Photosynthetic Behavior of Gmelina Arborea Roxb. Genotypes at 15-months-old Plantation, South Pacific of Costa Rica

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Abstract

The aim of this investigation was to determine the photosynthetic capacity of five genotypes at 15-months-old plantation of Gmelina arborea. A clonal trial was conducted, taking one individual (ramet) at random from each of five clones at each of five blocks, for a total of 25 trees assessed. The study focused on clonal response to the light curve, and their performance in terms of gas exchange. No statistically significant differences were recorded between genotypes investigated for any of the parameters obtained from the light response curves. At the species level, maximum photosynthetic rate at light saturation (A_{nmax}) averaged 25.23 mol µmol CO_2 $m^{-2}s^{-1}$ and light saturation point (LSP) recorded average was 1499.95 µmol CO_2 $m^{-2}s^{-1}$.Clone 5 showed the highest values for A_{nmax} and LSP (19% and 41% above the overall average respectively), becoming the most effective in terms of photosynthetic capacity from the five clones evaluated in the field. No statistically significant differences between clones for any of the gas exchange parameters obtained were detected.

Keywords: *Gmelina arborea*, photosynthetic capacity, clones, plantation

Resumen

El objetivo de la investigación fue determinar la capacidad fotosintética de cinco genotipos en una plantación de 15 meses de edad de Gmelina arborea. Se utilizó un ensayo clonal del cual se tomó un individuo al azar de cada uno de los cinco clones en cada uno de ls cinco bloques, para un total de 25 árboles evaluados. El estudio se enfocó en la respuesta a la curva de la luz de los clones y su desempeño en términos del intercambio de gases. No se registraron diferencias estadísticas entre los clones evaluados para ninguno de los parámetros obtenidos de las curvas de luz. A nivel de la especie, la tasa máxima fotosintética a saturación de luz (A_{nmax}) promedio fue 25.23 mol µmol CO_2 $m^{-2}s^{-1}$ y el punto de saturación de luz (LSP) promedio registrado fue 1499.95 µmol CO_2 $m^{-2}s^{-1}$, el clon 5 mostró los valores más deseablesparаA_{nmax}y LSP (19% y 41% sobre el promedio general respectivamente), convirtiéndose en el más efectivo en términos de capacidad fotosintética para los cinco clones evaluados en campo. No se registraron diferencias estadísticas entre clones para ninguno de los parámetros de intercambio de gases.

Palabras Clave: *Gmelina arborea*, capacidad fotosintética, clones, plantación

Introduction

Latin America is emerging as a leader in forest plantations, having more than 12 million hectares planted for industrial use with projections to reach 17 million hectares in 2020 (Flores 2011). Despite this boom, a very important amount, yet not documented, of these plantations have not obtained the expected productivity. The main causes are associated with inappropriate site selection, use of a poor planting material and lack of appropriate silvicultural programs that integrate scientific information such as essential disciplines of genetics and tree physiology (Pérez and Kanninen 2005). Similarly the establishment period in the field is a critical period, during which time trees implement strategies to adapt to the soil and climatic conditions of the site. In this first stage changes occur in both the morphological and physiological characteristics which directly influence growth rates (Cornelissen et al. 1996, cited by Araque et al. 2009).

The study of physiological characters must be a priority due to its relation to genotype and productivity in forest plantations (Dickman 1991, Martin et al. 2005, Huang et al. 2006, Aspinwall et al. 2011). Physiological processes are directly involved in tree growth and, consequently, the productivity of a plantation, being the most relevant the photosynthesis process associated with growth (Flood et al. 2011). Studies of the photosynthetic rate, along with other gas exchange parameters are significant as an early selection criterion (Lapido et al. 1984, Kundu & Tigerstedt 1998, cited by Flores 2012). Others such as stomatal conductance, is a parameter associated with the level of stomatal opening (López et al. 2007) and regulates to some extent the photosynthetic process as it relates to perspiration, which when excessive causes significant reductions in productivity (Azcón et al. 2000). Chlorophyll content has been the subject of several studies that relate its levels to net photosynthesis, finding some conflicting opinions (Buttery &Buzzell 1977, quoted by Flores 2012), citing the chlorophyll content of *Gmelina arborea* also depends on the age (Rojas et al. 2012).

Investigations on tree physiology must generate practical information that fits breeding programs, helping to increase growth of plants, mainly by selecting more efficient genotypes in terms of physiological processes in a given environment (Pallardy 2008, Pepper et al. 2012). However, at present, the research has been done with plants under controlled environmental conditions without adequate field calibration, which can lead to a waste of time and resources, since in most cases the results cannot be extrapolated to describe natural environments (El-Sharkawy 2006). Despite the usefulness of physiology in forestry production there are very few studies on superior genotypes for plantations, as in the case of new improved materials of *Gmelina arborea* and other species (Araque et al, 2009, Lopez et al. 2001). The only investigations recorded in Latin America are conducted by Flores (2012) and Rojas et al. (2012) both in Colombia. Early growth and physiological characteristics must be investigated to predict the development of genetic material in the field. *Gmelina arborea* Roxb. is an important timber tree of the family Lamiaceae (Kok 2012). It has become of great importance in many tropical areas around the world, as an option to ensure supply of raw material for the forest industry (Balcorta& Vargas 2004, Kumar 2007, Adebisi et al. 2011, Wee et al. 2012). Its importance lies in the rapid initial growth (Adebisi et al. 2011), and that it can easily adapt to a variety of site conditions, and a variety of uses (Indira 2006) providing producers and / or investors a quick return on their investment (Wee et al. 2012).

The aim of this investigation was to determine the photosynthetic capacity of five genotypes of *Gmelina arborea* at 15 months of age plantation, in order to improve the selection process of genotypes able to adapt to various adverse conditions without adverse effect on growth rate or biomass production.

Materials and Methods

Study area and Experimental Material

The present study was carried out at a clonal trial of *Gmelina arborea*, located in the community of Monterrey, Puerto Jiménez district, Golfitocounty, Province of Puntarenas, Costa Rica south Pacific region (N 83.39655° W 8.57701°). The study area has an average annual rainfall of 3500-4000 mm, mean annual temperature of 24-28°C (Kappelle et al. 2002) with an altitude of 20 meters. The region is classified as premontane wet forest transition to Basal (Holdridge 1967). The evaluated trees came from a clonal trial established by INISEFOR-UNA in September, 2011, under an experimental design of randomized complete blocks. Six individuals per clone in pairs were established on each block, ie three pairs of each clone per each block and repeated in six blocks. The location of the clonal trial and the distribution of the clones on each block are presented in figure 1 and figure 2 respectively. For the present study an individual ramet per each of the five genotypes, at each of the 5 blocks were evaluated, for a total of 25 trees.

Figure 1.View of the Spatial Location of INISEFOR-UNA Gmelina Arborea Clonal Trial, South Pacific of Costa Rica

Source: INISEFOR - UNA

Figure 2: Schematics of *Gmelina* Arborea Clonal trial in the Field, South Pacific of Costa Rica
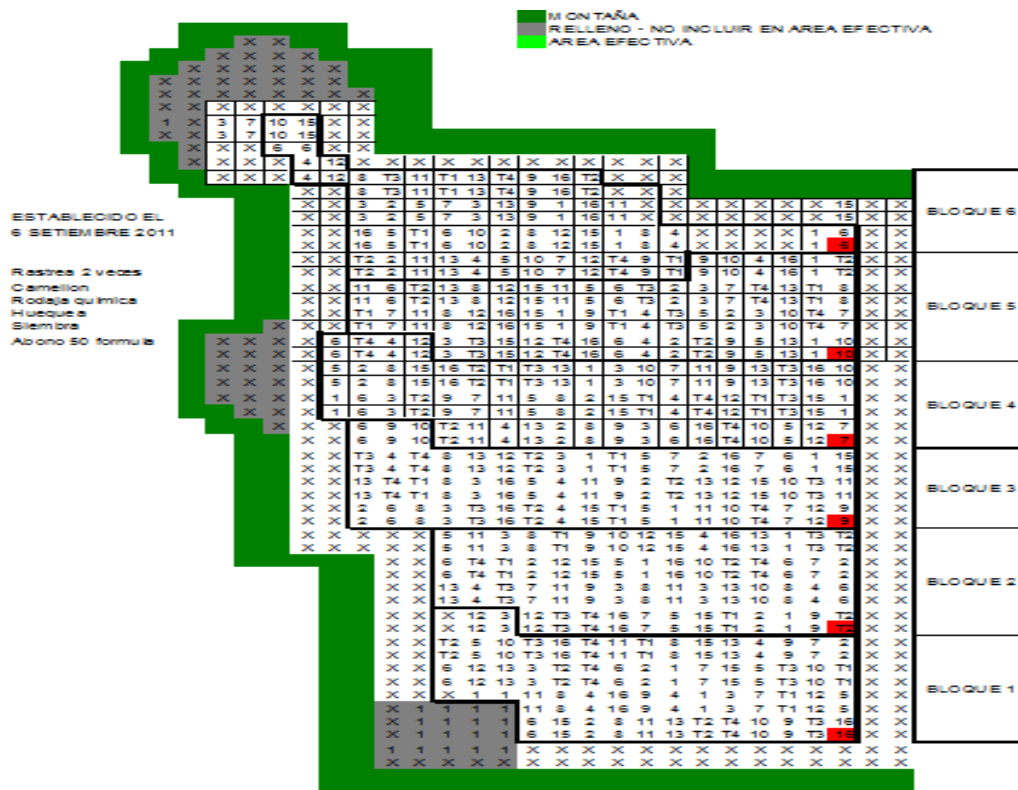
Source: INISEFOR - UNA

Measuring Physiological Parameters

Physiological parameters of *Gmelina arborea* for five genotypes at 15 months of age were obtained. This research encompassed both the to the light response curve of the clones as well as their performance in terms of gas exchange. Response Curve Light (A_n-PPFD). The average CO_2 used with the equipment, to obtain photosynthetic variables was 360 ppm $\pm$ 16.05 ppm with an air temperature of 30 ℃ within the cuvette, as these are the average conditions recorded at crown level during fieldwork days.

Measurements were made on fully developed, expanded and illuminated leaves, located at the top of the crwon (Blake &Bevilacqua 1990, Evans &Poorter 2001, Huang et al. 2006, Tharakan et al. 2008), where the young and highly photosynthetically active leaves are located (Herbohn et al. 2009). The third pair of levaeswityh no apparent damage on the blade were used for evaluations (Tharakan et al. 2008). A total of 17 levels of photosynthetic photon flux density incident (0, 50, 100, 150, 200, 250, 300, 350, 400, 600, 800, 1000, 1200, 1400, 1600, 1800, 2000 µmol photons $m^{-2}s^{-1}$) were evaluated, starting at 0 and increasing the intensity gradually until 2000 µmol photons $m^{-2}s^{-1}$. Five trees were evaluated for each clone. Data were fitted using the formula of the non-rectangular hyperbola (Thornley 1976, Marshall & Biscoe 1980,Pasian&Lieth1990, Flores 2012) shown below:

$F (PPFD, \Phi, A_{max}, R_d)$:

$$A_n = \frac{\Phi PPFD + A_{max} - \sqrt{(\Phi PPFD + A_{max})^2 - 4\Phi PPFD A_{max}\theta}}{2\theta} - R_d$$

where A_n is the net photosynthetic rate, Φ is the quantum yield of photosynthesis, PPFD is the density of photosynthetic photon flux, $A_{max}$is the maximum photosynthetic rate at light saturation, $R_d$is mitochondrial respiration rate and θ is a parameter describing the convexity of the curve (Leverenz1988, Zufferey et al. 2000, Flores 2012). LSP is the point of light saturation and was calculated using the equation proposed by Lieth and Pasian (1990):

$$LSP = 2\frac{(A_{max} + R_d)}{\Phi}$$

Gas Exchange

These measurements were performed on a clear day (Rojas et al. 2012) with an air temperature of 30 ℃ in the cuvette. Evaluation of gas exchange was performed using an infrared gas analyzer open type (CIRAS-2, PP Systems, USA) with a PLC6 (U) cuvette at a 360 ppm ± 8.83 ppm CO_2 concentration, and fixed light intensity of 1000 ± 4.57 µmol photons m^{-2} s^{-1}, with the main objective to prevent photo inhibition (Evans and Poorter 2001). The obtained physiological variables were: net photosynthesis (A_n= µmol CO_2 $m^{-2}s^{-1}$), stomatal conductance (G_s= mmol H_2O m^{-2} s^{-1}), transpiration (E = µmol H_2O m^{-2} s^{-1}) and water use efficiency = (µmol H_2O m^{-2} s^{-1}). The measurements were performed in a fully expanded leaf of the third pair from a branch located in the top tier of the crown (Evans &Poorter 2001, Rojas et al. 2012), evaluating five trees per genotype.

Statistical Analysis

The analysis was performed using InfoStat® (2012) statistical software. Physiological gas exchange data, after verification of parametric statistics assumptions were analyzed by an analysis of variance, and a comparison of means by Tukey test (p <0.05).

Results and Discussion

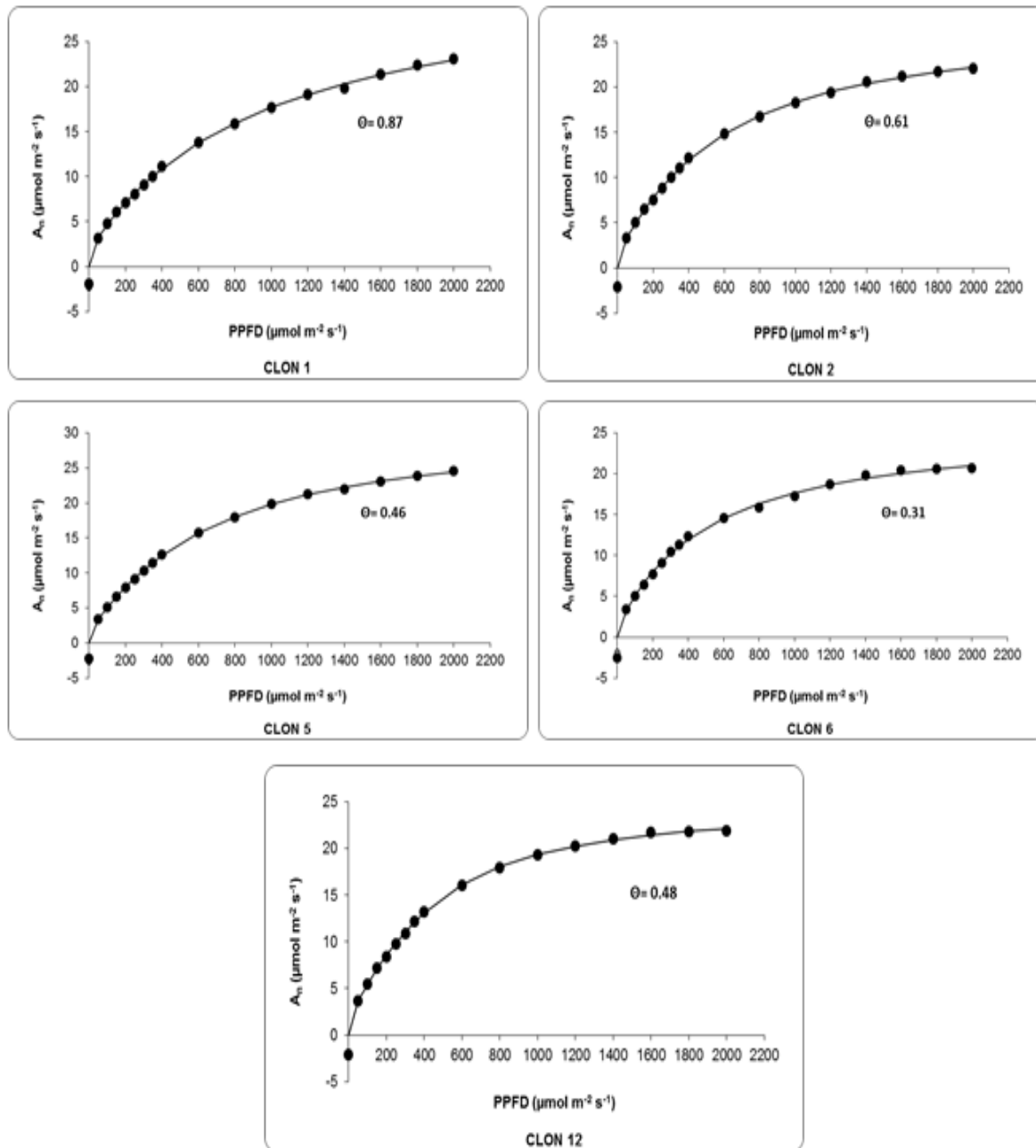**Light Response curve (A_n-PPFD)**

The curve of daily PPFD represents the average of 10 days of measurement. It was used for making decisions about which densities to use for the development of the light curves. The highest density of photosynthetic flow occurred between 11 am and 12 noon. Curves were constructed from 0 to 2000 µmol m^{-2} s^{-1}, given a restriction by the measuring equipment. The daily course of photosynthetic flux density (PPFD) is shown for the site where the test clones where the experimental material is located (Figure 3).
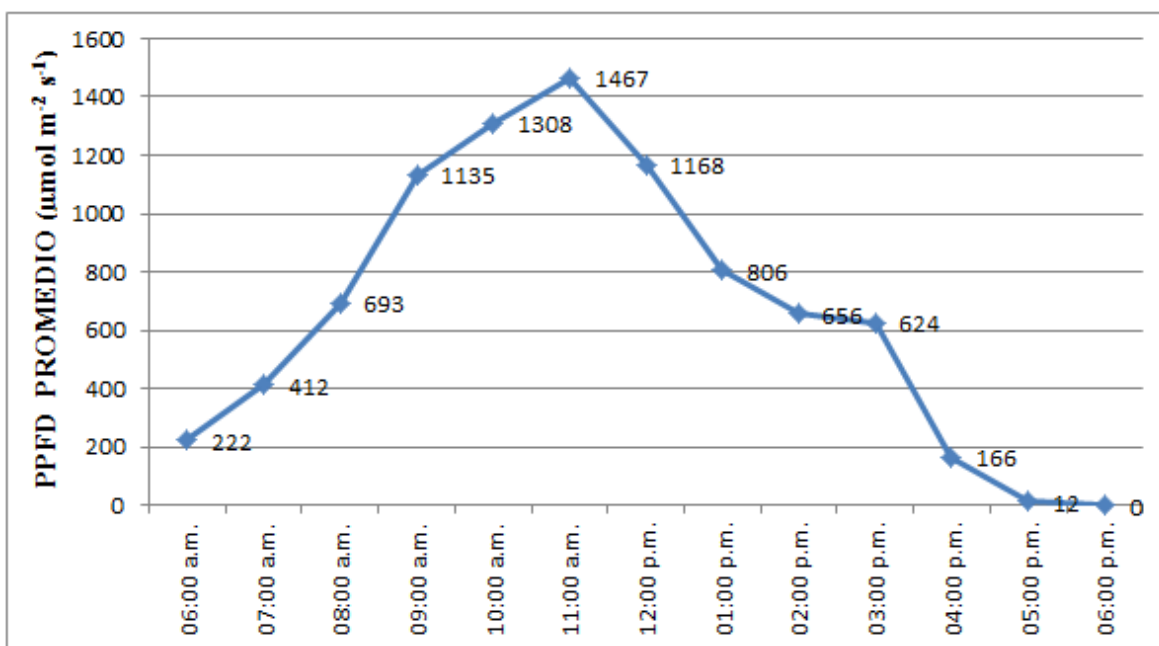
Figure 3: Average Daily Pattern of Photosynthetic Flux Density (PPFD) at the Site of Gmelina Arborea Clonal Assay INISEFOR-UNA, in Puerto Jimenez, Costa Rica Southern Pacific

In figure 4, curves of CO_2 assimilation as a function of incident photon flux density for five genotypes of *Gmelina arborea* (clones 1, 2, 5, 6 and 12) in a plantation at 15 months of age (Figure 4) are presented. Such curves help to determine which clones exhibit greater plasticity in terms of their physiological behavior (Dickman 1991), which allow them to successfully survive and compete in different environmental conditions (Corcuera et al. 2005).

Figure 4: Photosynthetic Response Curve (A_n) to Photosynthetic Photon Flux Density (PPFD) for Five Clones of Gmelina Arborea in a 15-Months-Old Plantation

A very similar behavior among curves of the five clones investigated was found, and the convexity values of the curves (Θ) showed no statistically significant differences, with a variation ranging from 0.31 and 0.87 (**Error! Reference source not found.**). The not so slope on the curve that occurred at the beginning of each curve coincides with the typical pattern of species acclimated to environments with high rates of incident photon flux, which denotes conditioning and utilization of photosynthetic flux density. From the light response curves values physiological traits for the five genotypes evaluated in field to 15 months of age (Table 1) are obtained.

Table 1: Physiological Parameters Estimated From Light Response Curves in Five *Gmelina Arborea* Clones in a 15-Months-Old Plantation

CLONE	Respiration (R_d) $\mu mol\ m^{-2}\ s^{-1}$			Quantum yield (Φ) mol/mol			Maximumphotosynthesis (A_{max}) $\mu mol\ CO_2\ m^{-2}\ s^{-1}$			Light Saturationpoint (LSP) $\mu mol\ m^{-2}\ s^{-1}$		
1	-1.6993	a	-3%	0.0300	a	-17%	26.08	a	3%	1684.58	a	12%
2	-1.6817	a	-4%	0.0360	a	-1%	22.36	a	-11%	1375.11	a	-8%
5	-2.1247	a	21%	0.0328	a	-9%	**30.08**	a	19%	**2110.26**	a	41%
6	**-1.5197**	a	-14%	0.0399	a	10%	24.31	a	-4%	1171.52	a	-22%
12	-1.7688	a	1%	**0.0421**	a	17%	23.32	a	-8%	1158.26	a	-23%
Average	**-1.7589**			**0.0362**			**25.23**			**1499.95**		

Means with a common letter are not significantly different (p> 0.05)
Percentage values represent its difference in reference to average value

No statistically significant differences were found among the investigated genotypes in any of the traits evaluated. The values recorded were over a range of 0.030 to 0.042 for the clones investigated. The recorded value by clone 12 was 17% higher than the average (0.0362) and 40% higher compared to the lowest (clone 1). These values are higher than those reported by Nogués and Baker (1995) and Tambussi and Graciano (2010), cited by Flores (2012), for C3 plants not subjected to water stress, who reported values from 0.025 to 0.030 $\mu mol\ m^{-2}\ s^{-1}$. However, plants can modify their patterns of quantum yield, significantly increasing its level in stressful situations, on a process known as compensatory photosynthesis (Retuerto et al. 2003). The maximum photosynthetic rate at light saturation (A_{nmax}) showed a variation between 22.36 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ for clone 2 and 30 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ in clone 5, with an average of 25.23 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$. Clone 5 had the highest maximum photosynthesis, stomatal limitations have lower suggesting for gas exchange; while clone 2 had the lowest A_{nmax} with a range of variation of 34.5% between them. The results of this study that reported by Gliessman (2002), cited by Flores (2012), who points out that C3 plants tend to have their maximum photosynthetic rates under moderate conditions of light and temperature, and inhibition pattern are opposed to high rates of lighting and heat.

Araque et al. (2009) determined the ecophysiological characteristics of four species, *Cedrelaodorata* which recorded the largest A_{nmax} with a value of 11.7 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$, also recording the highest growth yields. Lopez et al. (2001) evaluated the photosynthetic rate of five forest plantation species, recording values from 6.1 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ to 14 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$, with *Cordiaalliodora* having the highest An. Huang et al. (2006) evaluated the physiological behavior twelve tropical forest species under similar environmental conditions to this study, reporting for *Gmelina arborea* a rank of fourth on values of A_{nmax} (12.64 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$). Herbohn et al. (2009) evaluated the light response curves in different planting spacings, with improved genetic materials at 11 months, registering 20.5 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ as the best average value of An_{max} at 4m x 4m planting density. Consistently, in all the research cited, the recorded values are definitely lower than those determined for the genotypes of *G. arborea* of this study, which could help classify it as a successful invasive species in tropical environments, with recorded high growth rates and higher photosynthetic capacity compared to native species (Pepper et al. 2012). However, around one year of age is still very early to make comparisons between different materials of the species (Herbohn et al. 2009, Codesido et al. 2012). These results show differences in physiological behavior to changes in the incident radiation, due to differences in requirements of light and behavior of stomatal closure. Therefore, the incident radiation, and other climatic conditions must be taken into account when selecting either species to be established in a given production system (López et al. 2001).

As for the light saturation point (LSP) average recorded by the five genotypes investigated was 1499.95 $\mu molm^{-2}\ s^{-1}$, ranging from 1158.26 $\mu molm^{-2}\ s^{-1}$ for clone 12 and 2110.26 $\mu molm^{-2}\ s^{-1}$ for clone 5, ie clone 5 had a higher photosynthetic capacity, since it managed to keep active and increasing its CO_2 fixation at very high light intensities. Further research should evaluate the distribution of the different tissues of the biomass produced, in relation to their photosynthetic potential (Araque et al. 2009). The five clones investigated are part of a multi-stage genetic assembly of phenotypic and indirect genotype selection. These same clones showed desirable diametric growth in the field, which might suggest that photosynthetic mechanisms have a stable development.

This could explain the failure to find significant differences in any of the physiological parameters measured among the five clones investigated. That is why, it is necessary to increase the experimental sample in future research to corroborate or refute the previous approach (Adams et al. 2011, Flood et al. 2011). Although no statistically significant differences among clones was found on the parameters obtained from the light response curves, it is noteworthy that clone 5 showed higher values for A_{nmax} and LSP (19% and 41% above the overall average respectively). Clone 6, exhibited excellent values in respiration, quantum yield and maximum photosynthesis, although its LSP is low. That is why clone 5 was identified as to have the highest photosynthetic capacity of the five genotypes evaluated on the plantation. In contrast, clone 12 showed the least desirable values in all parameters except the quantum yield, which was located in the last position of the clones evaluated. In summary, the order of the clones, from most to least desirable, in terms of physiological parameters obtained from the light curves are as follows:

5 > 6 > 1 > 2 > 12

Figure 5 shows the light response curves obtained for the five clones; no appreciable aspects are denoted in the individual curves. Left curves are presented to 600 µmol photons m^{-2} s^{-1} (Figure 5A), to compare root cuttings in nursery condition, and right curves to 2000 µmol photons m^{-2} s^{-1}, for each of the five investigated clones (Figure 5B).
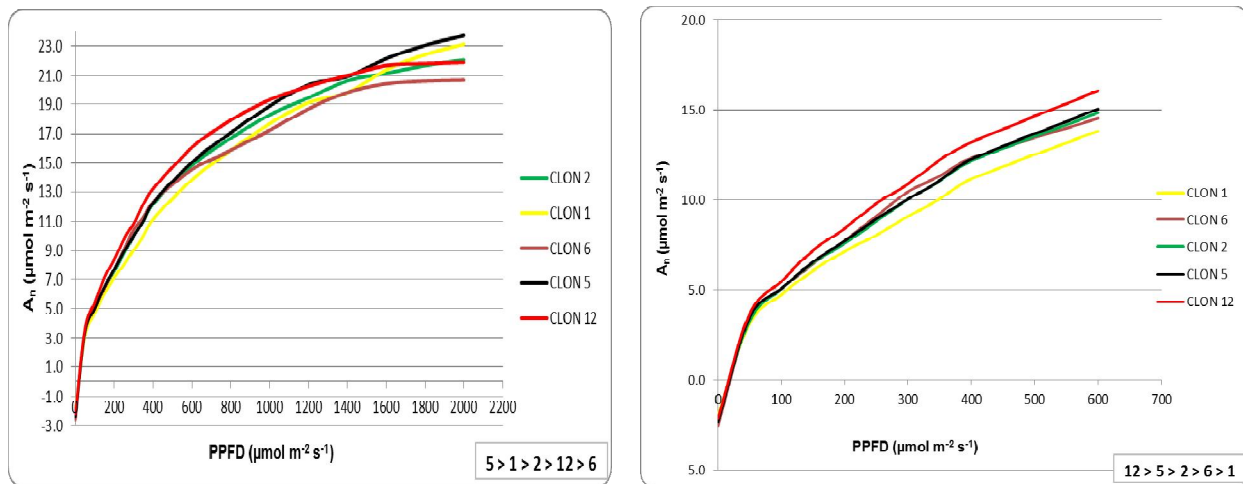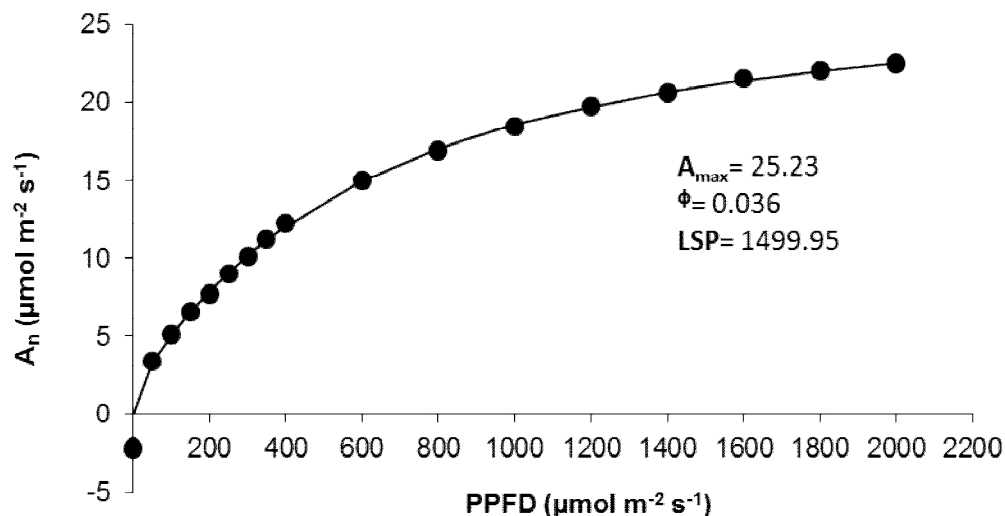

Figure 5: Photosynthesis Response Curve (A_n) to Photosynthetic Photon Flux Density (PPFD) for Fivegmelina Arborea Clones Evaluated Under Field Conditions at 15-Months-Old

Changes are identified in the pattern of the curves from the five clones as photon flux density is increased. The curve of clone 12 is higher than the rest up to 1400 µmol photons m^{-2} s^{-1}, where it begins to decrease its photosynthetic rate to be located second to last at 2000 µmol photons m^{-2} s^{-1} (Figure 5B). Meanwhile clone curve 5 is held in the second position up to 1400 µmol photons m^{-2} s^{-1}, which exceeds the clone 12 and is placed above the other curves up to 2000 µmol photons m^{-2} s^{-1}, point where it shows a clear trend of not having yet reached the LSP. This pattern is confirmed in the ranking of clones established in the preceding paragraph with respect to the variables obtained from the light curves for each genotype investigated.

The curve of clone 1 remains in the last position until about 700 µmol photons m^{-2} s^{-1}, at which point increases photosynthetic rate to be in the second position up to 2000 µmol photons m^{-2} s^{-1}, where it starts to decrease in photosynthetic rate per unit photon flux.

Using the five light response curves from each of the five clones investigated, the photosynthetic response curve at a given incident photon flux density was obtained, showing the average photosynthetic performance for the species under field conditions at 15 months age (Figure 6).

Figure 6: Average Response Curve Photosynthesis (A_n) to Photosynthetic Photon Flux Density (PPFD) Gmelina Arborea Plantation under Field Conditions at 15 Months Age

Gmelina arborea recorded average maximum photosynthesis (A_n) of 25.23 mol CO_2 µmol CO_2 $m^{-2}s^{-1}$ and a point of light saturation 1499.95 µmol CO_2 $m^{-2}s^{-1}$. This value was higher than those reported by other authors (Combalicer et al. 2010, Huang et al. 2006, Herbohn et al. 2009). The value of quantum yield (ϕ) average obtained for the species is 0.036. Initially could suggest a poor efficiency of the photosynthetic system, however, the slope value with the species can maintain its constant photosynthetic mechanism and achieve high values Amax. This suggests that melina is capable of using PAR values both low and high, which is a competitive-adaptive advantage.

Gas Exchange

Stomatal to moderate levels of water stress closure, osmotic adjustment and high efficiency in water use are some of the physiological parameters that should guide the clonal selection (Corcuera et al. 2005,Combalicer et al. 2010, Flores 2012); hence the importance of quantification and evaluation of such processes as clonal selection parameters. The process of evaluation of gas exchange parameters by net photosynthesis, stomatal conductance, transpiration and use of water efficiency; for the five genotypes were performed using a PAR of 1000± 4.57 µmol m-2s-1 and an average CO2 concentration of 360 ± 8.83 ppm.
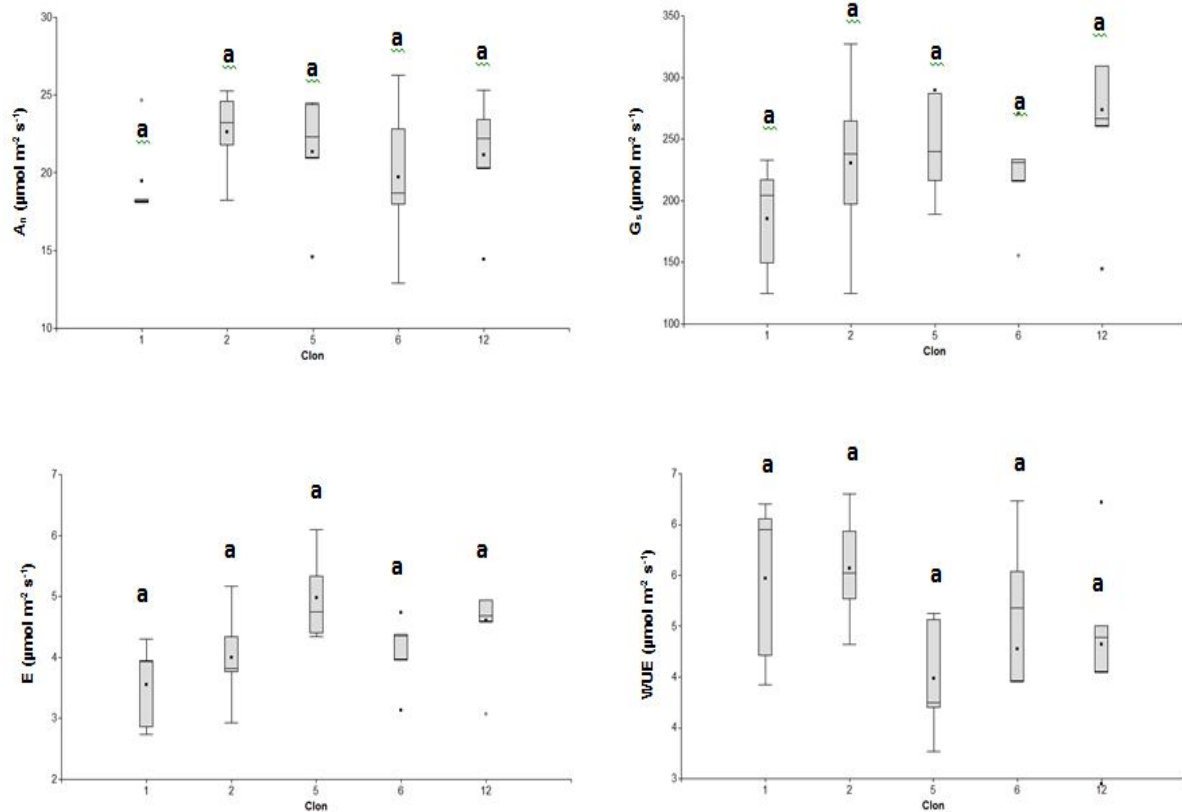
Means with a common letter are not significantly different (p> 0.05)

Figure 7: Net photosynthesis (A_n), stomatal conductance (G_s), transpiration (E) and water use efficiency (WUE) in five clones of Gmelina arborea plantation under field conditions at 15 months age

Significant variation in the data was recorded both among and within the five clones investigated for the four parameters, as a result from wide ranges between the minimum and maximum value in most of them. This caused that the test of means detected no statistically significant differences among clones for any of the parameters ($\alpha = 0.05$). Aspinwall et al. (2011) indicate that very little is known about how the uniformity of physiological rates vary depending on the genetic variation and viceversa, becoming the main explanation for the wide variations in gas exchange parameters.

Clones 5 and 2 recorded the highest values for all parameters, except WUE where clone 5 showed a low value. Clone 12 had smaller ranges of variation for the parameters evaluated, suggesting greater stability and less sensitivity to variables that could interfere reading by CIRAS-2, such as small changes in environmental conditions that require stabilization time for a correct data recording (Confederación Hidrográfica del Guadiana 2011). There is a similar pattern in the placement of the clones in the graphs of gas exchange (Figure 7), as well as the ranges of variation of Gs and E variables, confirming a strong relationship between the two (Combalicer et al. 2010) . However, it is assumed that the experimental error is large due to the few observations in the sample, to the point that it seems better than the accuracy of the equipment; values obtained from gas exchange process for the five clones of *Gmelina arborea* are presented below.

Table 2: Physiological Parameters Evaluated According to Gas Exchangein Fivegmelina Arborea Clones Ata 15-Months-Old Plantation, South Pacific Of Costa Rica

CLON	FOTOSINTESIS NETA (A_n) $\mu mol\ m^{-2}s^{-1}$			CONDUCTANCIA ESTOMATICA (G_s) mol/mol			TRANSPIRACION (E) $\mu mol\ m^{-2}s^{-1}$			USO EFICIENTE DEL AGUA (WUE) $\mu mol\ m^{-2}s^{-1}$		
5	21.36	a	**2%**	**289.53**	**a**	**16%**	4.98	a	**14%**	4.31	a	**-14%**
12	21.15	a	**1%**	273.60	a	**9%**	4.61	a	**5%**	4.76	a	**-5%**
6	19.73	a	**-5%**	270.73	a	**8%**	4.74	a	**8%**	4.70	a	**-7%**
2	**22.62**	**a**	**8%**	230.27	a	**-8%**	4.00	a	**-9%**	**5.76**	**a**	**15%**
1	19.47	a	**-7%**	185.53	a	**-26%**	**3.55**	**a**	**-19%**	5.62	a	**12%**
PROMEDIO	**20.87**			**249.93**			**4.38**			**5.03**		

Means with a common letter are not significantly different (p> 0.05)
Percentage values represent its difference in reference to average value

According to the gas exchange process evaluated, net photosynthesis (A_n) ranged from 19.47 $\mu mol\ m^{-2}s^{-1}$ to 22.62 $\mu mol\ m^{-2}s^{-1}$among the five clones, with an average of 20.87 $\mu mol\ m^{-2}s^{-1}$, higher than reported by several authors for both melina as other tropical species (Huang et al. 2006, Herbohn et al. 2009, Combalicer et al. 2010) value. Clone 5, as in the evaluation of the light response curves above recorded higher average values G_s and E for 16% and 14% respectively. A higher value on average in net photosynthesis was also recorded (21.36 $\mu mol\ m^{-2}s^{-1}$). According to light curves, the value of maximum photosynthesis which clone 5 can obtain on its light saturation point is 30.08 $\mu mol\ m^{-2}s^{-1}$. Combalicer et al. (2010) identified significant differences from net photosynthesis between four tropical species planting, however, such values are attributed to a greater number of foliar biomass from species with respect to the other, and thus issues such as the arrangement of leaves in the glass resulting in a mutual shadow on them as well as the morphology and chlorophyll content of the leaves. It does not apply in the present investigation as genotypes of the same species present similar leaf morphology.

Meanwhile Huang et al. (2006) evaluated 12 tropical species and maximum An values recorded for melina plantation of 16 $\mu mol\ m^{-2}s^{-1}$, lower value compared to that recorded in this investigation.. The differences in the values obtained in each study may be attributable to multiple site soil and climatic conditions, mainly temperature and irradiation recorded during the days of measurement. López et al. (2001) and Pepper et al. (2012) found that an increase in temperature and irradiation brings decrease of net photosynthesis and chlorophyll content, and inducing stomatal closure, and cause photoinhibition photorespiration, causing damage in the photosynthetic apparatus

Stomatal conductance (G_s) showed no statistically significant differences between clones (α = 0.05). To a high variability among clones investigated, ranging from 185.53 $\mu mol\ m^{-2}s^{-1}$ to 289. $\mu mol\ m^{-2}s^{-1}$, ie a variation of 56% between the two was recorded As in An clones 12 and 6 showed high and worthy of note in this parameter. As in the present investigation, Araque et al. (2009) identified no statistically significant differences in the evaluation of Gs to four tropical tree species. Sojka et al. (2005) reported a strong link between the rate of diffusion of oxygen from the soil and stomatal conductance, so that should make a comprehensive assessment of the soil and climatic variables for understanding variations in Gs, as there may be other factors involved with closure stomatal in *Gmelina arborea*; for example the concentration of CO_2 and some chemical signals (Farquhar & Sharkey 1982, cited by Rojas et al. 2012).

Similarly, transpiration (E), recorded no significant differences among the investigated genotypes (α = 0.05). Clone 5 had the highest value, which puts it at a disadvantage for sites prone to water stress, therefore when this clone be established in any condition, caution on its performance should be considered. Clone 1 showed the most desirable in terms of the value E. As with this research, Araque et al. (2009) failed to detect statistically significant difference regarding this variable in its evaluation of four tropical tree species. The overall average for E in this study was 4.38 $\mu mol\ m^{-2}s^{-1}$, considered low compared with the value of 3.50 $\mu mol\ m^{-2}s^{-1}$ on average reported by Flores (2012) for clones melina, 81 days old; presuming that possibly the material evaluated by Flores (2012) at one year of age presents significantly higher transpiration values since at older age the requirements of the process of gas exchange are higher (Flood et al. 2011, Rojas et al. 2012).

Rapid growth genotypes have a greater ability to limit water loss by transpiration compared with slow growing, presumably because of its efficiency in the regulation of stomatal closure, becoming genetic material with high efficiency in the use of water (WUE) (Blake and Bevilacqua 1990, Pepper et al. 2012). The value of E registered to melina by Huang et al. (2006) was 5.84 µmol $m^{-2}s^{-1}$ higher than in the present investigation. The differences between species and genotypes, as perspiration, could be explained by the total leaf area, which has a significant effect on loss of water due to perspiration. Greater total leaf area obviously implies a larger total surface transpiration (Araque et al. 2009, Combalicer et al. 2010), without neglecting the frequency and size of stomata (Tharakan et al. 2008 Araque et al. 2009). The stomatal frequency varies between species, age of the plant and leaf and the upper or lower side thereof (Ekenayake et al. 1998, cited by Combalicer et al. 2010).

Fernandez et al. (2010) add to the list the degree of unsaturation of water in the air (deficit vapor pressure), which is emerging as the main factor causing water consumption by transpiration in plants. The close relationship between morphological and physiological characteristics is crucial in the adaptation strategy that develops every species mainly is their first years of life. However, Araque et al. (2009) suggests that, for the four forest species assessed, reported no clear relationship between transpiration rate and the anatomical structure of the species.

Water use efficiency (WUE) is a characteristic of each species and depends largely on environmental conditions (Medrano 2007). It is ultimately determined by the stomatal behavior and plays a predominant role in areas where water supply is the main constraint to production (Combalicer et al. 2005). Genotypes of rapid growth record high values of WUE due to their low values of transpiration (Blake and Bevilacqua 1990), achieving more carbon fixation through photosynthesis, per unit of water transpired. In the present study, no significant differences (α = 0.05) for that parameter among the five clones tested were recorded. The average for genotypes plantation at 15 months of age was 5.03 µmol m^{-2} s^{-1}. The clone 2 had the highest value for this parameter with 15% more than the average WUE due to a low of transpiration. More efficient water use means equal or greater production than other genotypes, but with lower water consumption. Melina clones evaluated by Huang et al. (2006) reported high levels of perspiration, which directly affects less efficient water use for these clones (2.65 µmol m^{-2} s^{-1}) compared with those in the present investigation values (5.03 µmol m^{-2} s^{-1}). The ranking of the genotypes in terms of water use efficiency is as follows: 2 = 5.76 µmol m^{-2} s^{-1}> 1 = 5.62 µmol m^{-2} s^{-1}> 12 = 4.76 µmol m^{-2} s^{-1}> 6 = 4.70 µmol m^{-2} s^{-1}> 5 = 4.31 µmol m^{-2} s^{-1}. WUE values recorded in this investigation are considered low compared with those reported by Combalicer et al. (2010) for four tropical species, who reported a maximum value of 10.1 µmol $m^{-2}s^{-1}$, ie 90% higher than reported for melina genotypes in this investigation. These marked differences could be explained by the fact that WUE, is ultimately, determined by self-stomatal behavior of each species, being instrumental in the adaptation strategy to field conditions, mainly in the first years of life (Rojas et al. 2012). High WUE suggests a high photosynthetic efficiency (Blake & Bevilacqua 1990). The variability recorded by genotypes in each of the evaluated parameters, provides the ability to further develop research selection and improved genotypes for plantations to production level, for different soil and climatic conditions. However, it is clear that the study of a single parameter does not guarantee selection, so both morphological and physiological parameters that contribute more to the early selection of genotypes should be identified. Moreover, different adaptation strategies genotypes must also be taken into account in the selection criteria, depending on the objectives of the breeding program (Fernández et al. 2010).

Conclusions and Recommendations

Very similar behavior in the response curves of light of the five clones investigated were observed. Not pronounced slope recorded in the beginning of the curve coincides with the typical pattern of species acclimated to high ambient incident photon flux rates (PPFD).No statistically significant differences between genotypes assessed for any of the parameters obtained from light response curves were recorded.

The maximum photosynthetic rate at light saturation (A_{nmax}) ranged between 22.36 µmol CO_2 m^{-2} s^{-1} for clone 2 and 30.08 µmol CO_2 m^{-2} s^{-1} for clone 5, with an average of 25.23 µmol CO_2 m^{-2} s^{-1}. The results recorded to indicate that clone 5 had lower stomatal limitations for gas exchange.

The light saturation point (LSP) recorded average was 1499.95 µmol CO_2 m^{-2} s^{-1}, ranging from 1158.26 µmol m^{-2} s^{-1} for clone 12 and 2110.26 µmol m^{-2} s^{-1} for clone 5.

Clone 5 recorded the most desirable values in the A_{nmax} and LSP (19% and 41% above the overall average respectively). Clone 6 showed excellent values in transpiration, quantum yield and maximum photosynthesis, although its LSP is the lowest. Clone 5 had the highest photosynthetic capacity in plantation at 15-months-old.

Gmelina arborea recorded on average a maximum photosynthesis (A_{nmax}) of 25.23 µmol CO_2 m^{-2} s^{-1} and a point of light saturationof 1499.95 µmol m^{-2} s^{-1}in planting at15-months-old.

Net photosynthesis (A_n) ranged from 19.47 µmol m^{-2} $s^{-1}$to 22.62 µmol m^{-2} s^{-1}, with an average of 20.87 µmol m^{-2} s^{-1}. Stomatal conductance (G_s) unchanged from 185.53 molmol m^{-2} s^{-1} to 289.53 molmol m^{-2} s^{-1}. The average for transpiration of the investigated genotypes was 4.38 µmol m^{-2} s^{-1}. The water use efficiency average was 5.03 µmol m^{-2} s^{-1}, varying from 5.76 µmol m^{-2} s^{-1} to 4.31 µmol m^{-2} s^{-1}.

Clone 2 recorded the highest values for net photosynthesis (A_n) and water use efficiency (WUE); and presented the second best value in relation to transpiration (E) and stomatal conductance (G_s). This clone became asshowing the most efficient photosynthetic capacity in planting condition at 15-months-old.

Clone 1 could be recommended for sites prone to water scarcity constraints due to its excellent breathability and WUE values.

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