Water use in plantations of eucalypts and pines: a discussion paper from a tree breeding perspective

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SUMMARY

Plantation forests are being established on more marginal, harsh sites to accommodate expansion of agriculture. Because of this, tree breeders and silviculturists are interested in improving drought hardiness of trees. Breeding approaches to improve drought hardiness includes the assessment of trees as dead or alive in trials after severe droughts followed by the selection of the best surviving phenotypes for the establishment of seed orchards or land races. Physiologists estimate water utilization in trees in terms of water use efficiency (WUE). It is a function of biomass per unit of evapotranspiration and is calculated on a leaf or wood scale in clonal plots and stands. The gene complexes that control drought hardiness and WUE are probably different. It one respect, traditional breeding might have a limited impact on changing WUE since it will be difficult to alter rate of evapotranspiration through selection. In another respect, one could argue that selecting trees for high productivity is indirectly selecting for high WUE in some environments. Alternative approaches such as assessing heavy isotopes of carbon and oxygen in leaf tissue are being used by some scientists as a surrogate measure of water use in crops and trees. This paper presents the general findings from catchment studies on water uptake in pines and eucalypts and discusses how tree breeders might use results to further the development of drought hardy varieties grown in seasonally dry environments.

Keywords: breeding, drought hardiness, water use, genomic selection, clones

L'utilisation de l'eau dans les plantations d'eucalyptus et de pins: une discussion du point de vue de l'amélioration génétique des arbres

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Les plantations forestières sont établies sur les sites plus marginaux et rudes pour accommoder l'expansion agricole. A cause de ceci, les sélectionneurs d' arbres et les sylviculturistes sont intéressés par l'amélioration de la résistance à la sécheresse des arbres. Les approches de l'amélioration génétique pour la résistance à la sécheresse incluent l'évaluation des arbres dans les essais comme mort ou vivant après une sécheresse sévère, suivie par la sélection des meilleurs phénotypes survivants pour l'établissement des vergers à graines ou une rasse locale. Les physiologistes estiment l'utilisation d'eau pour les arbres dans des termes d'efficacité d'utilisation d'eau (WUE). C'est une fonction de la biomasse par l'unité d'évapotranspiration et est calculée à l'échelle des feuilles ou du bois dans les parcelles et peuplements clonaux. Les complexes géniques qui contrôlent la résistance à la sécheresse et la WUE sont probablement différents. D'un côté, l'amélioration génétique traditionnelle pourrait avoir un impact limité pour changer la WUE puisqu'il sera difficile de modifier le taux d'évapotranspiration à travers la sélection. D' un autre côté, on pourrait dire que sélectionner les arbres pour la haute productivité sélectionne indirectement pour la haute WUE dans quelques environnements. Les approches alternatives comme l'évaluation des isotopes lourds de carbone et d'oxygène dans les tissus foliaires sont utilisées par certains scientifiques comme une substitution pour la mesure d'usage d'eau dans les récoltes et les arbres. Cet article présente les conclusions générales des études au niveau des bassins sur la prise d'eau dans les pins et eucalyptes et discute comment les sélectionneurs des arbres pourraient utiliser des résultats pour promouvoir le développement des variétés résistantes a la sécheresse cultivées dans des environnements avec les saisons sèches.

Uso del agua en plantaciones de eucaliptos y pinos: un artículo de discusión bajo la perspectiva del mejoramiento genético forestal

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Las plantaciones forestales están siendo establecidas en sitios más marginales y áridos para favorecer la expansión de la agricultura. Por esta razón, los genetistas forestales y los silvicultores están interesados en mejorar la resistencia de los árboles a la sequía. Los métodos de mejoramiento genético para mejorar la resistencia a la sequía incluyen la evaluación de los árboles como muertos o vivos en los ensayos después de sequías severas seguidas por la selección de los mejores fenotipos sobrevivientes para el establecimiento de huertos semilleros o razas locales.

Los fisiólogos estiman la utilización del agua por los árboles en términos del uso eficiente del agua (WUE por las siglas en inglés). Es una función de la biomasa por unidad de evapotranspiración y es calculada en una escala de las hojas o la madera en lotes clonales y rodales. Los complejos de genes que controlan la resistencia a la sequía y el WUE son probablemente diferentes. Por un lado, el mejoramiento genético forestal tradicional podría tener un impacto limitado en el cambio del WUE ya que será difícil alterar la tasa de evapotranspiración a través de la selección. Por otro lado, uno podría argumentar que seleccionar árboles por alta productividad corresponde indirectamente a seleccionarlos por el WUE alto en algunos ambientes. Métodos alternativos tales como la evaluación de isótopos pesados de carbono y oxígeno en los tejidos de las hojas están siendo usados por algunos científicos como una medida de remplazo del uso del agua en los cultivos y los árboles. Este artículo presenta lo que se ha encontrado en general en los estudios de captación en toma del agua en pinos y eucaliptus y discute cómo los genetistas forestales podrían usar los resultados para avanzar en el desarrollo de variedades resistentes a la sequía plantadas en ambientes con sequías estacionales.

INTRODUCTION

In the last five years, there has been much more interest by forest industry to find tree species, populations and families that are well suited to dry environments. There are two reasons for this. First, the forestry land now available for planting is often marginal in some way for good tree survival and growth. Second, global climatic fluctuations are characterized by extreme weather events that often include periods of severe drought. The genetic material that is planted must be able to withstand/adapt to these climatic and environmental conditions and still produce the type of wood needed by the mill.

Tree breeders try to improve drought hardiness by finding better-adapted seed sources. As examples, efforts were made in the 1980s to make selections in natural populations of *Pinus caribaea* var. *hondurensis* (Sénéclauze) Barrett & Golfari on extremely dry sites in southeastern Guatemala and Honduras for marginally dry areas in eastern Venezuela and central Brazil (Dvorak *et al.* 1993). In New Zealand, mainland California sources of *P. radiata* D. Don have been crossed with more drought tolerant island sources from Mexico to improve survival in low rainfall areas of the country (Darling, per. comm.). In the *P. taeda* L. programs in the southern US, seed sources of the species from the drier regions of east Texas have often shown superior drought resistance/survival over more coastal sources when planted in marginal areas (Bilan 1983). *Eucalyptus camaldulensis* Dehnh. is often chosen as a parental species when hybrid progeny are desired for improved drought tolerance. The new interest in Corymbia species/hybrids is because of their supposed superior drought tolerance. When severe droughts do occur that include high levels of tree mortality, tree breeders usually walk through genetic field trials and assess trees as dead or alive, select the best phenotypes among the survivors, and create a "drought resistance" landrace or seed orchard to offer better protection against cyclic water deficits in the future.

Hydrologists and eco-physiologists have been examining water use in trees for decades. The concerns about stream flow and water yields of trees were raised as early as 1915 in South Africa, and were thoroughly debated during the Empire Forestry Conference in 1935 (see Dye and Versfeld 2007). Even though the South Africans, Indians, and Europeans were some of the pioneers in studying water usage in forest plantations, it has been primarily Australian scientists who have written a number of comprehensive reviews on the subject over the last several decades (see White *et al.* 2009, Vanclay 2009, Benyon *et al.* 2007, Whitehead and Beadle 2004, Davidson 1993, Keenan *et al.* 2004, O'Loughlin and Nambiar 2001, Poore and Fries 1985). The topic of water use in trees is complex because it requires a good understanding of the hydrological cycle (water input and loss), excellent knowledge of physical soil properties (soil texture, depth, and drainage) and a familiarity with the local vegetation and the tree species being grown and managed. This includes information on plantation spacing and post-planting treatments, nutrient status, crown size, leaf morphology, and rooting depth.

Oftentimes, it is not clear if the breeders' attempt to improve "drought hardiness" through the introduction of new seed sources and the selection of trees in local land races are exactly equivalent genetically to the eco-physiologists attempt to measure "water use efficiency" (WUE) in plantation trees. Part of the confusion comes from a lack of understanding about various definitions and the range and scales of different estimates of WUE. However, most agree that the water use issue in plantation forestry will be one of the most important questions in many countries in the coming decades.

This paper attempts to examine what role traditional tree breeding might have in developing more water efficient trees by looking at results from physiology, hydrology and silviculture research. First, a brief summary of our knowledge on water usage in eucalypts and pines is presented using results from catchment sites in various areas around the world. The review is not meant to be all-inclusive but efforts have been made to report on some of the recent work conducted in Latin America, which is often excluded in English language journals. Second, questions are raised about which water-use traits are most important to select for and easiest to genetically manipulate. Third, questions are asked about the potential return on investments from expensive programs to breed for water use traits. The intention of the paper is to update tree breeders and forest managers on the current state of the science and to generate discussion about what future breeding efforts are needed to improve adaptability and growth and better conserve water to maintain quality and stream flows.

TERMINOLOGY

The water cycle on Earth is essentially a closed system in that the same amount of water always exists (University of

Michigan 2006). The hydrological cycle is often represented by the equation:

$$P=ET+S+R+\Delta S+e \qquad (1)$$

Where P=precipitation, ET=evapotranspiration, S=stream-flow, R=groundwater recharge and ΔS=the change in soil water storage and e=environmental error

Precipitation includes all forms of atmospheric moisture. It can fall on the leaf and be evaporated (interception), run down the stem to the ground (stemflow) or fall between the crowns of trees to the ground (throughfall). Interception and subsequent evaporation is the greatest cause of water loss of precipitation. It is somewhat species dependent because surface area of the leaves varies with species (Davidson 1993). The greater the leaf area per square meter of ground covered, the greater the interception loss (Davidson 1993). During photosynthesis, plants transpire water. Transpiration rates are often used in eco-physiological studies as an indicator of stomata closure (Martins *et al.* 2008). Direct evaporation from the soil and transpiration from the plants is collectively called evapotranspiration (Keenan *et al.* 2004). Long-term mean stream flow and groundwater recharge is determined by the difference between incoming rainfall and total ET (Benyon *et al.* 2007). Stemflow and throughfall water can either runoff and influence streamflow or infiltrate downward into the soil and recharge the groundwater supply. Capillary action of tree roots can cause ground water to rise in certain circumstances.

To determine the relative water usage of tree species, eco-physiologists calculate a parameter called "water use efficiency" (WUE) (Landsberg 1999). It is defined as the dry matter produced by the tree per unit of water transpired. Because photosynthesis and transpiration are co-dependent on stomatal processes in the leaves, it is reasonable to assume that WUE will be relatively conservative and provide useful information on CO_2 uptake and transpiration (Landsberg 1999). In some cases it is calculated using estimates of wood volume (minus branches and leaves) divided by m³ of water transpired (Stape *et al.* 2004) or divided by estimates of annual evapotranspiration rates (Almeida *et al.* 2007). Eco-physiologists often present WUE values as clone or stand means based on large tree plots rather than on an individual tree basis.

Tree breeders should be aware that there are currently five different estimates of WUE in the literature (see White *et al.* 2009). These authors suggest that most data on WUE measures the instantaneous ratio of carbon assimilation to transpiration at the leaf scale (W_i). However, they contend that WUE of wood production expressed in m³ of wood volume per ML of evapotranspiration (W_w) is the more useful measure of water use when assessing the results of plantation management or breeding (White *et al.* 2009). The authors conclude that selection for W_i could lead to reduced W_w in some environments.

WUE as measured by the eco-physiologists has been used as a tool for breeding in crops that has led to increased grain

yields in wheat of 15% in harsh environments (Davies *et al.* 2011, Parry *et al.* 2005). It has also been proven to be a useful parameter in forestry eco-physiology studies when measured on a stand or clone basis. However, Landsberg (1999) expresses a concern that WUE values are not sufficiently stable to be useful as measures of individual tree performance in different environments, nor is it likely that the values associated with particular species are consistent enough to be useful as a basis for selecting trees for particular uses or for management.

Much of the data on water use in trees that are collected by eco-physiologists come from information taken in catchments. A "catchment" is a structure (or landform) where water is collected whereas a "watershed" is technically a ridge that separates one drainage area from another (Wikpedia, http://en.wikipedia.org/wiki/Drainage_basin 2011). Both terms are used interchangeably in the literature. It seems that a catchment could conceivably represent any landform, even a flat plain, since even there, water infiltrates and makes its way to ground water supplies. Catchment studies, which occur singly or sometimes paired, might cover 10 to several thousand hectares and often include several large treatments that compare plantation species versus native species or grasslands. Several authors note that published results do not necessarily reflect the water balance outside the catchment area (Van Dijk and Keenan 2007) and results at one location should not be extrapolated to other locations (Poore and Fries 1985). In the mid-1980s, Poore and Fries (1985) could only find data from several forest tree catchment experiments that had long-term (>10 years) information on eucalypts. Now much more information from paired catchment areas is available for both eucalypts and pines and have been the subject of thorough reviews (e.g. see Brown *et al.* 2005).

WATER USE COMPARISONS

As a baseline for comparison of water use in trees, one could examine water use in agricultural crops since planting of both forest plantations and crops often compete with each other on similar landscapes in the tropics and subtropics. Agriculture is responsible for 87% of the total fresh water used globally (University of Michigan 2006). Crops such as rice (*Oryza sativa* L.) citrus (*Citrus* spp.), alfalfa (*Medicago sativa* L.), sugar cane (*Saccharum officinarum* L.), and coffee (*Coffea* spp.) are particularly water demanding. For example, 2500 to 5000 L of water are needed to produce 1 kg of rice to counteract loses from evapotranspiration, percolation and seepage (Bouman 2009, University of Michigan 2006). The agricultural industry is trying to find ways to be more efficient in its water use by improving irrigation techniques and machinery and by developing more drought hardy crop varieties. However, to some, human population growth and increasing demands for food seems to be outdistancing improvements in water conservation technology. Estimates are that agricultural irrigation systems waste as much as 60% of the total water

pumped before it reaches the intended crop (University of Michigan 2006).

Although comparative measurements for trees are scarce, White *et al*. (2009) have estimated that 1.0 to 5m^3 of wood were produced per ML (10^6 L) of water utilized from transpiration, soil evaporation and canopy rain interception in *E. globulus*, *E. nitens* and *P. radiata* plantations across southern Australia. In a different study, Bren *et al*. (2011) calculated 1.25 m^3 of wood products were produced per ML of water utilized in a *P. radiata* sawlog compartment in southern Australia. Both of these studies are in winter rainfall environments with summer droughts. Some suggest that eucalypts are more efficient users of water than crops when total biomass produced is expressed as a function of water used (Davidson 1993). He presented the following information taken from results of crop water usage in Australia (see Table 1).

Based on his information, eucalypts generally are more efficient water users than a number of commonly grown crops based on total biomass. Critics argue that some of these values represent irrigated crops versus non-irrigated plantations, but point to the concern by forester managers that total water consumption (including irrigation) needs to be considered when assessing levies for water use. According to some, the playing field for water use assessment is not level when comparing crops for food versus crops for wood. As an example, in eastern South Africa, sugarcane is not defined as a water use crop although it is often heavily irrigated, but cane growers do not have to register or license or pay for the water they use while forestry does (Dye and Versfeld 2007). However, others state that the measure of water productivity is of little value in comparing crops and trees, as higher biomass yields may not necessarily mean higher economic returns when values of inputs and products are considered (Woodhouse and Hassan 1999).

TABLE 1 *Water use by plants through evapotranspiration measured in total biomass and expressed in litres/kg (after Davidson 1993)*

Plant	Water use per total biomass (litres/kg)
Cotton/Coffee/Bananas	3200
Sunflower	2400
Field Pea	2000
Paddy Rice	2000
Horse Bean	1714
Cow Pea	1667
Soy Beans	1430
Potato	1000
Sorghum	1000
Eucalypts	785
Finger Millet	592

PERTINENT RESULTS FROM CATCHMENT STUDIES

In the general reviews conducted on water use in plantations, most of the findings are in agreement that tree species produce less surface runoff, ground water recharge and streamflow than more shallow rooted forms of vegetation such as crops, pastures, and grasslands (see Benyon *et al*. 2007, Van Dijk and Keenan 2007, Brown *et al*. 2005, White 1993, Poore and Fries 1985). Where plantations are established in parts of a catchment that are hydro-geologically isolated from streams, most of the time the impacts on stream flow will be negligible or very little (O'Loughlin and Nambiar 1991). The results on streamflow are not surprising since trees have rougher and denser canopies, which result in higher interception losses (Van Dijk and Keenan 2007) because of a greater leaf area than crops and grasses. Regardless of the exact combination of physiological and environmental processes that promote water use in trees, the reduction of streamflow during the dry season, called low-flow, is especially critical to the public if the catchment areas serve as a collection point for community water supplies, a source of water to irrigate agricultural crops, or maintain unique plant and animal communities in special ecological zones that are National Parks or Reserves.

There are four general types of catchment studies broadly described by Brown *et al*. 2005 in their review: a) afforestation experiments b) deforestation experiments, c) regrowth experiments and d) forest conversion experiments. Today there are more long-term data available from forest industry on watershed/catchments studies of both pines and eucalypts (see Lima 2011, Voigtlaender 2007, Von Stackelberg 2005, Almeida and Soares 2003) than were available several decades ago. Analytical models that are more complex than earlier versions have been developed to predict and interpret trends from the catchments (Almeida *et al*. 2004, Brown *et al*. 2007, Landsberg *et al.* 2003). The challenges that face tree breeders in establishing useful field genetic trials also are present in the design of catchment trials. These include decisions on the duration of the experiments, replication orientation, size and number of replications, information on physical and chemical properties of the soil, slope of the land, prior knowledge of vegetation and historic land use etc. Because of the large physical size of replications in catchment studies, "environmental noise" limits the value of some of the published results (Van Dijk and Keenan 2007). Reporting on results of catchment studies of one to two years duration are important locally, but similar to reproductive biology studies conducted by tree breeders, longer-term timeframes for hydrology experiments are preferred.

Several of the salient points from recent findings of the four different types of catchment studies are summarized below.

- There are no results that consistently confirm or refute that eucalypt or pines use more water than indigenous species (Gyenge *et al*. 2008, Scott and Prinsloo 2008, Komatsu *et al*. 2004, Almeida and Soares 2003, Lima *et al*. 1990). It appears that some of the contradictory

results involve how water efficiency is measured and also vary around the issue that crown development of the native species seldom equals that of the plantations species when assessments are conducted, making direct comparisons difficult (see Myers *et al.* 1996). This is especially important to consider when drawing conclusions about exotic and native tree species in agroforestry studies. Furthermore, the hydrologic research must be long term to discern meaningful trends.

- There are interesting discussions on whether water loss is greater in eucalypt or pine plantations. The initial Australian research suggested that interception losses in eucalypt plantations were about 11 to 20% and pines were greater than 20% (Poore and Fries 1985). Further research suggested that higher interception loss in pines was balanced by lower soil evaporation than in eucalypts and that the combined water loss from interception and soil evaporation was about the same in pines and eucalypts (Benyon, 2006). Research in paired catchments in Chile (winter rainfall) with *P. radiata* and *E. globulus* showed interception losses of 16 to 17% for the pines and 10 to 11% for the eucalypts but the streamflow was greater in the pine catchment (Huber *et al.* 2010). The Chilean authors account for this by indicating evapotranspiration was greater in the eucalypt catchments. Streamflow reduction was also less for pines (*P. patula*) than eucalypts (*E. grandis*) in long-term studies on paired catchments in subtropical regions (summer rainfall) of Mpumalanga, South Africa. Maximum streamflow reduction was 80% for pines and 100% for eucalypts over native scrub forests and grasslands (Scott *et al.* 2005). The rapid desiccation of the catchments was thought to be more the result of increased transpiration than increased interception (Dye 1996, Scott and Lesch 1996 in Scott *et al*. 2005). If equal crown development is considered, there are probably few biologically significant differences between the two genera.

- There is really no comprehensive tree breeding studies over multiple sites that quantify the genetic relationship of clonal performance (productivity) to water use efficiency. However, there are a growing number of physiology studies that examine water-related traits using small numbers of clones (Gentil 2010, Carneiro *et al.* 2008, Reis *et al.* 2006, Almeida *et al.* 2004, Costa e Silva *et al.* 2004, Inoue *et al.* 1988). For example, Almeida *et al.* (2004) assessed five *E. grandis* clones multiple times over a 3.5 year time period in eastern Brazil and found differences in productivity that could be attributed to differences in biomass partition and stomatal conductance. Costa e Silva *et al.* (2004) found that a drought resistance clone of *E. globulus* ssp. *globulus* Labill. maintained higher leaf water status and growth rate than a drought sensitive clone of the same species. Inoue *et al.* (1988) assessed clones of *E. grandis* Hill ex Maid. and *E. saligna* Smith at 3 to 4 months of age in controlled environments. Differences

among clones were detected for net photosynthesis, daily CO_2 assimilation rates per plant and transpiration. Reis *et al.* (2006) assessed below-and above-ground growth of four *E. grandis x E. urophylla* S. T. Blake clones and one *E. camaldulensis x eucalyptus* spp. clone in Bahia, Brazil. Irrigation treatments were applied to the seedlings at 6 months of age. The *E. camaldulensis x eucalyptus* hybrids were characterized by deep root development in the soil profile and trees maintained their growth under water stress conditions. The physiology studies included both field trials and greenhouse experiments, were characterized by testing a few clones (< 6), and often used different methodologies or models that make it difficult to determine if there are consistent relationships between water use and productivity. There is little doubt that there are real differences among clones in water use efficiency, but there is no evidence at this time that clearly shows that breeding has the potential to maintain or increase plantation productivity while reducing evapotranspiration.

DISCUSSION

Some researchers warn that looking at only one aspect of the entire hydrological cycle, such as water yield, might lead to an incomplete picture of above and below ground processes (Lima 2011, Benyon *et al.* 2007). Even though the point is well taken, recent research in tropical and subtropical forest plantations has shown that water supply is the key resource in determining levels of plantation productivity (Stape *et al.* 2004, 2010) and it is the status of the water availability that most concerns government officials and the public.

Both eucalypts and pines appear to use less water to produce a given amount of biomass than some agricultural crops. However, because of their large size and more abundant leaves with greater leaf area, trees affect stream flow more severely than shorter vegetation when established close to rivers, lakes and estuaries. For this reason, nearly all commercial plantation programs in South America have strict legal limits on how close they can plant trees to a water source and generally, 20% of their total land area remains in native forests or grasslands (Lima 2011). The severity of problems associated with water availability appears to be greater in areas where the plantations are large in size and cover most of the catchment area or in places with seasonal rainfall. Smaller plantings in agroforestry settings seem to be of limited concern.

What traits should tree breeders use to assess water use efficiency in genetic trials? Can breeders alter the levels of evapotranspiration, which is a component of WUE? Is selecting trees for survival in the field after a long drought, which is often scored as a "Yes" or "No" by tree breeders, equivalent to choosing the best trees for WUE or some other water related trait? The two measures, drought hardiness and WUE, do not appear to be the same traits and are probably governed by different groups of gene complexes. Drought avoidance is the ability of plants to maintain relatively high tissue water

potential despite a shortage of soil moisture, whereas drought stress tolerance is the ability to withstand water deficit with low tissue water potential (Cregg 2004, Mitra 2001). In eucalypts, drought avoidance includes low values and large seasonal dynamic changes in leaf area index, near-vertical arrangement of leaves, high stomatal sensitivity to air saturation deficit, and deep rooting ability (Whitehead and Beadle 2004). In pines, drought avoidance traits include rapid root development, more lateral roots (van Buijtenen *et al.* 1976) and noticeable deposits of cuticular wax in and around needle stomata (Newton *et al.* 1986). When making selections for drought hardiness, tree breeders are probably selecting for a combination of traits; leaf traits that relate to the rate and degree of stomatal closure and root traits that deal with their development and rapid expansion.

Even though change of species or provenance and the creation of better-adapted land races have been successful in drought hardiness improvement in forestry, much less is known about gene processes in mature trees that control the trait and the potential gains from breeding. Heritabilities for drought hardiness appear to be moderate to high in most annual crops (Ahmadi and Bajelan 2008, Hussain *et al.* 2009, Suraporniboon *et al.* 2008) and also to be at least moderate in studies of trees, most of which have been experiments with seedlings grown in environmental chambers and nurseries. For trees, greenhouse studies to test drought resistance have been used successfully in duplicating survival observations in the field (Newton *et al.* 1986).

Other approaches need further studied. Some researchers are now looking at heavy isotopes of carbon and oxygen to measure water use efficiency as described below.

Carbon Isotopes

Plant drought stress can be reflected to the degree by which plants discriminate against the heavier isotope carbon 13CΔ during photosynthesis (Davies *et al*. 2011, Osorio and Pereira 1994, Rowell *et al.* 2009). Specifically, when the predominant isotope 12C is utilized more quickly than it is replenished in the photosynthesis process from the outside atmosphere, the greater the relative partial pressure of 13C is at the site of carboxylation and progressively more of the heavy isotope 13C is incorporated into organic matter (Osorio and Pereira 1994, Rowell *et al.* 2009). Therefore, drought stress related decreases in stomatal conductance and relative CO_2 concentrations in the leaf are often correlated with increases in carbon isotope 13C of newly formed photosynthates (Brugnoli *et al.* 1988, Farquhar *et al.* 1989 in Rowell *et al.* 2009).

The 13C isotope is measured using a mass spectrometer and is a convenient surrogate for estimating WUE (Farquhar 1989). Xu *et al.* (2000) found that variation in tree WUE for seven-year-old clones of *P. elliottii* Engelmann var. *elliottii x P. caribaea* hybrids, as reflected in 13CΔ, was largely attributed to genetic effects on leaf photosynthetic activity rather than stomatal conductance as reflected in foliar leaf $\delta18O$ (see below). The authors concluded that foliar 13CΔ appears promising as a physiological parameter for selecting clones of hybrid pine for improved WUE and increased growth in

drought prone environments in subtropical Australia. Even though the isotope has been discriminated on annual rings from wood cores for some angiosperms and gymnosperms, (Livingston and Spittlehouse 1993, MacFarlane *et al.* 1999 in Cregg 2004), it showed no variation across families in *P. radiata* (Rowell *et al.* 2009). Ideally, significant correlations between 13CΔ, either positive or negative, suggest that this trait could be used as a selection criterion in breeding for maintenance of productivity under conditions of water stress (Bond and Stock 1990, Xu *et al.* 2000 in Rowell *et al.* 2009). The efficacy of determining 13CΔ in stressed and non-stressed seedlings in a greenhouse environment is unclear.

Near Infrared (NIR) Analysis and Oxygen Isotopes

Water contains isotopes of hydrogen and oxygen of varying weights. The heavier isotopes of each element occur in water molecules in small proportions. There is a tendency for these heavier molecules of water to accumulate in leaves during transpiration (Farquhar *et al.* 2007). In crop and tree breeding, the carbon, hydrogen, and oxygen isotope measurements could provide a practical surrogate for measurements of the marginal water cost of carbon gain with the rate of transpiration (Cowan and Farquhar 1977). Heavy water enrichment increases with increased evapotranspiration (Sheshshayee *et al.* 2005).

The heavy oxygen stable isotope ($\delta18O$) and mineral accumulation (measured as ash content) in plant organic matter have been proposed as indirect methods for assessing photosynthetic and transpirative performance of crops (Cabrera-Bosquett *et al.* 2011). N content in vegetative tissues is of interest to water and nitrogen use efficiency breeding programs because of its effect on leaf photosynthesis, which determines fine grain yield (Bänziger *et al.* 2000 in Cabrera-Bosquett *et al.* 2011). In their work with maize, Cabrera-Bosquett *et al.* (2011) developed good predictive NIR models for both N and ash at the family level across different water treatments and adequate models for ($\delta18O$) suggesting they offer promising opportunities for maize breeding programs to improve water and nitrogen use efficiency and grain quality.

The possibility of utilizing NIR in water use assessment in tree breeding is attractive because many forestry organizations already have access to the equipment and technology, which has primarily been used to predict chemical wood properties of selected plus trees (Hodge and Woodbridge 2010). A further area of research would be to develop models for N and ash content in trees to determine if they accurately predict water use efficiency over time.

Little has been done to breed for water use efficiency in trees other than to employ more drought tolerant seed sources and develop land races. Further work on other water related traits is not a major feature of most commercial tree breeding programs because of the ambiguity of what exactly to select for and how to go about it. However, some would argue that any strategy that maximizes leaf area would maximize the water use efficiency of wood production (White *et al.* 2009). If this is true, then breeders are already indirectly selecting for

WUE by choosing trees based on volume production. Silvicultural practices such as crown management (Vanclay 2009), pruning, thinning and fertilization also increase WUE (White *et al.* 2009).

Still, there are a number of questions at both the research and policy levels for tree breeders. Do trees that use water more efficiently have the same wood quality (e.g. cell wall thickness or size) as trees not selected for the trait or will the chemical properties, stability and strength of the final product be somehow compromised? Will improvement gains in water use of trees through breeding (or silviculture) be reflected by equal levels of improvement in catchment areas as measured by increased annual streamflow and lowflow? Alternatively, is the environmental noise that surrounds catchment areas (soil, vegetation type, changing weather patterns) so pronounced that only major improvement in efficiencies in tree-water uptake (e.g. 20%) will be noticeable downstream? Will the development of improved water efficient trees/clones be recognized as an environmental benefit at the federal, local, and community levels? How will water use taxes be levied against forestry organization in the future? Will these be applied fairly across all industries and will they be based on measureable water use rather than on the area of plantations established? These policy questions are important because in the next decades, tree breeding programs are going to survive or be terminated based on their ability to demonstrate real economic returns on investment. If it is unclear on how the millions of dollars needed industry-wide to breed for some form of a water use trait would be measured in terms of its benefits to the public, the industry, or the environment, decision makers are going to question the feasibility of proceeding with the research. An analogy would be to spend years breeding for improved wood density to strengthen construction timber only to find out when completed that economic markets do not distinguish between different strengths and grades of timber. The policy questions are important to tree breeders because they directly or indirectly determine whether the end-product produced can be marketed economically.

To answer some of these questions, the following approaches could be considered by tree breeders:

- Continue to test species, populations and families for drought hardiness using traditional means.
- Determine the relation between productivity in clones and some form of WUE measurement.
- Determine if silvicultural management of stands is a more effective and less expensive way to alter water use than breeding.
- If breeding seems to be an economically feasible approach, work closely with physiologists to determine the genetic relationship between drought hardiness of trees selected in the field versus some measure of their water use. The measure of water use needs to be well-defined and methodologies used must be consistent across locations and years. Decide on traits that are easy to measure in the field and preferably have high juvenile/mature correlations.

- Development of robust field designs is needed. Catchment studies are broadly useful, but do not provide the understanding of physiological and genetic processes that would be helpful to quantify the potential effectiveness of tree breeding in the manipulation of water use in clonal plantings.
- Determine if intra-clonal competition alters superiority in water uptake. Some pines selected for high productivity in genetic tests in the United States performed poorly when competing against identical sibling clones in studies derived from somatic embryogenesis (Weir, per. comm.).
- Work with hydrologists to come up with practical ways to predict increases in streamflow by using the more water efficient varieties.
- Continue work to identify quantitative trait loci (QTL) for drought hardiness/water use efficiency traits using a genomic selection approach (see Grattapaglia and Resende 2011). QTL's have been identified for drought resistance in crops (e.g. Kamunya 2009, Kumar *et al.* 2007). However, these often are genotype specific and the challenge for molecular breeders is to find QTL's that control major effects that are independent of genetic origin (Ortiz *et al.* 2007). In genomic selection, QTL location can be disregarded, however, sufficient power is needed to detect QTL and to discriminate true effects from environmental noise (Grattapaglia and Resende 2011). The evolution of genomic selection in forest trees is still in its infancy and still will need some thorough testing to determine its actual practical application in tree breeding.

CONCLUSIONS

South Africa is the only country in the world where plantation forestry has been regulated as a stream flow reduction activity (Dye and Versfield 2007). Users are required to pay a fee (tax) for their water use. Other countries will presumably follow suit with their own models as management of the water resource becomes more critical. Tree breeders are aware of the importance of developing water efficient strains of trees but silviculture practices might offer the fastest and cheapest way of improvement. Early screening of clones for traits that govern water use in trees through a genomic selection approach might someday be feasible. Regardless of the approach, a major bottleneck is being able to demonstrate to the public that planting more water efficient clones identified in field trials will result in measureable increases in stream flow during the dry season or during periods of severe drought.

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REFERENCES

AHMADI, H. and BAJELAN, B. 2008. Heritability of drought tolerance in wheat. *American-Eurasian Journal of Agriculture and Environmental Science* **3**(4): 632–635.

ALMEIDA A.C., SOARES, J.V., LANDSBERG, J.J. and REZENDE, G.D. 2007. Growth and water balance of *Eucalyptus grandis* hybrid plantations in Brazil during a rotation for pulp production. *Forest Ecol. Manage* **251**: 10–21.

ALMEIDA A.C., LANDSBERG, J.J. and SANDS, P.J. 2004. Parameterization of 3-PG model for fast-growing *Eucalyptus grandis* plantations. *Forest Ecol. & Manage* **193**(1–2): 179–195.

ALMEIDA A.C. and SOARES, J.V. 2003. Comparação entre uso de água em plantações de *Eucalyptus grandis* e Floresta Ombrófila Densa (Mata Atlântica) na costa leste do Brasil. *Revista Árvore*. **27**: 159–170.

BÄNZINGER, M., EDMEADES, G.O., BECK, D. and BELLON, M. 2000. In: Breeding for drought and nitrogen stress tolerance in maize, from theory to practice. CIMMYT, Mexico, DF, Mexico.

BENYON, R., THEIVEYANATHAN and DOODY, T.M. 2006. Impacts of tree plantations on groundwater in south-eastern Australia. *Australian Journal of Botany* **54**: 181–192.

BENYON, R., ENGLAND, J., EASTHAM, J., POLGLASE, P. and WHITE, D. 2007. Tree water use in forestry compared to other dry-land agricultural crops in the Victorian context. Report prepared for the Department of Primary Industries Victoria to promote scientific knowledge in this area. Ensis Technical Report N. 159. 50 p.

BILAN, M.V. 1983. Root systems of a drought hardy ecotype of loblolly pine (*Pinus taeda* L.) In: Root ecology and its practical application. A contribution to the investigation of the whole plant. *Bundesanstalt Gumpenstein.* 543–551.

BOND, W.J. and STOCK, W.D. 1990. Preliminary assessment of the grading of *Eucalyptus* clones using carbon isotope discrimination. *S Af. J. For.* **154**: 51–54.

BREN, L., ELMS, S. and COSTENARO, J. 2011. How Much Water Is Needed to Produce a Cubic Metre of Radiata Pine Log? *Australian Forestry*, Vol. 74, No. 2, June 2011: 108–111.

BROWN, A.E., ZHANG, L.,McMAHON, T.A., WESTERN, A.W. and R.A. VERTESSY. 2005. A review of paired catchment studies for determining changes in water yield resulting from alternations in vegetation. *Journal of Hydrology* **310**: 28–61.

BROWN, A.E., PODGER, G.M., DAVIDSON, A.J., DOWLING, T.I. and ZHANG, L. 2007. Predicting the impact of plantation forestry on water users at local and regional scales An example for the Murrumbidgee River Basin, Australia. *Forest Ecol. Manage* **251**: 82–93.

BOUMAN, B. 2009. How much water does rice use? *Rice Today*. January-March. http://beta.irri.org/news/images/stories/ricetoday/8-1/SCIENCE_how_much_water_does_rice_use.pdf.

BRUGNOLIA, E., HUBICK, K.T., von CAEMMERER, S., WONG S.C. and FARQUHAR, G.D. 1988. Correlation between carbon isotope discrimination in leaf starch and sugars of C3 plants and the ratio of intercellular and atmospheric partial pressures of carbon dioxide. *Plant Physiology* **88**: 1414–1424.

CABRERA-BOSQUET, L., SÁNCHEZ, C., ROSALES, A., PALACIOS-ROJAS, N. and ARAUS, J.L. 2011. Near-infrared reflectance spectroscopy (NIRS) assessment of δ18O and nitrogen and ash contents for improved yield potential and drought adaptation in maize. *Journal of Agricultural and Food Chemistry* **59**(2): 467–474.

CARNEIRO, R.L.C., RIBEIRO, A., HUAMAN, C.A.M., LEITE, F.P., SEDIYAMA, G.C. and BASTOS, N.F. 2008. Consumo de água em plantios de eucalipto: parte 1 determinação da condutância estomática em tratamentos irrigado e não-irrigado. *Rev. Árvore* **32**: 1–10.

COSTA e SILVA, F., SHVALEVA, A., MAROCO, J.P., ALMEIDA, M.H., CHAVES, M.M. and PEREIRA J.S. 2004. Responses to water stress in two *Eucalyptus globulus* clones differing in drought tolerance. *Tree Physiology* **24**: 1165–1172.

COWAN, I.R. and FARQUHAR, G.D. 1977. Stomatal function in relation to leaf metabolism and environment. *Symp Soc Exp Biol* **31**: 471–505.

CREGG, B.M. 2004. Improving drought tolerance of trees: theoretical and practical considerations. In: Proc. XXVI IHC. Nursery Crops (Eds. T. Fernandez and C.G. Davidson). Acta Hort. 630.

DAVIDSON, J. 1993. Ecological aspects of eucalypt plantations. In: Proc. Regional Expert Consultations on *Eucalyptus*. Volume I. 35 p. http://www.fao.org/docrep/005/ac777e/ac777e06.htm.

DAVIES, W.J., ZHANG, J., YANG, J. and DODD, I.C. 2011. Novel crop science to improve yield and resource use efficiency in water-limited agriculture. *Journal of Agricultural Science* **149**: 123–131.

DVORAK, W.S., ROSS, K.D. and LIU, Y. 1993. Performance of *Pinus caribaea* var. *hondurensis* in Brazil, Colombia and Venezuela. Camcore Bulletin on Tropical Forestry No. 11. Department of Forestry, North Carolina State University. Raleigh, NC. USA. 47 p.

DYE, P.J. 1996. Response of *Eucalyptus grandis* trees to soil water deficits. *Tree Physiology* **16**: 233–238.

DYE, P.J., and VERSFELD, D. 2007. Managing the hydrological impacts of South African plantation forests: An overview. *Forest Ecol. Manage* **251**: 121–128.

FARQUHAR, G.D., CERNUSAK, L.A. and BARNES, B. 2007. Heavy water fractioning and plant during transpiration. *Plant Physiology* **143**: 11–18.

FARQUHAR, G.D., EHLERINGER, J.R. and HUBICK, K.T. 1989. Carbon isotope discrimination and photosynthesis. *Ann. Rev. Plant Physiology* **40**: 503–537.

GENTIL, M.S. 2010. Transpiração e eficiência do uso da água em árvores clonais de *Eucalyptus* aos 4 anos em áreas com e sem irrigação em Eunápolis, Bahia. Dissertação(Mestrado) – Escola Superior de Agricultura Luiz de Queiroz. Universidade de São Paulo Piracicaba. 71p. Acesso ao site http:\\www.teses.usp.br.

GRATTAPAGLIA, D. and RESENDE, M.D.V. 2011. Genomic selection in forest tree breeding. *Tree Genetics and Genomes* **7**: 241–255.

GYENGE, J.E., FERNÁNDEZ, M.E., SARASOLA, M. and SCHLICHTER, T.M. 2008. Testing a hypothesis of the relationship between productivity and water use efficiency in Patagonian forests with native and exotic species. *Forest Ecology and Manage* **255**: 3281–3287.

HODGE, G.R. and WOODBRIDGE, W.C. 2010. Global near infrared models to predict lignin and cellulose content of pine wood. *J. of Near Infrared Spectroscopy* **18**: 367–380.

HUBER, A., IROUMÉ, A., MOHR, C. and FRÊNE, C. 2010. Effect of *Pinus radiata* and *Eucalyptus globulus* plantations on water resource in the Coastal Range of Biobío region, Chile. / Efecto de plantaciones de *Pinus radiata* y *Eucalyptus globulus* sobre el recurso agua en la Cordillera de la Costa de la región del Biobío, Chile. *Bosque* **31**(3): 219–230.

HUSSAIN, I., MUHAMMAD, A., MUHAMMAD S. and ASHFAQ, A. 2009. Gene action studies for agronomic traits in maize under normal and water stress conditions. *Pakistan Journal of Agricultural Sciences* **46**(2): 107–112.

INOUE, M.T., and RIBEIRO, F.A. 1988. Fotossíntese e transpiração de clones de *Eucalyptus grandis* e *E. saligna*. *IPEF*. **40**: 15–20.

KAMUNYA, S.M., WACHIRA, F.F., PATHAK, R.S., SHARMA, R.K., KORIR, R., KINYANGI, T., KIPLANG'AT, J., SHARMA, V., CHALO, R. and AHUJA, PS. 2009. Genetic mapping and identification of quantitative loci for yield and drought tolerance in tea (*Camellia sinensis* (L) O. Kuntze). *Tea* **30**(1): 19–41.

KEENAN, R., PARSONS, M., GERRAND, A., O'LOUGHLIN, E., BEAVIS, S., GUNAWARDANA, D., GAVRAN, M. and BUGG, A. 2004. Plantation and water use: a review prepared for Forest and Wood Products Research and Development Corporation by the Bureau of Rural Sciences. Canberra, Australia. 94 p.

KOMATSU, H., TANAKA, N. and KUME, T. 2004. Do coniferous forests evaporate more water than broad-leaved forests in Japan? *Journal of Hydrology* **291**(1–2): 1–27.

KUMAR, R., VENUPRASAD, R. and ATLIN, G.N. 2007. Genetic analysis of rainfed lowland rice drought tolerance under natural occurring stress in eastern India: heritability and QTL effects. *Field Crop Research* **103**(1): 42–52.

LANDSBERG, J.J., WARING, R.H. and COOPS, N.C. 2003. Performance of forest productive model 3-PG applied to wide range of forest types. *For. Ecol. Manage* **172**: 199–214.

LANDSBERG, J.J. 1999. Relationships between water use efficiency and tree production. The Ways Trees Use Water.

Four review papers (ed. J. Landsberg). Water and Salinity Issues in Agroforestry No. 5. RIRDC Publication 93/37. pp. 52–62.

LIMA, W.P. 2011. Plantation forestry and water: science, dogmas, challenges. Instituto BIOATLÂNTICA. Rio de Janeiro, Brazil. 65 p.

LIMA W.P., ZAKIA, M.J.B., LIBARDI, P.L. and SOUSA FILHO, A.P. 1990. Comparative evapotranspiration of *Eucalyptus*, Pine and "Cerrado" vegetation measured by the soil water balance method. *IPEF* International **1**: 5–11.

LIVINGSTON, N.J. and SPITTLEHOUSE, D.L. 1993. Carbon isotope fractionation in tree rings in relation to growing season water balance. In:. Stable Isotopes and Plant-Carbon Relations (eds. JR Ehleringer, AE Hall, and GD Farquhar). Academic Press, San Diego, CA, USA. pp: 141–153.

MACFARLANE, C., WARREN C.R., WHITE, D.A., and ADAMS, M.A. 1999. A rapid and simple method for processing wood to crude cellulose for analysis of stable carbon isotopes in tree rings. *Tree Physiology* **19**: 831–835.

MARTINS, F.B., STRECK, N.A., SILVA, J.C., MORAIS,W. W, SUSIN, F., NAVROSKI, M.C. and VIVIAN, M.A. 2008. Deficiência hídrica no solo e seu efeito sobre transpiração, crescimento e desenvolvimento de mudas de duas espécies de eucalipto. *Rev. Bras. Ciênc. Solo*. **32**(3): 1297–1306.

MITRA, J. 2001. Genetics and genetic improvement of drought resistance in crop plants. *Current Science* **80**(6): 759–764.

MYERS, B.J., THEIVEYANATHAN, S., O'BRIEN, N.D. and BOND, W.J. 1996. Growth and water use of *Eucalyptus grandis* and *Pinus radiata* plantations irrigated with effluent. *Tree Physiology* **16**: 211–219.

NEWTON RJ., MEIER, C.E., VAN BUIJTENEN, J.P. and MCKINLEY, C.R. 1986. Moisture-stress Management: silviculture and genetics. In: Proc. Of the Physiology Working Group, "Stress Physiology and Forest Productivity". Society of American Foresters National Convention, Fort Collins Colorado, USA. July 28–31, 1985. pp. 35–60

O'LOUGHLIN, E. and NAMBIAR, E.K.S. 2001. Plantations, Farm Forestry and Water. RIRDC/LWA/FWPRDC Publication No. 01/137. Canberra, Australia. 26 p.

ORTIZ, R., IWANGA, M., REYNOLDS, M.R.,WU, H. and CROUCH, J.H. 2007. Overview on crop genetic engineering for drought-prone environments. CIMMYT, SAT eJournal-ejournal.icrisat.org. Texcoco, Mexico. 30 p.

OSORIO, J. and PEREIRA, J.S. 1994. Genotypic differences in water use efficiency and 13C discrimination in *Eucalyptus globulus. Tree Physiology* **14**: 871–882.

PARRY, M.A.J., FLEXAS, J. and MEDRANO, H. 2005. Prospects for crop production under drought: research priorities and future directions. *Annals of Applied Biology* **147**: 211–226.

POORE, M.E.D. and FRIES, C. 1985. The ecological effects of *eucalyptus*. FAO Forestry Paper 59. Rome, Italy 87 p.

REIS, G.G., REIS, M.G.F., FONTAN, ICI, MONTE, M.A., GOMES, A.N. and OLIVEIRA, C.H.R. 2006. Crescimento de raízes e da parte aérea de clones de híbridos de *Eucalyptus grandis* x *Eucalyptus urophylla* e de *Eucalyptus camaldulensis* x *Eucalyptus* spp submetidos a dois regimes de irrigação no campo. *Rev. Árvore*. **30**(6): 921–931.

ROWELL, D.M., AIDES, P.K., TAUZ,M., ARNDT, S.K. and ADAMS, M.A. 2008. Lack of genetic variation in tree ring □13 C suggests a uniform, stomatally-driven response to drought stress across *Pinus radiata* genotypes. *Tree Physiology* **29**: 191–198.

SCOTT, D.F., and LESCH, W. 1997. Streamflow responses to afforestation with *Eucalyptus grandis* and *Pinus patula* and to felling in the Mokobulaan experimental catchments, South Africa. *Journal of Hydrology* **199**: 360–377.

SCOTT, D.F, BRUIJNZEEL, L.A. and J. MACKENSEN. 2005. The hydrological and soil impacts of forestation in the tropics. In: Forests, Water and People in the Humid Tropics (eds. M. Bonell & LA Bruijnzeel). Cambridge University Press, UK. 925 p.

SCOTT, D.F. and PRINSLOO, F.W. 2008. The longer-term effects of pine and eucalypt plantations on streamflow. *Water Resources Research* VOL. 44, (7) XXX, doi:10.1029/2007WR006781.

SHESHSHAYEE, M.S., BINDUMADHAVA, H., RAMESH R, PRASAD, T.G., LAKSHMINARAYANA, M.R. and UDAYAKUMAR, M. 2005. Oxygen isotope enrichment (Delta O-18) as a measure of time-averaged transpiration rate. *J. Exp Bot* **56**: 3033–3039.

STAPE, J.L., BINKLEY, D., RYAN, M.G., FONSECA, S., LOOS, R.A., TAKAHASHI, E.M., SILVA, C.R., SILVA, S.R., HAKAMADA, R.E., FERREIRA, J.M.A., LIMA, A.M.N., GAVA, J.L., LEITE, F.P., ANDRADE, H.B., ALVES, J.M., SILVA, G.G.C. and AZEVEDO, M.R. 2010. The Brazil *Eucalyptus* Potential Productivity Project: Influence of water, nutrients and stand uniformity on wood production. *Forest Ecol. Manage* **259**: 1684–1694.

STAPE, J.L., BINKLEY, D. and RYAN, M.G. 2004. *Eucalyptus* production and the supply, use and efficiency of use of water, light and nitrogen across a geographic gradient in Brazil. *Forest Ecol. Manage* **193**: 17–31.

SURAPORNIBOON, P., JULSRIGIVAL, S., SENTHONG, C. and KARLADEE, D. 2008. Genetics of silicon content in upland rice under drought condition. *SABRAO Journal of Breeding and Genetics* **40**(1): 27–35.

UNIVERSITY OF MICHIGAN. 2006. Human Appropriation of the World's Fresh Water Supply. http://www. globalchange.umich.edu/globalchange2/current/lectures/freshwater_supply.

VAN DIJK, A.I.J.M. and KEENAN, R.J. 2007. Planted forests and water in perspective. *Forest Ecol. Manage* **251**: 1–9.

VOIGTLAENDER, M. 2007. Caracterização hidrológica e biogeoquímica de microbacias: uma comparação entre Mata Atlântica e *Pinus taeda* L. Dissertação (Mestrado em Recursos Florestais) – Escola Superior de Agricultura Luiz de Queiroz, Piracicaba. 74 p.

VAN BUIJTENEN, J.P., BILAN, M.V. and ZIMMERMAN, R.H. 1976. Morpho-physiological characteristics related to drought tolerance in *Pinus taeda* L. In: Cannel, MGR and FT Lat (Eds) Tree Physiology and Yield Improvement. Academic Press. New York. Pp. 349–359.

VANCLAY, J.K. 2009. Managing water use from forest plantations. *Forest Ecology & Management* **257**: 385–389.

VON STACKELBERG, N.O. 2005. Simulation of the hydrologic effects of afforestation in the Tacuarembó River basin, Uruguay. (MS Thesis). North Carolina State University. Raleigh, NC. USA 155 p.

WHITE, K.J. 1993. Silviculture of *eucalyptus* planting-Learning in the region. Regional expert consultation on *eucalyptus*. Volume I. http://www.fao.org/docrep/005/ac777e/ac777e07.htm.

WHITE, D., BATTAGLIA, M., BRUCE, J., BENYON, R., BEADLE, C, McCRATH, J., KINAL, J., CROMBIE, S., AND DOODY, T. 2009. Water-use efficient plantations-separating the wood from the leaves. Forest &Wood Products Australia. Project No. PNC073-0708. Melbourne, Australia 25 p.

WHITEHEAD, D. and Beadle CL. 2004. Physiological regulation of productivity and water use in *Eucalyptus*: a review. *Forest Ecol. Manage* **193**: 113–140.

WOODHOUSE, P. AND HASSAN, R. 1999. Implementation of South Africa's National Water Act. Catchment Management Agencies: Interests, Access and Efficiency. Inkomati Basin Pilot Study. Rural Resources, Rural livelihoods Working Paper 12. http://www.sed.manchester.ac.uk/idpm/research/publications/wp/rr/documents/rr_wp12.pdf.

WIKPEDIA. 2011. http://en.wikipedia.org/wiki/Drainage_basin.

XU, Z.H., SAFFIGNA, P.G., FARQUHAR, G.D., SIMPSON, J.A., HAINES, R.J., WALKER, S., OSBORNE, D.O. and GUINTO, D. 2000. Carbon isotope discrimination and oxygen isotope composition in clones of the F1 hybrid between slash pine and Caribbean pine in relation to tree growth, water-use efficiency and foliar nutrient concentration. *Tree Physiology* **20**: 1209–1218.