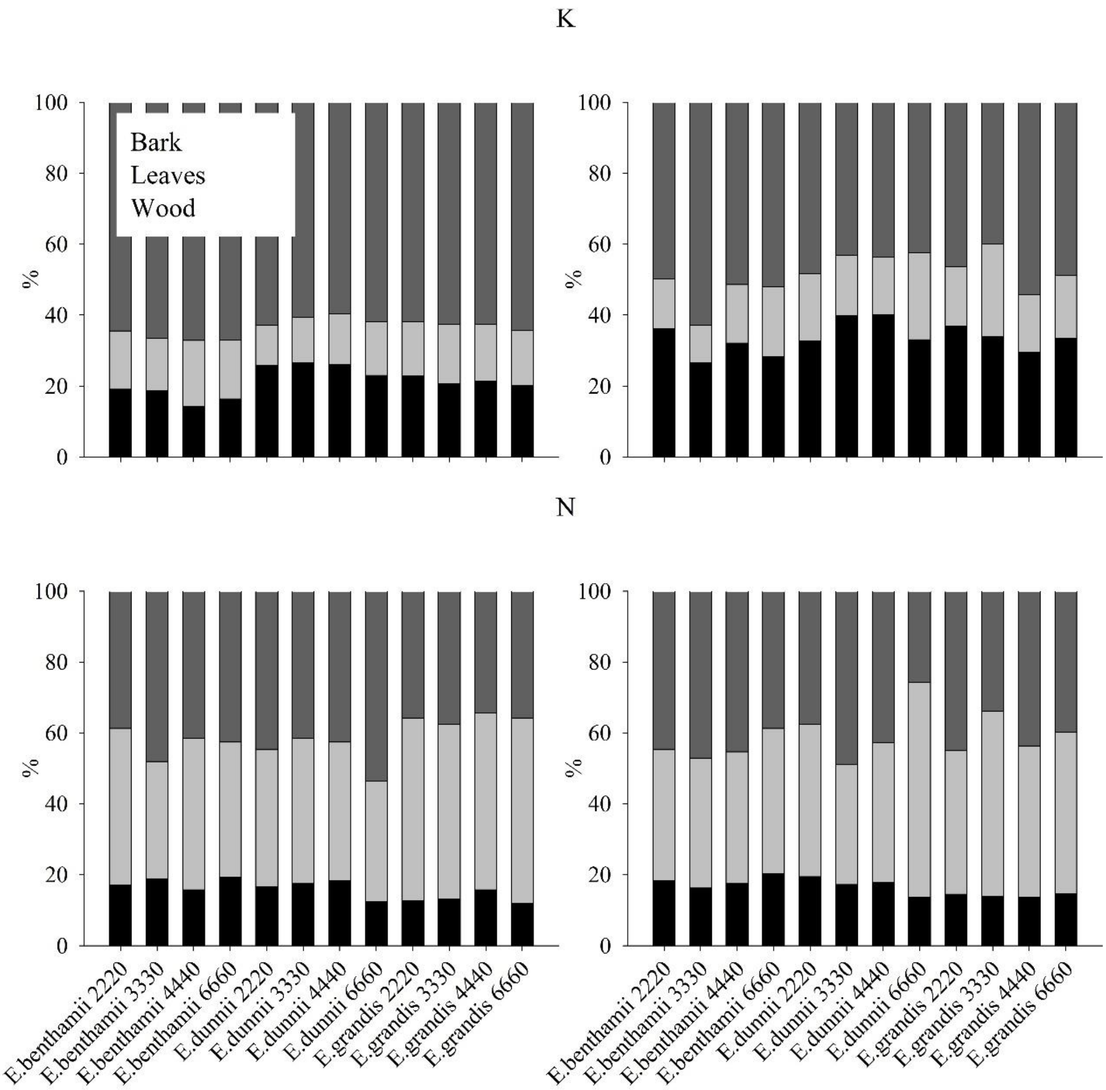


Figure 3. Relative proportion of the weight per hectare (%) of K and N of the wood, leafs and bark fractions of the species and planting densities at the sites Tacuarembó (left) and Paysandú (right) at the age of 74 and 76 months, respectively.

3.3 Nutrients use efficiency

The UE of each species and planting density for the site of Tacuarembó and Paysandú at the age of 75 and 76 months, respectively, were presented in Figures 4 and 5. On the Tacuarembó site, the analysis of variance indicates that there were differences between species for P (*P*=0.0039) and Ca^{+2} (*P*=0.0057), Mg^{+2} (*P*=0.009). The contrasts of means showed that *E. grandis* was the species with the highest UE values for the 3 nutrients mentioned above. At Paysandú site, the analysis of variance detected significant differences between species for Ca^{+2} (*P*=0.0078) and Mg^{+2} (*P*=0.0003). The K^{+} were the only nutrient influenced by planting density (*P*=0.045). The interaction species and planting density has a significant effect on the UE of P (*P*=0.0212). The joint analysis of the two sites shows that a greater UE occurs from the Paysandú site (*P*=0.0247, *P*<0.0001, *P*<0.0001) for the P, K^{+} and N, respectively. The Tacuarembó site obtains a larger UE of Ca^{+2} (*P*=0.0022). The UE of the Mg^{+2} were the same for the two sites (Figure 6). In both sites it was obtained that the efficiency of nutrient utilization was decreasing in the following order: P> Mg^{+2}> N; at Tacuarembó site there was a greater UE of the Ca^{+2} than of the N whereas in the site of Paysandú the occurred an opposite pattern. The simple linear correlation values between the UE of each nutrient and the total biomass production was presented in Table 5. With all the nutrients except for the K^{+} at the Tacuarembó site, a correlation value of zero were obtained between the NUE and the total productivity of biomass. The results of the ANOVA at each site was presented in Table S18 (Supplementary Material). In both sites significant differences were obtained in the UE with the highest and lowest values for P, Mg^{+2} and K^{+}, Ca^{+2}, respectively.

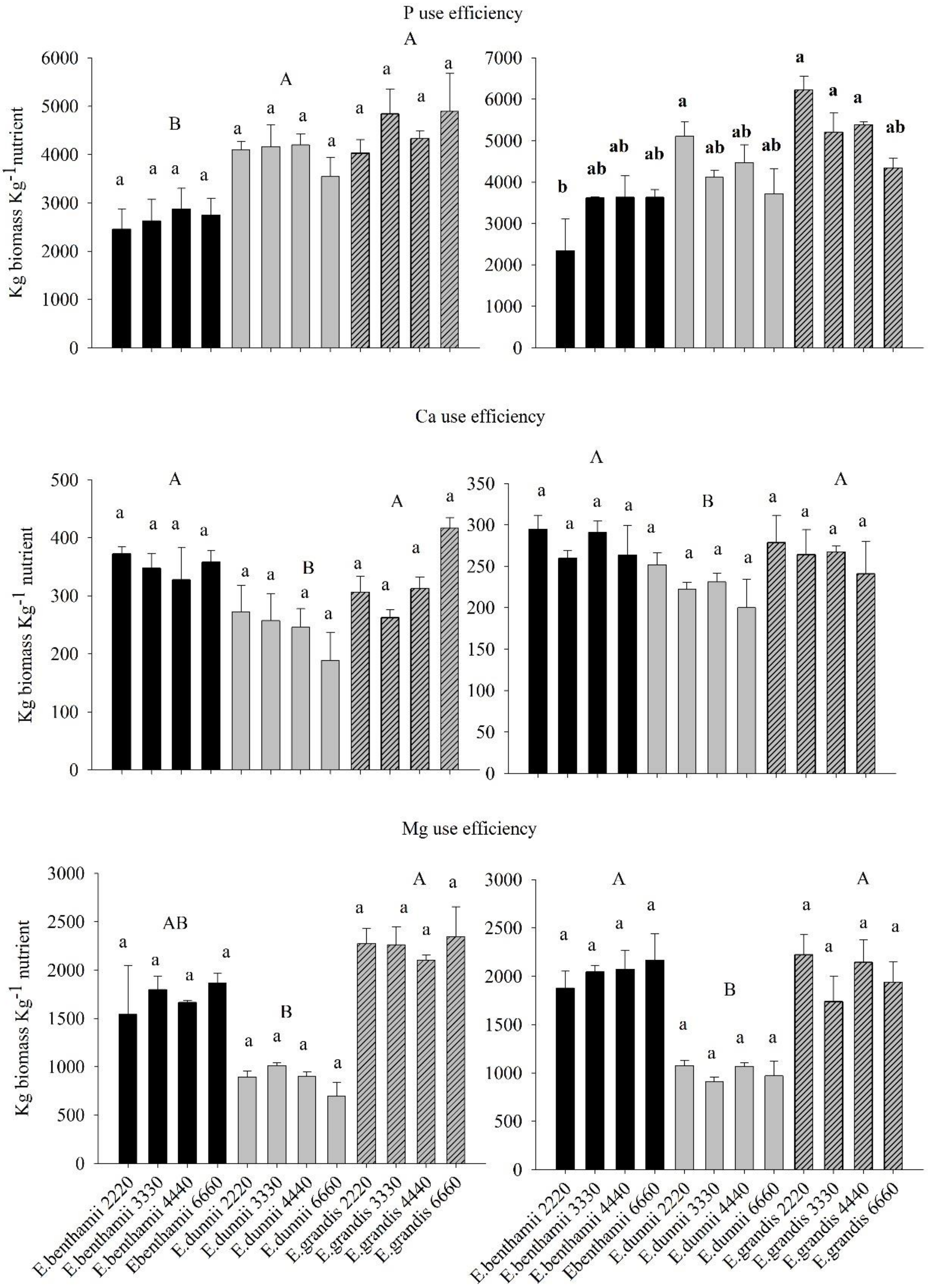


Figure 4. UE of P, Ca+2 and Mg in Tacuarembó (left) and Paysandú (right) at the age of 74 and 76 months, respectively. Different capital letters indicate differences between species and different lowercase letters indicate differences between planting densities according to the Tukey test after the anova with a significance level of 5%. Different letters in bold indicate differences between species and planting densities

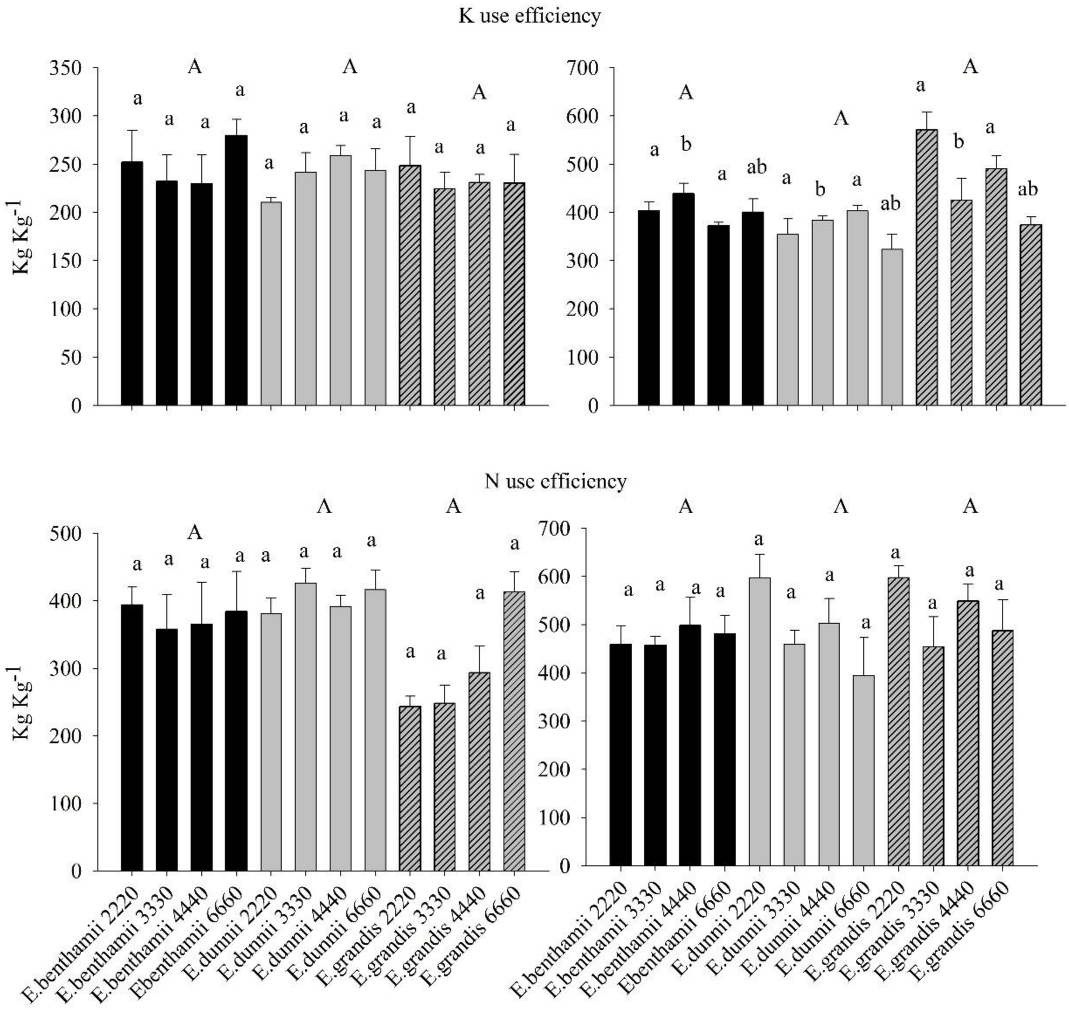


Figure 5. UE of K and N in Tacuarembó (left) and Paysandú (right) at the age of 74 and 76 months, respectively. Different capital letters indicate differences between species and different lowercase letters indicate differences between planting densities according to the Tukey test after the anova with a significance level of 5%.

Table 5. Simple linear correlation values (with the associated probability value) between the UE of each nutrient and the total biomass production in both sites.

	Nutrients									
	P		**Ca**		**Mg**		**K**		**N**	
Sites	r_{PT}	*p-value*	r_{CaT}	*p-value*	r_{MgT}	*p-valor*	r_{KT}	*p-value*	r_{NT}	*p-value*
Tacuarembó	-0.08	0.64	-0.11	0.51	-0.17	0.30	**0.39**	**0.02**	0.01	0.97
Paysandú	0.05	0.76	-0.10	0.54	-0.12	0.47	-0.09	0.61	-0.16	0.36

4. Discussion

4.1 Production of biomass and proportion of tree's fractions

At the Tacuarembó site, the highest total biomass productivity was obtained with *E. benthamii* and *E. dunnii* (173.3 and 174.1 Mg ha^{-1}, respectively) (Table 1). Wood production was higher for these species (134.3 and 132.8 Mg ha^{-1}, respectively) compared with *E. grandis* (109.1 Mg ha^{-1}), although this difference was not significant. The weight of the bark had a behavior similar to that of the wood at the same time that the weight of the leaves was very similar between species. With the wood, bark and total biomass tree's fractions it was obtained that the highest weight values were associated with the highest planting densities. The weight of the leaves was the same for the different planting densities. The highest level of wood production with bark and total biomass was obtained with *E. benthamii* at the density of 6660 trees ha^{-1} (215.4 and 223.2 Mg ha^{-1}, respectively). The average increase in wood and bark productivity of the extreme planting densities (6660 vs. 2220 trees ha^{-1}) were 62%, that of the total biomass were 57% and that of the leaves were 50%. The increase in biomass productivity in relation to the increase in plant density has been widely reported for eucalyptus species (Bernardo et al., 1998, Caron et al., 2015, Eufrade Junior et al., 2016). The reduction in spacing determines that the weight loss that occurs in the tree at the individual level were compensated in greater proportion by the increase in plant density (Goulart et al., 2003, Rocha, 2011, Navarro et al., 2016). The proportion of the weight per hectare of wood and leaves was very similar for the species and densities of plantation with an average value of 77 and 4%, respectively. Branches were the only fraction affected by the spacing, determining that the highest values correspond to the lowest planting densities. *E. benthamii* and *E. dunii* have the highest values of bark proportion (12%). Similar values of proportions of the different tree's fractions were obtained by Schumacher et al., (2011) evaluating eucalyptus species at the age of 6 years and with a planting density similar to those of this study. The reduced effect of spacing on the biomass tree's fractions was also verified by several authors evaluating eucalyptus species with high planting densities (Albaugh et al., 2017; Eufrade Junior et al., 2016). Values of proportions have also been reported similar tree's fractions with planting densities of 2200, 1800 and 1300 trees per hectare, with ages comparable to those of the present experiment (Santana et al., 1999, Ladeira et al., 2001, Salvador et al., 2016). At Paysandú site an important similarity was observed in the total biomass values of the different species and planting densities. The highest values are reached with *E. dunnii* at 6660 trees per hectare (235.3 Mg ha^{-1}), but no significant differences were detected with the rest of the species and planting densities. The productivity of wood, leaves and branches were also the same for all the combinations evaluated. The weight of the bark does not show a definite relationship with the density of plantation. These results confirm those reported by Bentancor et al., (2019) in this same experiment at the age of 49 months. Similar results evaluating high planting densities (5000 to 15000 trees per hectare) were also reported by Rodríguez et al., (2013) and Albaugh et al., (2017) evaluating *E. globulus* although at a younger age than this our study. The proportions of the weight of the different tree's fractions maintain the same tendency as that registered at Tacuarembó site in the sense that the bark was the only fraction affected by the type of species. The highest values correspond to *E. benthamii* and *E. dunnii* with 13 and 12%, respectively. The similarity in the values of total biomass production between the different planting densities indicates that it was possible to reach high levels of this variable with low planting densities, which would imply a reduction in the costs of installation of the crop. The values of the proportions of weight obtained in both experiments was the reflection of the short age of the trees which was different from those reported with eucalyptus species at older (Gama-Rodriguez and de Barros, 2002). According to Silva et al., (2004) and Gonçalves et al., (2005) in the stage of growth after the closing of the canopy, an accumulation of biomass begins to occur mainly in the shaft of the trees, which determines the greater weight relative to this fraction in relation to the total biomass.

4.2 Nutrient contents

The results of the nutrient contents obtained in the different tree's fractions in general confirm the hypothesis that the concentrations of the different nutrients were very similar for all the planting densities evaluated in both sites (Tables S2-S7, Supplementary material). At Tacuarembó site, the effect of the species was significant for the P, K^+ and Mg^{+2} in the bark, Mg^{+2} in the leaves and P, Ca^{+2}, Mg^{+2} and N in wood. In all cases the highest values are registered with *E. benthamii* and *E. dunnii* except the K^+ in the bark where *E. grandis* has the highest value. The average values P obtained are: 0.04, 0.16 and 0.021%; of Ca^{+2} 1.66, 0.73 and 0.15%; of Mg^{+2} 0.22, 0.20 and 0.05%; of K^+ 0.72, 1.61

and 0.32%; of N 0.32, 2.68 and 0.13%, in bark, leaves and wood, respectively. This determines that the leaves contain the highest proportion of P, K^+ and N while the bark has a high content of Ca^{+2} and Mg^{+2}. The wood was the one that contains the lowest levels of all the nutrients. Results obtained by Ualde (2015) evaluating *E. globulus* of 8 years old also confirm the results obtained in this experiment. On average for the species and densities of plantation the content of nutrients of the leaves were 8 and 2 times higher than wood and the bark. The contents obtained in this experiment was within the expected range, although with some deviations, with eucalyptus species with densities and age similar to those of this experiment (Leite et al., 2011; Sochacki et al., 2012; Salvador et al., 2016). As expected, according to the literature results on average, the concentration of Ca^{+2} and Mg^{+2} in the fractions of the tree has the following decreasing order: Bark> leaves> wood while for the P, K^+ and N the order is: leaves > bark> wood (Schumacher y Poggiani, 1993; Laclau et al., 2000; González-García et al., 2015). At Paysandú site the effect of the species was significant only for the content of Mg^{+2} in leaves and Ca^{+2} in bark. *E. grandis* and *E. dunnii* was the species with the highest values of the nutrients and tree's fractions mentioned. The average values for the species and planting densities of P are: 0.04, 0.15 and 0.02%; of Ca^{+2} 1.83, 0.89 and 0.16%; Mg^{+2} 0.23, 0.24 and 0.03%; of K^+ 0.98, 1.57 and 0.21%; of N 0.27, 2.16 and 0.10%, in bark, leaves and wood, respectively. These contents were similar to those recorded on the Tacuarembó site, probably explained by the similarity in the chemical composition of both types of soils, although a statistical analysis confirming it was not carried out. In this site the tendency was maintained that the Ca^{+2} concentrates to a greater extent in the bark and the P, K^+ and N in the leaves. Mg^{+2} were in similar proportions in the bark and leaves. This accumulation of nutrients in the different fractions of the tree has been widely reported in the literature with species of Eucalyptus at different ages (Hernández et al., 2009, Guimaraes et al., 2015, González-García et al., 2015; Eufrade Junior et al., 2016, Albaugh et al., 2017). The ratio in the average content of all the nutrients of the leaves compared with wood and bark was 9 and 1.5 times, respectively.

4.3 Extraction of nutrients

The extraction of nutrients in all tree's fractions, the results obtained allow accepting the hypothesis that the species and density of plantation affect this parameter. At the Tacuarembó site, the highest quantities of P, Mg^{+2} and N was produced with *E. benthamii* (62, 102 and 443 kg ha^{-1}, respectively) and *E. dunnii* (41, 192 and 394 kg ha^{-1}, respectively) (Table 2). The levels of Ca^{+2} and K^{+} was the same for all species. According to Dovey, (2009) *E. dunnii* exports more major nutrients than *E. grandis* although this depends on several factors acting together. The extraction of nutrients (except for Ca^{+2}) were positively associated with planting density. The nutrient extraction ranges in the total biomass of the extreme planting densities (2220 vs. 6660 trees ha^{-1}) were: 36 to 58 kg ha^{-1}, 558 to 658 kg ha^{-1}, 97 to 160 kg ha^{-1}, 514 to 762 kg ha^{-1} and 290 to 475 kg ha^{-1}, for P, Ca^{+2}, Mg^{+2}, K^{+} and N, respectively. The extraction increases in percentage for the extreme densities (2220 vs 6660 trees ha^{-1}) was 60, 64, 48 and 64% for P, Mg^{+2}, K^{+} and N, respectively. The harvest of only the wood would imply a significant reduction in the levels of extraction of nutrients. For the planting densities mentioned, this reduction on average would be: 37, 55, 46, 36 and 58% for P, Ca^{+2}, Mg^{+2}, K^{+} and N, respectively. The convenience of leaving the leaves and bark fractions in the field has also been confirmed by Silva et al., (1983), Faria et al., (2008) and Eufrade Junior et al., (2016). The proportion of weight per hectare of nutrients was variable in each of the tree's fractions evaluated and were affected only by the species (Figures 2 and 3, Tables S12 to S14, Supplementary material). In general, was observed that P were concentrated in wood, Ca^{+2} in the bark, Mg^{+2} in bark and wood, K^{+} in wood and N in wood and leaves. Similar relationships were also reported by (Bargali and Singh, 1991, Gama-Rodrigues and de Barros, 2002, González, 2008) with eucalyptus species. In wood, the average proportions of P, Ca^{+2} and K^{+} were: 59, 32 and 63%, respectively. The proportion of Mg^{+2} was 30, 59 and 39% and that of N was: 44, 45 and 36% for *E. benthamii*, *E. dunnii* and *E. grandis*, respectively. The significantly higher values of N were obtained with *E. benthamii* and *E. dunnii* while that of Mg^{+2} with *E. dunnii*. In the cortex fraction the values of Ca^{+2}(58, 54 and 65%), Mg^{+2} (49, 36 and 36%), K^{+} (17, 25 and 22%) and N (18, 16 and 13%) were obtained with *E. benthamii*, *E. dunnii* and *E. grandis*, respectively. The average value for P was 18%. In the leaves fraction the values of P (16, 21 and 32%) and Mg^{+2} (12, 6 and 25%) correspond to *E. benthamii*, *E. dunnii* and *E. grandis*, respectively. For P these last two species have the values significantly higher while for Mg^{+2} the highest value was obtained with *E. grandis*. The mean values of Ca, K^{+} and N were 9, 15 and 42%, respectively. The absence of the effect of planting density on the proportions of nutrients in different tree's fractions was also verified by Albaugh et al. (2017) evaluating *E. globulus* with 5000 and 15000 trees ha^{-1}. At Paysandú site the highest Mg^{+2} extraction was obtained with *E. dunnii* (171.8 kg ha^{-1}) (Table 3). In this site a positive relation was observed for the extraction of K^{+} (529, 675, 521 and 734 kg ha^{-1}) and N (295, 376, 307, 443 kg ha^{-1}) for the densities of 2220, 3330, 4440 and 6660 trees ha^{-1}, respectively. The extraction increases for extreme planting densities (6660 vs. 2220 trees ha^{-1}) of these two nutrients was 39 and 50%, respectively. The use of the wood would imply a greater reduction in the levels of extraction of nutrients compared to Tacuarembó site. For the planting densities mentioned, this reduction on average would be: 47, 67, 59, 52 and 62% for P, Ca^{+2}, Mg^{+2}, K^{+} and N, respectively. The major extraction of nutrients increased with the population according to reported by Leite et al., (1998); Santana et al., (1999); Eufrade Junior et al., (2016), evaluating species of Eucalyptus to the extent that there was also an increase in biomass production explained by planting density. This determines that eucalyptus plantations with populations close to 1000 trees per hectare in general have lower levels of extraction of nutrients than those recorded our study (González, 2008, Hernandez et al., 2009, Ualde, 2015). With the P and Ca^{+2} a significative effect of the species interaction and planting density was observed showing that the highest levels of extraction occur with the lowest spacings. The proportion of the weight per hectare of the nutrients presents greater variation than in the previous site since there were a greater effect of the density of plantation and its interaction with the species (Figures 2 and 3, Tables S15 to S17, Supplementary Material). In this site it was also observed that in wood a high concentration of P, Mg^{+2}, K^{+} and N occurs, while the bark accumulates in higher average the Ca^{+2} and in the leaves a high proportion of K^{+}. In *E. dunnii* wood was recorded the higher proportion (55%) and N linked to planting density (42, 44, 44 and 36% for 2220, 3330, 4440 and 6660 trees ha^{-1}, respectively). In the cortex fraction, the proportion of the highest values of Mg^{+2} and N correspond to *E. benthamii* (61%) and *E. benthamii* and *E. dunnii* N (18 and 18%), respectively. The proportion of Ca^{+2} depends on the density of plantation without having a defined pattern of variation. In the leaves fraction, the highest values of P and Mg^{+2} correspond to *E. grandis* and *E. dunnii* N (30 and 28%) and *E. grandis* (25%), respectively.

The K availability is the one that emerges as the first limitation for growth in all species and planting densities in both sites compared to Ca and Mg (Table 5). The different evolution of K in both sites is due to the differences in productivity and availability of this nutrient in the two soil types (Table S1, Supplementary material). The relationship between the nutrient extracted versus available in soil of Ca and Mg shows that there would be no restrictions on these in the long term. Harvesting the wood and bark fractions implies a lower extraction and therefore a greater availability of these nutrients in the future compared to the total biomass of the tree.

4.4 Nutrient use efficiency

The UE of the use of nutrients at Tacuarembó site were not affected by the density of plantation (Figures 4 and 5). According to Santana et al., (2000 and 2002), the UE basically depends on the type of genetic material, soil nutrient limitations and water availability. The highest values are obtained with P in *E. grandis* and *E. dunii* and Mg^{+2} in *E. grandis* and *E. benthamii*. The lowest values of UE were registered with the K^{+} and Ca^{+2} and with very similar values for the first of both in all the esecies. The highest UE values of Ca^{+2} was obtained with *E. grandis* and *E. benthamii*. The low UE of Ca^{+2} were due to its high concentration in the bark of these eucalyptus species (Hernandez et al., 2009) added to its low mobility in the phloem (Caldeira et al., 2002). According to this same author the N has a relatively low UE and similar to that of the Ca^{+2} due to the high content in the green leaves and to the internal retroslation. It has also been determined that the low UE were associated with the high availability of the nutrient in the soil (Morais et al., 1990) at the same time that a low content of nutrients in the different tree's fractions could be a reflection of nutritional deficiencies (Caradus, 1992). However, Lambert and Turner (2016), determined that the UE and the nutritional status in some cases behave as independent parameters although these same authors in another study verified that this relationship were variable depending on the nutrient considered (Turner and Lambert, 2014). Similar to that reported by Santana et al., (2002), no relationship between biomass productivity and UE of nutrients were detected in this site except for the case of K^{+} (Table 4). The values obtained with all the nutrients was similar to those reported by Morais et al, (1990); and Laclau et al., (2000) in eucalyptus species with 7 years of age. At Paysandú site, similar results were obtained in that the P and Mg^{+2} reach the highest values, followed by N, Ca^{+2} and the K^{+} with the lowest value (Figures 4 and 5). The UE ranking of these nutrients was also verified by (Melo et al., 1995, Faria et al., 2008) evaluating Ecualyptus species. In turn it was observed that *E. grandis* and *E. benthamii* was the most efficient species with the use of Ca^{+2} and Mg^{+2} although with higher levels of the first of both compared with Tacuarembó site. In this site the UE of P were affected by the combination of the species and density of plantation although with very similar values in all cases. The UE of the use of the N were the same for all the evaluated combinations, whereas the one of the K^{+} were affected by the plantation density but without showing a defined pattern of variation. The high UE in the nutrient use of *E. grandis* were also reported by Silva et al. (1983) evaluating several eucalypt spies at planting densities of 1333 trees per hectare at the age of 10 years. As at Tacuarembó site, in this case there were a very low relation between the total biomass productivity and the UE of the different nutrients (Table 4). This lack of relationship between the two parameters were consistent with the results obtained by Santana et al. (2002) evaluating *E. grandis* and *E. saligna* at 78 months of age. The analysis of the UE for the two sites shows that in Paysandú there were a greater UE in the use of P, K^{+} and N and, on the contrary, in the case of Ca^{+2}(Figure 6). Considering the two sites together, it was observed that the higher average productivity of the Pasyandú site were accompanied by a higher UE in the use of the three nutrients mentioned above. Also, on this site it was possible to achieve higher productivity with similar levels of Mg^{+2} utilization. The higher productivity of this site was basically explained by the higher survival achieved by the three species (Chapter 1) due to better weed control in the early stages of growth. The availability of nutrients and the precipitation regime of both sites would not be explaining the differences registered between both sites. The combination of high UE and total bimoasa productivity of *E. benthamii* would be an indication of the lower relative rate of extraction of nutrients in proportion to the biomass produced (Zaia and Gama-Rodriguez, 2004, Rosim et al., 2016).

5. Conclusions

The results obtained confirm the hypothesis that the nutrients concentration does not depend on the species or planting density and that these parameters affect the extraction of nutrients. In both sites the production of total biomass was the same for all species while in Tacuarembó a close relationship between this parameter and the planting density were obtained. The same behavior was observed with the production of wood at the same time as a total independence between the production of branches and leaves with the species and densities of plantation. In the same way, the proportions of weight of the different tree's fractions of the tree was not affected by the species and spacings in both sites. The concentration of the different nutrients remains unchanged for all planting densities in each of the tree's fractions evaluated from both sites. The effect of the species in contrast shows differences between them for the nutrients in the different tree's fractions. Leaves and wood contained the highest and lowest levels of nutrients, respectively, being the ratio between both of 9 to 1. The nutrients Ca^{+2} and Mg^{+2} was concentrated in the bark while the P, K^{+} and N in the bark. The amounts of nutrients extracted in the total biomass show a close relationship with the density of plantation in both sites except for Ca^{+2} and Mg^{+2} in Tacuarembó and Paysandú, respectively. The use of a plantation density of 6660 trees ha^{-1} determines increases in the levels of extraction of nutrients of the order of 40 to 60% compared with 2220 trees ha^{-1}. The use of only the wood fraction would allow similar levels of reduction in the extraction of nutrients and therefore a more sustainable use of the soil in the long term. In Tacuarembó the highest extractions of P, Mg^{+2} and N were obtained with *E. benthamii* and *E. dunnii* associated with the higher productivity reached by these species. In Paysandú the highest level of extraction were obtained with *E. dunnii* for the case of Mg^{+2}. The highest UE values of nutrient utilization were obtained with P and Mg^{+2} at both sites. *E. grandis* were the species that shows the highest values for P, Ca^{+2} and Mg^{+2} while plant density has a reduced effect on the UE. In both sites there were a lack of relationship between the biomass productivity levels and the UE.

6. References

Achat, D. L., C. Deleuze; G. Landmann; N. Pousse; J. Ranger; L. Augusto. 2015. Quantifying consequences of removing harvesting residues on forest soils and tree growth - a meta-analysis. Elsevier. Forest Ecology and Management 348: 1241–41.

Albaugh, T.J.; R.A. Rubilar; C. A. Maier; E. A. Acuña; R. L. Cook. 2017. Biomass and nutrient mass of *Acacia dealbata* and *Eucalyptus globulus* bioenergy plantations. Biomass and Bioenergy 97: 162–171.

Andrade, T.C.G.R.; N.F. D. Barros; L.E. Dias; M.I.R. Azevedo. 2013. Biomass yield and calorific value of six clonal stands of *Eucalyptus urophylla* s. t. Blake cultivated in northeastern Brazil. Cerne 19 (3): 467–472.

Bargali, S.; S. Singh. 1991. Aspects of productivity and nutrient cycling in a 8-year-old Eucalyptus plantation in a moist plain area adjacent to Central Himalaya, India. Canadian Journal of Forest Research 21: 1365–1372.

Barrow, N.J. 1978. Problems of efficient fertilizer use. In International Colloquium on Plant Analysis and Fertilizer Problems, 37–52. Auckland, New Zealand.

Bellote, A.F.J.; J. R. Sarruge; H. P. Haag; G. D. D. Oliveira. 1980. Extração e exportação de nutrientes pelo *Eucalyptus grandis* Hill Ex-Maiden em função da idade: 1 - Macronutrientes. Ipef 20: 1–23.

Bentancor, L., J. Hernández; A. del Pino; A. Califra; F. Resquín; P. González-Barrios. 2019. Biomass and Bioenergy Evaluation of the biomass production, energy yield and nutrient removal of *Eucalyptus dunnii* Maiden grown in short rotation coppice under two initial planting densities and harvest systems. Elsevier Ltd. Biomass and Bioenergy. 122:165–174.

Benton, J.; B. Wolf; H.A. Mills. 1985. Plant analysis handbook. A practical sampling, preparation, analysis and interpretation guide.

Bernardo, A.L.; M.G. F. Reis; G.G. Reis; R.B. Harrison; D. J. Firme. 1998. Effect of spacing on growth and biomass distribution in *Eucalyptus camaldulensis*, *E. pellita* and *E. urophylla* Plantations in southeastern Brazil. Forest Ecology and Management 104: 1–13.

Chapter 6. Evaluation of the nutrient content in biomass of Eucalyptus species from short rotation plantations in Uruguay

Binkley, D.; J. L. Stape; M. G. Ryan; H. R. Barnard; J. Fownes. 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. Ecosystems 5 (1): 58–67.

Binkley, D.; J.L. Stape; W.L. Bauerle; M.G. Ryan. 2010. Explaining growth of individual trees: light interception and efficiency of light use by Eucalyptus at four sites in Brazil. Forest Ecology and Management 259 (9): 1704–1713.

Bouillet, J. P.; J. P. Laclau; J. L.M. Gonçalves; M. Z. Moreira; P. C.O. Trivelin; C. Jourdan; E. V. Silva; M. C. Piccolo; S. M. Tsai; A. Galiana. 2008. Mixed-species plantations of *Acacia mangium* and *Eucalyptus grandis* in Brazil. 2: nitrogen accumulation in the stands and biological N2 fixation. Forest Ecology and Management 255 (12): 3918–3930.

Bouvet, A.; N. Nguyen-The; F. Melun. 2013. Nutrient concentration and allometric models for hybrid Eucalyptus planted in France. Annals of Forest Science 70 (3): 251–260.

Caldeira, M.V.W.; R.M.R. Neto; M.V. Schumacher. 2002. Avaliação da eficiência nutricional de três procedências australianas de Acácia-Negra (*Acacia mearnsii* de Wild.). Árvore 26 (5): 615–620.

Camargo, M.L. P. de; C. B. de Moraes; E. S. Mori; I. A. Guerrini; E.J. de Mello; S. Oda. 2004. Considerações sobre eficiência nutricional em Eucalyptus. Científica 32 (2): 191–196.

Caradus, J. R. 1992. Heritability of, and relationships between phosphorus and nitrogen concentration in shoot, stolon and root of white clover (*Trifolium repens* L.). Plant and Soil 146 (1–2): 209–217.

Caron, B. O.; E. Eloy; V. Q. D. Souza; D. Schmidt; R. Balbinot; A. Behling; G. C. Monteiro. 2015. Quantificação da biomassa florestal em plantios de curta rotação com diferentes espaçamentos quantification of forest biomass in short rotation plantations with different spacings. Comunicata Scientiae 6(1): 106-112.

Corrêa, R.S.; M.V. Schumacher; D.R. Momolli. 2013. Deposição de serapilheira e macronutrientes em povoamento de *Eucalyptus dunnii* Maiden sobre pastagem natural degradada no bioma Pampa. Scientia Forestalis/Forest Sciences 41 (97): 65–74.

da Silva, F.C. 2009. Manual de Análises químicas de solos, plantas e fertilizantes. In Embrapa Informação Tecnológica, 370.

Dovey, S. B. 2009. Estimating biomass and macronutrient content of some commercially important plantation species in South Africa. Southern Forests 71 (3): 245–251.

Dovey, S. B. 2012. Effects of clear felling and residue management on nutrient pools, productivity and sustainability in a clonal eucalypt stand in South Africa. PhD´s Thesis. Faculty of AgriSciences. University of Stellenbosch.South Africa. 248 p.

Ericsson, T. 1994. Nutrient dynamics and requirements of forest crops. New Zealand Journal of Forestry Science 24 (2/3): 133–68.

Eufrade Junior, H. J.; R. X. de Melo; M. M.P. Sartori; S.P. S. Guerra; A.W. Ballarin. 2016. Sustainable use of eucalypt biomass grown on short rotation coppice for bioenergy. Biomass and Bioenergy 90: 15–21.

Faria, G. E. D., N.F. D. Barros; V. L. P. Cunha; I. S. Martins; R.D. C. C. Martins. 2008. Avaliação da produtividade, conteúdo e eficiência de utilização de nutrientes em genótipos de *Eucalyptus Spp*. no Vale Do Jequitinhonha, MG. Ciencia Florestal 18 (3): 369–79.

Gama-Rodrigues, A.C.; N.F. Barros. 2002. Ciclagem de nutrientes em floresta natural e em plantios de Eucalipto e de Dandá no sudeste da Bahia, Brasil. Revista Árvore 26: 193–207.

Grove, T.S.; B.D. Thomson; N. Malajczuk. 1996 Nutritional physiology of Eucalyptus: uptake, distribution and utilization. pp. 77-108. En: Attiweill, P.M. 1996. Nutrition of Eucalyptus. CSIRO 440 p.

Guimaraes, C.C.; M.V. Schumacher; R. Witshoreck; H.P. Souza; J. C. Santo. 2015. Biomassa e nutrientes em povoamento de *Eucalyptus dunnii* Maiden no Pampa Gaucho. Revista Árvore 39 (5): 873–882.

Gonçalves, J. L. D. M.; J. L. Stape; V. Benedetti; V.A. Fessel; J.L. Gava. 2005. Reflexos do cultivo mínimo e intensivo do solo em sua fertilidade e na nutricao das árvores. In: Nutricao e Fertilizacao Florestal. Piracicaba, Brazil: IPEF.

González-García, M.; A. Hevia; J. Majada; F. Rubiera; M. Barrio-Anta. 2015. Nutritional, carbon and energy evaluation of *Eucalyptus nitens* short rotation bioenergy plantations in northwestern Spain. IForest - Biogeosciences and Forestry 9: 3033–10.

González, D.A. 2008. Extracción y reciclaje de nutrientes por cosecha de *Eucalyptus globulus* y *Eucalyptus maidenii*. Tesis de Maestría. Universidad de la República. Facultad de Agronomía, Montevideo, Uruguay. 57 p.

Goulart, M.; C. R. Haselein; J. M. Hoppe; J. A. Farias; D. T. Pauleski. 2003.Massa específica básica e massa seca de madeira de *Eucalyptus grandis* sob o efeito do espaçamento de plantio e da posição axial no tronco. Ciência Florestal, Santa Maria. 13 (2): 167–175.

Hernández, J.; A.del Pino; L. Salvo; G. Arrarte. 2009. Nutrient export and harvest residue decomposition patterns of a *Eucalyptus dunnii* Maiden plantation in temperate climate of Uruguay. Forest Ecology and Management 258 (2): 92–99.

INUMET. 2018. https://www.inumet.gub.uy/clima/estadisticas-climatologicas

Laclau, J.P.; J. P. Bouillet; J. Ranger. 2000. Dynamics of biomass and nutrient accumulation in a clonal plantation of Eucalyptus in Congo. Forest Ecology and Management 128 (3): 181–196.

Ladeira, B.C.; G.G. dos Reis; M.G. F. Reis; N.F. de Barros. 2001. Producao de biomassa de eucalipto sob tres espacamentos em uma sequencia de idade. Árvore 25 (1): 69–78.

Lambert, M.; J. Turner. 2016. Nutrient cycling in a New South Wales subtropical rainforest: organic matter and phosphorus. Australian Journal of Botany 64: 100–110.

Leite, F.P.; N.F. Barros; R.F. Novais; A.S. Fabres. 1998. Seção IV - Fertilidade do solo e nutrição de plantas. acúmulo e distribuição de nutrientes em *Eucalyptus grandis* sob diferentes densidades populacionais. Revista Brasileira de Ciencia Do Solo 22 (3): 419–26.

Leite, F.P.; I. Ribeiro Silva; R. F. Novais; N. F. D. Barros; J.C.L. Neves; E. M. de A. Villani. 2011. Nutrient relations during a Eucalyptus cycle at different population densities. Revista Brasileira de Ciência Do Solo 35 (3): 949–959.

Leles, P. S. D. S.; G. G. D. Reis; M. D. G. F. Reis; E. J. D. Morais. 2001. Crescimento, produção e alocação de matéria seca de *Eucalyptus camaldulensis* e *E. pellita* sob diferentes espaçamentos na região de Cerrado, MG. Scientia Forestalis 59: 77–87.

Loneragan, J.F. 1968. Nutrient requiremnts of plants. Nature 220: 1307–1308.

Ludvichak, A. A.; M. V. Schumacher; G. Dick; D. R. Momolli; H.P.D. Souza; C. D. C. Guimarães. 2016. Nutrient return through litterfall in a *Eucalyptus dunnii* Maiden stand in sandy soil. Revista Árvore 40 (6): 1041–1048.

Melo, V. D. F.; R. F. D. Novais; N. F. D. Barros; M. P. F. Fontes; L. M. D. Costa. 1995. Balanço nutricional, eficiência de utilização e avaliação da fertilidade do solo em P, K, Ca e Mg em plantios de eucalipto no Rio Grande Do Sul. Ipef 48/49: 8–17.

Merino, A.; M. A. Balboa; R. R. Soalleiro; J. G.Á. González. 2005. Nutrient exports under different harvesting regimes in fast-growing forest plantations in southern Europe. Forest Ecology and Management 207 (3): 325–339.

Meullemiestre, A. 2014. Valorisation des déchets de la filière 'bois' en deux étapes: isolation des molécules extractibles puis fabrication de charbon actif: cas du pin maritime. PhD´s Thesis. Université de La Rochelle. Français. 244 p.

MGAP. 1976. Carta de Reconocimiento de suelos del Uruguay a escala 1/1000.000 y clasificación de suelos del Uruguay. Montevideo, Uruguay.

Morais, E.J.; N.F. Barros; R.F. Novais; R.M. Brandi. 1990. Biomassa e eficiência nutricional de espécies de eucalipto em duas regiões bioclimáticas de Minas Gerias. Revista Brasileira de Ciencia Do Solo 14: 353–362.

Navarro, A.; A. M. Stellacci; P. Campi; C. Vitti; F. Modugno; M. Mastrorilli. 2016. Feasibility of SRC species for growing in mediterranean conditions. Bioenergy Research 9 (1): 208–223.

Pallarés, O.R.; E.J. Berreta; G.E. Maraschin. 2005. The South American Campos ecosystem. In Grasslands of the World. FAO, 171–219.

Poggiani, F. 1980. Florestas para fins energéticos e ciclagem de nutrientes. IPEF - Série Técnica 1 (2): 1–11.

Poggiani, F., H.T.Z. Couto; W.S. Suiter Filho. 1983. Biomass and nutrient estimates in short rotation intensively cultured plantation of *Eucalyptus grandis*. Revista Do Ipef 23 (23): 29–36.

R Core Team. 2012. R: A Language and environment for statistical computing. Viena, Austria: R Foundation for Statistical Computing.

Rocha, M.F.V. 2011. Influecia do espacamento e da idade nas produtividades e propiedades da madeira de *Eucalyptus grandis* x *Eucalyptus camaldulensis* para energía. Tese de Mestrado. Universidade Federal de Vicosa - MG, Brasil.86 p.

Rodríguez, A.; J. Cancino; E. Acuña; R. Rubilar; F. Muñoz. 2013. Evaluación del crecimiento de plantaciones dendroenergéticas de *Eucalyptus globulus*, según densidad de plantación y turno de rotación en suelos contrastantes de la región del Bio Bio, Chile. Ciencia e Investigación Forestal INFOR 19 (1): 7–13.

Rosim, C. C.; T. Y. Hsing; R. C. de Paula. 2016. Nutrient use efficiency in interspecific hybrids of eucalypt. Revista Ciência Agronômica 47 (3): 540–547.

Safou-Matondo, R.; P. Deleporte; J. P. Laclau; J. P. Bouillet. 2005. Hybrid and clonal variability of nutrient content and nutrient use efficiency in Eucalyptus stands in Congo. Forest Ecology and Management 210 (1–3): 193–204.

Salvador, S. M.; M.V. Schumacher; M. Viera. 2016. Biomassa e estoque de nutrientes em plantios clonais de *Eucalyptus saligna* Smith. em diferentes idades. Scientia Forestalis 44 (110): 311–321.

Santana, R.; N.F. D. Barros; J. C., J.C.L. Neves. 2002. Eficiência de utilização de nutrientes e sustentabilidade da produção em procedências de eucalyptus grandis e eucalyptus saligna Em Sítios Florestais Do Estado de São Paulo. Revista Árvore 26 (4): 447–457.

Santana, C.R.; N.F. D. Barros; R.F. Novais; H. G. Leite; N. B. Comerford. 2008. Alocação de nutrientes em plantios de eucalipto no Brasil. Sociedade Brasileira de Ciência Do Solo 32: 2723–2733.

Santana, R. C.; N.F. Barros; N. B. Comerford. 2000. Above-ground biomass, nutrient content, and nutrient use efficiency of eucalypt plantations growing in different sites in Brazil. New Zealand Journal of Forestry Science 30 (1): 225–236.

Santana, R. C.; N. F. De Barros; J. C. L. Neves. 1999. Biomassa e conteúdo de nutrientes de procedências de *Eucalyptus grandis* e *Eucalyptus saligna* em alguns sítios florestais do estado de São Paulo. Scientia Forestalis/Forest Sciences, 56: 155–169.

Schumacher, M. V.; R. Witschoreck; F. N. Calil. 2011. Biomassa em povoamentos de Eucalyptus spp. de pequenas propriedades rurais em Vera Cruz, RS. Ciencia Florestal 21 (1): 17–22.

Schumacher, M.V.; F. Poggiani. 1993. Biomass yield and nutrients remotion by *Eucalyptus camadulensis* Dehnh, *Eucalyptus grandis* Hill Ex Maiden and *Eucalyptus torelliana* f. Muell, cultivated in Anhembí, SP. Ciência Florestal, Santa Maria 3 (1): 21–34.

Silva, H. D.; F. Poggiani; L. C. Coelho. 1983. Eficiência de utilização de nutrientes em cinco espécies de Eucalyptus. Boletim de Pesquisa Florestal (Bol. Pesq. Fl.) 7: 1–8.

Silva, H. D.; C. A. Ferreira; R. S. Corrêa; A. F. J. Bellote; E.L. Tussolini. 2004. Alocação de biomassa e ajuste de equações para estimativa de biomassa em compartimentos aéreos de *Eucalyptus benthamii*. Boletim Pesquisas Florestais 49: 83–95.

Silva, H. D.D.; F. Poggiani; L. C. Coelho. 1983. Biomassa, concentração e conteúdo de nutrientes em cinco espécies de Eucalyptus plantadas em solos de baixa fertilidade. Boletim de Pesquisa Florestal 6/7: 9–25.

Silva, P. H. M.; F. Poggiani; P.L. Libardi; A. N. Gonçalves. 2013. Fertilizer management of eucalypt plantations on sandy soil in Brazil: initial growth and nutrient cycling. Elsevier. Forest Ecology and Management 301: 67–78.

Sochacki, S.J.; J. R. J. Harper; K.R.J. Smettem; B. Dell; H. Wu. 2012. Evaluating a Sustainability index for nutrients in a short rotation energy cropping system. GCB Bioenergy 5 (3): 315–326.

Turner, J.; M. J. Lambert. 2008. Nutrient cycling in age sequences of two Eucalyptus plantation species. Forest Ecology and Management 255 (5–6): 1701–1712.

Turner, J.M.; M.J. Lambert. 2014. Analysis of nutrient use efficiency (NUE) in *Eucalyptus pilularis* forests. Australian Journal of Botany 62 (7): 558–569.

Ualde, J.P. 2015. Extracción de nutrientes por plantaciones comerciales de diferentes edades de *Eucalyptus globulus* labill en suelos de la zona este de Uruguay. Tesis Ingeniero Agrónomo. Universidad de la República. Facultad de Agronomía-Uruguay. Montevideo, Uruguay. 81 p.

Viera, M.; M. V. Schumacher; M.V. W. Caldeira; L. F. Watzlawick. 2013. Teores de nutrientes em povoamentos monoespecíficos e mistos de *Eucalyptus urograndis* e *Acacia mearnsii* em sistema agrossilvicultural. Ciencia Florestal 23 (1): 67–76.

Wang, D.; F. H. Bormann; A.E. Lugo; R.D. Bowden. 1991. Comparison of nutrient-use efficiency and biomass production in five tropical tree taxa. Forest Ecology and Management 46 (1–2): 1–21.

Wise, P. K.; M. G. Pitman. 1981. Nutrient removal and replacement associated with short-rotation eucalypt plantations. Australian Forestry 44 (3): 142–52.

Wright, A.F.; J.S. Bailey. 2001. Organic carbon, total carbon, and total nitrogen determinations in soils of variable calcium carbonate contents using a Leco CN-2000 dry combustion analyzer. Communications in Soil Science and Plant Analysis 32: 3243–3258.

Zaia, F. C.; A. C. Gama-Rodrigues. 2004. Ciclagem e balanço de nutrientes em povoamentos de eucalipto na região norte Fluminense. Revista Brasileira de Ciência Do Solo 28 (3): 843–852.

Chapter 6. Evaluation of the nutrient content in biomass of Eucalyptus species from short rotation plantations in Uruguay

Supplementary material

Appendix 1

Arroyo Malo soil morphologic description

A 0 – 46 cm: Brown (7,5 YR 4/3) moist; sandy loam; massive – simple grain; common, medium (5 mm), faint dark brown (7,5 YR 3/4) motling, diffuse edge; few color depletions; many fine and very fine roots.

AB 46 – 64 cm: Dark grey (10 YR 4/1) moist; sandy clay loam; very weak angular blocks – massive; few color depletions; common fine and very fine roots.

Bt 64 - 91 cm: Greyish Brown to dark greyish brown (2,5 Y 4,5/2), moist; medium moderate angular blocks; clayely; continuos thin clay skins; many distinct red (2,5 YR 4/8) coarse (5-10 mm) motling; some prominent dark brown (7,5 YR 5/6) coarse to very coars, with clear to abrupt edge; gradual transition.

BC 91 - 109 cm: Light brownish grey (2,5 Y 6/3) moist; sandy clay-clayely; coarse strong angular blocks; thin patched clay skins; many, distinct redish yellow (7,5 YR 6/8), diffuse edge; gradual to clear transition.

C 109 - 122 cm + : Mixed colors: Olive yellow (2,5 Y 7/8) mist and light yellowish brown (2,5 Y 6/3) moist; sandy clay loam – sandy loam; moderate – weak angular blocks; many, coarse (5-10 mm), distinct red (2,5 YR 5/8) motling, clear edge, some brown (7,5 YR 4/3).

Chapter 6. Evaluation of the nutrient content in biomass of Eucalyptus species from short rotation plantations in Uruguay

Appendix 2

La Merced soil morphologic description

A 0 – 43 cm: Brown (7,5 YR 4/3) moist; sandy loam; massive – simple grain; common, medium (2 mm), strong brown (7,5 YR 4/6) motling, diffuse edge; many fine and very fine roots.

E 46 – 67 cm: Grayish brown (10 YR 5/2) moist; sandy loam; strong brown (7,5 YR 4/6) motling, diffuse edge; few color depletions; common fine and very fine roots; abrupt transition.

Bt 67 - 107 cm: Greyish brown (10 YR 5/2), moist; medium moderate angular blocks; sandy clayely to clayely; continuos thin clay skins; strong brown (7.5 YR 5/8) motling, common, less than 5 mm, with a clear edge; common roots, gradual transition; clear transition.

BC 107 – 133 cm + : Grayish brown (10 YR 5/2) moist; clayely with coarse sand; red (2.5 YR 5/8) and abundant moltings, common roots.

Table S1. Main physical and chemical characteristics of Paysandú and Tacuarembó by soil horizon. (Bentancor et al., 2019)

Site	Horizont	Depth	Clay	Silt	Sand	Bulk density	Orgánic C	pH†		Extractable cations							Base	Stock of exchangeable cations		
								H_2O	KCl	Al	Ca	Mg	K	Na	Total bases	CECe	Sat.	Ca	Mg	K
		cm	--------- g kg^{-1} ---------			Mg m^{-3}	g kg^{-1}			------------------- cmol$_c$ kg^{-1} -------------------							%	-----Mg ha^{-1}-----		
Paysandú	A	43	13.1	27.2	59.7	1.45	6.4	4.8	3.7	0.8	2.1	0.8	0.1	0.2	3.2	4.0	80.0	2.6	0.1	0.1
	E	24	12.6	25.3	62.1	1.50	2.9	4.8	3.7	0.8	1.9	0.8	0.1	0.2	3.0	3.8	79.0	1.4	0.6	0.07
	Bt	40	30.3	31.7	38.0	1.45	3.5	5.1	4.1	0.6	9.6	3.2	0.4	0.3	13.4	14.1	95.0	1.1	3.7	0.5
	BC	26	29.0	36.2	34.8	1.47	1.7	5.4	4.2	0.3	11.0	3.7	0.4	0.4	15.4	15.7	98.1	8.4	2.8	0.3
Tacuarembó	A	46	14.7	24.3	61.0	1.45	7.0	4.7	3.8	1.0	2.7	1.0	0.3	0.2	4.2	5.3	79.2	3.6	0.8	0.8
	AB	18	18.0	29.6	52.4	1.45	5.8	4.6	3.8	1.0	3.0	1.3	0.3	0.2	4.8	5.8	82.8	1.6	0.4	0.3
	Bt	27	35.6	40.1	31.1	1.45	4.6	4.8	3.7	0.9	5.3	2.6	0.4	0.4	8.5	10.4	81.7	4.1	1.2	0.6
	BC	18	36.4	31.7	32.0	1.44	4.6	5.1	4.1	0.7	6.5	3.1	0.3	0.6	10.5	11.2	93.8	3.4	1.0	0.3
	C	13	27.5	36.8	35.8	1.44	4.6	5.1	4.1	0.6	5.1	2.5	0.3	0.2	8.0	8.6	93.0	1.9	0.6	0.2

Table S2. Results of the ANOVA and Tukey test of the weight proportion of fractions (%) at Tacuarembó site

Species	Planting Density (Trees ha^{-1})	Wood			Bark			Leaves			Branchs		
		Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd
E. benthamii	2220	ns	ns	ns	AB	ns	ns	ns	ns	ns	ns	a	ns
	3330	ns	ns	ns	AB	ns	ns	ns	ns	ns	ns	ab	ns
	4440	ns	ns	ns	AB	ns	ns	ns	ns	ns	ns	ab	ns
	6660	ns	ns	ns	AB	ns	ns	ns	ns	ns	ns	b	ns
E. dunnii	2220	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	a	ns
	3330	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ab	ns
	4440	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ab	ns
	6660	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	b	ns
E. grandis	2220	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	a	ns
	3330	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ab	ns
	4440	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ab	ns
	6660	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	b	ns

Table S3. Results of the ANOVA and Tukey test of the weight proportion of fractions (%) at Paysandú site

Species	Planting Density (Trees ha^{-1})	Wood			Bark			Leaves			Branchs		
		Species	Planting density	Sp*Pd	Species	Planting density	Sp*Pd	Species	Planting density	Sp*Pd	Species	Planting density	Sp*Pd
E. benthamii	2220	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	3330	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	4440	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	6660	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
E. dunnii	2220	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	3330	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	4440	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	6660	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
E. grandis	2220	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
	3330	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
	4440	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
	6660	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns

Table S4. Nutrient content ± (S.E.) in bark for each species and planting density at Tacuarembó site (74 months old).

Species	Planting density (trees ha^{-1})	P	Ca	Mg	K	N
		---(%)---				
E. benthamii	2220	0.046 (0.004) A a	1.40 (0.15) A a	0.19 (0.006) A a	0.72 (0.08) B a	0.33 (0.024) abc
	3330	0.054 (0.008) A a	1.42 (0.12) A a	0.23 (0.018) A a	0.71 (0.13) B a	0.39 (0.018) ab
	4440	0.049 (0.002) A a	1.43 (0.10) A a	0.24 (0.010) A a	0.62(0.05) B a	0.35 (0.047) abc
	6660	0.051 (0.004) A a	1.47 (0.03) A a	0.24 (0.070) A a	0.55 (0.03) B a	0.43 (0.007) a
E. dunnii	2220	0.040 (0.005) AB a	1.67 (0.15) A a	0.33 (0.042) B a	0.87 (0.05) A a	0.33 (0.030) abc
	3330	0.036 (0.003) AB a	1.50 (0.15) A a	0.26 (0.013) B a	1.10 (0.02) A a	0.31 (0.031) abc
	4440	0.038 (0.004) AB a	2.04 (0.54) A a	0.32 (0.059) B a	0.87 (0.09) A a	0.34 (0.030) abc
	6660	0.041 (0.003) AB a	1.63 (0.13) A a	0.33 (0.005) B a	0.87 (0.12) A a	0.29 (0.004) abc
E. grandis	2220	0.028 (0.001) B a	2.019 (0.25) A a	0.141 (0.008) C a	1.07 (0.04) A a	0.25 (0.018) bc
	3330	0.029 (0.003) B a	2.054 (0.24) A a	0.127 (0.025) C a	0.95 (0.02) A a	0.27 (0.020) bc
	4440	0.041 (0.004) B a	2.054 (0.28) A a	0.170 (0.006) C a	0.94 (0.03) A a	0.36 (0.035) ab
	6660	0.033 (0.010) B a	1.259 (0.05) A a	0.131 (0.024) C a	0.96 (0.11) A a	0.22 (0.034) c

Table S5. Nutrient content ± (S.E.) in leave for each species and planting density at Tacuarembó site (74 months old).

Species	Planting density (trees ha^{-1})	P	Ca	Mg	K	N
		---(%)---				
E. benthamii	2220	0.16 (0.006) A a	0.62 (0.059) A a	0.17 (0.016) A a	1.59 (0.31) A a	2.93 (0.065) A a
	3330	0.17 (0.024) A a	0.68 (0.124) A a	0.18 (0.005) A a	1.80 (0.18) A a	2.66 (0.209) A a
	4440	0.16 (0.018) A a	0.62 (0.079) A a	0.19 (0.009) A a	1.79 (0.22) A a	2.76 (0.415) A a
	6660	0.17 (0.020) A a	0.65 (0.053) A a	0.17 (0.009) A a	1.65 (0.23) A a	2.94 (0.458) A a
E. dunnii	2220	0.11 (0.007) A a	0.70 (0.038) A a	0.14 (0.017) A a	1.52 (0.17) A a	2.56 (0.090) A a
	3330	0.16 (0.016) A a	0.82 (0.035) A a	0.18 (0.031) A a	1.62 (0.15) A a	2.67 (0.278) A a
	4440	0.16 (0.013) A a	0.84 (0.055) A a	0.18 (0.022) A a	1.55 (0.17) A a	2.63 (0.300) A a
	6660	0.14 (0.010) A a	0.89 (0.138) A a	0.19 (0.017) A a	1.71 (0.20) A a	2.45 (0.278) A a
E. grandis	2220	0.20 (0.052) A a	0.84 (0.113) A a	0.28 (0.013) B a	1.39 (0.07) A a	2.77 (0.373) A a
	3330	0.13 (0.017) A a	0.78 (0.108) A a	0.22 (0.015) B a	1.34 (0.03) A a	2.34 (0.254) A a
	4440	0.17 (0.014) A a	0.58 (0.065) A a	0.28 (0.031) B a	1.59 (0.11) A a	2.93 (0.186) A a
	6660	0.15 (0.017) A a	0.72 (0.034) A a	0.25 (0.043) B a	1.55 (0.10) A a	2.58 (0.225) A a

Table S6. Nutrient content ± (S.E.) in wood for each species and planting density at Tacuarembó site (74 months old).

Species	Planting density (trees ha^{-1})	P	Ca	Mg	K	N
		(%)				
E. benthamii	2220	0.037 (0.008) A a	0.077 (0.029) B a	0.12 (0.055) B a	0.28 (0.04) A a	0.12 A a (0.006)
	3330	0.032 (0.006) A a	0.024 (0.016) B a	0.11 (0.003) B a	0.28 (0.03) A a	0.17 A a (0.035)
	4440	0.028 (0.004) A a	0.025 (0.068) B a	0.13 (0.001) B a	0.27 (0.03) A a	0.14 A a (0.003)
	6660	0.030 (0.004) A a	0.022 (0.022) B a	0.15 (0.001) B a	0.25 (0.04) A a	0.14 A a (0.017)
E. dunnii	2220	0.018 (0.0004) B a	0.078 (0.043) A a	0.12 (0.011) A a	0.28 (0.01) A a	0.14 AB a (0.015)
	3330	0.017 (0.002) B a	0.070 (0.066) A a	0.13 (0.007) A a	0.26 (0.04) A a	0.12 AB a (0.007)
	4440	0.016 (0.002) B a	0.076 (0.003) A a	0.11 (0.06) A a	0.23 (0.01) A a	0.13 AB a (0.009)
	6660	0.023 (0.005) B a	0.126 (0.246) A a	0.16 (0.039) A a	0.25 (0.04) A a	0.14 AB a (0.019)
E. grandis	2220	0.016 (0.005) B a	0.019 (0.010) B a	0.11 (0.001) B a	0.25 (0.06) A a	0.09 B a (0.003)
	3330	0.013 (0.001) B a	0.023 (0.027) B a	0.11 (0.001) B a	0.30 (0.04) A a	0.11 B a (0.010)
	4440	0.014 (0.002) B a	0.020 (0.013) B a	0.09 (0.001) B a	0.28 (0.02) A a	0.10 B a (0.012)
	6660	0.013 (0.001) B a	0.021 (0.010) B a	0.15 (0.001) B a	0.29 (0.06) A a	0.09 B a (0.015)

Table S7. Nutrient content ± (S.E.) in bark for each species and planting density at Paysandú site (76 months old).

Species	Planting density (trees ha^{-1})	P	Ca	Mg	K	N
		(%)				
E. benthamii	2220	0.043 (0.006) A a	1.52 (0.11) A a	0.25 (0.029) A a	0.86 (0.012) A a	0.30 (0.021) A a
	3330	0.039 (0.003) A a	1.92 (0.016) A a	0.21 (0.007) A a	0.76 (0.038) A a	0.25 (0.008) A a
	4440	0.054 (0.005) A a	1.58 (0.077) A a	0.22 (0.013) A a	0.73 (0.040) A a	0.27 (0.042) A a
	6660	0.043 (0.004) A a	1.88 (0.237) A a	0.20 (0.017) A a	0.63 (0.026) A a	0.30 (0.015) A a
E. dunnii	2220	0.032 (0.004) A a	1.87 (0.096) A a	0.26 (0.04) A a	0.83 (0.050) A a	0.26 (0.018) A a
	3330	0.039 (0.002) A a	1.65 (0.156) A a	0.29 (0.012) A a	1.35 (0.035) A a	0.30 (0.015) A a
	4440	0.034 (0.005) A a	1.82 (0.076) A a	0.25 (0.021) A a	0.99 (0.141) A a	0.26 (0.006) A a
	6660	0.035 (0.003) A a	1.71 (0.119) A a	0.25 (0.008) A a	1.03 (0.248) A a	0.28 (0.019) A a
E. grandis	2220	0.034 (0.003) A a	2.04 (0.106) A a	0.18 (0.016) A a	0.83 (0.315) A a	0.24 (0.014) A a
	3330	0.033 (0.004) A a	1.88 (0.181) A a	0.23 (0.042) A a	1.35 (0.249) A a	0.28 (0.009) A a
	4440	0.039 (0.009) A a	2.28 (0.282) A a	0.19 (0.034) A a	0.99 (0.145) A a	0.24 (0.010) A a
	6660	0.040 (0.002) A a	1.77 (0.189) A a	0.23 (0.032) A a	1.03 (0.044) A a	0.26 (0.009) A a

Table S8. Nutrient content ± (S.E.) in leaves for each species and planting density at Paysandú site (76 months old).

Species	Planting density (trees ha^{-1})	P	Ca	Mg	K	N
		(%)				
E. benthamii	2220	0.16 (0.023) A a	0.86 (0.024) A a	0.18 (0.018) B a	1.49 (0.076) A a	2.25 (0.132) A a
	3330	0.16 (0.010) A a	0.75 (0.094) A a	0.20 (0.008) B a	1.79 (0.142) A a	2.55 (0.272) A a
	4440	0.16 (0.006) A a	0.71 (0.088) A a	0.16 (0.016) B a	1.73 (0.152) A a	2.29 (0.110) A a
	6660	0.14 (0.005) A a	0.73 (0.040) A a	0.16 (0.010) B a	1.61 (0.198) A a	2.27 (0.136) A a
E. dunnii	2220	0.14 (0.006) A a	0.85 (0.111) A a	0.16 (0.023) AB a	1.70 (0.444) A a	1.87 (0.081) A a
	3330	0.15 (0.010) A a	1.26 (0.177) A a	0.25 (0.009) AB a	1.75 (0.144) A a	2.07 (0.056) A a
	4440	0.15 (0.014) A a	1.21 (0.198) A a	0.22 (0.042) AB a	1.59 (0.164) A a	2.10 (0.064) A a
	6660	0.16 (0.013) A a	1.14 (0.191) A a	0.25 (0.034) AB a	1.74 (0.152) A a	2.12 (0.211) A a
E. grandis	2220	0.13 (0.022) A a	0.72 (0.024) A a	0.30 (0.051) A a	1.23 (0.055) A a	2.08 (0.005) A a
	3330	0.11 (0.003) A a	0.80 (0.136) A a	0.30 (0.036) A a	1.19 (0.143) A a	1.99 (0.039) A a
	4440	0.14 (0.011) A a	0.74 (0.093) A a	0.35 (0.009) A a	1.58 (0.241) A a	2.22 (0.061) A a
	6660	0.14 (0.008) A a	0.91 (0.037) A a	0.30 (0.012) A a	1.46 (0.323) A a	2.06 (0.226) A a

Table S9. Nutrient content ± (S.E.) in wood for each species and planting density at Paysandú site (76 months old).

Species	Planting density (trees ha^{-1})	P	Ca	Mg	K	N
		(%)				
E. benthamii	2220	0.027 (0.005) b	0.12 (0.007) B a	0.017 (0.001) A a	0.20 (0.020) b	0.12 (0.021) A a
	3330	0.021 (0.001) b	0.12 (0.004) B a	0.017 (0.001) A a	0.28 (0.036) a	0.13 (0.015) A a
	4440	0.020 (0.005) b	0.12(0.003) B a	0.017 (0.003) A a	0.20 (0.005) b	0.11 (0.019) A a
	6660	0.020 (0.001) b	0.11 (0.006) B a	0.016 (0.002) A a	0.21 (0.013) b	0.10 (0.006) A a
E. dunnii	2220	0.012 (0.002) ab	0.16 (0.013) A a	0.065 (0.013) A a	0.19 (0.015) b	0.08 (0.012) A a
	3330	0.017 (0.001) b	0.23 (0.005) A a	0.077 (0.003) A a	0.22 (0.011) ab	0.13 (0.015) A a
	4440	0.015 (0.002) b	0.17 (0.010) A a	0.063 (0.003) A a	0.17 (0.010) b	0.11 (0.022) A a
	6660	0.013 (0.001) b	0.25 (0.072) A a	0.067 (0.013) A a	0.24 (0.021) ab	0.09 (0.015) A a
E. grandis	2220	0.010 (0.0003) a	0.16 (0.039) AB a	0.020 (0.005) A a	0.19 (0.026) b	0.09 (0.003) A a
	3330	0.011 (0.001) ab	0.14 (0.010) AB a	0.019 (0.001) A a	0.19 (0.019) b	0.09 (0.009) A a
	4440	0.012 (0.0003) ab	0.14 (0.014) AB a	0.019 (0.003) A a	0.23 (0.022) ab	0.10 (0.009) A a
	6660	0.013 (0.001) b	0.18 (0.045) AB a	0.018 (0.0005) A a	0.23 (0.005) ab	0.10 (0.007) A a

Table S10. Nutrient weight by fraction and post hoc test (Tukey test) for species and planting density at Tacuarembó site (at age 74 months).

	Species											
	E.benthamii				***E.dunnii***				***E.grandis***			
Planting density (trees ha^{-1})	**2220**	**3330**	**4440**	**6660**	**2220**	**3330**	**4440**	**6660**	**2220**	**3330**	**4440**	**6660**
P_{wood} (Kg ha^{-1})	35.2 A b	31.8 A b	39.5 A ab	57.5 A a	17.2 B b	20.5 B b	21.9 B ab	36.0 B a	17.8 C b	12.3 C b	16.0 C ab	15.7 C a
Ca_{wood} (Kg ha^{-1})	122.5 B a	118.6 B a	201.7 B a	165.9 B a	158.8 A a	275.5 A a	211.2 A a	309.3 A a	81.9 C a	118.6 C a	102.6 C a	88.6 C a
Mg_{wood} (Kg ha^{-1})	69.6 B a	28.0 B a	35.6 B a	40.9 B a	73.2 A a	83.3 A a	108.3 A a	189.0 A a	19.9 B a	21.7 B a	23.5 B a	25.1 B a
K_{wood} (Kg ha^{-1})	309.5 A c	364.1 A bc	523.0 A ab	539.4 A a	349.3 A c	367.0 A bc	403.4 A ab	513.4 A a	314.4 A c	320.5 A bc	371.8 A ab	417.7 A a
N_{wood} (Kg ha^{-1})	113.6 A b	169.5 A ab	207.8 A a	266.7 A a	137.3 A b	140.9 Aab	190.5 A a	257.4 A a	96.1 B b	103.7 B ab	117.3 B a	133.4 B a
P_{bark} (Kg ha^{-1})	7.1 A b	9.5 A ab	11.0 A ab	14.1 A a	6.3 A b	6.8 A ab	9.0 A ab	12.0 A a	3.8 B b	3.8 B ab	6.0 B ab	5.6 B a
C_{abark} (Kg ha^{-1})	217.3 A a	249.1 A a	319.9 A a	408.9 A a	264.3 A a	290.6 A a	507.8 A a	452.7 A a	274.6 A a	276.4 A a	309.7 A a	211.9 A a
Mg_{bark} (Kg ha^{-1})	29.2 A b	40.2 A ab	54.6 A ab	66.1 A a	52.1 A b	50.2 A ab	77.6 A ab	93.0 A a	19.7 B b	17.3 B ab	25.6 B ab	22.3 B a
K_{bark} (Kg ha^{-1})	91.5 B a	101.6 B a	111.7 B a	131.2 B a	143.0 A a	161.4 A a	175.9 A a	190.8 A a	115.9 B a	105.6 B a	127.2 B a	130.3 B a
N_{bark} (Kg ha^{-1})	50.3 A b	66.2 A b	78.4 A a	120.7 A a	50.8 A b	59.3 A b	81.7 A a	59.6 A a	33.9 B b	36.1 B b	53.3 B a	37.6 B a
P_{leave} (Kg ha^{-1})	7.1 A a	8.1 A a	12.7 A a	14.2 A a	5.3 A a	8.1 A a	10.4 A a	9.9 A a	9.6 A a	7.7 A a	9.7 A a	9.5 A a
Ca_{leave} (Kg ha^{-1})	27.8 A a	30.8 A a	48.8 A a	52.2 A a	32.6 A a	42.4 A a	55.3 A a	61.5 A a	42.6 A a	46.0 A a	34.6 A a	46.3 A a
Mg_{leave} (Kg ha^{-1})	7.5 B b	8.0 B ab	14.6 B a	13.7 B a	6.5 B b	9.4 B ab	11.8 B a	13.3 B a	14.1 A b	12.7 A ab	16.4 A a	16.2 A a
K_{leave} (Kg ha^{-1})	78.9 A a	81.0 A a	144.5 A a	133.6 A a	63.6 A a	77.6 A a	97.0 A a	126.5 A a	77.1 A a	85.3 A a	94.6 A a	101.8 A a
N_{leave} (Kg ha^{-1})	129.7 A a	116.9 A a	213.8 A a	238.2 A a	119.5 A a	139.1 A a	175.0 A a	164.0 A a	138.7 A a	136.3 A a	169.7 A a	166.3 A a

Different letters indicate significant post-hoc differences between the planting density (lower case) and species (capital letter) at alpha=0.05 based on a Tukey HSD test

Table S11. Nutrient weight by fraction and post hoc test (Tukey test) for species and planting density at Paysandú site (at age 76 months)

	Species											
	E.benthamii				***E.dunnii***				***E.grandis***			
Planting density (trees ha^{-1})	**2220**	**3330**	**4440**	**6660**	**2220**	**3330**	**4440**	**6660**	**2220**	**3330**	**4440**	**6660**
P_{wood} (Kg ha^{-1})	34.3 a	28.8 a	20.8 ab	34.7 a	18.1 b	19.9 ab	18.4 b	21.9 ab	11.9 b	18.0 b	18.9 b	16.3 b
Ca_{wood} (Kg ha^{-1})	160.3 A a	161.8 A a	128.6 A a	198.4 A a	233.5 A a	272.5 A a	214.5 A a	394.3 A a	198.4 A a	232.9 A a	233.4 A a	217.5 A a
Mg_{wood} (Kg ha^{-1})	21.5 B a	24.5 B a	17.1 B a	27.6 B a	95.2 A a	89.5 A a	77.9 A a	106.5 A a	24.3 B a	31.5 B a	34.0 B a	22.2 B a
K_{wood} (Kg ha^{-1})	250.4 ab	406.8 a	205.1 b	355.8 a	275.3 ab	257.3 ab	216.2 b	398.7 a	239.8 ab	312.1 ab	361.7 a	281.6 ab
N_{wood} (Kg ha^{-1})	153.1 A a	171.7 A a	119.1 A a	173.1 A a	113.1 A a	150.6 A a	127.9 A a	150.3 A a	107.3 A a	153.9 A a	156.7 A a	118.3 A a
P_{bark} (Kg ha^{-1})	9.1 A b	9.2 A ab	9.4 A ab	12.8 A a	7.3 AB b	b.9 AB ab	6.7 AB ab	9.8 AB a	4.9 B b	7.7 B ab	6.8 B ab	6.7 B a
Ca_{bark} (Kg ha^{-1})	321.2 ab	445.7 ab	274.1 b	582.7 a	419.4 ab	293.2 ab	368.5 ab	496.4 ab	290.0 ab	434.5 ab	425.1 ab	298.4 ab
Mg_{bark} (Kg ha^{-1})	52.6 A a	47.7 A a	38.0 A a	61.0 A a	59.8 A a	51.5 A a	49.5 A a	71.4 A a	26.3 A a	52.2 A a	37.4 A a	38.3 A a
K_{bark} (Kg ha^{-1})	182.1 A a	172.1 A a	128.0 A a	193.1 A a	186.5 A a	238.1 A a	199.1 A a	311.2 A a	190.8 A a	264.4 A a	196.5 A a	192.6 A a
N_{bark} (Kg ha^{-1})	63.0 a b	59.1 ab	46.0 b	90.9 a	58.5 ab	53.1 ab	53.5 ab	79.5 ab	34.6 b	63.2 ab	48.6 ab	43.1 b
P_{leave} (Kg ha^{-1})	9.2 A a	8.7 A a	6.5 A a	11.1 A a	9.6 A a	7.4 A a	8.6 A a	28.1 A a	6.3 A a	13.0 A a	9.7 A a	9.4 A a
Ca_{leave} (Kg ha^{-1})	49.4 B a	39.2 B a	29.4 B a	58.9 B a	59.0 A a	63.0 A a	68.8 A a	235.3 A a	33.8 AB a	104.0 AB a	51.7 AB a	58.8 AB a
Mg_{leave} (Kg ha^{-1})	10.4 B b	10.8 B ab	6.6 B b	12.9 B a	10.7 AB b	12.5 AB ab	12.7 AB b	50.2 AB a	14.1 A b	36.6 A ab	23.3 A b	19.4 A a
K_{leave} (Kg ha^{-1})	70.4 A a	67.8 A a	65.9 A a	135.3 A a	106.9 A a	101.7 A a	80.7 A a	231.3 A a	86.0 A a	203.8 A a	109.1 A a	103.4 A a
N_{leave} (Kg ha^{-1})	126.8 A a	133.5 A a	97.6 A a	183.5 A a	130.0 A a	104.8 A a	118.1 A a	355.5 A a	97.2 A a	238.6 A a	153.4 A a	135.7 A a

Different letters indicate significant post-hoc differences between the planting density (lower case) and species (capital letter) at alpha=0.05 based on a Tukey HSD test

Table S12. Results of post hoc test (Tukey test) of nutrient weight per hectare (%) in wood at Tacuarembó site

		P			Ca			Mg			K			N		
Species	Planting Density (Trees ha^{-1})	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd
E. benthamii	2220	ns	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	A	ns	ns
	3330	ns	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	A	ns	ns
	4440	ns	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	A	ns	ns
	6660	ns	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	A	ns	ns
E. dunnii	2220	ns	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	A	ns	ns
	3330	ns	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	A	ns	ns
	4440	ns	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	A	ns	ns
	6660	ns	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	A	ns	ns
E. grandis	2220	ns	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	B	ns	ns
	3330	ns	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	B	ns	ns
	4440	ns	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	B	ns	ns
	6660	ns	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	B	ns	ns

Table S13. Results of post hoc test (Tukey test) of nutrient weight per hectare (%) in bark at Tacuarembó site

			P			Ca			Mg			K			N	
Species	Planting Density (Trees ha^{-1})	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd
E. benthamii	2220	ns	ns	ns	AB	ns	ns	A	ns	ns	B	ns	ns	A	ns	ns
	3330	ns	ns	ns	AB	ns	ns	A	ns	ns	B	ns	ns	A	ns	ns
	4440	ns	ns	ns	AB	ns	ns	A	ns	ns	B	ns	ns	A	ns	ns
	6660	ns	ns	ns	AB	ns	ns	A	ns	ns	B	ns	ns	A	ns	ns
E. dunnii	2220	ns	ns	ns	B	ns	ns	B	ns	ns	A	ns	ns	A	ns	ns
	3330	ns	ns	ns	B	ns	ns	B	ns	ns	A	ns	ns	A	ns	ns
	4440	ns	ns	ns	B	ns	ns	B	ns	ns	A	ns	ns	A	ns	ns
	6660	ns	ns	ns	B	ns	ns	B	ns	ns	A	ns	ns	A	ns	ns
E. grandis	2220	ns	ns	ns	A	ns	ns	B	ns	ns	AB	ns	ns	B	ns	ns
	3330	ns	ns	ns	A	ns	ns	B	ns	ns	AB	ns	ns	B	ns	ns
	4440	ns	ns	ns	A	ns	ns	B	ns	ns	AB	ns	ns	B	ns	ns
	6660	ns	ns	ns	A	ns	ns	B	ns	ns	AB	ns	ns	B	ns	ns

Table S14. Results of post hoc test (Tukey test) of nutrient weight per hectare (%) in leaves at Tacuarembó site

		P			Ca			Mg			K			N		
Species	Planting Density (Trees ha^{-1})	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd	Species	Planting density	S*Pd
E. benthamii	2220	B	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
	3330	B	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
	4440	B	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
	6660	B	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
E. dunnii	2220	A	ns	ns	ns	ns	ns	C	ns	ns	ns	ns	ns	ns	ns	ns
	3330	A	ns	ns	ns	ns	ns	C	ns	ns	ns	ns	ns	ns	ns	ns
	4440	A	ns	ns	ns	ns	ns	C	ns	ns	ns	ns	ns	ns	ns	ns
	6660	A	ns	ns	ns	ns	ns	C	ns	ns	ns	ns	ns	ns	ns	ns
E. grandis	2220	A	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	3330	A	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	4440	A	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	6660	A	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns

Table S15. Results of post hoc test (Tukey test) of nutrient weight per hectare (%) in wood at Paysandú site

Species	Planting Density (Trees ha^{-1})	P Species	P Planting density	P S*Pd	Ca Species	Ca Planting density	Ca S*Pd	Mg Species	Mg Planting Density	Mg S*Pd	K Species	K Planting density	K S*Pd	N Species	N Planting density	N S*Pd
E. benthamii	2220	ns	ns	ns	ns	ns	bc	B	Ns	ns	A	ns	bcd	ns	ab	ns
	3330	ns	ns	ns	ns	ns	bc	B	Ns	ns	A	ns	a	ns	a	ns
	4440	ns	ns	ns	ns	ns	bc	B	Ns	ns	A	ns	abc	ns	a	ns
	6660	ns	ns	ns	ns	ns	c	B	ns	ns	A	ns	ab	ns	b	ns
E. dunnii	2220	ns	ns	ns	ns	ns	bc	A	ns	ns	C	ns	bcd	ns	ab	ns
	3330	ns	ns	ns	ns	ns	a	A	ns	ns	C	ns	cd	ns	a	ns
	4440	ns	ns	ns	ns	ns	bc	A	ns	ns	C	ns	cd	ns	a	ns
	6660	ns	ns	ns	ns	ns	b	A	ns	ns	C	ns	cd	ns	b	ns
E. grandis	2220	ns	ns	ns	ns	ns	ab	B	ns	ns	B	ns	bcd	ns	ab	ns
	3330	ns	ns	ns	ns	ns	bc	B	ns	ns	B	ns	d	ns	a	ns
	4440	ns	ns	ns	ns	ns	bc	B	ns	ns	B	ns	ab	ns	a	ns
	6660	ns	ns	ns	ns	ns	ab	B	ns	ns	B	ns	bcd	ns	b	ns

Table S16. Results of post hoc test (Tukey test) of nutrient weight per hectare (%) in bark at Paysandú site

Species	Planting Density (Trees ha^{-1})	P Species	P Planting density	P S*Pd	Ca Species	Ca Planting density	Ca S*Pd	Mg Species	Mg Planting density	Mg S*Pd	K Species	K Planting density	K S*Pd	N Species	N Planting density	N S*Pd
E. benthamii	2220	ns	ns	ns	ns	ns	b	A	ns	ns	ns	ns	ns	A	ns	ns
	3330	ns	ns	ns	ns	ns	a	A	ns	ns	ns	ns	ns	A	ns	ns
	4440	ns	ns	ns	ns	ns	ab	A	ns	ns	ns	ns	ns	A	ns	ns
	6660	ns	ns	ns	ns	ns	b	A	ns	ns	ns	ns	ns	A	ns	ns
E. dunnii	2220	ns	ns	ns	ns	ns	a	B	ns	ns	ns	ns	ns	A	ns	ns
	3330	ns	ns	ns	ns	ns	b	B	ns	ns	ns	ns	ns	A	ns	ns
	4440	ns	ns	ns	ns	ns	b	B	ns	ns	ns	ns	ns	A	ns	ns
	6660	ns	ns	ns	ns	ns	b	B	ns	ns	ns	ns	ns	A	ns	ns
E. grandis	2220	ns	ns	ns	ns	ns	b	B	ns	ns	ns	ns	ns	B	ns	ns
	3330	ns	ns	ns	ns	ns	b	B	ns	ns	ns	ns	ns	B	ns	ns
	4440	ns	ns	ns	ns	ns	ab	B	ns	ns	ns	ns	ns	B	ns	ns
	6660	ns	ns	ns	ns	ns	b	B	ns	ns	ns	ns	ns	B	ns	ns

Table S17. Results of post hoc test (Tukey test) of nutrient weight per hectare (%) in leaves at Paysandú site

Species	Planting Density (Trees ha^{-1})	P Species	P Planting density	P S*Pd	Ca Species	Ca Planting density	Ca S*Pd	Mg Species	Mg Planting density	Mg S*Pd	K Species	K Planting density	K S*Pd	N Species	N Planting density	N S*Pd
E. benthamii	2220	B	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
	3330	B	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
	4440	B	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
	6660	B	ns	ns	ns	ns	ns	B	ns	ns	ns	ns	ns	ns	ns	ns
E. dunnii	2220	A	ns	ns	ns	ns	ns	C	ns	ns	ns	ns	ns	ns	ns	ns
	3330	A	ns	ns	ns	ns	ns	C	ns	ns	ns	ns	ns	ns	ns	ns
	4440	A	ns	ns	ns	ns	ns	C	ns	ns	ns	ns	ns	ns	ns	ns
	6660	A	ns	ns	ns	ns	ns	C	ns	ns	ns	ns	ns	ns	ns	ns
E. grandis	2220	A	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	3330	A	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	4440	A	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns
	6660	A	ns	ns	ns	ns	ns	A	ns	ns	ns	ns	ns	ns	ns	ns

Table S18. Mean values of NUE (± standard error) for each site. Different letters indicate statistical differences according Tukey test by site for a P<0.05.

	EUN (Kg biomass Kg^{-1} nutrient)									
Sites	P		Ca		Mg		K		N	
Tacuarembó	3730 (171.8)	a	306 (13.1)	bc	1613 (108.2)	a	240 (6.2)	c	409 (11.9)	b
Paysandú	4331 (195)	a	257 (7.3)	c	1680 (94.3)	a	283 (8)	c	496 (15.2)	b

“¡Qué cosas, hermano,
que tiene la vida!
Yo no la quería
cuando la encontré
hasta que una noche
me dijo, resuelta:
Ya estoy muy cansada
de todo... Y se fue.
¡Qué cosas, hermano,
que tiene la vida!
Desde aquella noche
la empecé a querer.

¡Cuántos sacrificios
hice pa' olvidarla!
¡En cuántos fandangos
mis noches perdí!
¡Quién hubiera dicho
que por su cariño
diera tantos tumbos
como los que di!
He tirao la vida
por los cafetines
pa' mostrarle a todos
que ya la olvidé,
pero todo es grupo
y al quedarme a solas
he llorao, hermano,
como una mujer.

Dos años enteros
la tuve a mi lado
y nunca, ni en sueños,
quererla pensé.
¡Quién iba a decirme
que loco yo un día
la vida daría
por verla otra vez!...
¡Qué cosas, hermano,
que tiene la vida...
¡Desde aquella noche
la empecé a querer!”

Luis Cesar Amadori, 1932

Capítulo 7. Discusión general

1. Introducción

El sector forestal en Uruguay se ha consolidado como uno de los más importantes de la economía, ocupando el tercer lugar en el total de las exportaciones de origen agropecuario. Actualmente el monto exportado por los productos de origen forestal representa el 13% del total (MGAP-DIEA, 2019) y con una tendencia al crecimiento en los próximos años (Fuletti y Petraglia, 2018). El crecimiento de este sector se ha basado en tres aspectos fundamentales: i) el buen comportamiento de varias especies entre las cuales se destacan los eucaliptos y pinos, ii) el marco normativo que fue instrumentado hacia finales de la década de los años 80 con el fin de promover la instalación de plantaciones forestales y posterior industrialización de las mismas, y iii) un contexto político y social tradicionalmente estable. Esta normativa fue el resultado, entre otras cosas, la clasificación de suelos denominados de prioridad forestal los cuales ocupan actualmente una 4.2 millones de hectáreas representando aproximadamente un 25% de los suelos cultivables del país (Califra y Durán, 2010). Tanto los resultados empíricos como los experimentales han mostrado que es posible obtener altos niveles de productividad con varias especies de eucaliptos (entre otros géneros) en las diferentes zonas de aptitud forestal (Balmelli y Resquin 2002 y 2006). Actualmente las especies que ocupan la mayor parte de la superficie forestada con este género son: *Eucaliptus globulus, E. grandis, E. dunnii, E. maidenii, E. tereticornis, E. camaldulensis* y *E. benthamii*. Las tres primeras son las que actualmente predominan, aunque recientemente se están utilizando a escala comercial híbridos de *E. grandis* con *E. camaldulensis, E. globulus* y *E. tereticornis* (Boscana y Boragno, 2018).

A partir del año 2005 en Uruguay se comenzó a implementar una política energética con el objetivo de reducir la dependencia del petróleo mediante la promoción del uso de fuentes renovables de energía (autóctonas y no tradicionales) de manera sustentable tanto económica como medioambiental de las mismas (MIEM, 2008). Cabe destacar que los combustibles de origen fósil (petróleo y gas natural) en los años anteriores a esta reforma en promedio representaban el 58% del total de la matriz energética del país. Los resultados de estas acciones en cuanto a la incorporación de nuevas fuentes de energía ha sido la instalación de un importante nivel de potencia eléctrica proveniente básicamente de la quema de biomasa de industrias forestales y de parques eólicos. Actualmente, alrededor del 55% de la potencia generada en el mercado eléctrico proviene de las siguientes fuentes: biomasa, eólica y solar al mismo tiempo que el peso del petróleo en dicho mercado es inferior al 10% (ADME, 2019). Por otro lado, se ha avanzado en la incorporación de biocombustibles como el etanol, proveniente de cultivos (maíz, trigo, sorgo y caña de azúcar), y el biodiesel, con materias primas de diverso origen (vegetal, animal y urbano). La proporción de bioetanol y biodiesel en el total de los combustibles de origen fósiles es de 9 y 12%, respectivamente (ANCAP, 2017). Recientemente se comenzó con la promoción del uso de residuos generados en actividades agrícolas, industriales y urbanas para la generación de biogás, diésel sintético, gas de síntesis y biofertilizantes (BIOVALOR, 2019). Por otro lado, a partir del año 2010 la Agencia Nacional de Investigación e Innovación (ANII) ha financiado la investigación (tanto pública como privada) y la formación de recursos humanos en áreas relacionadas a la energía como una forma de apoyo a la diversificación de la matriz energética del país anteriormente mencionada. Esto ha dado como resultado que fueron evaluados distintos procesos de obtención de diferentes tipos de combustibles a partir de materias primas de origen forestal. Estos estudios han permitido evaluar residuos provenientes de labores selvícolas (biomasa proveniente de raleos), de industrias de celulosa y madera sólida y de cultivos energéticos.

Los cultivos energéticos más estudiados han sido el pasto elefante (*Penisetum purpureum*), la caña de castilla (*Arundo donax*), el switchgrass (*Panicum virgatum*) (Siri-Prieto, 2014), y más recientemente algunas especies de eucaliptos (Resquin, 2015). Los cultivos con especies de eucaliptos han mostrado un interesante potencial para la generación de energía en distintas regiones del mundo: Chile (Rodríguez et al., 2013; Albaugh et al., 2017; Acuña et al., 2018), Brasil (Müller, 2005; Guerra et al., 2014; Foelkel, 2015, Eufrade Junior et al. 2016), Francia (Pérez et al., 2010), Italia (Spinelli et al., 2009), y España (Pérez et al., 2011; Ciria, 2011; Jiménez et al., 2013; Rodríguez et al., 2014) y Australia (Harris, 2007), entre otros.. De acuerdo a Seixas (2008), del total de la superficie de cultivos energéticos plantadas a nivel mundial aproximadamente el 40% es con especies de eucaliptos. Las principales ventajas de las especies plantadas a escala comercial es que combinan varias características de interés: se adaptan a un amplio rango de condiciones ambientales, tienen altas tasas de crecimiento, valores medios de densidad de la madera, interesantes propiedades tecnológicas (contenido de energía), alta capacidad de rebrote, alta tolerancia a la competencia y tener un balance energético positivo (Cabrera et al., 2014; Foelkel, 2015). Los cultivos energéticos con eucaliptos, independientemente de la especie de que se trate, tienen como objetivo la producción de grandes cantidades de biomasa en turnos relativamente cortos. Esto permite el uso de superficies relativamente reducidas y al mismo tiempo asegurar un suministro de materia prima a costos competitivos (Ciria, 2011). Esto implica que las densidades de plantación estén por encima de los 2000 a 3000 árboles ha^{-1} y turnos que van desde los 2 a 8 años, dependiendo de la especie, el marco de plantación y las condiciones de crecimiento. La viabilidad económica de este de tipo de plantaciones implica que la rotación del cultivo debe extenderse a dos o tres turnos posteriores a la primera cosecha ya que las mismas tienen altos costos de instalación. La identificación del momento óptimo de cosecha debe tener en cuenta tanto la producción de biomasa, las características del fuste (lo cual determina el tipo de maquinaria de cosecha y procesamiento) y las propiedades tecnológicas de la misma (Baettig et al., 2010). La producción de biomasa forestal con fines energéticos podría ser una de las alternativas para la diversificación de la matriz energética de Uruguay, tal y como sucede en algunos países de la región y del mundo (Dimitrou y Aronsson, 2005; Marcos, 2006; IDAE, 2007; Nava-García y Doldán-García, 2014). A diferencia de la silvicultura de los cultivos denominados tradicionales de producción de madera sólida y celulosa, las plantaciones energéticas plantean en muchos casos una serie de interrogantes que es necesario responder previo a su implementación en sistemas comerciales. La principal diferencia entre esos sistemas de producción radica en las altas densidades de plantación utilizadas lo cual determina la acumulación de grandes cantidades de biomasa en períodos relativamente cortos. El espaciamiento es una de las prácticas de manejo que mayor incidencia tienen sobre la competencia entre individuos, la sobrevivencia, la distribución de biomasa en las fracciones del árbol, la dinámica de nutrientes, el momento de cosecha y la productividad final (Gonçalves et al., 2004). Resultados obtenidos con algunas de las especies de eucaliptos que también son plantadas en Uruguay, pero con altas densidades en países de la región muestran que es posible obtener altos niveles de productividad (15 a 35 ton ha^{-1} $año^{-1}$) en turnos relativamente cortos (inferiores a 8 años) (Leles et al., 2001; Müller, 2005; Carón et al., 2015; Foelkel, 2015; Rodríguez et al., 2013; Santelices et al., 2015; Eloy et al., 2014; Albaugh et al., 2017). Estos antecedentes, sin bien no son directamente extrapolables a las condiciones del país, indicarían que esos sistemas de producción tendrían un alto potencial de producción de biomasa y por tanto de energía por unidad de superficie y tiempo.

2. Potencialidad de las especies

Para la evaluación de la productividad de este tipo de cultivos se debe tener en cuenta aspectos tales como las diferencias de los tipos de suelos existentes y los parámetros climáticos, además de indicadores de la sostenibilidad ambiental de la producción de biomasa. Los requerimientos de sitio de varias de las especies de eucaliptos de mayor importancia comercial son lo suficientemente amplias como para lograr buenas condiciones de adaptación las condiciones de Uruguay en el escenario de clima actual. Una prueba de esto son los altos rendimientos que se registran en general en las distintas regiones del país. Los requerimientos ambientales de *E. grandis* y *E. dunnii* (Tabla 1) muestran que las diferentes regiones del país tienen condiciones de sitio propicias para la instalación de las mismas. De acuerdo a Brazeiro et al., (2012) las eco-regiones con mayor potencial para estas especies son las cuencas sedimentarias del oeste y gondwánica que se corresponden con el litoral oeste y norte del país, respectivamente

Estas razones, junto con los aspectos logísticos, han determinado que las plantaciones comerciales de estas especies se concentran en dichas zonas (MGAP-DIEA, 2017) y que, por lo tanto, se consideren representativas para la evaluación de cultivos energéticos. Las características de los sitios han mostrado en estudios previos que interactúan con los distintos materiales genéticos de varias de las especies de eucaliptos que se plantan en los suelos de aptitud foresta del país (Balmelli, 1995; Balmelli y Resquin, 2002). La respuesta de una especie o material genético a las condiciones de un sitio puede estar influenciada por un número grande de factores incluyendo la interacción entre los mismos. Desde el punto de vista práctico interesa identificar la(s) variable(s) que mejoran el crecimiento a los efectos de planificar la elección de los sitios a forestar y obtener altos rendimientos. En *E. grandis* los resultados obtenidos en esta tesis muestran que los parámetros del suelo que tienen un peso más importante con la producción son aquellos que tienen una relación directa con la capacidad de exploración de las raíces (Tabla 2, Capítulo 1). Por tanto, los suelos con mayor profundidad de los horizontes A-B y menor contenido de arcilla y limo (o sea con una mayor proporción de la fracción arena) son los que determinan los mayores crecimientos. A su vez, este tipo de suelos poseen una alta capacidad de acumulación de agua y un buen drenaje, aunque con escasa retención debido al tamaño de los microporos. La incidencia de estos factores también ha sido identificada por Laclau et al., (2013) observando que las raíces de menor tamaño en esta especie alcanzan profundidades de

Tabla 1. Requerimientos de clima y suelo de *E. grandis* y *E. dunnii*

Especie	Parámetro	Variable	Intervalo	
E. grandis	Clima	Precipitación (mm)	1020	1780
		Temperatura mínima ºC	2	10
		Temperatura máxima ºC		30
	Suelo	Ph	ácido	
		Profundidad	40 cm	
		textura	Limosa, franca o ligeramente arcillosa	
	Topografía	Altitud (m)	0	600
		Pendiente (%)	0	30
E. dunnii	Clima	Precipitación (mm)	845	1950
		Temperatura mínima ºC	-0.5	7
		Temperatura máxima ºC	24	29
	Suelo	Ph	neutro	
		Profundidad	-	-
		textura	Bien drenados	
	Topografía	Altitud (m)	0	800
		Pendiente (%)	-	-

Fuente: FAO, 1981; Jovanovic et al., 1999; Bustillos-Herrera et al., 2007.

hasta profundidades de 1 m. La asociación positiva con la disponibilidad de agua también ha sido reportada por Bustillos-Herrera et al., (2007); Armin y Abdolrassoul, (2010) y Rachid, (2016). Suelos con estas características forman parte de varios de los grupos que componen los distintos suelos de aptitud forestal en varias regiones del país (Durán, 2008), aunque predominan en las zonas norte y litoral lo cual se ve reflejado en el mapa de probabilidad actual de ocurrencia de esta especie (Figura 4, Capítulo 1). En cuanto a la orientación, si bien la noreste a noroeste tienen un efecto positivo sobre el crecimiento debido a la mayor exposición a la radiación solar a que están expuestos los árboles, en términos prácticos tiene una utilidad relativa teniendo en cuenta la disposición de los laboreos que se realizan para evitar los efectos de la erosión. De todos modos, este parámetro tiene un peso muy inferior comparado con el resto de las variables seleccionadas. *E. dunnii* muestra una menor dependencia de los parámetros del suelo, teniendo en cuenta que varias de las variables de mayor importancia relativa que explican el crecimiento son la temperatura en distintas épocas del año, aunque también hay una fuerte asociación con el espesor del horizonte A (Tabla 2, Capítulo 1). Este parámetro muestra ser el más restrictivo para esta especie ya que las zonas óptimas para la misma se encuentran en los suelos comparativamente más profundos del país como son los de las zonas norte y litoral. A su vez estas zonas tienen valores medios de temperaturas mayores que el resto, en particular en los meses de otoño (Castaño et al., 2011), lo cual se asocia positivamente con el crecimiento de esta especie.

Los modelos de predicción de hábitat evaluados en general muestran una buena precisión mostrando similares resultados en cuanto a los indicadores de la bondad de ajuste (Figura 4, Capítulo 1), De los 11 modelos evaluados los mejores resultados en ambas especies se obtuvieron con los modelos ensamblados, mostrando la superioridad de esta técnica con respecto a la de los modelos individuales (Tabla 3, Capítulo 1). La evidente susceptibilidad de *E. dunnii* frente al aumento de temperatura en los meses de verano se ve reflejado en los mapas de probabilidad de distribución en función del cambio climático previsto para las próximas décadas. Los diferentes escenarios de aumento de la temperatura para los años 2050 y 2070 parecen tener un importante efecto sobre la presencia de esta especie en las diferentes regiones forestales con respecto a la situación actual (Figura 6, Capítulo 1). Estos resultados ponen en duda la viabilidad de esta especie en el largo plazo, concordando con lo obtenido por Jovanovic et al., (2000), los cuales concluyen que la región ocupada por Uruguay tiene condiciones que desde el punto de vista del clima no son las adecuadas para la especie. La mayor dependencia de *E. grandis* de los parámetros del suelo con respecto a las del clima se ve reflejada en los mapas de probabilidad de distribución en función del cambio climático previsto para las próximas décadas. Los posibles escenarios de aumento de la temperatura para las próximas décadas no parecen tener mayor efecto sobre la presencia de esta especie en las distintas zonas forestales del país con respecto a la situación actual (Figura 7, Capítulo 1). Los requerimientos de sitio de esta especie han permitido que se adapte a amplio rango de condiciones en todo el mundo siendo una de las especies más plantadas en regiones de clima templado (Schönau, 1984). Una de las restricciones de la especie es su reducida tolerancia a las bajas temperaturas en etapas tempranas del crecimiento (Brussa, 1994) que se manifiestan con mayor intensidad durante los meses de invierno en las zonas topográficas más bajas. No obstante, las predicciones de cambio en el clima para la región de Uruguay indican que se produciría un aumento en las temperaturas medias mínimas lo cual atenuaría esta restricción sobre la especie (Giménez et al., 2009). Esto podría estar explicando que la probabilidad de ocurrencia de esta especie a futuro sea prácticamente la misma comparado con la distribución de hábitat óptimo que se observa actualmente.

3. Sobrevivencia de las plantaciones

Los valores de sobrevivencia de Tacuarembó al final del período de evaluación estuvieron comprendidos entre el 30 y el 60% mientras que en Paysandú alcanzaron valores de 70 a 90% y en ambos sitios *E. benthamii* y *E. dunnii* registraron los mayores valores. El análisis de los resultados de la sobrevivencia, la cual determina importantes diferencias en los resultados de ambos sitios, no depende de la densidad de plantación en los primeros 76 meses de crecimiento (Figura 1, Capítulo 2). Esto confirma los resultados obtenidos por varios autores en el sentido de que estas especies de eucaliptos son relativamente tolerantes a la competencia al menos en los primeros años del crecimiento. La evolución de los valores de ambos sitios parece estar vinculada al efecto de competencia de tipo asimétrica, que ocurre entre árboles de diferente grado de desarrollo (Weiner et al., 2001; Soares et al., 2016). De acuerdo a Tomé y Verwjjst (1996), este tipo de competencia determina la ocurrencia de árboles suprimidos los cuales tienen una relativa persistencia y tolerancia a la sombra. La evolución del coeficiente de variación del *Vi* (datos no presentados) sustenta la hipótesis de la existencia de una gran variación de este parámetro, asociado positivamente con la densidad de plantación. La mayor tasa de mortalidad ocurrida en el sitio de Tacuarembó desde las primeras etapas del crecimiento fue el resultado de una inadecuada preparación de las condiciones de plantación tanto previa como posterior a la misma. Las condiciones de temperatura y precipitaciones fueron muy similares para ambos sitios de modo que no explican las diferencias observadas en la cuanto al comportamiento de este parámetro (Figuras S5 y S6, Material suplementario, Capítulo 3). Esto muestra la importancia de lograr las condiciones óptimas de instalación de este tipo de cultivos, teniendo en cuenta la brevedad de los turnos y la intensa competencia a la que se ven sometidos los árboles desde el inicio. *E. grandis* es la especie que, en promedio, registra los menores valores de sobrevivencia en ambos sitios en la última etapa del crecimiento (46 y 7%, en Tacuarembó y Paysandú, respectivamente)

(Tabla 1, Capítulo 3). No obstante, esto no tiene incidencia en los niveles de crecimiento comparado con las otras dos especies como será analizado posteriormente.

4. Crecimiento

Los modelos de predicción del *Vi* tuvieron mejores estadísticos de ajuste fueron de tipo lineal y logarítmico en función del *dn* y dn^2h para cada sitio, especie y densidad de plantación. Todos los valores de R^2_{adj} obtenidos fueron superiores a 0.94 y los del error (*RCME*) y sesgo (*E)* muy próximos a 0 en todos los casos (Tabla 4 Capítulo 2). El ajuste del *Vi* en función de estas variables en especies forestales ha sido reportado por varios autores (Vega-Nieva et al., 2015) aunque también se han identificado otras variables que contribuyen a la mejora en la precisión de los mismos (González García et al., 2013). En este caso, las variables edad y número de árboles por hectárea no realizaron una contribución significativa a la predicción de los modelos. El mayor grado de ajuste considerando el conjunto de datos de todos los inventarios (1er al 5to año de crecimiento) y las diferentes densidades de plantación (2220 a 6660 árboles por ha^{-1}) de cada especie implica que los modelos puedan ser utilizados con cierta flexibilidad de condiciones. A su vez, los mismos tienen como únicas variables predictoras a parámetros de inventario que son relativamente sencillos de obtener a campo. El hecho de que se obtenga una mayor capacidad de predicción del *Vi* para cada sitio estaría explicado por las diferencias en las curvas de crecimiento propias de las condiciones de crecimiento de los mismos. Esto, sin duda, pudo estar influenciado por las diferencias registradas en la tasa de mortalidad observada desde las primeras etapas del crecimiento por las razones comentadas anteriormente. De todos modos, los modelos obtenidos en cada una de las especies son muy similares para los dos sitios indicando cierta semejanza en la relación entre el *Vi* vs las variables predictoras de ambos conjuntos de datos.

A diferencia de lo observado con la sobrevivencia, el crecimiento individual mostró el efecto de la competencia entre individuos entre las diferentes densidades de plantación (Tabla 3, Capítulo 2). En Tacuarembó, las variables *dbh, H, Vi* y esbeltez estuvieron afectadas solamente por la densidad de plantación, mientras que, en Paysandú, la *H* y la esbeltez dependieron del defecto combinado de la especie y de la densidad de plantación. El mayor efecto de los diferentes espaciamientos en el primero de los sitios mencionados está relacionado con la evolución de la densidad teniendo en cuenta que la “distancia” en términos del número de árboles entre las densidades extremas (6660 vs 2220 árboles por ha^{-1}) va en aumento con el paso del tiempo. Este cambio en las proporciones de árboles vivos se debió a la relativa alta tasa de mortalidad de las densidades más bajas de plantación. Las mayores tasas de sobrevivencia registrada en Paysandú determinaron que las relaciones entre las densidades de plantación se mantuvieran relativamente estables con el paso del tiempo. Por otro lado, es conocida la menor dependencia de la *H* al manejo silvicultural y su mayor relación con las condiciones del sitio (Alcorn et al., 2007; Neto et al., 2010). Como consecuencia del mayor efecto del espaciamiento sobre el *dbh* que sobre la *H*, se observó una mayor esbeltez de los árboles (relación *H*/*dbh*) con las mayores densidades de plantación, aunque también se detecta un efecto simultáneo de esta y de la especie. Este menor ahusamiento del fuste podría tener efectos negativos sobre la resistencia mecánica de la madera (Warren et al., 2009; Díaz Bravo et al., 2012), aunque en este estudio estaría asociado a cambios en la densidad de la madera como será analizado oportunamente.

El volumen acumulado tuvo un comportamiento diferente en cada sitio, asociado a los efectos combinados de la especie y la densidad de la plantación (Tacuarembó) y de la especie (Paysandú) (Tabla 3, Capítulo 2). No obstante, en la mayoría de los casos la mayor productividad se obtuvo con las densidades de plantación más altas. En Tacuarembó, los niveles más altos de productividad se obtienen con las tres especies en las mayores densidades de plantación, y en Paysandú, en cambio, *E. grandis* fue la especie que en promedio tuvo la mayor tasa de crecimiento para todas las densidades de plantación (371.8 m^3 ha^{-1}). La respuesta del crecimiento en función de la densidad de plantación que se obtuvo en este sitio no fue significativa. Esto se explica por la similitud que se observó en el crecimiento alcanzado con *E. dunnii* en los diferentes espaciamientos. Con esta especie se registró una reducción en el crecimiento individual de similar magnitud al aumento de la densidad de plantación. Esto podría ser una señal de una menor tolerancia a la competencia entre individuos compara con las otras especies debido a la mayor sobrevivencia alcanzada en este sitio.

La evolución de las curvas de crecimiento también muestra diferencias entre sitios, explicadas en buena medida por las respectivas tasas de sobrevivencia. En Tacuarembó, la alta tasa de mortalidad dio lugar a un estancamiento en la tasa de crecimiento (IMA) próximo al 4to año, indicando el momento óptimo de cosecha. Esto ocurre de manera muy similar para todas las especies y densidades de plantación. En Paysandú, el momento de cosecha sucede aproximadamente a la misma edad, pero con mayores niveles de productividad de las especies y densidades de plantación (Figuras 5 a 10, Capítulo 2). Si bien el efecto de la competencia determina una reducción en el crecimiento individual, esto no se tradujo en un acortamiento del turno de cosecha como señala Harris, (2007). De todos modos, con los menores espaciamientos se obtienen altos rendimientos en períodos más cortos coincidiendo con lo reportado por varios autores (Sochacki et al., 2007; Eufrade Junior et al., 2013).

5. Densidad de la madera y producción de biomasa

La densidad de la madera es un parámetro de interés ya que está relacionada (junto con el volumen) con la producción de biomasa (Lopes et al., 2017), y fundamentalmente con la calidad de la madera como combustible ya que determina el contenido energético por unidad de volumen (Viana et al., 2018). Esto, a su vez, tiene implicaciones sobre el almacenamiento y el transporte de la madera en la medida que altos valores de esta variable redundan en una reducción de los costos de manejo de la misma. El estudio de la evolución de la densidad de la madera cobra importancia debido a que condiciona la productividad de un rodal en etapas posteriores a la del estancamiento del volumen (Lopes et al., 2017). Resultados obtenidos por varios autores muestran que la densidad de la madera es afectada tanto por la densidad de plantación como por la edad de los árboles (Paulino, 2012; Santana et al., 2012; Rocha et al., 2016), las cuales a su vez están estrechamente vinculadas (Machado et al., 2012). En este estudio, el análisis de los valores de la densidad de la madera mostró un comportamiento notoriamente diferente entre ambos sitios (Tabla 4, Capítulo 3). Los valores más altos se obtuvieron en Paysandú, lo que podría explicarse por alguna de las condiciones del sitio, tal y como ha sido registrado en estudios anteriores con estas especies de eucaliptos (Resquin et al., 2005). De los posibles factores ambientales que se asocian positivamente con la densidad de la madera se citan la disponibilidad de agua y de nutrientes (du Toit et al., 2001; Gava y Gonçalves, 2008; Sansígolo y Ramos, 2010; Drew et al., 2011), así como la temperatura (Thomas et al., 2004 y 2007), los cuales favorecen las altas tasas de crecimiento. No obstante, algunos reportes indican una relación positiva entre el estrés hídrico y la densidad de la madera de *E. grandis* (Searson et al., 2004). De la observación de las características de cada sitio se desprende que la temperatura durante el período de evaluación ha sido el parámetro que podría explicar estas diferencias, como fue comentado anteriormente. El régimen de precipitaciones fue muy similar en ambos casos (Figuras S1 y S2, Material suplementario Capítulo 2), al mismo tiempo que los dos tipos de suelos habrían hecho un aporte de nutrientes del mismo tenor al crecimiento de los árboles (Bentancor, 2017). El incremento de la densidad de la madera con el aumento del espaciamiento es atribuido a la mayor uniformidad de la densidad en el sentido medula-corteza y a la formación precoz de madera adulta la cual tiene fibras con paredes de mayor espesor (Cassidy et al., 2013). Este último factor también se menciona como el principal responsable del aumento de la densidad de la madera en los primeros años del crecimiento de los eucaliptos (Sette Jr. et al., 2012).

El ajuste de los modelos de estimación del peso individual del fuste tiene características similares a las del volumen individual en el sentido de que en todos los casos se obtuvo una precisión alta desde el punto de vista del R^2_{adj}, *RCME* y *E* (Tablas S2 y S3, Material suplementario Capítulo 3). Las variables que mostraron mayor capacidad de predicción fueron el *dbh* y la *H*, con relaciones de tipo logarítmico entre estas y el peso individual. A diferencia de lo ocurrido con el volumen individual, el mejor ajuste de los modelos se obtuvo para cada densidad de plantación por separado. Esta diferencia podría estar relacionada con el diferente comportamiento de la densidad de la madera con respecto al diámetro y la altura de los árboles en las diferentes densidades de plantación. Los modelos ajustados para el sitio de Paysandú dieron como resultado una ligera subestimación de los valores de peso más altos concordando con lo obtenido por Cunia, (1964) y Cailliez, (1980), los cuales argumentan que esto es un resultado frecuente de los modelos de tipo logarítmicos.

El peso individual tiene un comportamiento muy similar al del volumen individual ya que los valores más altos se obtuvieron con los espaciamientos mayores (Tabla 7, Capítulo 3). El análisis de los valores de Tacuarembó detectó un efecto significativo de la interacción especie y densidad de plantación, indicando que el peso individual depende del efecto combinado de ambos factores. El valor de peso más alto se obtuvo con *E. dunnii* a 2220 árboles ha^{-1} (112 kg $arbol^{-1}$), aunque con las densidades más bajas se obtuvieron valores estadísticamente iguales en todas las especies. En Paysandú, los efectos de la especie y de la densidad de plantación fueron significativos e independientes entre sí, de modo que los valores más altos se alcanzaron con *E. grandis* (74 kg $arbol^{-1}$), y con los mayores espaciamientos (95 y 39 kg $arbol^{-1}$, 2220 vs 6660, árboles ha^{-1}, respectivamente). La mayor diferencia de peso observada entre las densidades de plantación en este sitio se explicó por el efecto de la densidad de la madera. En este sitio, el mayor peso individual de los espaciamientos más altos fue acompañado de una mayor densidad de la madera. En Tacuarembó, en cambio, las diferencias de peso se explican básicamente por el crecimiento individual. La diferencia registrada en los valores medios de ambos sitios se explica por la menor competencia ocurrida en Tacuarembó debido a la mayor tasa de mortalidad.

El peso por hectárea, en ambos sitios, estuvo influenciado por el efecto combinado de la especie y la densidad de plantación (Tabla 7, Capítulo 3). En ambos ensayos, los valores más altos de productividad se alcanzaron para las tres especies en las densidades de plantación más altas. En todos los casos, se observó que la reducción en el peso individual en función del aumento de la competencia fue compensada por el incremento en el número de árboles, al igual que lo sucedido con el volumen. Esto indicaría la tolerancia relativa a la competencia que muestras estas especies, aun con las densidades más altas, hasta una edad de 76 meses a pesar del aumento de la heterogeneidad en el tamaño de los árboles con la reducción del espaciamiento. La respuesta al incremento de la población de árboles es diferente en cada sitio, en Tacuarembó se obtuvo un incremento medio del 60%, mientras que en Paysandú fue del 16% entre las densidades extremas (6660 vs 2220 árboles ha^{-1}). Esta diferencia en parte se debe al efecto negativo que tiene en este sitio la reducción del espaciamiento, al mismo tiempo que una relativa independencia en el sitio de Tacuarembó. En ambos casos, la productividad por hectárea también estuvo condicionada por la sobrevivencia, de modo que la menor mortalidad registrada en Paysandú redunda en mayores tasas de crecimiento para todas las densidades de plantación. La evolución del IMA, en general, mostró incrementos crecientes hasta los 76 meses, con las densidades de plantación indicando que no se había alcanzado el momento óptimo de cosecha. En cambio, en *E. benthamii* en Tacuarembó, se observó cierto estancamiento en la tasa de crecimiento próximo a la edad de 57 meses.

6. Contenido de energía

El contenido de energía de la madera es una de las variables de mayor interés en la evaluación de la biomasa forestal, dado que incide en los costos de transporte, el almacenamiento y el rendimiento energético, en particular en un cultivo de alta densidad de plantación (Viana et al., 2018). Estos factores determinan la viabilidad económica de este tipo de cultivos, de manera que interesa evaluar el efecto de algunos parámetros silviculturales a los efectos de identificar sistemas eficientes de producción de energía. Una de las variables que más incide en el contenido energético de la madera es el poder calórico, el cual depende básicamente de algunos parámetros de la composición química como la lignina, los extractivos y la relación S/G de la lignina (Castro et al., 2015; Santos et al., 2016). La semejanza de los valores obtenidos en Tacuarembó confirmar el concepto de que esta variable es relativamente independiente de algunas prácticas silviculturales como el espaciamiento (Tabla 3, Capítulo 4) (Rocha et al., 2016), así como el tipo de especie de eucalipto (Pérez et al., 2014). Sin embargo, algunas características de la madera en Paysandú determinaron que el poder calórico fue más alto en las densidades mayores (Tabla 3, Capítulo 4). De los parámetros evaluados, existen dos que, de acuerdo a la literatura, podrían estar explicando este comportamiento, la densidad de la madera y la relación *H*/*dbh*. El efecto de la densidad de la madera sería indirecto, ya que las variaciones de esta en edades tempranas se asocian en forma negativa con el contenido de cenizas y con la relación S/G (Soares et al., 2014). Los minerales que integran esta fracción son de tipo inertes, y contribuyen negativamente con el contenido calórico de la madera (Kumar et al., 2010). Por otro lado, se ha determinado que la unidad guaiacila (G) tiene una mayor relación carbono/oxígeno que la unidad siringila (S), lo cual le confiere mayor poder calórico debido al carbono es el principal elemento combustible (Protásio et al., 2017). El efecto de la mayor relación *H*/*dbh* registrada en Paysandú determinó que los árboles tengan una alta proporción de fuste por encima de la región del *dbh*. La madera de esta región que está relativamente próxima a la zona de la médula, y tiene una alta proporción de madera juvenil, la cual contiene mayores niveles de lignina y extractivos que la madera madura (Larson et al., 2001), relacionados positivamente con el contenido calórico de la madera como fuera comentado previamente. Los cambios ocurridos en Paysandú con el aumento de la edad estarían explicados básicamente por los cambios observados en la densidad de la madera.

La densidad energética de la madera acompaña básicamente la evolución de la densidad de la madera, la cual está más influenciada por la edad, la especie y la densidad de plantación que el poder calórico. Este parámetro mostró un aumento con la edad en ambos sitios, pero con niveles poco relevantes desde el punto de vista práctico (Brand, 2010). En Tacuarembó, el incremento de la edad no implica cambios en el contenido energético de la madera por unidad de volumen, mientras que en Paysandú se produjo un aumento del 14% hasta la edad de 76 meses (Tabla 6, Capítulo 4). El rendimiento energético está directamente relacionado con la productividad de biomasa, de manera que los valores más altos se obtuvieron con los espaciamientos menores para las tres especies en ambos sitios. Las diferencias de rendimiento energético entre espaciamientos fueron crecientes con el paso del tiempo, determinada por la evolución propia de cada especie y densidad de plantación (Figura 3, Capítulo 4). La evolución de la tasa de incremento del rendimiento energético en Tacuarembó mostró un aumento hasta la edad de 48 meses, momento a partir del cual registra una ralentización hasta el final del período de evaluación. Esto podría ser un indicador del momento de cosecha, aunque para esto se requiere del análisis conjunto con el incremento corriente anual de esta variable. La evolución de esta variable en Paysandú mostró, en general, aumentos crecientes hasta el final del período, aunque los mismos fueron significativamente iguales a partir del mes 48. Los valores más altos de densidad y rendimiento energético fueron alcanzados en Paysandú, explicados por la densidad de la madera y las tasas de crecimiento registrados en este sitio como fuera comentado anteriormente. El incremento en el número de árboles no se tradujo, en ninguno de los casos, en aumentos en igual proporción del volumen, del peso o del rendimiento energético por ha^{-1}. Esto sugiere la necesidad de analizar algunos de los costos de instalación de este tipo de cultivo, teniendo en cuenta que con las densidades extremas de plantación (2220 vs 6660 árboles ha^{-1}) se triplica los costos de las plantas, la fertilización y de las operaciones asociadas a las mismas.

7.Extracción de nutrientes

Otro aspecto relevante al momento de evaluar este tipo de cultivos está relacionado con la sustentabilidad de los mismos. En general, en los sistemas forestales ocurre un importante reciclado de nutrientes a través de la deposición de ramas, corteza y hoja que contribuyen al aporte requerido por las plantas (Ludvichak et al., 2016). Esto es de particular importancia en los suelos de baja fertilidad natural, que frecuentemente son destinados a la instalación de las especies forestales (Silva et al., 2013). En Uruguay, los sistemas forestales convencionales instalados con especies de eucaliptos son de ciclos relativamente largos (de 10 a 25 años), y tienen como único producto comercial a la madera sin corteza. La utilización de solamente el fuste a esas edades determina que la extracción de nutrientes sea relativamente baja, teniendo en cuenta la reducida concentración de minerales de esta fracción del árbol (Hernández et al., 2009). Los sistemas de corta rotación, en cambio, tienen la particularidad de que los turnos son más cortos y con una mayor población de árboles que los convencionales, y que se cosechan todas las fracciones aéreas del árbol. Esto determina que los niveles de extracción de algunos nutrientes sean de tal magnitud que en suelos de baja capacidad de aporte mineral pueda verse comprometida la fertilidad debido a los altos niveles de producción en el mediano plazo.

Los pesos de las fracciones madera y corteza son los únicos relacionados a la especie y en general de forma directa con la densidad de plantación tal y como fue analizado en párrafos anteriores (Tabla 1, Capítulo 5). La proporción del peso de las diferentes fracciones en la biomasa total es prácticamente la misma para las especies y densidades de plantación estudiadas en esta tesis, indicando que la competencia no afecta la partición en la distribución de la biomasa hasta la edad de 76 meses (Figura 1, Capítulo 5). Los contenidos de nutrientes de las diferentes fracciones de las especies y densidades de plantación fueron similares en ambos sitios, debido probablemente a la semejanza en la composición química de ambos tipos de suelos (Bentancor, 2017), aunque esta afirmación no tiene rigor estadístico. En ambos casos se observó que las concentraciones de nutrientes no de la densidad de plantación, y que las mismas estaban afectadas por la especie (Tablas S2-S7, Material suplementario Capítulo 5). Por otro lado, se confirmó el hecho de que las hojas concentren la mayor proporción de P, K y N, mientras que la corteza contiene niveles altos de Ca y Mg. También se verificó que la madera es la fracción con las concentraciones menores de los nutrientes evaluados. En promedio, la relación en la concentración de nutrientes en las hojas con respecto a la madera para las especies y densidades de plantación estudiadas fue de 9 a 2. La extracción de nutrientes, a diferencia de lo observado para las concentraciones, dependió de la especie y de la densidad de plantación, ya que estos factores determinan diferencias en la productividad de biomasa (Tablas 2 y 3, Capítulo 5). En Tacuarembó, el aumento de la densidad de plantación de 2220 a 6660 árboles ha^{-1} provocó, en promedio, un incremento de la extracción de 60, 64, 48 y 64% para el P, Mg, K y N, respectivamente. En términos absolutos, los niveles de extracción más importantes fueron de Ca, K y N, con valores de 558 a 658 kg ha^{-1}, 514 a 762 kg ha^{-1} y 290 a 475, respectivamente. Cosechando solamente la fracción madera, en promedio, se produciría una reducción en la extracción del orden de: 55, 36 y 58% para los nutrientes mencionados. En Paysandú, también se observó una alta extracción de K y N con el aumento de la densidad de plantación, con valores de 529 vs 734 kg ha^{-1}; 295 vs 443 kg ha^{-1} para las densidades de 2220 y 6660 árboles ha^{-1}, respectivamente, representando un aumento de 39 y 50% para ambos nutrientes. En este sitio, la reducción en los niveles de extracción mediante la cosecha de la fracción madera fue de 47, 67, 59, 52 y 62% para el P, Ca, Mg, K y N, respectivamente. La eficiencia de utilización de los nutrientes, en general, mostró poca relación con la densidad de plantación en ambos sitios, destacándose *E. benthamii* y *E. grandis* con los valores más altos en ambos sitios (Figuras 4 y 5, Capítulo 5). La eficiencia de utilización de los nutrientes no mostró relación con la productividad de biomasa de manera que es posible identificar combinaciones de especie y densidad de plantación de alto rendimiento con bajos contenidos de nutrientes.

Los resultados obtenidos señalan la importancia de lograr un buen establecimiento del cultivo a través de las actividades de preparación del suelo y el control de malezas y de hormigas previo y posterior a la plantación. Este aspecto es crítico ya que incide en la productividad tanto del primero como de los turnos siguientes a la primera cosecha (Sims et al., 2001). De acuerdo a estos autores lograr una alta sobrevivencia es de vital importancia para lograr altos niveles de rendimiento en varios turnos de cosecha y reducir las actividades de plantación las cuales tienen un alto costo. Los resultados obtenidos mostraron la performance de las especies y densidades de plantación en una primera rotación desde el punto de vista de la generación de energía (que es el objetivo de producción) y de un aspecto de la sustentabilidad de los mismo como es la extracción de nutrientes. El tipo de árboles que forman parte de la primera rotación es notoriamente diferente al rebrote originado en los turnos sucesivos a la primera cosecha. Los rebrotes formados a partir del tocón determinan que exista una alta competencia entre individuos resultando en varios individuos de diámetro reducido, con una alta proporción de corteza, ramas y hojas. Las especies de eucaliptos usadas comercialmente en general tienen una alta tasa de rebrote y en algunos casos son manejados de forma de mantener dos o tres individuos por tocón dependiendo del objetivo de producción (madera sólida, celulosa o leña) (Ríos-Saucedo et al., 2017). Resultados obtenidos por varios autores con varias especies de Eucalyptus muestran que el turno siguiente a la primera cosecha tienen un nivel de producción de biomasa total superior con respecto a esta (Sims et al., 2001). Estos resultados muestran que en los casos en los que se obtiene un nivel de sobrevivencia superior al 50% es posible alcanzar altos niveles de producción y de ese modo evitar los costos de una nueva plantación (Sims et al., 1999). Dependiendo de la densidad de plantación utilizada en este tipo de cultivos la fracción de biomas a cosechar podría ser el fuste con corteza o el árbol entero. Esto está condicionado por los diámetros obtenidos con los diferentes espaciamientos lo que a su vez también depende de la tasa de crecimiento y del largo de la rotación. En la etapa de rebrote (posterior a la primera cosecha) la biomasa está compuesta por una alta proporción de corteza, ramas y hojas lo que determina una materia más heterogénea compara con la del fuste y con propiedades tecnológicas diferentes (Eufrade Junior et al., 2018). El escenario de los turnos siguientes a la primera cosecha, por tanto, plantea una serie de interrogantes que deben ser evaluados en el mediano plazo desde el punto de vista productivo, tecnológico y ambiental para determinar la viabilidad de este tipo de cultivos. En este sentido, el ensayo instalado en Paysandú surge como el más apropiado para continuar con este tipo de evaluaciones teniendo en cuenta que presenta características interesantes como una alta tasa de sobrevivencia y está instalado en un suelo representativo de una de las regiones forestales del país.

8. Referencias

Acuña, E., R. Rubilar; J. Cancino; T.J. Albaugh; C.A. Maier. 2018 Economic assessment of *Eucalyptus globulus* short rotation energy crops under contrasting silvicultural intensities on marginal agricultural land. Elsevier. Land Use Policy. 76:329–337.

Administración del Mercado Eléctrico (ADME). Available at: http://adme.com.uy/ (Consultada: 25 January 2019).

Albaugh, T. J.; R.A. Rubilar; C.A. Maier; E.A. Acuña; R.L. Cook, R. L. 2017. Biomass and nutrient mass of *Acacia dealbata* and *Eucalyptus globulus* bioenergy plantations, Biomass and Bioenergy, 9:162–171.

Alcorn, P. J.; P. Pyttel; J. Bauhus; G.B. Smith; D. Thomas; R. James; A. Nicotra.2007. Effects of initial planting density on branch development in 4-year-old plantation grown *Eucalyptus pilularis* and *Eucalyptus cloeziana* trees. Forest Ecology and Management, 252: 41–51.

Baettig, R.; M. Yáñez; M. Albornoz. 2010.Cultivos dendroenergéticos de híbridos de álamo para la obtención de biocombustibles en Chile : estado del arte. Bosque, 31(2): 89–99.

Balmelli, G. 1995. Ensayos de orígenes de *Eucalyptus globulus*. Evaluación al 3er año', Serie Técnica INIA 68, p. 19. http://www.ainfo.inia.uy/digital/bitstream/item/2973/1/111219240807134928.pdf

Balmelli, G.; F. Resquin. 2004. Evaluación del crecimiento de especies de Eucalyptus en diferentes zonas de prioridad forestal, Serie Aftercare Forestal INIA - JICA, 14, p. 20. http://www.ainfo.inia.uy/digital/bitstream/item/4330/1/Aftercare-del-Proyecto-de-Mejoramiento-Genetico-Forestal-en-el-Uruguay-2000-2002-Nro.-14.pdf. Accessed May 28th, 2018.

Balmelli, G.; F. Resquin. 2006. Productividad de diferentes especies de Eucalyptus sobre areniscas de Tacuarembó-Rivera, Serie Técnica 159. INIA Tacuarembó, 159, pp. 305-312. http://www.ainfo.inia.uy/digital/bitstream/item/7774/1/ST-159-305-312.pdf. Accessed April 20th, 2018.

Brazeiro, A.; D. Panario; A. Soutullo; O. Gutierrez; A. Segura; P. Mai. 2012. Clasificación y delimitación de las eco-regiones de Uruguay. Informe Técnico. Convenio MGAP/PPR – Facultad de Ciencias/Vida Silvestre/ Sociedad Zoológica del Uruguay/CIEDUR. 40p.

Brussa, C. 1994. Eucalyptus. Especies de cultivo más frecuente en Uruguay y regiones de clima templado. Montevideo (Uruguay): Hemisferio Sur. 328 p

Bustillos-Herrera, J. A.; J.R.Valdez-Lazalde; A. Aldrete; M.de J. Gonzalez-Guillen. 2007. Land suitability for eucalyptus (*Eucalyptus grandis* Hill ex Maiden) plantations: Definition through the analytic hierarchy process and gis. Agrociencia, 41(7): 787–796.

Cabrera, A.; C. Tozzini; S. Espinoza; R. Santelices; E. Bonari. 2014. Cálculo del balance energético de una plantación de *Populus deltoides* clon Lux con fines energéticos en un sitio con ambiente mediterráneo. Bosque, 35(2): 133–139.

Cailliez, F. 1980. Estimacion del volumen forestal y prediccion del rendimiento con referencia especial a los trópicos vol. 1 - estimacion del estimación volumen. Estudio FAO: Montes 22/1, p. 93.

Califra, H.; A. Durán. 2010. 10 Años de Investigación en Producción Forestal. Productividad y preservación de los recursos suelo y agua. Jornada de Actualización técnica. Dpto de Suelos y Aguas. Facultad de Agronomía. Universidad de la Republica. Montevideo, Uruguay. 65 p.

Caron, B.; E. Eloy; V. De Souza; D. Schmidt; R. Balbinot; A. Behling; G.C. Monteiro. 2015. Quantification of forest biomass in short rotation plantations with different spacings | Quantificação da biomassa florestal em plantios de curta rotação com diferentes espaçamentos. Comunicata Scientiae, 6(1): 106-112.

Cassidy, M.; G. Palmer; R.G.B. Smith. 2013. The effect of wide initial spacing on wood properties in plantation grown *Eucalyptus pilularis*. New Forests, 44(6): 919–936.

Castaño, J. P.; A. Ceroni; M. Furest; J. Aunchayna; R. Bidegain. 2011. Caracterización agroclimática del Uruguay 1980-2009. Serie Técnica INIA. Montevideo, Uruguay., 193, p. 33. http://www.ainfo.inia.uy/digital/bitstream/item/2538/1/18429021211104157.pdf

Castro, A. F. N. M.; R.V.O. Castro; A.D.C. Oliveira; R.C. dos Santos; A.M.M.L.

Carvalho; P.F. Trugilho; I.C.N.A. Melo. 2016. Correlations between age, wood quality and charcoal quality of eucalyptus clones. Árvore, 40(3):551–560.

Ciria, P. 2011. Desarrollo de los cultivos energéticos leñosos en España. Vida RURAL, CEDER-CIEMAT (Soria). Unidad de Biomasa:10–15.

Cunia, T. 1964. Weighted Least Squares and Construction of Volume Tables. Forest Science, 10(2): 180–191.

Díaz Bravo, S.; M. Espinosa; L. Valenzuela; J. Cancino; J.P. Lasserre. 2012. Efecto del raleo en el crecimiento y algunas propiedades de la madera de Eucalyptus nitens en una plantación de 15 años. Maderas. Ciencia y tecnología, 14(3):373-388

Dimitriou, I.; P. Aronsson. 2005.Willows for energy and phytoremediation in Sweden. Unasylva, 56(221): 47–50.

Drew, D. M.; G. Downes; R. Evans. 2011.Short-term growth responses and associated wood density fluctuations in variously irrigated *Eucalyptus globulus*. Trees - Structure and Function, 25(2):153–161.

Durán, A. 2008. Índice de productividad CONEAT: origen de los índices, concepto de productividad, nomenclatura y utilización. Facultad de Agronomía.Universidad de la República. Material elaborado en base a presentación del Prof. Artigas Durán. URL: http://www.fagro.edu.uy/~edafologia/curso/Material%20de%20lectura/ TEORICOS/coneat2008.ppt.

Eloy, E.; D.A. Da Silva; D. Schmidt; R. Trevisan; B.O. Caron; E. Elli. 2016. Effect of planting age and spacing on energy properties of *Eucalyptus grandis* W. Hill Ex Maiden. Árvore, 40(4): 749–758.

Eufrade Junior, H. J.; A. Ballarin; S.P.S. Guerra; G. Oguri. 2013. Influência Do Espaçamento Na Densidade Básica Da Madeira Em Sistemas Florestais De Curta Rotação in 8° Congresso Internacional de Bioenergia São Paulo – SP – 05 A 07 de Novembro, pp. 5–9.

Eufrade Junior, H. J.; R.X. de Melo; M.M.P. Sartori; S.P.S. Guerra; A.W. Ballarin. 2016. Sustainable use of eucalypt biomass grown on short rotation coppice for bioenergy. Biomass and Bioenergy, 90: 15–21.

Eufrade-Junior, H. de J., S.P.S Guerra; C.A. Sansígolo; A.W. Ballarin, A. W. 2018. Management of Eucalyptus short-rotation coppice and its outcome on fuel quality. Renewable Energy, 12:309–314.

FAO. 1981. El eucalipto en la repoblación forestal. Colección FAO: Montes N° 11. Organizacion de las Naciones Unidas para la Agricultura y la Alimentacion. Roma, Italia. 790 p.

Foelkel, C. 2015. Qualidade da Biomassa Florestal do Eucalipto para Fins Energéticos. Eucalyptos Newsletter No 49, pp. 78–107. http://www.eucalyptus.com.br/artigos/news49_Biomassa_Florestal_Eucalipto.pdf

Gava, J. L.; J.L.M. 2008. Soil attributes and wood quality for pulp production in plantations of *Eucalyptus grandis* clone. Scientia Agricola, 65(3): 306–313.

Giménez, A.; J.P. Castaño; E. Baethgen; B. Lanfranco. 2009. Cambio climático en uruguay, posibles impactos y medidas de adaptación en el sector agropecuario. Serie Técnica INIA 178, pp. 1–23. http://www.ainfo.inia.uy/digital/bitstream/item/3014/1/18429071209133815.pdf

Gonçalves, J. L. de M.; J.L. Stape; J.P. Laclau; P. Smethurst; J.L. Gava. 2004. Silvicultural effects on the productivity and wood quality of eucalypt plantations. Forest Ecology and Management, 193(1–2):45–61.

Guerra, S. P. S.; E. A. Garcia; K.P. Lanças; M.A. Rezende; R. Spinelli. 2014. Heating value of eucalypt wood grown on SRC for energy production. Elsevier Ltd. Fuel 137:360–363.

Harris, F 2007, The effect of competition on stand, tree, and wood growth and structure in subtropical Eucalyptus grandis plantations', PhD thesis, Southern Cross University, Lismore, NSW. 193 p.

Hernández, J.; A. del Pino; L. Salvo; G. Arrarte. 2009. Nutrient export and harvest residue decomposition patterns of a *Eucalyptus dunnii* Maiden plantation in temperate climate of Uruguay. Forest Ecology and Management, 258(2):92–99.

Instituto para la Diversificación y Ahorro de la Energía, IDAE. 2007. Biomasa: Cultivos energéticos. Madrid. Available at: www.idae.es.

Jiménez Bocanegra, J. A.; F. Perea Torres; J. Lobo García; L. Pavón Prada; V.H. Durán Zuazo. 2013. Evaluación del cultivo de eucalipto para la producción de biomasa en Andalucía, Vida RURAL 1:62–66.

Jovanovic, T.; R. Arnold; T. Booth. 2000. Determining the climatic suitability of *Eucalyptus dunnii* for plantations in Australia, China and Central and South America. New Forests, 19(3):215–226.

Kumar, R.; K.K. Pandey; N. Chandrashekar; S. Mohan. 2010. Effect of tree-age on calorific value and other fuel properties of *Eucalyptus* hybrid. Journal of Forestry Research, 21(4): 514–516.

Laclau, J.-P.; E.A. da Silva; G. Rodrigues Lambais; M. Bernoux; G. le Maire; J.L. Stape;

J.P. Bouillet; J. L. de M. Gonçalves; C. Jourdan; Y. Nouvellon. 2013. Dynamics of soil exploration by fine roots down to a depth of 10 m throughout the entire rotation in *Eucalyptus grandis* plantations. Frontiers in Plant Science, 4:1–13.

Larson, P. R.; D.E. Kretschmann; A.C. Iii; J.G. Isebrands. 2001.Formation and Properties of Juvenile Wood in Southern Pines A Synopsis. Rhinelander, Wisconsin.

Lopes, E. D.; M.L. Laia; A.S. Santos; G.M. Soares; R.W.P Leite; N.D.S. Martins. 2017. Influência do espaçamento de plantio na produção energética de clones de *Corymbia* e *Eucalyptus*. Floresta, 47(1):95-104

Ludvichak, A. A.; M.V. Schumacher; G. Dick; D.R. Momolli; H. Pablo De Souza; C. Guimarães. 2016. Nutrient return through litterfall in a *Eucalyptus dunnii* maiden stand in sandy soil. Revista Árvore, 40(6):1041–1048.

Machado, F. D. C.; S. Philipe; S. Guerra; N. Ceragioli; G. Oguri, G. 2012. Influência do espaçamento na produtividade e alocação de biomassa em um plantio de *Eucalyptus grandis* in Congresso Internacional de Bioenergia, pp. 1–6.

Marcos, F. 2006.Generación de energía eléctrica con biomasa a medio y largo plazo. Anales de mecánica y electricidad:22–27.

MGAP-DIEA. 2017. Anuario Estadístico Agropecuario, Http://Www.Mgap.Gub.Uy/Sites/Default/Files/Diea-Anuario2017Web01a.Pdf. doi: 10.1016/S0367-326X(02)00066-7.

Ministerio de Industria y Mineria (MIEM). 2008. Uruguay: Política Energética 2005-2030. Ministerio de Industria, Energía y Minería - Dirección Nacional de Energía. Available at: http://www.dne.gub.uy.

Müller. M.D. 2005. Produção de madeira para geração de energia elétrica numa plantação clonal de eucalipto em Itamarandiba, MG. Tese de Doutorado. Universidade Federal de Viçosa. 108 p. http://www.bibliotecaflorestal.ufv.br/bitstream/handle/123456789/31/129121_c.pdf?sequence=2&isAllowed=y.

Nava-García, F. J.; X.R. Doldán-García. 2014. Cultivos energéticos. Agricultura, socidad y desarrollo, 11(1): 26–34.

Neto, S. N. d. O.; G.G. Reis; M. d. G. F. Reis; H.G. Leite; J.C.L. Neves. 2010. Crescimento e Distribuição Diamétrica de *Eucalyptus camaldulensis* em Diferentes Espaçamentos e Níveis de Adubação na Região de Cerrado de Minas Gerais. Floresta, 40(4):755–762.

Paulino, E. J. 2012. Influência do espaçamento e da idade na produção de biomassa e na rotação econômica em plantios de Eucalipto. Dissertação de Mestrado. Universidade Federal Dos Vales Do Jequitinhonha e Mucuri. Diamantina, MG, Brasil. 60 p.

Perez, D.; A. Guillemain; A. Berthelot; N. N´Guyen-The; F. Morogues; C. Gomes. 2010. Evaluation of forestry biomass quality for the production of second-generation biofuels. Cellulose chemistry and technology, 44(1–3):1–14.

Pérez, S.; C.J. Renedo; A. Ortiz; F. Delgado; I. Fernández. 2014. Energy potential of native shrub species in northern Spain. Elsevier Ltd. Renewable Energy. 62:79–83.

Pérez, S.; C.J. Renedo; A. Ortiz; M. Mañana; F. Delgado; C. Tejedor. 2011. Energetic density of different forest species of energy crops in Cantabria (Spain). Biomass and Bioenergy, 35: 4657–4664.

Protásio, T. P.; P.F. Trugilho; A.C.C. De Araújo; T.A. Bastos; S.C. Da Silva Rosado; J.F.N. Pinto. 2017. Classification of Eucalyptus clones by the ratio syringyl/guaiacyl and growth characteristics for energy use. Scientia Forestalis, 45(114):327–341.

Resquin, F. 2015. Producción de biomasa con especies de eucalipto. Disponible en: http://www.inia.uy/estaciones-experimentales/direcciones-regionales/inia-tacuarembó/jornada-de-biomasa-forestal-2015. Acceso: 8 Febrero 2016.

Resquin, F.; J. Mello; I. Fariña; J. Mieres, L. Assandri. 2005. Caracterización de la celulosa de especies del género Eucalyptus plantadas en Uruguay. Serie Técnica INIA Nro 159, p. 82. http://www.inia.uy/Publicaciones/Documentos%20compartidos/18429160709160425.pdf

Ríos-Saucedo, J. C.; E. Acuña-Carmona; J. Cancino-Cancino; R. Rubilar-Pons; J. J. Corral-Rivas; R. Rosales-Serna. 2017. Dinámica de brotación y densidad básica de la madera en rebrotes de tres especies dendroenergéticas. Agrociencia, 51(2):215–227

Rocha, M.F.V.; B.R. Vital; A. C. O. de Carneiro; A.M.M.L. Carvalho; M.T. Cardoso; P.R.G. Hein. 2016. Effects of plant spacing on the physical , chemical and energy properties of *Eucalyptus* wood and bark. Journal of Tropical Forest Science, 28(3): 243–248.

Rodríguez, A.; J. Cancino; E. Acuña; R. Rubilar; F. Muñoz. 2013. Evaluación del crecimiento de plantaciones dendroenergéticas de *Eucalyptus globulus*, según densidad de plantación y turno de rotación en suelos contrastantes de la región del Bio Bio, Chile. Ciencia e Investigación Forestal INFOR, 19(1):7–13.

Rodríguez, C. R.; V.H. Durán; C. Bielders; J.A. Jiménes; F. Perea; J.R. Francia. 2014. Bioenergy farming using woody crops . A review. Agronomy for sustainable development, 35(1): 95–119.

Sansígolo, C. A.; E.S. Ramos. 2011. Quality of wood and pulp from a clone of *Eucalyptus grandis* planted at three locations. Cerne, 1: 47–60.

Santelices, R.; S. Espinoza; Cabrera, A. 2015. Especies del género Eucalyptus con potencial energético para ser establecidas en el secano Mediterráneo de la Región del Maule. Centro de Desarrollo para el Secano Interior. Universidad Católica del Maule. 65 p.

Santos. R.; A. Carneiro; B.R. Vital; R, Castro; G. Vidaurre; P.F. Trugilho; A. Castro. 2016. Influência das propriedades químicas e da relação siringil/guaiacil da madeira de eucalipto na produção de carvão vegetal. Ciência Florestal, 26(2):657–669.

Santos Santana, W. M.; N. Calegario; M. D. Chaves Arantes; P.F. Trugilho. 2012. Effect of age and diameter class on the properties of wood from clonal *Eucalyptus*. Cerne. Universidade Federal de Lavras, 18(1): 1-8

Schönau, A. P. G. 1984. Silvicultural considerations for high productivity of *Eucalyptus grandis*. Forest Ecology and Management, 9: 295–314.

Searson, M. J.; D.S. Thomas; K.D. Montagu; J.P. Conroy. 2004. Wood, density and anatomy of water-limited eucalypts. Tree Physiology, 24(11):1295–1302.

Seixas, F. 2008. Harvesting and Use of Forestry Biomass for Energy Production in the USA. Southern Research Station USDA Forest Service Auburn, Alabama, USA 2008. 118 p.

Sette Jr, R. C.; I.R. de Oliveira; M. Tomazello Filho; F. Minoru; J.P. Laclau. 2012. Efeito da idade e posição de amostragem na densidade e caracteristicas anatômicas da madeira de *Eucalyptus grandis*. Revista Árvore, 36(6): 1183–1190.

Silva, P. H. M. da; F. Poggiani; P.L. Libardi; A.N. Gonçalves. 2013. Fertilizer management of eucalypt plantations on sandy soil in Brazil: Initial growth and nutrient cycling. FElsevier B.V. Forest Ecology and Management. 301: 67–78.

Sims, R. E.; T.G. Maiava; B.T. Bullock. 2001. Short rotation coppice tree species selection for woody biomass production in New Zealand. Biomass and Bioenergy, 20(5): 329–335.

Sims, R. E. H.; K. Senelwa; T. Maiava; B.T. Bullock. 1999. Eucalyptus species for biomass energy in New Zealand - Part II: Coppice performance. Biomass and Bioenergy, 17(4): 333–343.

Siri-Prieto, G. 2014. Bioenergía en Uruguay: Oportunidades y Riesgos’, in I Congreso Uruguayo de Suelos. VI Encuentro de la SUCS. Colonia 6-8 Agosto 2014. Colonia, Uruguay. Available at: http://docplayer.es/66590539-Bioenergia-en-uruguay-oportunidades-y-riesgos.html.

Soares, V. C.; M.L. Bianchi; P.F.Trugilho; A. Júnior; J. Höfler, J. 2014. Correlações entre as propriedades da madeira e do carvão vegetal de híbridos de eucalipto. Árvore, 38(3): 543–549.

Sochacki, S. J.; R.J. Harper; K.R.J. Smettem. 2007. Estimation of woody biomass production from a short-rotation bio-energy system in semi-arid Australia. 31: 608–616.

Spinelli, R.; S.M. Ward; P.M. Owende. 2009. A harvest and transport cost model for *Eucalyptus* spp. fast-growing short rotation plantations. Biomass and Bioenergy. Elsevier Ltd, 33(9): 1265–1270.

Thomas, D. S.; K.D. Montagu; J.P. Conroy. 2004. Changes in wood density of *Eucalyptus camaldulensis* due to temperature—the physiological link between water viscosity and wood anatomy. Elsevier. Forest Ecology and Management. 193(1–2):157–165.

Thomas, D. S.; K.D. Montagu; J.P. Conroy. 2007. Temperature effects on wood anatomy , wood density , photosynthesis and biomass partitioning of *Eucalyptus grandis* seedlings. Tree Physiology, 27: 251–260.

du Toit, B.; A. Arbuthnot; D. Oscroft; R.A. Job; 2001. The effects of remedial fertilizer treatments on growth and pulp properties of *Eucalyptus grandis* stands established on infertile soils of the Zululand coastal plain. The Southern African Forestry Journal, 192(1): 9–18.

Viana, H.; A. Rodrigues; D.M.M. Lopes; R. Godina; L.J.R. Nunes; J.C. Matias. 2018. *Pinus pinaster* and *Eucalyptus globulus* Energetic Properties and Ash Characterization. Proceedings - 2018 IEEE International Conference on Environment and Electrical Engineering and 2018 IEEE Industrial and Commercial Power Systems Europe, EEEIC/I and CPS Europe 2018. IEEE, pp. 1–4. doi: 10.1109/EEEIC.2018.8494618.

Warren, E.; R.G.B. Smith; L.A. Apiolaza; J.C.F. Walker. 2009. Effect of stocking on juvenile wood stiffness for three Eucalyptus species. New Forests, 37(3): 241–250.

“Rara
como encendida
te hallé bebiendo
linda y fatal...
Bebías
y en el fragor del champán,
loca, reías por no llorar...
Pena
me dio encontrarte
pues al mirarte
yo vi brillar
tus ojos
con un eléctrico ardor,
tus bellos ojos que tanto adoré.

…Hoy vas a entrar en mi pasado,
en el pasado de mi vida...
Tres cosas lleva mi alma herida:
amor... pesar... dolor...
Hoy vas a entrar en mi pasado
y hoy nuevas sendas tomaremos**...”**

Enrique Cadícamo, 1942

Capítulo 8. Conclusiones generales

Las principales conclusiones alcanzadas en esta tesis doctoral han sido las siguientes:

1. El análisis conjunto del crecimiento y de las condiciones del sitio en plantaciones intensivas de *E. dunnii* y *E. grandis* en Uruguay permitió identificar las variables ambientales de mayor peso relativo en la producción de biomasa.
2. El crecimiento de *E. grandis* estuvo relacionado positivamente con la profundidad de los horizontes superficiales y en forma negativa con los contenidos de arcilla y de limo. Esto determina que el potencial de la especie se corresponda con una amplia región de los suelos forestales del país. El crecimiento de *E. dunnii* mostró también una asociación positiva con la profundidad del horizonte superficial, influenciada por la temperatura de los meses de verano y otoño. Esta relativa independencia de *E. grandis* de los parámetros climáticos determina que su hábitat potencial en Uruguay sea menos sensible a los posibles cambios que ocurran en el clima aún en los escenarios de mayor aumento de la temperatura. *E. dunnii*, en cambio, muestra una importante restricción de ocurrencia a futuro debido a la mayor susceptibilidad con respecto a las variables del clima. No obstante, en las condiciones actuales ambas especies presentan condiciones de adaptación a las distintas regiones forestales del país.
3. La sobrevivencia estuvo condicionada por las actividades de preparación del sitio previo y posterior a la plantación indicando la alta susceptibilidad de esta variable frente a la intensidad del manejo silvicultural en estas etapas del cultivo. La mayor competencia en los menores espaciamientos no afectó a la tasa de mortalidad de los árboles en los primeros 6 años de crecimiento. Esto muestra que en condiciones normales de preparación del suelo, de control de malezas y de control de hormigas es posible obtener altos valores de sobrevivencia con las tres especies evaluadas.
4. La densidad de plantación también mostró un efecto evidente sobre el crecimiento individual, aunque en mayor medida sobre el diámetro que sobre la altura. Los efectos de la reducción sobre estos parámetros no mantuvieron la misma proporción que la del número de árboles en las diferentes densidades de plantación evaluadas. La competencia entre árboles también se manifestó a través de la heterogeneidad del crecimiento individual como resultado de la competencia asimétrica entre individuos de distinto porte.

5. La falta de proporcionalidad entre el número de árboles y el crecimiento individual resultó en que con las mayores densidades de plantación se obtuvieron en los niveles de crecimiento más altos, aunque este parámetro también estuvo estrechamente relacionado con la sobrevivencia. La evolución de las curvas de crecimiento (crecimiento acumulado, IMA e ICA) mostró la falta de relación entre la duración del turno y la densidad de plantación.
6. La densidad de la madera tuvo un comportamiento diferente en cada sitio y fue afectada de forma diferente por la edad y la densidad de plantación. En Tacuarembó, la especie fue el único factor que tuvo incidencia sobre la misma; mientras que en Paysandú tanto la especie, como la densidad de plantación y la edad mostraron tener efecto sobre este parámetro.
7. La competencia entre individuos mostró un efecto negativo sobre el peso individual del fuste, manteniendo una relación muy a similar a lo observado con el volumen individual para cada densidad de plantación. En Paysandú, las diferencias de peso también estuvieron explicadas por los cambios ocurridos en la densidad de la madera obtenidos en los distintos espaciamientos. El diámetro normal y la altura resultaron ser muy buenos predictores tanto del volumen como del peso individual mostrando que el ajuste de los modelos fue más eficiente para el sitio, especies y densidades de plantación por separado. El peso por hectárea también estuvo positivamente relacionado con la densidad de plantación, del mismo modo el volumen para las tres especies. La diferencia en las curvas del peso acumulado por hectárea fue creciente con el paso del tiempo y se explican por la evolución del peso individual para cada densidad de plantación. Las diferencias de la sobrevivencia explican en buena medida las diferencias registradas en la productividad de biomasa y en el turno de ambos sitios.
8. El poder calórico de la madera mostró ser un parámetro relativamente estable para las especies, las densidades de plantación y las edades evaluadas. Esto implica que los mayores rendimientos de energía por hectárea se alcanzaron con los espaciamientos más reducidos. La densidad de la madera y el poder calórico tuvieron un peso similar en la densidad energética.
9. El peso por hectárea de las diferentes fracciones del árbol también mostró una relación directa con las densidades de plantación, al mismo que la proporción del peso de cada componente se mantiene prácticamente sin cambios en cada espaciamiento.

10. El contenido de los macronutrientes de los diferentes tejidos del árbol no se vio alterado por la densidad de plantación, indicando que no ocurren grandes cambios desde el punto de vista del metabolismo nutricional. No obstante, se detectaron diferencias entre especies. Las fracciones corteza y hojas concentran la mayor parte del Ca, Mg y P, N y K, mientras que la madera es la porción del árbol con las concentraciones menores de estos elementos, lo que hace recomendable mantener los residuos de cosecha en campo para favorecer el reciclaje de los mismos.
11. Los mayores niveles de extracción de nutrientes se observaron con las densidades más altas, asociadas a la productividad de biomasa obtenidos con los espaciamientos más reducidos. La eficiencia de utilización de los nutrientes fue independiente del nivel de productividad de biomasa de forma tal que es posible identificar combinaciones de especies y densidades de plantación que optimicen estas dos características al mismo tiempo. Los niveles de extracción de nutrientes con las mayores densidades de plantación mostraron que el agotamiento del stock de las bases ocurriría en un plazo menor que con las densidades más bajas de plantación, en particular para el caso del K. El uso de la fracción madera y corteza, en un esquema de cosecha similar a los convencionales, muestran una menor necesidad de reposición de estas bases al suelo contribuyendo a la sostenibilidad de este tipo de cultivos en el mediano y largo plazo.
12. Los resultados obtenidos permiten identificar las especies y densidades de plantación que maximizan el rendimiento de energía por unidad de superficie y al mismo tiempo determinar los turnos de cosecha para alcanzar estos resultados. Los altos niveles de producción registrados muestran que es posible abastecer plantas generadoras de energía de pequeño porte (10 MWh) con superficies relativamente reducidas en turnos de 4 a 6 años.