

## Water use of tree lines: importance of leaf area and micrometeorology in sub-humid Kenya

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### Abstract

In this research the relative importance of leaf area and microclimatic factors in determining water use of tree lines was examined in sub-humid Western Kenya. Measurements of tree water-use by a heat-balance technique, leaf area, bulk air saturation deficit, daily radiation, and soil water content were done in an experiment with tree lines within crop fields. The tree species were *Eucalyptus grandis* W. Hill ex Maiden, *Grevillea robusta* A. Cunn. and *Cedrella serrata* Royle, grown to produce poles on a phosphorus-fixing Oxisol/Ferralsol with (+P) or without (-P) phosphorus application. Doubling the leaf area of *Cedrella* and *Grevillea* doubled water use in a leaf area (LA) range of 1–11 m<sup>2</sup> per tree. The response of *Eucalyptus* water use ( $W$ ) to increases in leaf area was slightly less marked, with  $W = LA^n$ ,  $n < 1$ . Transpiration rate per unit leaf area (Tr) was the other important determinant of water use, being affected by both tree species and phosphorus fertilization. A doubling of the saturation deficit (SD) halved the water use of all trees except for *Cedrella* +P, in which water use increased. A direct effect of soil water content on water use was only found in *Grevillea* -P, with a small increase (60%) as available water increased from 1.4 to 8.9% above wilting point (32%). This low direct response to soil water content is probably due to the extensive tree-root systems and the deep clayey soils supplying sufficient water to meet the evaporative demand. Indirect responses to soil water content via decreases in leaf area occurred in the dry season. The results showed that water use of tree lines was more determined by leaf area and transpiration rate per unit leaf area than by micro meteorological factors. The linear response of tree water use to leaf area, over a wide range leaf areas, is a specific characteristic of tree line configurations and distinguished them from forest stands. In tree lines light interception and canopy conductance increase with leaf area much more than a similar leaf area increase would have caused in a closed forest canopy.

### Introduction

Tree lines bordering crop fields are important in many farming systems. They may compete with crops for water, especially in drier environments.

In more humid tropical environments with P-fixing soils such as in western Kenya, decrease in soil water content due to tree water use may limit crop growth, due to soil drying induced P-deficiency (Radersma et al. 2005). Therefore, an under-

standing of the main determinants of water-use by tree lines in this environment is crucial.

Water-use of plants is determined by (1) available energy (radiation  $R$ ) and the fraction of total  $R$  which is used for evaporation of water (latent heat  $\lambda E$ ), (2) saturation deficit (SD) and aerodynamic resistance ( $r_a$ ), which depends on relative humidity, temperature, wind-speed and height and structure of the plant-surface, (3) leaf-area (index) and (4) plant species characteristics which determine the hydraulic resistance of water through the soil-plant-atmosphere continuum. The latter two factors determine the canopy resistance ( $r_c$ ).

The most straightforward and still the most comprehensive energy budget equation was developed by Penman and modified by Monteith. This equation is useful in predicting water-use of canopies (Mc Naughton and Jarvis 1983; Jensen and Rosbjerg 1991). Other more complex energy balance models have been used to predict water use from canopies (Cienciala et al. 1994; Whitehead et al. 1994), tree lines (Smith et al. 1997) and single trees (Landsberg and Mc Murtrie 1984; Vrecenak and Herrington 1984). When all factors mentioned above were measured and energy balance equations were used for the calculations, the predictions are highly accurate. However, for more practical purposes, simpler approaches to assessing water use and its main determinants are desirable.

Mc Naughton and Jarvis (1983) developed a simplified approach to energy budgets for closed canopies, to understand and predict the effects of changing watershed vegetation from forest to grass. They introduced an  $\Omega$  factor ranging from 0 to 1 which indicated whether canopies were more (closer to 0) or less (closer to 1) coupled to the surrounding atmosphere, with its effect on canopy water-use. Canopy water-use was in general higher and more sensitive to changes in wind-speed and SD if  $\Omega$  approached 0 (e.g. forest), and was generally lower and more sensitive to changes in  $R$  if  $\Omega$  approached 1 (e.g. grass).

There are differing views on the main factors that determine tree water use in forest stands. Kelliher et al. (1995) showed that meteorological variables are more important than leaf area. In contrast, Hatton et al. (1998) and Calder (1992) found a strong dependence of water use on leaf area (or basal cross-sectional area of the tree trunk) in Eucalyptus. This is probably due to

differences in the ranges of leaf area indices (LAI) of the forest canopies they studied.

However, tree lines or single trees differ in several ways from forest canopies. The relatively simple Penman-Monteith equation or the use of the  $\Omega$  factor are not appropriate because in single trees and tree lines advection is high, and thus trees or tree lines are likely to be closely coupled to the atmosphere. This suggests that air humidity, wind, tree height and tree structure will be important determinants of tree water-use. Leaf area may also be an important determinant of water use in tree lines. An increase in leaf area (LA) per tree in tree lines increases the amount of radiation intercepted by the tree more than an increase in leaf area index (LAI) in forest canopies. Upon an increase in leaf area in tree lines the interception of radiation per square meter becomes more complete as in forest canopies, but also the area covered by the tree line increases. Hence an increase in leaf area in tree lines results in interception of radiation over a larger surface.

Complicating the understanding of water use by tree lines are interaction effects between meteorological factors and leaf conductance. In tree lines and single trees, with their low aerodynamic resistance between atmosphere and leaf surface, responses to reduce stomatal conductance and transpiration may control tree water use. Trees are likely to be specialized in control responses because they are more closely coupled to the atmosphere than low crops (Mc Naughton and Jarvis 1983). This response may be even more noticeable in tree lines than in closed canopies. The main control mechanism is via canopy resistance, as a function of stomatal resistance and leaf area. Stomatal resistance may increase at increasing saturation deficits (Dye and Olbrich 1993; Cienciala et al. 1994; Meinzer et al. 1997), or at decreasing soil water availability (Jing and Ma 1990; Mc Murtrie and Landsberg 1992). Other plant responses to high atmospheric water demand or low soil water supply are leaf rolling (Dingkuhn et al. 1989; Sobrado 1990) and leaf shedding (Hatton and Wu 1995), which reduces the leaf area.

The objectives of the research described here were, (1) to examine the relative importance of saturation deficit, radiation, soil water content, leaf area and transpiration rate per unit leaf area in determining the water use of tree lines and (2)

to understand why some factors are more important than others and the extent this is specific to tree lines. The investigations were carried out in sub-humid Western Kenya using lines of *Eucalyptus grandis*, *Cedrella serrata* and *Grevillea robusta* grown in maize fields with or without phosphorus application. Phosphorus is the resource most limiting maize growth in this environment, but application of P to the crop also affects tree growth, water-use and competition-mechanisms between trees and maize (Radersma 2002).

## Materials and methods

### Site description

An experiment was conducted on a farmer's field in Nyabeda, Western Kenya, (latitude 0.08° N, longitude 34.24° E, altitude 1300 m). The site is sub-humid with an annual rainfall of about 1500 mm, distributed over two main cropping seasons; the long rainy season from March to June/July (900 mm) and the short rainy season from September to December/January (600 mm). The experiment was established in March 1997 on level land, which had previously been alternately cropped with maize or left fallow and was of generally low fertility status.

Meteorological parameters were monitored in a station 500 m away from the experiment. Average short-wave radiation during the day (12–13 h) was usually between 0.35 and 0.55 kJ m<sup>-2</sup> s<sup>-1</sup>, with occasional days of 0.2–0.3 kJ m<sup>-2</sup> s<sup>-1</sup> in the long rainy season. Daily minima of relative humidity varied only slightly from around 50% in drier periods (January–March, sometimes July/August) to 60–70% in wetter periods. Mean daily wind speed at 2 m height was around 1 m s<sup>-1</sup> during most of the year, but in January, February (dry season) and May (probably accompanying thunder-storms) wind speeds of 2–4 m s<sup>-1</sup> were more common.

The soil was a deep Oxisol/Ferralsol with a ground water table more than 20 m deep. The soil consisted of 580 g kg<sup>-1</sup> clay, 160 g kg<sup>-1</sup> sand and 260 g kg<sup>-1</sup> silt in the top 0–0.15 m. Clay contents increased to 730 g kg<sup>-1</sup> towards depth (3 m). Bulk density remained lower than 1.3 kg dm<sup>-3</sup> over the first 1.6 m depth due to high sesquioxide content.

Further details are given in Radersma and Ong (2004).

### Experimental set-up and field layout

The experiment was a 4×2 factorial design, with four replicates. The treatments were a complete factorial combination of two phosphorus levels (with and without P fertilizer) and four tree-crop systems (a maize plot with a tree line in the center of either *Cedrella serrata*, *Grevillea robusta*, or *Eucalyptus grandis*, and a sole maize treatment without a tree-line).

Phosphorus was applied in the +P treatments at a dose of 250 kg ha<sup>-1</sup> at the start of the experiment in April 1997 and an extra dose of 50 kg ha<sup>-1</sup> in April 2000. Nitrogen (70 kg ha<sup>-1</sup> yr<sup>-1</sup>) and potassium (15 kg ha<sup>-1</sup> yr<sup>-1</sup>) were applied regularly to all treatments.

The plot size was 13.5 m×15 m. The trees in the tree line had a spacing of 0.5 m in the first year thinned to 1 m thereafter. Maize hybrid 511 or 512 was used in the long rainy seasons and sorghum seredo in the short rainy seasons. Maize spacing was 0.75 m×0.25 m and sorghum spacing was 0.60 m×0.15 m in all treatments. The distance between the tree-line and the first crop row was 75 cm for maize and 60 cm for sorghum.

### Plant and plot management

Seeds of *Grevillea robusta* (prov. Loitokitok from ICRAF MPT GRU) and *Eucalyptus grandis* (prov. Kaimosi Kakamega from KEFRI/Muguga) were sown on 23 October 1996, and seeds from *Cedrella serrata* (prov. Arboretum de Ruhunde from Rwanda) were sown on 10 December 1996, in a nursery. Seedlings were transplanted to the field in April 1997. Pruning was done according to farmers' rules to produce poles and reduce shading of crops. All branches up to 3/4 of the tree height were cut. Pruning dates were 22 December 1997, 14 May and 30 September 1998 and 20 April and 27 October 1999. The plots were weeded manually by hoe, twice during each cropping season. Root interference between plots was avoided by trenching around the plots in February 1999 and in February 2000.

### Measurements

Figure 1 shows a summary of the measurements done and the relations derived necessary for relating leaf-area to tree water use. Specific leaf area (SLA) of each tree species was derived from destructive sampling of the trees (Figure 1 measurement 2). From each treatment (6) and each replicates (4) two leaf samples of 10–100 g fresh weight were taken. One of these was oven-dried and weighed again to derive dry-weight: fresh-weight ratio. Part of the other 24 samples were used for determination of the weight : surface relation (6 smaller samples for *Cedrella*, 5 samples of different size for *Grevillea* and 4 large samples for *Eucalyptus*) were glued on paper and scanned by Delta-T scanner, using Delta-T image analysis software to measure the surface area.

Relations between stem-diameter just below canopy ( $\phi_c$ ) and canopy height ( $h_c$ ) (height between the base and the top of the canopy) with leaf-area (LA) were derived from destructive sampling at the end of the long rainy seasons in 1998, 1999 and 2000 (Figure 1 measurement 1). Canopy height and stem diameter just below the canopy were measured, the tree was cut and all leaves stripped and weighed. A sub-sample of the leaves was taken, weighed, dried and weighed again to get the dry-weight: fresh-weight ratio.

Water use of the trees (W) was measured by the heat balance technique (Baker and van Bavel 1987) (Figure 1 measurement 3). Heater coil and thermo couples were covered by styrofoam and aluminum foil to prevent heat losses or heat

additions from incoming radiation (Khan and Ong 1995). Hourly data were collected using a Campbell C21X data logger. From July 1998 to July 1999 heat-balance measurements were done every 2 months on 3 trees of 4 treatments. An extra dry-period measurement on 3 trees of all 6 treatments was done in February/March 2000. In May–June 2000 (wet season) sap-flow of 3 trees in all 6 treatments, was measured for 2 weeks. After the first week, the lower parts of the canopies of two of the three trees were severely pruned resulting in canopies of 1/2 or 1/3 of their original canopy height, to cross-check the importance of leaf-area as determinant of tree water-use. Daily water-use was calculated by taking the sum of sap-flow during daily hours, adjusted for different base-line values of the sap-flow graphs. The base-line value is the average value of the graph above zero during night-hours when sap-flow should be about zero in our situation. Mathematically daily water-use was therefore calculated by adding the sap-flow measurements of all 24 hours, and extracting 24 times the base-line value. Sap-flow and  $\phi_c$  and  $h_c$  (to estimate LA) were measured, at the same time on the same trees.

To determine the importance of radiation ( $R$ ), saturation deficit (SD) and soil water content ( $\theta$ ) on tree water-use, hourly data (short-wave radiation, temperature, relative-humidity, wind speed) were collected from a meteorological station 0.5 km away during the periods of sap-flow measurements. These data were used to calculate total daily  $R$ , daily average wind-speed and average daily SD. SD was calculated as  $(e_{a(T_{\min})} + e_{a(T_{\max})})/2 - e_d$  with  $e_a$

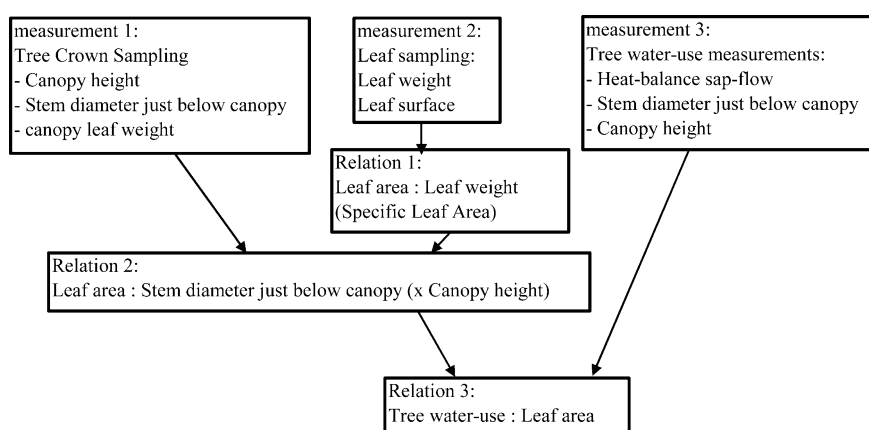


Figure 1. Measurements done and relations derived to calculate daily and total water use of trees at similar pole-sizes at Nyaabeda, Western Kenya.

and  $e_d$  calculated from  $T_{min}$ ,  $RH_{max}$ ,  $T_{max}$  and  $RH_{min}$  (FAO 1992).

Soil water contents were measured by neutron probe every month over eight 0.2 m intervals up to 1.6 m depth at three distances from the tree lines in all treatments between August 1998 and August 2000 (Radersma and Ong 2004). Soil water content at the times of sap-flow measurement were derived by linear interpolation over time of these monthly soil water content measurements, the estimations made separately for each plot.

#### Statistical analysis and calculations

Statistical analyses were done using Genstat (2000). Specific leaf areas (SLA), the ratio leaf area:leaf-weight, both dry and fresh were analyzed by analysis of variance. Regression analysis was used to develop relationships for prediction of leaf area per tree (LA) from stem diameter just below the canopy ( $\varnothing_c$ ) alone, or multiplied with canopy-height ( $h_c$ ), or from conical volume ( $1/3 \times (1/2 \times \varnothing_c)^2 \times \pi \times h_c$ ). LA was derived from leaf weight, using the fresh-leaf SLA relation or the dry-leaf SLA relation. The two best fits were both used to calculate LA from  $\varnothing_c$  alone, or multiplied by  $h_c$ . The average of these two calculations was used as assessment of LA and related to water-use ( $W$ ) measurements.

First, the relations between LA and  $W$  were analyzed for all 6 treatments (tree-species $\times$ P-level) together to examine whether there were significant differences between the treatments in transpiration rate ( $Tr$ ). Only data from a leaf-area range of 0 to 12 m<sup>2</sup> were used for all treatments. However, maximum leaf-area of Cedrella +P was only 4.3 m<sup>2</sup>, Cedrella -P and Grevillea +P and -P reached 8–11 m<sup>2</sup>. Secondly, after the analysis showed that the relations between  $Tr$  and  $W$  differed between treatments, the best fitting relations were determined for each treatment separately. For these analyses, period averages of daily sap-flow measurements (averages of the different daily values within one sap-flow measurement period) were used.

Multiple regression with  $W$  as response and leaf area (LA), soil water content ( $\theta$ ), radiation ( $R$ ) and saturation deficit (SD) as explanatory variables was used to examine the extent to which variables other than LA contribute to understanding varia-

tion in  $W$ . The number of observations used for this analysis was slightly less than in the  $W/LA$  (=  $Tr$ ) regressions, because some of the meteorological data were faulty and could not be used. The regression was done separately for each treatment. Soil water contents ( $\theta$ ) were expressed in m<sup>3</sup> m<sup>-3</sup> above wilting-point ( $\sim 0.32$  m<sup>3</sup> m<sup>-3</sup>).

## Results

### Allometric relations to calculate leaf area

Specific leaf areas for Eucalyptus, Grevillea and Cedrella are shown in Table 1.

The best relations to derive leaf area (LA), measured by taking total leaf weight multiplied by specific leaf area (SLA), from canopy height ( $h_c$ ) and/or stem diameter just below canopy ( $\varnothing_c$ ) are shown in Table 2. For Cedrella and Grevillea leaf area was best predicted by a relation in which  $\varnothing_c$  was multiplied by  $h_c$  (height at the top of the tree minus height at the base of the canopy). For Eucalyptus leaf area was best derived by relations with  $\varnothing_c$  alone. For each species two equations were used to calculate leaf area, one using total leaf biomass and SLA derived from fresh leaves and the second using total leaf biomass and SLA derived from dry leaves. The leaf-area estimate used in further analysis was the mean of the leaf-areas calculated by these two equations. All relations have the form  $y = cx^n$  (Landsberg and Mc Murtrie 1984). For Eucalyptus  $x$  is  $\varnothing_c$  alone and  $n = 2$ , while for Cedrella and Grevillea  $x$  is best represented by the product  $\varnothing_c \cdot h_c$  with  $n = 1$ . All

Table 1. Relation between leaf weight and leaf surface (specific leaf area = SLA) using fresh and dried leaves of Cedrella, Eucalyptus and Grevillea in Nyabeda, Western Kenya.

	$n$	SLA-fresh (m <sup>2</sup> kg <sup>-1</sup> )	SLA-dry (m <sup>2</sup> kg <sup>-1</sup> )
Cedrella	3	5.5	13.3
Eucalyptus	3	4.5	13.4
Grevillea	4	3.2	9.0
	sed 3–3	0.24	0.66
	sed 3–4	0.22	0.61

sed 3–3 = standard error when  $n = 3$  for both species, sed 3–4 = standard error when Grevillea ( $n = 4$ ) is compared with Cedrella or Eucalyptus ( $n = 3$ ).

Table 2. Best fitting relations between allometric measurements ( $x$ ) and leaf area ( $\text{cm}^2$ ) ( $y$ ) in Nyabeda, Western Kenya.

species / LA-range ( $\text{m}^2$ )	$x$ = canopy diameter (cm)		$x$ = canopy diameter $\times$ height ( $\text{cm}^2$ )		SLA used
	Equation	$r^2$	Equation	$r^2$	
Cedrella [0.27;8.95]			$y = 81.536x^{1.0519}$	0.862	Dry
			$y = 86.908x^{1.0364}$	0.827	Fresh
Eucalyptus [1.20;62.6]	$y = 5637.2x^{2.3765}$	0.965			Dry
	$y = 6134x^{2.1969}$	0.974			Fresh
Grevillea [0.20;11.43]			$y = 106.19x + 335.68$	0.887	Dry
			$y = 75.763x + 2412.9$	0.883	Fresh
	$x$ = canopy diam. (cm)		$x$ = canopy diam. * height ( $\text{cm}^2$ )		
	$y$ = leaf area ( $\text{cm}^2$ )		$y$ = leaf area ( $\text{cm}^2$ )		

Leaf-area was calculated as the mean of the two leaf-areas calculated by two equations: one using specific leaf area (SLA) derived from dry leaves and the second using SLA derived from fresh leaves.

relationships are therefore dimensionally equivalent ( $\text{m}^2$ ).

#### Relation of water use ( $W$ ) with leaf area ( $LA$ )

The relation between  $W$  and  $LA$  is plotted in Figure 2. Accumulated analysis of variance, explaining  $W$  by  $LA$ , treatment and  $LA \times$  treatment, showed significantly different transpiration rates per unit leaf area ( $Tr = W: LA$ ) for the different treatments (tree species $\times$ P-application level). Because of these significant differences, the best relations between  $LA$  and  $W$  were assessed by regression per treatment, using the whole range of leaf areas for each Cedrella +P or -P and Grevillea +P or -P, and up to a leaf area of  $28 \text{ m}^2$  for

Eucalyptus +P or -P. The limit of  $28 \text{ m}^2$  was used as it is the leaf area of Eucalyptus at maximum stem/pole size reached in this experiment by Cedrella and Grevillea. These relations between  $LA$  and  $W$  are given in Table 3. For Cedrella -P a linear relation using untransformed leaf area values fitted best. For Cedrella +P and the two Eucalyptus treatments a power relation using untransformed leaf area values fitted best, and for Grevillea the best fitting relation was linear using square-root (leaf-area). However, the regression lines in Figure 2 show that in all treatments water-use increases nearly linearly with increasing leaf area over a large range of leaf area.

The steeper the slope of the line relating  $W$  to  $LA$  in Figure 2, the higher the water use per unit leaf area ( $Tr$ ). Thus Cedrella +P had the highest

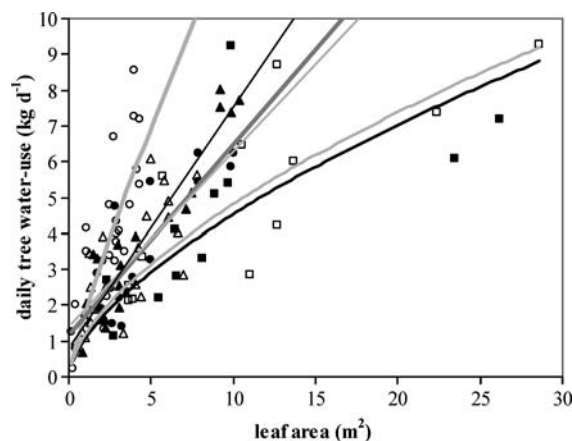


Figure 2. Relation between daily water use and leaf area. -P are the treatments without P application, +P are the treatments with P application. The best relations between daily water use and leaf area as given by the lines are linear or power relations (see legend). ● Ced-P; ○ Ced+P; ■ Euc-P; □ Euc+P; ▲ Grev-P; △ Grev+P; — Power (Euc-P); — Power (Euc+P); — Power (Ced+P); — Linear (Ced-P); — Linear (Grev+P); — Linear (Grev-P).

Table 3. Regression relations between daily water-use ( $W$ ) and leaf-area ( $LA$ ) of pole-trees in Nyabeda, Western Kenya.

Species	P	Water-use ( $g\ d^{-1}$ ):leaf-area ( $m^2$ )	
		Equation	$r^2$
Cedrella	-P	$W = LA*531 + 1177$	0.75
	+P	$W = 1766*LA^{0.85}$	0.73
Eucalyptus	-P	$W = 1058*LA^{0.63}$	0.62
	+P	$W = 1173*LA^{0.61}$	0.60
Grevillea	-P	$W = rtLA*2856-1862$	0.84
	+P	$W = rtLA*1793-68$	0.51

-P = treatments without P application, +P = treatments with P application, W = water use, LA = leaf area, rtLA = square root of leaf-area.

Tr and both Eucalyptus treatments the lowest Tr. Both Grevillea treatments and Cedrella -P showed intermediate levels of Tr. Application of P affected Tr of Cedrella. Cedrella +P had a significantly higher Tr than Cedrella -P. In contrast, Grevillea +P seemed to have a slightly lower Tr than Grevillea -P, but this was not significant. These different slopes (Tr) reflect that daily water-use of Cedrella +P is as high as that of Cedrella -P at half the leaf area. Grevillea +P and -P show a similar relation between leaf area and water use as Cedrella -P, but the Tr of Eucalyptus is generally lower. Thus although the leaf area of Eucalyptus reaches higher values than the other trees, the daily water use is equal to or less than them.

#### Multiple regression of $W$ by $LA$ , daily shortwave radiation ( $R$ ), saturation deficit ( $SD$ ) and soil water content ( $\theta$ )

Tree water use  $W$  could be explained by multiple regression with  $LA$ ,  $\theta$  ( $m^3\ m^{-3}$  above wilting point at  $\sim 0.32\ m^3\ m^{-3}$ ),  $R$  and  $SD$ . Ranges of these explanatory variables and the related ranges of predicted water use  $W$  with standard errors are shown in Table 4 for each treatment. In Grevillea -P environmental variables explained 12.5% more of the variance in water-use than leaf area alone. In all other treatments the extra variance explained was 4-6%. An increase in  $SD$  from around 0.5 kPa to around 1 kPa seemed to result in a lower water use in Grevillea, which is significant in Grevillea -P (42 % lower water-use), less clear in Grevillea +P, Eucalyptus +P and Cedrella -P

(31-34 % lower water-use). Cedrella +P seemed to use more water upon an increase in  $SD$ , but this is not significant. The  $SD$  range of Eucalyptus -P was too small to be conclusive, and the low replication ( $n = 8$ ) made the results of this analysis questionable.

Changes in daily radiation ( $R$ ) over the range occurring in our environment, showed a significant effect in Grevillea -P. In Grevillea -P an increase in  $R$  of slightly more than 50% resulted in a predicted increase of water use just less than 50 %. Eucalyptus +P showed a similar relation but this was not significant.

Table 4 shows that volumetric soil water content ( $\theta$ ) had a direct effect on tree water use in the data series of Grevillea -P (which showed in all analysis the least unexplained variance). There was a significant increase in water use with an increase in  $\theta$  from 1.4 to 8.9 (% above wilting point). At  $\theta$  close by wilting point some extremely low water use data at large stem diameter occurred in Eucalyptus.

#### Discussion and conclusions

In our tree line situation, where the Penman-Monteith equation was not applicable and the energy balance equations with a higher level of sophistication, requiring measurement of all energy fluxes and resistances (Smith et al. 1997), were not feasible, multiple regression of water use of trees in a tree line explained by leaf area, meteorological parameters and soil water content gave an indication of the importance of the determinants of water use in a sub-humid climate. Comparing the variance accounted for by leaf-area alone (51-84%) with the variance accounted for by leaf-area, saturation deficit, radiation and the direct effect of soil water content, showed that the last three factors together explained at most 12.5% more of the variance in water-use (Table 4). In the Grevillea -P treatments, which showed the least unexplained variance, all variables leaf area, saturation deficit, daily radiation and soil water content had a significant effect.

The large effect of leaf area and the smaller effect of soil water content, saturation deficit and daily radiation on water use of the tree lines in this experiment in a sub-humid climate, were probably due to two reasons. The first reason is the differing

Table 4. Multiple regression of water use by trees with leaf area, soil water content and evaporative demand: ranges of explanatory factors and related predicted range of tree-water-use, in Nyabeda, Western Kenya.

	Explanatory factor	Range of explanatory factor	Range of predicted water-use	
			kg d <sup>-1</sup>	s.e
Cedrella -P <i>n</i> = 16 75.3%	LA (m <sup>2</sup> )	[0.2; 10]	[1.6; 6.1]	0.45, 0.59
	<i>R</i> (MJ m <sup>-2</sup> d <sup>-1</sup> )	[17; 22]	[3.6; 3.2]	0.43, 0.62
	SD (kPa)	[0.54; 0.89]	[4.2; 2.9]	0.63, 0.49
	$\theta > wp$ (m <sup>3</sup> m <sup>-3</sup> )	[0.044; 0.091]	[4.0; 3.1]	0.63, 0.42
Cedrella + P <i>n</i> = 18 78.2%	LA (m <sup>2</sup> )	[0.25; 4.3]	[0.6; 5.6]	0.44, 0.39
	<i>R</i> (MJ m <sup>-2</sup> d <sup>-1</sup> )	[16; 23]	[4.6; 2.4]	0.82, 0.56
	SD (kPa)	[0.38; 0.80]	[2.3; 3.7]	1.2, 0.54
	$\theta > wp$ (m <sup>3</sup> m <sup>-3</sup> )	[0.014; 0.091]	[4.1; 2.8]	0.99, 0.64
Eucalyptus -P <i>n</i> = 8 53.2%	rtLA (m)	[1.7; 3.1]	[1.9; 5.1]	2.6, 1.8
	<i>R</i> (MJ m <sup>-2</sup> d <sup>-1</sup> )	[17; 19]	[6.8; 0.05]	2.7, 3.5
	SD (kPa)	[0.62; 0.77]	[3.1; 6.0]	1.1, 2.8
	$\theta > wp$ (m <sup>3</sup> m <sup>-3</sup> )	[0.059; 0.10]	[-2.0; 10.0]	3.5, 3.7
Eucalyptus + P <i>n</i> = 16 68.2%	rt3LA (m <sup>2/3</sup> )	[1.5; 4.2]	[3.5; 9.9]	0.72, 1.07
	<i>R</i> (MJ m <sup>-2</sup> d <sup>-1</sup> )	[16; 22]	[5.0; 6.9]	1.0, 1.1
	SD (kPa)	[0.39; 1.1]	[6.8; 4.5]	1.2, 1.9
	$\theta > wp$ (m <sup>3</sup> m <sup>-3</sup> )	[0.014; 0.10]	[6.4; 5.6]	1.4, 0.98
Grevillea -P <i>n</i> = 19 95.3%	rtLA (m)	[0.90; 3.2]	[0.9; 7.1]	0.23, 0.27
	<i>R</i> (MJ m <sup>-2</sup> d <sup>-1</sup> )	[16; 24]	[3.2; 4.7]	0.19, 0.32
	SD (kPa)	[0.54; 0.87]	[4.6; 2.7]	0.26, 0.30
	$\theta > wp$ (m <sup>3</sup> m <sup>-3</sup> )	[0.014; 0.089]	[2.7; 4.3]	0.28, 0.19
Grevillea + P <i>n</i> = 18 65.4 %	rtLA (m)	[0.89; 2.8]	[1.4; 5.5]	0.43, 0.52
	<i>R</i> (MJ m <sup>-2</sup> d <sup>-1</sup> )	[17; 24]	[3.4; 3.0]	0.49, 0.43
	SD (kPa)	[0.56; 0.98]	[3.8; 2.7]	0.50, 0.49
	$\theta > wp$ (m <sup>3</sup> m <sup>-3</sup> )	[0.014; 0.086]	[3.4; 3.1]	0.44, 0.33

LA = untransformed leaf-area, rtLA = LA<sup>1/2</sup>, rt3LA = LA<sup>1/3</sup>, SD = average daily saturation deficit, *R* = daily shortwave radiation,  $\theta > wp$  = soil water content above wilting point, (*n* = 16) = number of period averages used for the regression, 75.3% = percent of variance accounted for by multiple regression. -P are the treatments without P application, +P are the treatments with P application.

widths of ranges of the determining variables in our experiment (Table 4). Leaf area ranges of the growing tree lines were large with a more than ten-fold increases, from 0.2 to 10 m<sup>2</sup> for Cedrella, from 1 to 10 m<sup>2</sup> for Grevillea and from 3 to 28 m<sup>2</sup> for Eucalyptus. In contrast, ranges in saturation deficit and daily radiation only showed a doubling of values.

Large radiation ranges were mainly found when daily fluctuations were measured. The diurnal variation in our sap-flow measurements closely followed radiation, similar to patterns found by Dye and Olbrich (1993), Smith et al. (1997) and Vertessy et al. (1997). However, daily radiation sums showed a narrower range. Using average daily radiation for the sap-flow period (means of 5–7 days) the range was 16.5–24.0 MJ m<sup>-2</sup> d<sup>-1</sup> (Table 4). Such a 50% increase in daily radiation resulted in a 46% increase in water use in Grevillea -P, the treatment where the effect was significant.

The narrow range in daily radiation is a climatic feature of the environment, with a predominantly clear sky even in the wet season.

The small range in saturation deficit [0.5; 1.0] kPa (Table 4), was probably due to the proximity of Lake Victoria (60 km away). Doubling of saturation deficit caused a 30–40% decrease in predicted water use in most treatments. Only in Cedrella + P it caused a 60% increase in predicted water-use. Other studies (Cienciala et al. 1994; Smith et al. 1997) considered saturation deficit as an important determinant of water use, but these studies worked with a larger range of saturation deficit and a smaller leaf-area range.

The range of available soil water content was 0.014 to 0.091 m<sup>3</sup> m<sup>-3</sup> above wilting point at 0.32 m<sup>3</sup> m<sup>-3</sup> (Table 4), but did not affect water use strongly in a direct way. Increasing available soil water content 6 times as in the range [0.014; 0.089] m<sup>3</sup> m<sup>-3</sup> in Grevillea -P, the treatment where the



effect was significant, resulted in an increase in water use of only slightly more than 1.5 times (Table 4). This is a less strong response than the response of water-use to equal changes in different explanatory variables, with doubling the saturation deficit halving water-use, and doubling the leaf area doubling water-use. Soil water content is more likely to affect plant water-use directly in water-limiting environments and coarse soils, or on shallow soils and if root systems are superficial (Vrecenak and Herrington 1984; Dye 1996). The main effect of strong decreases in soil water content on tree water use may be indirect, by causing leaf-shedding. This happened in our environment only in the long dry season (January–March). During the rest of the year in this sub-humid climate on the prevailing deep clayey soils, the extensive root-system was able to extract sufficient water to meet the demand (Radersma and Ong, 2004).

The second reason for the high importance of leaf area is related to the characteristics of tree lines and the way in which they differ from a forest canopy. In tree lines, an increase in leaf area decreases the canopy resistance as in a forest canopy, but in tree lines the surface area of the canopy also increases as the width of the tree line increases. Thus the amount of radiation intercepted and the amount of energy available for water evaporation at the leaf surfaces also increases. In this way the increase in radiation interception by tree lines was much larger than that from a similar increase in leaf area in a closed canopy. In a closed canopy increasing leaf area only increases the leaf area index ( $\text{m}^2$  leaf per  $\text{m}^2$  soil), reducing the radiation reaching the forest floor.

To compare the effect of leaf-area increases on water use of tree lines with forest canopies, leaf-area per tree was translated into leaf area index (LAI). The spread of the canopies of our tree lines was assessed to be 1 m on each side and tree-spacing within the line was 1 m. Thus each tree covered  $2 \text{ m}^2$  and at a leaf-area per tree of  $12 \text{ m}^2$ , the LAI of the tree lines was about 6. Up to this LAI of 6 (at LA of 12), water-use of the tree lines responded more or less linearly to leaf area increases (Figure 2). Kelliher et al. (1995) showed that linear response of canopy resistance to LAI in forest canopies occurs only up to LAI  $\sim 2$ ; the response decreases strongly between LAI 2 and 6 and ceases altogether at LAI  $> 6$ . Thus, the linear

response of water-use to leaf area index occurs up to LAI of 6 in our tree lines and only up to LAI 2 for forest canopies. One reason for the fast decrease of water-use responses to increases in leaf-area in forest canopies is self-shading. Another reason is the higher aerodynamic resistance within canopies. Self-shading and aerodynamic resistance are lower in tree lines.

Because of the importance of leaf-area, transpiration rate per unit leaf-area ( $T_r$ ) is another important determinant of tree water-use in tree lines. The  $T_r$  of our tree lines differed with tree species and P-application level, seen as different slopes of regression lines in Figure 2. Clear differences in  $T_r$  in different species were also found by Myers et al. (1996). Their *Eucalyptus grandis* had a three times higher leaf area than their *Pinus radiata*, but transpired only 22% more water. Thus transpiration rate of their *Pinus radiata* was much higher than of their *Eucalyptus grandis*. On the other hand, Meinzer et al. (1997) and Hatton et al. (1998) did not find large differences in transpiration rate of different tree species. However, Hatton et al. (1998) compared only different *Eucalyptus* species and Meinzer et al. (1997) compared four species in a tropical rain-forest, where boundary layer resistance was high and stomatal resistance was low. Thus boundary layer resistance determined tree water use to a large extent and species differences in water use per unit leaf area and stomatal responses were of lower importance.

Multiple regression of water use explained by leaf area, meteorological parameters and soil water content is risky, because some of these variables do not affect transpiration in one direction or in a linear way, and need careful interpretation. An increase in saturation deficit increases the evaporative demand and hence increases transpiration. On the other hand, trees respond to increases in saturation deficit or drying soil by closing their stomata or shedding leaves and in this way transpiration can be decreased.

An increase in saturation deficit was accompanied by a decreased water use (Table 4). Hence, the effect of saturation deficit on stomatal resistance and/or leaf-shedding, decreasing transpiration, was generally stronger than its transpiration-enhancing effect through an increase in evaporative demand. Only in *Cedrella* +P was the transpiration enhancing effect stronger than the tree-response effects. This effect of phosphorus application on

Cedrella, reducing its water-use limiting responses, probably caused the high transpiration rate we found in Cedrella + P.

Plants often show a non-linear response of water use to soil drying, with a threshold above which soil drying has little effect on water-use and below which its effects on water-use are serious (Jing and Ma 1990; Raison and Myers 1992). This non-linear response including a threshold may become especially important if soil drying causes leaf-shedding and reduction of leaf area. In this research soil water content did not have much direct effect on the water-use of the tree lines as described above. However the indirect effect of more severe dry periods on leaf shedding certainly played a role in the dry seasons. In the dry season Cedrella leaves and twigs were shedding along the stem from the bottom upwards. Thus calculated leaf-area (Table 2) and water use in the dry season were lower. In the multiple regression the reduction in water use caused in this indirect way via leaf-shedding were ascribed to reductions in leaf area and not to soil water content. On the other hand, the measured very low water use of some large Eucalyptus trees in the dry season, was probably due to reduced leaf area which was not accounted for in our calculations of leaf area. Calculation of leaf area in the dry season for Eucalyptus was not correct because allometric relations between leaf area and stem diameter just below the canopy (Table 2) were derived from wet-season measurements. In Eucalyptus the leaves were shed but the stem diameter just below the canopy, used to calculate leaf-area, remained the same. The indirect effect of soil water content on leaf shedding may especially play a role once the soil-resistance starts to determine plant water-uptake, instead of plant-resistances (Hillel et al. 1976).

In conclusion, we showed that leaf area per tree and the transpiration rate, both differing by species and P-application level, were the main determinants of daily water use in tree lines in the sub-humid climate of western Kenya. The importance of leaf area in determining water use of tree lines in our experiment was pronounced because of the relatively large range in leaf area, in comparison with the much smaller ranges of daily radiation and saturation deficit. If tree-lines occurred in circumstances with larger ranges in saturation deficit and radiation and on coarser or shallower

soils with water limitation as main determinant of leaf area, then these factors and soil water content would assume more importance in determining tree water-use. However, even then, the linear response of water-use to leaf-area over a wide leaf-area range would make the leaf area an important determinant of water-use.

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