

Effects of Vapour Pressure Deficit and Soil Water Content on Leaf Water Potential between Selected Provenances of *Eucalyptus microtheca* in an Irrigated Plantation, Eastern Kenya

Kari Tuomela and Markku Kanninen

Tuomela, K. & Kanninen, M. 1995. Effects of vapour pressure deficit and soil water content on leaf water potential between selected provenances of *Eucalyptus microtheca* in an irrigated plantation, eastern Kenya. *Silva Fennica* 29(3): 217–224.

The aim of the study was to compare the behaviour of three selected provenances of *Eucalyptus microtheca* that were likely to respond differently to drought. For this purpose, we studied the effects of vapour pressure deficit and soil water content on leaf water potential in an irrigated plantation at Bura, eastern Kenya.

An international provenance trial of *Eucalyptus microtheca*, established as a part of Finnida-supported Bura Forestry Research Project in eastern Kenya in August 1984, was used as a plant material in the study. The eastern provenance showed generally the lowest leaf water potential on a daily basis. Statistically significant differences in the daily leaf water potential fluctuation were detected. The eastern provenance exhibited the greatest and the northern one the smallest values. The minimum daily leaf water potential of the provenances responded well to changes in gravimetric soil water content, the western provenance being the most sensitive one. The relationship of the observed results and annual rainfall distribution in the geographical regions of the studied provenances is discussed.

Keywords drought adaptation, *Eucalyptus microtheca*, leaf water potential, provenance selection.

Authors' addresses Tuomela, University of Helsinki, Department of Forest Ecology/Tropical Silviculture, P.O. Box 28, FIN-00014 University of Helsinki, Finland; Kanninen, CATIE, 7170 Turrialba, Costa Rica **Fax** +358 0 708 5646 **E-mail** kari.tuomela@helsinki.fi
Accepted November 27, 1995

1 Introduction

Water stress is considered to be a primary factor that controls productivity and geographical distribution of plant species in arid and semi-arid lands, ASALs (Bachelard 1986, Bewley and Krochko 1982, Kramer and Kozlowski 1979). Because considerable land areas are subjected to varying periods of drought (Grove 1985) it is hardly surprising that a strong evolutionary impetus against drought has resulted in a considerable array of adaptations (Berry and Björkman 1980). Drought-avoidance, found generally in higher plants, is achieved primarily through adaptations that retard water loss or increase water absorption (Bewley and Krochko 1982).

The diurnal fluctuation in the plant water status is a function of the water imbalance resulting from the excess of transpiration over absorption (Ritchie and Hinckley 1975). Water status of the plant can be assessed by water potential (Ψ) which has gained wide acceptance as a fundamental measure (Hsiao 1973). Transpiration is a process of diffusion which is governed by the humidity gradient between a transpiring surface and surrounding air, and leaf diffusion resistance (Larcher 1983). Under sufficient water supply, stomata remain open when Ψ responds directly to flow resulting from the atmospheric demand, a daily pattern of Ψ showing a distinct peak around noon. Decreasing soil moisture availability causes stomatal closure when leaf resistance dominates so that Ψ reflects leaf resistance more closely than it does evaporative demand. A plateauing phase around noon often dominates the daily patterns of Ψ (Ritchie and Hinckley 1975).

The pressure chamber is an appropriate device to measure Ψ (Scholander et al. 1965, Tyree and Hammel 1972). Usually it is considered to be approximately equal to Ψ (Kramer and Kozlowski 1979, Ladiges 1974, 1975, Moreshet 1981, Sinclair 1980) although it ignores osmotic effects. Actually, the pressure chamber determinations are estimates of the total water potential of the xylem sap (Ritchie and Hinckley 1975).

According to Larcher (1983), hydrostable plants can, to a great extent, maintain favorable water balance throughout the day when their stomata respond with a great sensitivity to lack of water. Hydrolabile plants do not restrict tran-

spiration until they become very dry. Ritchie and Hinckley (1975) divided plants into regulators and conformers based on daily behaviour of Ψ ; the peculiar behaviour of conformers is their relative inability to control water balance whereas regulators are able, by various means, to regulate Ψ despite soil or atmospheric conditions.

Eucalyptus microtheca F. Muell. is a tree of arid and semi-arid lands of Australia which occurs naturally from the west to the east coast of Australia (Boland et al. 1984). *E. microtheca* is found on a variety of soil types, from coarse sand to heavy clay soils. It has been introduced successfully, for example, in Africa and the Middle East (Boland et al. 1984). In Sudan, where it is extensively planted in irrigated plantations, it has been considered one of the most drought resistant of all tried *Eucalyptus* spp. (Armitage 1987, Seed section report ... 1979). Because of its strong and heavy wood that is resistant to termites it is suitable for fencing, poles and firewood. *E. microtheca* is considered particularly important for fuelwood, shelterbelt and soil stabilization for ASALs (Forest genetic ... 1981). Earlier studies indicate that distinct differences in growth rate within the species exist that relate to geographical regions in Australia (Tuomela et al. 1993). However, the full potential of the species has not yet been explored because the seed for most exotic plantings has come from a limited part of the natural range (Seed section report ... 1979, Firewood crops ... 1980). Suitable provenances of *E. microtheca* for irrigation projects could offer great potential to increase fuelwood supply in ASALs.

The aim of the study was to compare the behaviour of three selected provenances of *Eucalyptus microtheca* that were likely to respond differently to drought. For this purpose, we studied the effects of vapour pressure deficit and soil water content on leaf water potential in an irrigated plantation at Bura, eastern Kenya.

2 Material and Methods

The study area is located in Bura Tana District (1°08'S; 39°45'E; altitude 100 m). The area is semi-arid, with a bimodal rainfall pattern of about

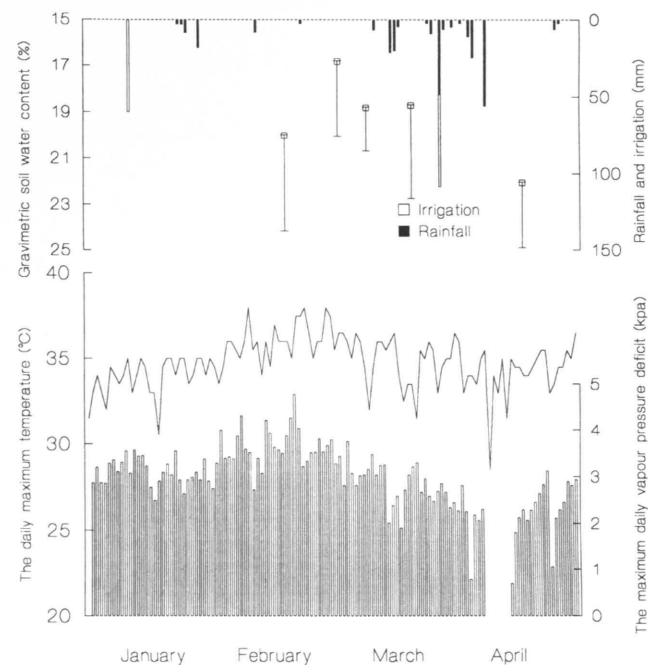


Fig. 1. The daily maximum temperature, the maximum daily vapour pressure deficit, rainfall, irrigation and gravimetric soil water content (vertical lines represent SE) at the trial, January–April 1990.

400 mm a⁻¹ (Otsamo et al. 1993). Temperature changes are modest. Mean monthly maximum and minimum temperature during 1983 to 1989 were 33.4 °C and 22.5 °C, respectively. The absolute maximum temperature recorded was 39.5 °C, and the respective minimum 17.0 °C. Mean potential evaporation was 2336 mm a⁻¹. The soil types of the research area vary from sandy clay loams to clays (Bura irrigation ... 1977).

An international provenance trial of *Eucalyptus microtheca*, established as a part of Finnida-supported Bura Forestry Research Project in eastern Kenya in August 1984, was used as a plant material in the study (Otsamo et al. 1993). The trial was established in randomized complete block design with five replications, each of which had sixteen provenance plots consisting of twenty

trees. One block had to be totally excluded due to the possible, biasing effect of a feeder canal on water conditions, and erroneous pruning during the experiment. Stand density was equal to 1 600 trees ha⁻¹. The trial was irrigated approximately at seven week intervals throughout the experimental period, 1984 to 1992. The irrigation was undertaken with siphons corresponding to a rainfall of about 60 mm. Changes in environmental variables over the study period, January to April 1990, are presented in Fig. 1.

Based on earlier results (Kaarakka et al. 1990, Tuomela et al. 1993), three provenances, Carnarvon Basin (EXM), Alice Springs-Ayers Rock (ALI) and Walgett-Mungindi (WAL) were selected for detailed analysis. Data on these provenances and on the climate in their natural occurrence in Australia is presented in Table 1.

Table 1. Data of the provenances used in the study (Seed section report ... 1979).

Variable	EXM	Provenance ALI	WAL
Geographical source	Carnarvon Basin, Western Australia	Alice-Springs- Ayers Rock, Northern Territory	Walgett-Mungindi, New South Wales- Queensland
Latitude (°S)	22°18'–24°42'	23°51'–25°11'	28°36'–30°05'
Longitude (°E)	113°51'–114°22'	132°09'–133°48'	148°07'–149°01'
Rainfall (mm a ⁻¹)	325	263	469
Rainy days (number a ⁻¹)	25	35	54
Mean annual maximum temperature (°C)	30.7	28.7	27.2
The driest quarter precipitation (mm)	4	27	86
Altitude a.s.l. (m)	10–20	457–520	130–180
MAI (m ³ ha ⁻¹) ¹⁾	6.0	9.8	14.1

¹⁾ Mean Annual Increment (MAI) of selected provenances of *E. microtheca* at the age of 48 months (Kaarakka et al. 1990).

The leaf water potential was measured with the pressure chamber technique Scholander et al. (1965), over a period of 7 weeks, February–April 1990. The pressure chamber determinations were assumed to equal to the total water potential (Ψ) (Ritchie and Hinckley 1975).

The measurements of the experiment were carried out on 12 February, 1 and 23 March, and 2, 5 and 17 April. Each provenance consisted of two sample trees per replication chosen systematically from the center of the plot. Two even aged, healthy and vital leaves, fourth or fifth leaves counted from the tip of the branch, were sampled from each tree. The sample leaves were removed from the height of about 2 meters above the ground level with a knife and measured on the site within 2 minutes. Thus, at each measurement time two sample leaves from four trees per provenance were measured. A leaf was enclosed into the pressure chamber and pressure was increased with a rate of about 0.05 Mpa s⁻¹ until first drop of water emerged from the leaf xylem.

Leaf water potential was measured five times per day on 1 and 23 March, 5 and 17 April with two and half hour intervals between 7:00 hrs–17:00 hrs and four times on 12 February and 2 April between 9:30 hrs–17:00 hrs.

Soil samples for determining gravimetric soil water content were taken five times during the experimental period, 17 February, 2, 9 and 20 March and 16 April from the same plots used for water potential measurements. Each sample con-

sisted of four randomly selected subsamples taken at the depth of about 30 cm.

Air temperature and relative humidity were measured daily with a min–max thermometer and a hygrometer, respectively. Saturation vapour pressure was calculated according to the model presented by Dilley (1968). For calculating maximum vapour pressure deficit we used humidity reading at 15:00 hrs, assuming that this was the hottest moment of the day.

Regression analysis was used to determine the dependence of the daily minimum leaf water potential (Ψ_{\min}) on vapour pressure deficit and on gravimetric soil water content. It was tested both with simple and with multiple regression models. In addition, the means of the daily water potential fluctuation ($\Psi_{\max} - \Psi_{\min}$) and Ψ_{\min} were analysed with the analysis of variance. Possible interactions between gravimetric soil water content and vapour pressure deficit, and the provenances were tested with analysis of variance.

The analyses were carried out with SYSTAT statistical software package (Wilkinson 1990).

3 Results

The daily behaviour of leaf water potential exhibited similar trend in all provenances. WAL showed generally the lowest and ALI the highest water potential values on a daily basis (Fig. 2).

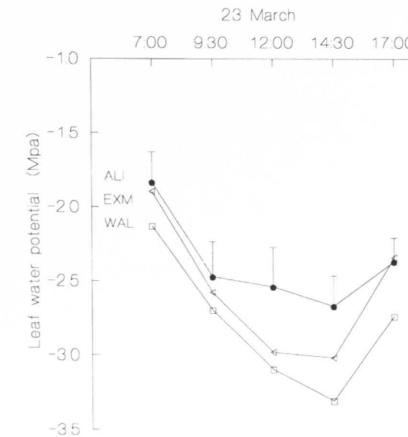


Fig. 2. Daily behaviour of leaf water potential (Mpa). Standard error of the ALI provenance is presented with vertical lines. WAL (\square), ALI (\bullet) and EXM (\triangleleft).

Statistically significant differences in the daily water potential fluctuation were detected between provenances (Table 2). WAL exhibited the greatest and ALI the smallest values (Table 3). The absolute range in the daily water potential fluctuation and in the daily minimum leaf water potential varied from 0.15 Mpa to 2.8 Mpa and from –2.05 Mpa to –4.55 Mpa, respectively. In the regression analyses, gravimetric soil water content predicted the daily minimum water potential better than the maximum daily vapour pressure deficit (Table 4). The minimum daily leaf water potential of all provenances responded well to changes in gravimetric soil water content, EXM being the most sensitive one (Fig. 3). Statistically significant interactions between gravimetric soil water content and provenances ($p < 0.05$), and between vapour pressure deficit and provenances ($p < 0.01$) were detected.

4 Discussion

The daily behavior of leaf water potential followed rather well changes in gravimetric soil water content and in vapour pressure deficit. In

Table 2. Analysis of variance for the daily water potential fluctuation.

Source	SS	DF	MS	F	P
Provenance	0.180	2	0.090	5.954	0.038
Replication	0.477	3	0.159	10.490	0.008
Error	0.091	6			

Table 3. Mean and standard error (in parenthesis) of the minimum daily water potential and the daily water potential fluctuation of studied provenances. Differences in mean values designated with the same letter are not statistically significant at $p < 0.05$ as determined by Tukey's HSD-test.

Provenance	The minimum daily water potential (Mpa)	The daily water potential fluctuation (Mpa)
EXM	–3.106 (0.077)a	1.191 (1.121)ab
ALI	–2.956 (0.190)a	1.008 (0.091)b
WAL	–3.352 (0.136)a	1.306 (0.156)a

general, the results of this study were in line with those obtained for *Eucalyptus* spp. elsewhere in drylands (Grunwald and Karschon 1982, Myers and Neales 1984). The observed high within provenance variation in the daily leaf water potential is probably due to a relatively small sample size used in the study. In addition, each provenance was composed of seeds collected from several adjacent locations in Australia (Seed section report ... 1979), increasing variation in the measured variables.

On a daily basis, the WAL provenance exhibited substantially lower leaf water potential and greater leaf water potential fluctuation than the EXM and ALI provenances. As it is generally assumed, lower leaf water potential may indicate lower turgor pressure in leaves and thus greater water stress (Jarvis 1975). On the other hand, greater leaf water potential fluctuation may provide greater water potential gradient between roots and leaves leading to faster uptake of water (cf. Delucia and Heckathorn 1989, Tuomela et al. 1993).

The effects of vapour pressure deficit and gravi-

Table 4. Parameters for simple and multiple regression equations using three different models (a–c). Coefficient of determination (r^2) and the significance of the models (p) are presented. Standard error of regression coefficient is presented in parenthesis.

Model (a): The minimum daily water potential = constant + a · the maximum daily vapour pressure deficit + b · gravimetric soil water content

Provenance	Model		constant	Regression coefficients	
	r^2	p		a	b
EXM	0.53	<0.0005	-4.508 (0.779) $p < 0.0005$	-0.186 (0.092) $p = 0.054$	0.100 (0.032) $p = 0.004$
ALI	0.46	<0.0005	-4.608 (0.401) $p < 0.0005$	0.227 (0.102) $p = 0.036$	0.049 (0.012) $p < 0.0005$
WAL	0.25	= 0.028	-4.096 (0.555) $p < 0.0005$	-0.143 (0.139) $p = 0.314$	0.065 (0.023) $p = 0.009$

Model (b): The minimum daily water potential = constant + a · the maximum daily vapour pressure deficit

Provenance	Model		constant	Regression coefficients a
	r^2	p		
EXM	0.19	= 0.002	-2.551 (0.177) $p < 0.0005$	-0.198 (0.061) $p = 0.002$
ALI	0.01	= 0.479	-2.772 (0.267) $p < 0.0005$	-0.066 (0.092) $p = 0.479$
WAL	0.02	= 0.343	-3.102 (0.271) $p < 0.0005$	-0.089 (0.093) $p = 0.343$

Model (c): The minimum daily water potential = constant + b · gravimetric soil water content

Provenance	Model		constant	Regression coefficients b
	r^2	p		
EXM	0.45	<0.0005	-5.677 (0.553) $p < 0.0005$	0.132 (0.029) $p < 0.0005$
ALI	0.36	= 0.001	-3.909 (0.266) $p < 0.0005$	0.048 (0.013) $p = 0.001$
WAL	0.22	= 0.012	-4.445 (0.439) $p < 0.0005$	0.061 (0.023) $p = 0.012$

metric soil water content on the minimum daily leaf water potential were studied using regression analysis. The results showed that EXM was the most sensitive to drying conditions. According to earlier results from the same trial, the western provenances, including EXM, have an inferior growth rate as compared to the northern and eastern ones (Johansson and Tuomela 1995). Thus, the sensitivity to drying conditions may

refer to a disadvantageous behaviour in competitive milieu (Fischer and Turner 1978).

Annual rainfall distribution varies considerably between the geographical regions of the studied provenances. In western Australia, the origin of the EXM provenance, the annual rainfall pattern is monsoonal with distinct wet and dry seasons. In northern and eastern Australia, the origins of the ALI and WAL provenances, the an-

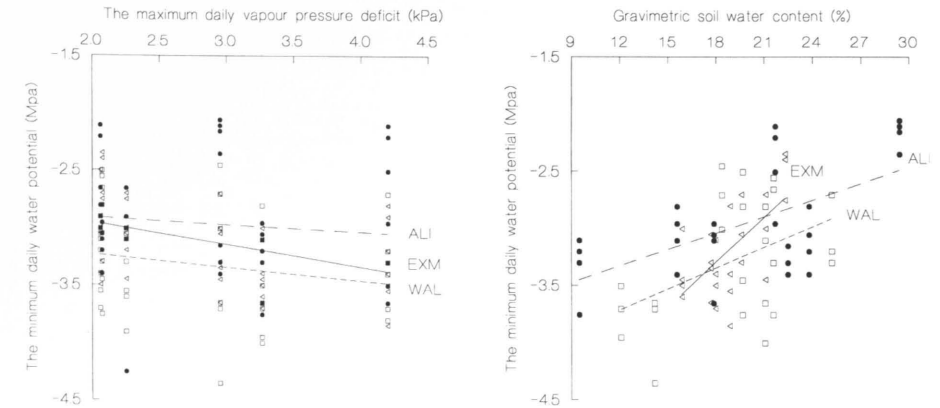


Fig. 3. The effects of the maximum daily vapour pressure deficit and gravimetric soil water content on the minimum daily water potential in the studied provenances. WAL (□), ALI (●) and EXM (◐).

nual rainfall is more evenly distributed. The observed sensitivity of EXM to drying conditions may indicate adaptation to conditions of annual prolonged drought. WAL and ALI, native to environments with frequent but short dry spells, responded less to changes in moisture conditions. They enabled to maintain the minimum daily leaf water potential rather constant throughout the experiment.

Acknowledgements

The authors wish to express their appreciation to the staff of Kenya Forestry Research Institute at Bura and Mr. Vesa Kaarakka for providing the support during the field work. Prof. Olavi Luukkanen gave valuable suggestions in the planning phase of the work. Statistical advice from Mr. Hannu Rita is gratefully acknowledged. The study was funded by the Finnish International Development Agency and the Academy of Finland.

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