

# Comparison of Growth Responses of *Khaya senegalensis* Seedlings and Stecklings to Four Irrigation Regimes

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*Khaya senegalensis* is an important tree species for timber production, native to West Africa, but mahogany shoot borer attacks prevent successful plantations. This research was aimed at comparing the growth of two propagule types, seedlings and stecklings, of *Khaya senegalensis* subjected to four irrigation regimes, 25, 50, 75 and 100% field capacity in Burkina Faso. The relative growth rate, biomass allocation and intrinsic water use efficiency of the propagules were assessed in a full-factorial pot experiment in block design. Except the relative growth rate of stem basal diameter and specific leaf area, for which mean values were significantly higher for seedlings than stecklings, the two propagule types had similar growth patterns regarding relative growth rates of stem length, leaf, stem, root and the total plant biomass. There was no significant difference between propagule types concerning biomass fraction to total plant biomass of leaf, stem and root, root to stem ratio, leaf area productivity and carbon isotope ratio ( $\delta^{13}\text{C}$ ). However, the irrigation regimes significantly affected all parameters. In contrast to 75 and 100% field capacity irrigation regimes, the low water supply of 25 and 50% field capacity resulted in plant stress, which was evident from the significant reduction in plant growth and biomass production and an increase in the root biomass to total plant biomass ratio and  $\delta^{13}\text{C}$ . It can be concluded that seedlings and stecklings have comparable growth patterns, while water stress is a major growth-limiting factor highlighting the need for selecting drought and borer resistant genotypes for successful plantations.

**Keywords** rooted cuttings, water stress, Senegal mahogany

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## 1 Introduction

*Khaya senegalensis* A.Juss. (Meliaceae), also known as acajou cailcedrat (French) or Senegal mahogany (English), is the most suitable indigenous tree species for timber production in Burkina Faso. Growing up to 35 m in height and 1.5 m in diameter on fertile soil, with an 8–16 m clean bole, its wood is hard, dense and red, resistant to fungi and termites. It is valued for carpentry, joinery, furniture making, cabinet work, ship building and in the production of decorative veneers (Nikiema and Pasternak 2008). But its natural regeneration is poor, and mahogany shoot borer *Hypsipyla robusta* (Moore) attacks prevent the success of plantations within the native area in West Africa (Newton et al. 1993, Nikiema and Pasternak 2008). Cloning resistant individuals to *Hypsipyla* has been sought as a solution for enhancing plantation establishment and production (Newton et al. 1993, Danthu et al. 2003).

Accordingly, our preliminary investigations have indicated that juvenile *K. senegalensis* plants are amenable to clonal propagation, allowing screening from seedling populations and multiplication of eventual resistant genotypes by stem cuttings. However, in savanna areas which are subjected to seasonal drought, such as Burkina Faso, water stress is known to be a key factor limiting plant growth, survival and productivity (Wilson and Witkowski 1998), and it often adversely affects forest plantations and agroforestry practices. It is considered to be a major cause of failure during re-establishment while also affecting seedling ability to use water efficiently, crucial to their post-planting survival (Margolis and Brand 1990, Sun et al. 1996). In addition, survival and initial growth of seedlings may be associated with one or more other factors, such as the mode of propagation, plant quality and age, silvicultural practices, browsing, fire and other disturbances (Zida et al. 2008, Bayala et al. 2009). Since the climate predictions for African savanna areas suggest an increase in the severity of droughts (Sheffield and Wood 2008), the ability to adapt to drought ought to be an important consideration when selecting genotypes to plant.

Because of problems associated with vegetative propagation such as cyclophysis or topophysis, field testing has been necessary to evaluate prop-

agule types and to quantify differences between vegetative propagules and seedlings (Frampton Jr and Foster 1993). As for a short term evaluation, pot trials have been a useful tool for clone testing prior to extensive field evaluation (Weih and Nordh 2002), a pot experiment was initiated to compare the growth pattern of seedlings and stecklings (plantable rooted cuttings) of *K. senegalensis* submitted to water stress by means of relative growth rate (RGR) and intrinsic water-use efficiency (WUE) based on carbon isotope ratio ( $\delta^{13}\text{C}$ ) in leaves. Stable carbon isotope ratio is a measure of the heavy isotope ( $^{13}\text{C}$ ) to the light isotope ( $^{12}\text{C}$ ) ratio (Lajtha and Michener 1994).

Relative growth rates are frequently used to compare the growth of seedlings that differ in initial size in order to eliminate any growth differences related to size and to determine which seedlings are inherently more efficient (Hunt 1982). Seedlings and stecklings of *K. senegalensis* may vary in production of biomass, resource allocation and adaptations to drought. Water use efficiency is a functional characteristic which is related to plant growth and performance under drought conditions. It is defined as the amount of carbon biomass produced per unit water transpired by the crop and corresponds to the transpiration efficiency in  $\text{C}_3$  plants (Farquhar et al. 1989). In theory, increasing WUE could affect plant growth. Moreover, measurement of WUE has been simplified by the discovery of a strong correlation between WUE and stable carbon isotope discrimination in  $\text{C}_3$  plants (Farquhar et al. 1989, Devitt et al. 1997). Commonly used for screening cultivars of dryland crops and rangeland grass species (Lajtha and Michener 1994), carbon isotope discrimination is becoming a valuable tool in tree breeding (Brendel et al. 2002, Raddad and Luukkanen 2006). The selection of genotypes with high  $\delta^{13}\text{C}$  and, therefore, high WUE, would have the potential to increase growth of total tree biomass in arid environments, such as the Sudanian zones of Burkina Faso (Farquhar et al. 1982, Hall et al. 1994, Sun et al. 1996). Thus, in order to generate information that could be used for the selection of improved plant materials suitable for propagation and successful plantations in Burkina Faso, an experiment was conducted to determine the effect of four irrigation regimes on growth, biomass allocation, foliar  $\delta^{13}\text{C}$  of two

propagule types, stecklings and seedlings, of *K. senegalensis*.

## 2 Materials and Methods

### 2.1 Plant Material and Experimental Design

The experiment was performed outdoors at the Forest Productions Department (DPF) of the Environmental and Agricultural Research Institute (INERA) in Ouagadougou, Burkina Faso. Seedlings and stecklings originated from a common seed source purchased from the National Seed Centre (CNSF) in Burkina Faso. Seeds were collected in 2008 from Tiakaré village (11°11'N–1°12'W) in Nahouri province, Burkina Faso. The seedlings were grown first in black perforated polythene bags (7 cm diameter × 25 cm height), which were filled with a mixture of sand, arable soil and manure (2:2:1 v/v/v), in the nursery at DPF. Ten-centimeter-long cuttings were collected from 3-month old seedlings and rooted in a 1:1 (v:v) perlite/sand medium in a mist greenhouse for two months. Rooted cuttings or stecklings were planted in plastic bags (20 cm diameter × 30 cm height), filled as previously described. After sprouting and then growing for about four months, 54 healthy stecklings, all approximately the same size, were chosen and replanted into 6-L plastic buckets filled with the arable soil, sand and manure mix. Concomitantly, five-month old seedlings (54 in total) which had previously been grown in plastic bags (7 cm diameter × 25 cm height) were transferred into 6-L plastic buckets. The bottom of each bucket has been manually perforated by means of five holes. Both, propagule types, seedlings and stecklings originating from seeds and rooted cuttings, respectively, were then placed in full sun and grown for 12 weeks, from September 28, 2009. The buckets were placed flat on the ground. All plants were watered once a day until October 12, when six individuals of each propagule type were selected at random for the initial harvest, which data were used in the assessment of growth rate. At this time, the mean length of stems was  $21.6 \pm 0.6$  cm (seedlings) and  $17.7 \pm 0.7$  cm (stecklings). The remaining 48 seedlings and 48 stecklings were used in a

completely randomized block design experiment with two factors, propagule type (seedlings and stecklings) and irrigation regime (25, 50, 75 and 100% field capacity). Three plants were randomly assigned accordingly to each of the eight experimental treatment units and arranged randomly in each of the four blocks (3 plants × 2 propagule types × 4 irrigation regimes × 4 blocks).

Field capacity was estimated by measuring the amount of water held in the soil of 12 control pots, which had been fully wetted, covered and weighed after 2 days of drainage. From October 13 until December 20, 2009, the pots were weighed every 72 hours and watered according to the appropriate irrigation regime by supplementing the soil's water content with a percentage (25, 50, 75 or 100%) of the field capacity adjusted for the plant biomass. Plant diameters were measured; biomass was, however, estimated from regressions of the basal diameters and fresh biomass of seedlings and stecklings determined at initial harvest and these data were used for two consecutive irrigation periods.

### 2.2 Harvest Procedure and Carbon Isotope Analysis

The initial harvest was carried out on October 13, 2009 and involved 6 seedlings and 6 stecklings; the second was on 22 December, 10 weeks after the treatments began. At both harvests, the stem length and basal diameter of all plants were recorded. Harvested plants were separated into leaves, stems and roots. The root systems were gently washed with tap water. The total leaf area of fresh leaves was measured with a laser area meter (CI-202, CID Inc., USA). The dry biomass of the stems, leaves and roots was determined after drying at 70 °C for 48 hours. The total dry biomass of the plant was calculated by summing the stem, root and leaf dry biomass. The dry biomass is henceforward referred as biomass.

As chemical analyses are expensive, only foliar samples of seedlings and stecklings subjected to watering regimes 50 and 100 % field capacity were analyzed, to determine their carbon isotope ratios, using a mass spectrometer in the Radio Carbon Dating Laboratory at the University of Helsinki, Finland. The carbon isotope ratio of the

sample ( $\delta^{13}\text{C}_{\text{sample}}$ ) was expressed as

$$\delta^{13}\text{C}_{\text{sample}} (\text{‰}) = [(R_{\text{sample}}/R_{\text{PDB}}) - 1] \times 1000 \quad (1)$$

where  $R_{\text{sample}}$  is the carbon isotope molar abundance ratio  $^{13}\text{C}/^{12}\text{C}$  of the sample and  $R_{\text{PDB}}$  is the Pee Dee Belemnite standard for carbon, the usual standard to which all measurements are referred (Lajtha and Michener 1994, Raddad and Luukkanen 2006).

### 2.3 Data Analysis

In order to compensate for differences in initial plant development, a functional growth analysis approach was used to compare plant growth between the two harvests (Hunt 1982). The relative growth rate (RGR) was calculated for stem, leaf, root, total plant biomass, leaf area, stem length and diameter. The RGR from initial to final harvest was calculated according to Hunt (1982):

$$\text{RGR}_A = (\ln A_F - \ln A_I) / (t_F - t_I) \quad (2)$$

$A_F$  denotes the measured trait at final (F) harvest and  $A_I$  denotes it at the initial (I) harvest calculated as the mean of the six plants per plant type for the destructive variables; ( $t$ ) is the time in weeks at final (F) and initial (I) harvest. Thus in the following text, the RGR of the stem, leaf, root and whole plant biomass, leaf area, stem length and diameter are referred to as RGRsb, RGRlb, RGRrb, RGRpb, RGRla, RGRsl and RGRsd, respectively. Leaf area productivity (plant biomass growth rate per unit of leaf area, LAP), specific leaf area (leaf area per unit of leaf biomass, SLA), leaf area ratio (leaf area per unit of plant biomass, LAR), leaf biomass ratio (leaf biomass per unit of plant biomass, LBR), stem biomass ratio (stem biomass per unit of plant biomass, SBR), root biomass ratio (root biomass per unit of plant biomass, RBR), and root to stem ratio (root biomass per unit stem biomass, RSR) were calculated using data collected at the final harvest and taken as additional variables to the RGR.

For all variables, two way-analysis of variance (ANOVA) was performed in order to compare propagule types (seedlings and stecklings),

irrigation regimes (25, 50, 75 and 100% field capacity) and the interactions between these two factors. Data were checked for normality and analyzed using the GLM procedure of the Statistical Analysis System (SAS Institute Inc., 2002–2008). Johnson transformed data were used for variables (RGRlb, RGRrb, RGRpb, RGRsl, RGRsd, SLA, LAP, and  $\delta^{13}\text{C}$ ) that did not fulfill the requirement for normality. Significant differences, when  $p < 0.05$ , were tested further using Tukey's HSD multiple comparison test.

## 3 Results

### 3.1 Plant Growth and Biomass Allocation

Except for the growth rate of the stem basal diameter and the specific leaf area, plant responses related to growth, biomass production, biomass fractions and  $\delta^{13}\text{C}$  did not differ significantly between seedlings and stecklings (Tables 1–2). Seedlings had higher stem basal diameter RGRs and a greater specific leaf area than stecklings (Table 3). With respect to the other variables associated with RGR and biomass allocation, seedlings were found to be similar to stecklings. The overall mean biomass fractions for seedlings and stecklings, respectively, were  $0.32 \pm 0.01$  and  $0.31 \pm 0.02$  for stem biomass ratio,  $0.34 \pm 0.01$  and  $0.32 \pm 0.02$  for root biomass ratio,  $1.06 \pm 0.07$  and  $1.08 \pm 0.05$  for root to stem ratio,  $0.34 \pm 0.02$  and  $0.37 \pm 0.03$  for leaf biomass ratio,  $34.5 \pm 3.0$  and  $31.5 \pm 4.4 \text{ cm}^2 \text{ g}^{-1}$  for leaf area ratio, and  $3.5 \pm 0.5$  and  $4.8 \pm 0.9 \text{ mg cm}^{-2} \text{ wk}^{-1}$  for leaf area productivity.

Conversely, irrigation regimes significantly affected all the variables relating to growth, biomass production and allocation except root to stem ratio (Tables 1–2). Investigation of the plant growth responses to irrigation treatments showed two distinct groups; the group supplied with high amounts of water (those plants subjected to 75 and 100% field capacity irrigation regimes) and the group supplied with less water (plants subjected to 25 and 50% field capacity irrigation regimes). Where a high water supply was maintained, higher relative growth rates of leaf and root biomass resulted, as well as higher growth

**Table 1.** ANOVA F-values for the effects of *Khaya senegalensis* propagule types (seedling and steckling) and irrigation regimes (25, 50, 75 and 100% field capacity) on the relative growth rate of plant, stem, root and leaf biomass, leaf area, stem length and stem basal diameter in Ouagadougou, Burkina Faso.

Source of variation	df	Relative growth rate of						
		Plant biomass	Stem biomass	Root biomass	Leaf biomass	Leaf area	Stem length	Stem diameter
Propagule type	1	0.44 <sup>ns</sup>	2.21 <sup>ns</sup>	0.05 <sup>ns</sup>	4.15 <sup>ns</sup>	0.17 <sup>ns</sup>	0.44 <sup>ns</sup>	6.91 <sup>*</sup>
Irrigation	3	17.13 <sup>***</sup>	11.99 <sup>***</sup>	10.71 <sup>***</sup>	24.83 <sup>***</sup>	36.83 <sup>***</sup>	14.14 <sup>***</sup>	16.25 <sup>***</sup>
Propagule × Irrigation	3	1.15 <sup>ns</sup>	0.69 <sup>ns</sup>	1.63 <sup>ns</sup>	1.58 <sup>ns</sup>	2.55 <sup>ns</sup>	1.21 <sup>ns</sup>	0.33 <sup>ns</sup>

\*p<0.05, \*\*p<0.01, \*\*\*p<0.001, ns (not statistically significant, p>0.05).

**Table 2.** ANOVA F-values for the effects of *Khaya senegalensis* propagule types (seedling and steckling) and irrigation regimes (25, 50, 75 and 100% field capacity) on stem biomass ratio (SBR), leaf biomass ratio (LBR), root biomass ratio (RBR), root to stem ratio (RSR) leaf area ratio (LAR), specific leaf area (SLA), leaf area productivity (LAP) and foliar carbon isotope ratio ( $\delta^{13}\text{C}$ ) in Ouagadougou, Burkina Faso.

Source of variation	df	SBR	LBR	RBR	RSR	LAR	SLA	LAP	$\delta^{13}\text{C}$
Propagule type	1	0.22 <sup>ns</sup>	0.96 <sup>ns</sup>	0.81 <sup>ns</sup>	0.09 <sup>ns</sup>	1.00 <sup>ns</sup>	9.99 <sup>**</sup>	0.56 <sup>ns</sup>	2.48 <sup>ns</sup>
Irrigation	3(1)	12.32 <sup>***</sup>	12.69 <sup>***</sup>	3.48 <sup>*</sup>	1.01 <sup>ns</sup>	20.62 <sup>***</sup>	5.46 <sup>**</sup>	17.02 <sup>***</sup>	30.30 <sup>***</sup>
Propagule × Irrigation	3(1)	1.87 <sup>ns</sup>	1.14 <sup>ns</sup>	0.26 <sup>ns</sup>	3.46 <sup>*</sup>	3.60 <sup>*</sup>	2.00 <sup>ns</sup>	3.39 <sup>*</sup>	4.89 <sup>*</sup>

\*p<0.05, \*\*p<0.01, \*\*\*p<0.001, ns (not statistically significant, p>0.05). (1) df for  $\delta^{13}\text{C}$

**Table 3.** The effects of *Khaya senegalensis* propagule types (seedling and steckling) and irrigation regimes (25, 50, 75 and 100% field capacity) on the relative growth rate of stem basal diameter RGRsd ( $\text{wk}^{-1}$ ), specific leaf area, SLA ( $\text{cm}^2 \text{g}^{-1}$ ) and foliar carbon isotope ratio,  $\delta^{13}\text{C}$  (‰) in Ouagadougou, Burkina Faso.

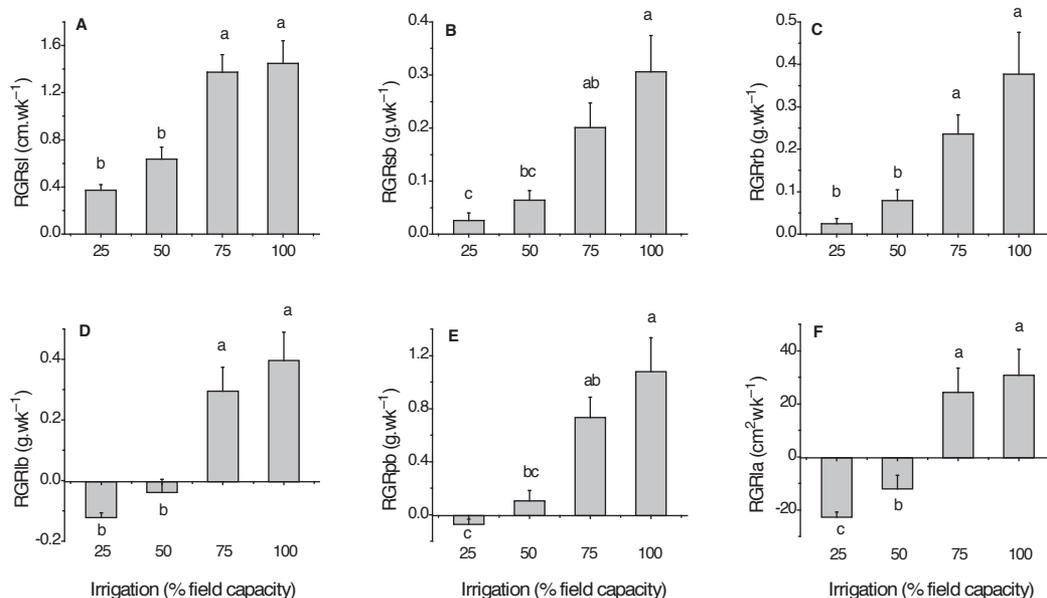
		RGRsd	SLA	$\delta^{13}\text{C}$
Propagule type	Seedling	0.052 ± 0.007 <sup>a</sup>	101.5 ± 7.6 <sup>a</sup>	-27.49 ± 0.23 <sup>a</sup>
	Steckling	0.040 ± 0.007 <sup>b</sup>	80.6 ± 6.4 <sup>b</sup>	-27.21 ± 0.33 <sup>a</sup>
Irrigation	25%	0.018 ± 0.004 <sup>b</sup>	67.9 ± 10.8 <sup>b</sup>	-26.80 ± 0.28 <sup>a</sup>
	50%	0.031 ± 0.005 <sup>b</sup>	94.3 ± 15.4 <sup>ab</sup>	
	75%	0.066 ± 0.007 <sup>a</sup>	104.1 ± 4.5 <sup>a</sup>	
	100%	0.070 ± 0.004 <sup>a</sup>	97.7 ± 1.3 <sup>a</sup>	-27.90 ± 0.07 <sup>b</sup>

Within the same column mean ± SE followed by different letters indicates significant differences at the 5% level according to Tukey's multiple comparison test.

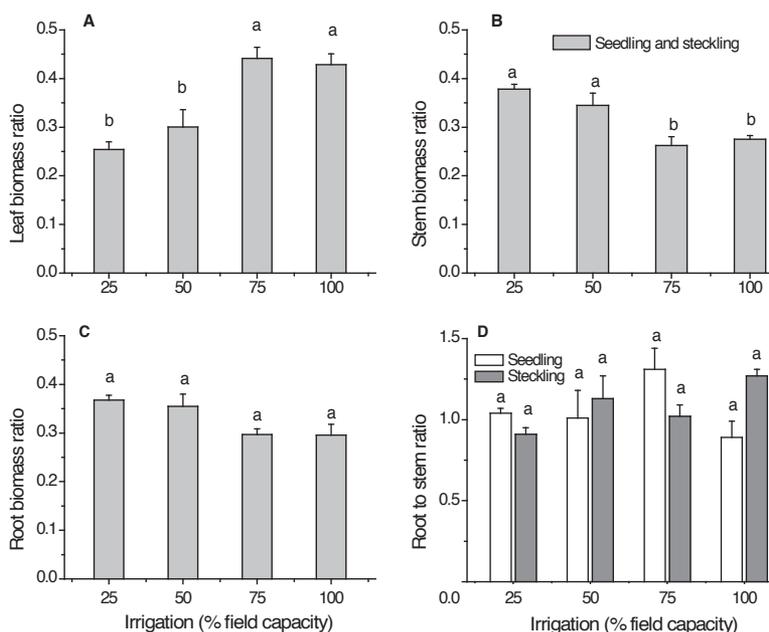
rates of stem length, stem basal diameter and leaf area, than when the water supply was low (Fig. 1, Table 3). The low water supply induced negative values for the RGR of leaf biomass (Fig. 1D) and leaf area (Fig. 1F). Reduction in leaf area was even more significant in plants supplied with a 25% than a 50% field capacity watering regime (Fig. 1F). Consequently, the leaf, root and stem

biomass fractions were significantly affected by the low water supply, resulting with a decrease in the leaf biomass fraction and increases in the stem and root biomass fractions (Fig. 2).

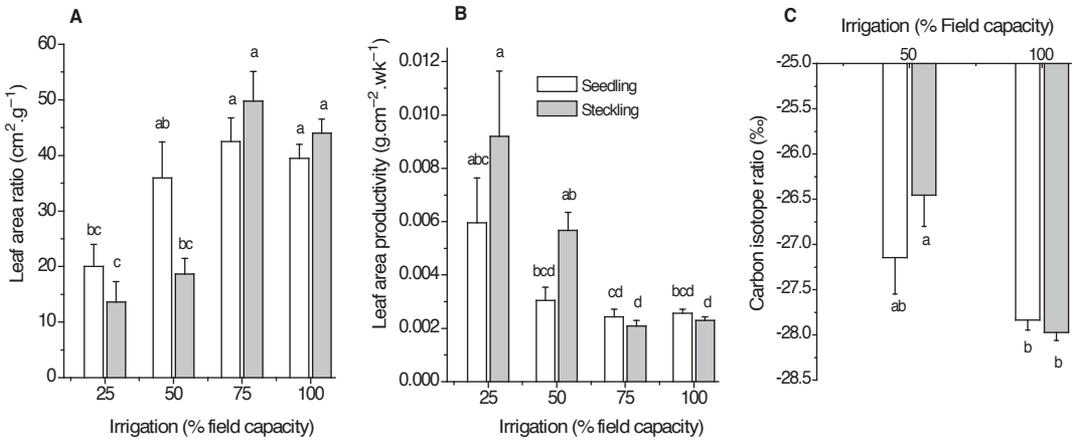
The effect of interactions between propagule types and irrigation regimes was significant for three parameters: root to stem ratio, leaf area ratio and leaf area productivity (Table 2). The group



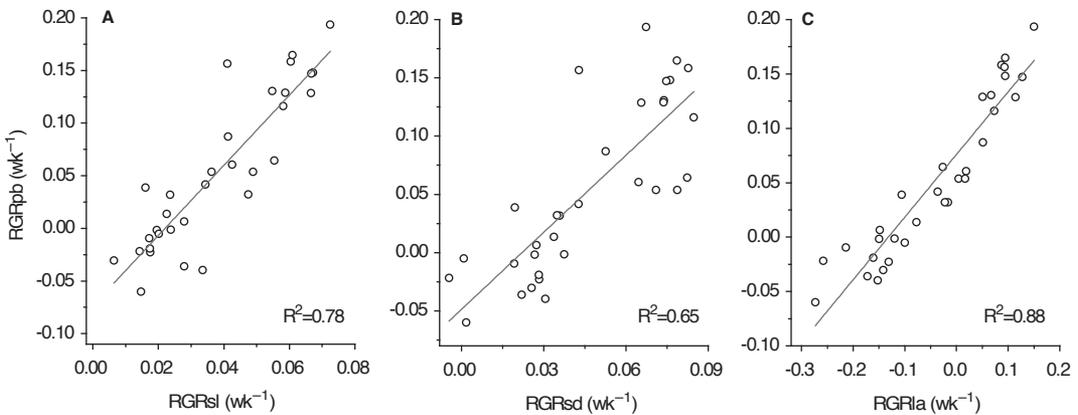
**Fig. 1.** The effect of irrigation regimes (25, 50, 75, 100% field capacity) on the relative growth rate of stem length (A), stem biomass (B), root biomass (C), leaf biomass (D), plant biomass (E) and leaf area (F) of seedlings and stecklings of *Khaya senegalensis* in Ouagadougou, Burkina Faso. Bars represent standard errors of means. Different letters indicate significant differences at the 5% level according to Tukey’s multiple comparison test.



**Fig. 2.** The effect of irrigation regimes (25, 50, 75, 100% field capacity) on leaf biomass ratio (A), stem biomass ratio (B), root biomass ratio (C), and root to stem ratio (D) of seedlings and stecklings of *Khaya senegalensis* in Ouagadougou, Burkina Faso. Bars represent standard errors of means. Different letters indicate significant differences at the 5% level according to Tukey’s multiple comparison test.



**Fig. 3.** The effect of propagule types of *Khaya senegalensis* (seedling and steckling) and irrigation regimes (25, 50, 75 and 100% field capacity) on leaf area ratio (A), leaf area productivity (B) and foliar carbon isotope ratio (C) in Ouagadougou, Burkina Faso. Bars represent standard errors of means. Different letters indicate significant differences at the 5% level according to Tukey’s multiple comparison test.



**Fig. 4.** Relationships between relative growth rate of total plant biomass (RGRpb) and the relative growth rates of stem length (RGRsl), stem basal diameter (RGRsd) and leaf area (RGRla) of *Khaya senegalensis* seedlings and stecklings after 10 weeks of growth under four irrigation regimes, 25, 50, 75 and 100% field capacity in Ouagadougou, Burkina Faso.

with a low water supply (25–50% field capacity) had lower leaf area ratios and higher leaf area productivity than the group which received a high water supply (Fig 2D, Fig 3AB). However, there was no clear difference between seedlings and stecklings with respect to these variables when any of the four irrigation regimes were considered alone, even though seedlings had higher leaf area ratios and lower leaf area productivity than stecklings when receiving a low water supply.

Furthermore, the RGRs of stem length, stem basal diameter and leaf area were found to be significantly correlated ( $p < 0.0001$ ) with the RGR of plant biomass, indicating a high degree of association between the biomass of the whole plant and these three non-destructive variables (Fig. 4).

### 3.2 Carbon Isotope Ratio ( $\delta^{13}\text{C}$ )

Mean foliar  $\delta^{13}\text{C}$  values ranged from  $-29.2$  to  $-25.3$  ‰. They were affected significantly by the irrigation regimes and the interaction (propagule types  $\times$  irrigation regimes) but similar between propagule types (Table 2). Mean values were significantly increased by the low water supply of 50% field capacity with  $-26.8$  ‰ compared to  $-27.9$  ‰ for 100% field capacity watering regime. This increase was clearly distinguished for stecklings in contrast to seedlings which had similar  $\delta^{13}\text{C}$  mean value for the two water supply conditions, 50 and 100% field capacity (Fig. 3C).

## 4 Discussion

### 4.1 Main Effect of Propagule Types

The overall pattern in the results showed large and significant differences between plants grown under different irrigation regimes, but only a small difference between seedlings and stecklings of *K. senegalensis*. Stecklings and seedlings had comparable mean RGRs for stem length, leaf, root, stem and total plant biomass, biomass allocation and intrinsic water use efficiency, indicating that these two types of propagule had a similar growth pattern during the early growth phase. Differences between seedlings and stecklings are diverse and

differ between tree species, and sometimes within the same species or from nursery to field plantations (Frampton Jr and Foster 1993, Russell 1993, Hennon et al. 2009). While some studies, usually of field plantations, have shown that seedlings grow faster, others have reported growth equal to or slower than that of stecklings. For example, in a nursery trial, yellow-cedar stecklings grew taller and had a greater root collar diameter than seedlings, but both were found to grow to similar sizes in a field comparison trial in British Columbia (Russell 1993); conversely, in Alaskan field experiments, stecklings were reported to be smaller in size than seedlings (Hennon et al. 2009). Our findings are consistent with the results obtained frequently for radiata pine (Fielding 1970, Talbert et al. 1993), yellow cypress (Karls-son and Russell 1990) and loblolly pine (Frampton et al. 2000). It was reported that generally, growth in stecklings of radiata pine was similar to that of seedlings when cuttings were taken from juvenile trees which were less than 10 years old (Talbert et al. 1993). It has also been found that the method of propagation itself (seeds or cuttings) had no strong influence on the growth rate of radiata pine when stecklings were propagated from juvenile plant material in Australia (Fielding 1970). This contrasts with the results obtained for *Faidherbia albida* (Delile) A. Chev. (Ouédraogo 1993), African wild olive (Negash 2003) and narrow-leaved ash (Cicek et al. 2006), where stecklings showed better growth than seedlings; conversely, in field tests on farms, white spruce seedlings exhibited higher relative growth rates than stecklings (Beaulieu and Bernier-Cardou 2006). However, according to these previous studies, more variations could be expected within clones or between stecklings of differing origin than in seedlings, because the growth of stecklings is influenced by their genetic potential, the maturity of the donor plant, the morphology of the regenerated root system, the vigor of the propagules and the elapsed time after planting.

The higher specific leaf area of seedlings compared to stecklings may have been due to reduction in the leaf area and density of stecklings as shown in leaf area ratio and leaf area productivity (Fig 3). Indeed, variations in specific leaf area have frequently been assumed to explain most of the interspecific variation in the RGR of seedlings

or clones (Poorter and Remkes 1990, Cornelissen et al. 2003, Karacic and Weih 2006). Since these previous investigations have shown that seedlings of fast-growing species or clones showed higher specific leaf area, seedlings would be expected to grow faster than stecklings. Unexpectedly, in the present study the pattern of RGR was similar for seedlings and stecklings, except for stem collar diameter. The higher RGR of stem diameter for seedlings might be due to a growth variation between seedling stems derived from hypocotyls and the shoots of the rooted stem cuttings, because hypocotyl tissues are able to adjust the osmotic potential in response to varying external water potentials in some species such as *Colophospermum mopane* (Kirk ex Benth.) (Johnson et al. 1996). This feature might not be maintained for a prolonged growth period.

#### 4.2 Main Effect of Irrigation Regimes

In contrast to propagule type, water stress had a significant effect on plant growth during the ten-week period of the experiment. Significant differences were detected between the well watered (75 and 100% field capacity) plants and those with a low water supply (25 and 50% field capacity) in terms of their relative growth rate and biomass allocation. The response of the two propagule types to water stress was a decline in growth and biomass production and an increase in the root biomass fraction and intrinsic WUE. The RGR of the stem, root, leaf, total plant biomass, leaf area, stem length and diameter, and the leaf biomass ratio were significantly decreased, while stem biomass ratio, root biomass ratio and  $\delta^{13}\text{C}$  increased significantly. Similar results have been reported in several previous studies (Roupsard et al. 1998, Gindaba et al. 2005, Karacic and Weih 2006, Sanon 2009, Yang and Miao 2010).

It is well established that plants respond to a reduced water supply with either structural or physiological acclimation or both. When severely water stressed, plants minimize water loss by reducing their total leaf area, shedding the lower leaves and reducing the formation of new leaves. Consequently, this reduction in leaf area diminishes the total photosynthetic output which in turn results in a decreased growth rate; usually this is

consistent with, as in our study, a positive correlation between plant biomass and leaf area (Farquhar et al. 1989, Chapin III 1991, Hall et al. 1994, Kozlowski and Pallardy 2002). It has also been stated that drought induces a reduction in leaf growth through a hormonal signal from the roots, as water stress causes a decrease in cytokinin transport from roots to shoots and/or an increase in leaf abscisic acid content; these changes in hormone balance would result in changes in cell wall extensibility and, therefore, in growth (Chapin III 1991). Alternatively, an increase in root biomass ratio could be a better strategy for maintaining growth under water-limiting conditions, as this can increase water and nutrient absorption, returning carbon and nutrient contents to more favorable levels for storage in order to support rapid growth when conditions do become favorable (Chapin III et al. 1987, Kozlowski and Pallardy 2002).

#### 4.3 Interaction Effect of Propagule Types and Irrigation

The interaction effect between propagule types and irrigation regimes was significant for four parameters: root to stem ratio, leaf area ratio, leaf area productivity and  $\delta^{13}\text{C}$ . However, the variations observed were more obvious between stressed and well watered conditions for stecklings than for seedlings, indicating that stecklings may respond faster to water stress than seedlings and that the variation in growth and WUE would be more noticeable in stressed conditions. According to the relationship found between  $\delta^{13}\text{C}$  and the intrinsic WUE (Hall et al. 1994, Devitt et al. 1997), stecklings exhibiting a similar  $\delta^{13}\text{C}$  could be expected to have a similar WUE to seedlings. But, before drawing any conclusions or making recommendations for practical applications, more investigations over a longer drought period are needed in order to determine variation in growth, biomass allocation,  $\delta^{13}\text{C}$ , plant survival and capacity to recover. Moreover, the RGR of total plant biomass is associated with indirect growth parameters, such as leaf area, stem length and diameter, suggesting that these could be reliable parameters, measurable without damaging plants, for assessing seedling and steckling growth in a nursery environment.

As a whole growth patterns of seedlings and stecklings are comparable. The growth of rooted cuttings from juvenile donors follows a similar trend to that of seedlings under both well watered and water stressed conditions. However, water stress was found to be an important factor limiting the establishment and growth of both types of propagule. A low water supply, resulting in 25 and 50% field capacity, produced stress in all plants, as they exhibited a reduction of plant growth and biomass production, and an increase in the root biomass fraction and WUE. This highlights the need to select genotypes for drought-tolerance in addition to mahogany shoot borer-resistance in order to ensure the success of *K. senegalensis* plantation establishment for timber production in its native areas in Africa.

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## References

- Bayala, J., Dianda, M., Wilson, J., Ouedraogo, S.J. & Sanon, K. 2009. Predicting field performance of five irrigated tree species using seedling quality assessment in Burkina Faso, West Africa. *New Forests* 38(3): 309–322.
- Beaulieu, J. & Bernier-Cardou, M. 2006. Comparison of early height growth between white spruce seedlings and rooted cuttings. *Canadian Journal of Forest Research* 36(12): 3246–3250.
- Brendel, O., Pot, D., Plomion, C., Rozenberg, P. & Guehl, J.M. 2002. Genetic parameters and QTL analysis of delta C-13 and ring width in maritime pine. *Plant Cell and Environment* 25(8): 945–953.
- Chapin III, F.S. 1991. Integrated responses of plants to stress. *Bioscience* 41(1): 29–36.
- , Bloom, A.J., Field, C.B. & Waring, R.H. 1987. Plant responses to multiple environmental factors. *Bioscience* 37(1): 49–57.
- Cicek, E., Tilki, F. & Cicek, N. 2006. Field performance of narrow-leaved ash (*Fraxinus angustifolia* Vahl.) rooted cuttings and seedlings. *Journal of Biological Sciences* 6(4): 750–753.
- Cornelissen, J.H.C., Cerabolini, B., Castro-Diez, P., Villar-Salvador, P., Montserrat-Marti, G., Puyravaud, J.P., Maestro, M., Werger, M.J.A. & Aerts, R. 2003. Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science* 14(3): 311–322.
- Danthu, P., Diaite-Sanogo, D., Sagna, M., Sagna, P. & Dia-Gassama, Y.K. 2003. Micropropagation of *Khaya senegalensis*, an African mahogany from dry tropical zones. *Journal of Tropical Forest Science* 15(1): 164–175.
- Devitt, D.A., Smith, S.D. & Neuman, D.S. 1997. Leaf carbon isotope ratios in three landscape species growing in an arid environment. *Journal of Arid Environments* 36(2): 249–257.
- Farquhar, G.D., O'Leary, M.H. & Berry, J.A. 1982. On the relationship between carbon isotope discrimination and the inter-cellular carbon-dioxide concentration in leaves. *Australian Journal of Plant Physiology* 9(2): 121–137.
- , Ehleringer, J.R. & Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40(1): 503–537.
- Fielding, J.M. 1970. Trees grown from cuttings compared with trees grown from seed (*Pinus radiata* D Don). *Silvae Genetica* 19(2–3): 54–63.
- Frampton, J., Li, B. & Goldfarb, B. 2000. Early field growth of loblolly pine rooted cuttings and seedlings. *Southern Journal of Applied Forestry* 24(2): 98–105.
- Frampton Jr, L.J. & Foster, G.S. 1993. Field testing vegetative propagules. In: Ahuja, M.R. & Libby, W.J. (eds.). *Clonal forestry I. Genetics and biotechnology*. Springer-Verlag, Berlin–Heidelberg, p. 110–134.
- Gindaba, J., Rozanov, A. & Negash, L. 2005. Photosynthetic gas exchange, growth and biomass allocation

- of two Eucalyptus and three indigenous tree species of Ethiopia under moisture deficit. *Forest Ecology and Management* 205(1–3): 127–138.
- Hall, A.E., Richards, R.A., Condon, A.G., Wright, G.C. & Farquhar, G.D. 1994. Carbon isotope discrimination and plant breeding. *Plant Breeding Reviews* 12: 81–113.
- Hennon, P.E., McClellan, M.H., Spores, S.R. & Orlikowska, E.H. 2009. Survival and growth of planted yellow-cedar seedlings and rooted cuttings (stecklings) near Ketchikan, Alaska. *Western Journal of Applied Forestry* 24(3): 144–150.
- Hunt, R. 1982. Plan growth curves: the functional approach to plant growth analysis. Edward Arnold, London, UK. 248 p.
- Johnson, J.M., Pritchard, J., Gorham, J. & Tomos, A.D. 1996. Growth, water relations and solute accumulation in osmotically stressed seedlings of the tropical tree *Colophospermum mopane*. *Tree Physiology* 16(8): 713–718.
- Karacic, A. & Weih, M. 2006. Variation in growth and resource utilisation among eight poplar clones grown under different irrigation and fertilisation regimes in Sweden. *Biomass and Bioenergy* 30(2): 115–124.
- Karlsson, I. & Russell, J. 1990. Comparisons of yellow cypress trees of seedling and rooted cutting origins after 9 and 11 years in the field. *Canadian Journal of Forest Research* 20(1): 37–42.
- Kozłowski, T.T. & Pallardy, S.G. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. *Botanical Review* 68(2): 270–334.
- Lajtha, K. & Michener, R.H. (eds.). 1994. Stable isotopes in ecology and environmental science (1st ed.). Cambridge. Blackwell Scientific Publications.
- Margolis, H.A. & Brand, D.G. 1990. An ecophysiological basis for understanding plantation establishment. *Canadian Journal of Forest Research* 20(4): 375–390.
- Negash, L. 2003. Vegetative propagation of the threatened African wild olive [*Olea europaea* L. subsp. *cuspidata* (Wall. ex DC.) Cififieri]. *New Forests* 26(2): 137–146.
- Newton, A.C., Baker, P., Ramnarine, S., Mesen, J.F. & Leakey, R.R.B. 1993. The Mahogany shoot borer – Prospects for control. *Forest Ecology and Management* 57(1–4): 301–328.
- Nikiema, A. & Pasternak, D. 2008. *Khaya senegalensis* (Desr.) A. Juss. In: Louppe, D., Oteng-Amoako, A. A. & Brink, M. (eds.). *Plant resources of tropical Africa*. Vol. 7. PROTA Foundation, Wageningen. p. 339–344.
- Ouédraogo, S.J. 1993. La multiplication végétative de *Faidherbia albida*: Evolution comparée des parties souterraines et aériennes de plants issus de semis et de bouturage. *Bois et Forêts des Tropiques* 237: 31–42.
- Poorter, H. & Remkes, C. 1990. Leaf-area ratio and net assimilation rate of 24 wild-species differing in relative growth-rate. *Oecologia* 83(4): 553–559.
- Raddad, E.A.Y. & Luukkanen, O. 2006. Adaptive genetic variation in water-use efficiency and gum yield in *Acacia senegal* provenances grown on clay soil in the Blue Nile region, Sudan. *Forest Ecology and Management* 226(1–3): 219–229.
- Roupsard, O., Joly, H.I. & Dreyer, E. 1998. Variability of initial growth, water-use efficiency and carbon isotope discrimination in seedlings of *Faidherbia albida* (Del.) A. Chev., a multipurpose tree of semi-arid Africa. Provenance and drought effects. *Annales Des Sciences Forestières* 55(3): 329–348.
- Russell, J.H. 1993. Clonal forestry with yellow-cedar. In: Ahuja, M. R. & Libby, W. J. (eds.). *Clonal forestry II. Conservation and application*. Springer-Verlag, Berlin–Heidelberg. p. 188–2001.
- Sanon, Z. 2009. Fonctionnement physiologique du karité (*Vitellaria paradoxa* Gaertn. F Hepper) sous différents régimes d'eau. Engineer Degree Thesis. Université Polytechnique, Bobo Dioulasso.
- Sheffield, J. & Wood, E.F. 2008. Global trends and variability in soil moisture and drought characteristics, 1950–2000, from observation-driven simulations of the terrestrial hydrologic cycle. *Journal of Climate* 21(3): 432–458.
- Sun, Z.J., Livingston, N.J., Guy, R.D. & Ethier, G.J. 1996. Stable carbon isotopes as indicators of increased water use efficiency and productivity in white spruce (*Picea glauca* (Moench) Voss) seedlings. *Plant, Cell and Environment* 19(7): 887–894.
- Talbert, C.B., Ritchie, G.A. & Gupta, P. 1993. Conifer vegetative propagation: an overview from a commercialization perspective. In: Ahuja, M. R. & Libby, W. J. (eds.). *Clonal forestry I*. Springer-Verlag, Berlin–Heidelberg. p. 145–181.
- Weih, M. & Nordh, N.-E. 2002. Characterising willows for biomass and phytoremediation: growth,

nitrogen and water use of 14 willow clones under different irrigation and fertilisation regimes. *Biomass and Bioenergy* 23(6): 397–413.

Wilson, T.B. & Witkowski, E.T.F. 1998. Water requirements for germination and early seedling establishment in four African savanna woody plant species. *Journal of Arid Environments* 38(4): 541–550.

Yang, F. & Miao, L.F. 2010. Adaptive responses to progressive drought stress in two poplar species originating from different altitudes. *Silva Fennica* 44(1): 23–37.

Zida, D., Tigabu, M., Sawadogo, L. & Oden, P.C. 2008. Initial seedling morphological characteristics and field performance of two Sudanian savanna species in relation to nursery production period and watering regimes. *Forest Ecology and Management*, 255(7): 2151–2162.

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