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SALINITY EFFECTS ON TRANSPIRATION IN *EUCALYPTUS CAMALDULENSIS* AND *COMBRETUM QUADRANGULARE*

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บทคัดย่อ

การศึกษาเปรียบเทียบอัตราการคายน้ำของไม้ทนเค็มสองชนิด โดยแยกออกเป็นไม้พื้นเมือง และไม้นำมาจากต่างประเทศ ได้แก่ ไม้สะแกนา และไม้ยูคาลิปตัส คามาลดูเลนซิส ตามลำดับ โดยได้ทำการศึกษาเปรียบเทียบทั้งระยะกล้าไม้ในเรือนกระจก ใช้สารละลายเกลือคลอไรด์รวมกับธาตุอาหารสูตรของมหาวิทยาลัยรัฐคาโรไลน่าเหนือ จนมีความเข้มของความเค็ม 0, 0.5, 1.0, 1.5 และ 2.0% ตามลำดับ ณ ระดับอุณหภูมิ 18, 24, 30, และ 36°C และความเข้มของแสง 300, 500, 1000, 1500, และ 2000 μmol/m^2/s และศึกษาระยะเป็นต้นไม้แล้ว ในพื้นที่ดินเค็มและไม่เค็ม ที่ระดับอุณหภูมิและความเข้มของแสงตามธรรมชาติ ณ ท้องที่จังหวัดขอนแก่น และร้อยเอ็ด ในภาคตะวันออกเฉียงเหนือ

ผลการศึกษาพบว่า ในเรือนกระจก อัตราการคายน้ำของกล้าไม้ทั้งสองชนิดเพิ่มขึ้นที่ระดับความเค็มต่ำ และลดลงเมื่อความเค็มสูงขึ้น แต่จะมีการคายน้ำเพิ่มขึ้นเมื่ออุณหภูมิสูงขึ้นจาก 18–36°C แต่สำหรับปริมาณความเข้มของแสงแล้ว อัตราการคายน้ำจะเพิ่มขึ้นช่วงความเข้มของแสง 300–1500 μmol/m^2/s และลดลงที่ 2000 μmol/m^2/s เมื่อเปรียบเทียบการคายน้ำของกล้าไม้ทั้งสองแล้ว กล้าไม้ยูคาลิปตัส คามาลดูเลนซิส มีอัตราการคายน้ำสูงกว่าไม้สะแกนา ที่ทุกระดับอุณหภูมิและแสง

ผลการศึกษาในพื้นที่ปรากฏว่า อัตราการคายน้ำของไม้ทั้งสองชนิดเพิ่มขึ้น เมื่ออุณหภูมิและความเข้มของแสงสูงขึ้น และมีการคายน้ำมากในช่วงเวลา 10.00–14.00 น. โดยมีการคายน้ำสูงสุด เวลา 12.00 น. ทั้งบนพื้นที่ดินเค็มและไม่เค็ม อัตราการคายน้ำของไม้ยูคาลิปตัส คามาลดูเลนซิส สูงกว่าไม้สะแกนา อิทธิพลของดินเค็มไม่ชี้ผลแจ้งชัดว่ามีผลต่อการคายน้ำของไม้ทั้งสองชนิด นอกจากที่อุณหภูมิสูงสุดเฉลี่ยที่วัดได้ 39°C และความเข้มของแสงเฉลี่ยสูงสุด 2000 μmol/m^2/s อัตราการคายน้ำบนพื้นที่ดินไม่เค็มมีมากกว่าพื้นที่ดินเค็ม

Key word : Salinity, transpiration, water – use efficiency, *Eucalyptus camaldulensis*, *Combretum quadrangulare*

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ABSTRACT

The aim of this study was to investigate the transpiration rates in two salt – tolerant tree species, *Eucalyptus camaldulensis* Dehnh. and *Combretum quadrangulare* Kurz. A greenhouse experiment with different levels of NaCl salinity (0, 0.5, 1.0, 1.5 and 2.0%) was set up and the results were compared with those of a field study on non – saline and saline soils.

In the greenhouse experiment, transpiration increased at low salinity but decreased at high salinity levels. Transpiration rates always increased with temperature. With irradiance they only increased up to medium photon flux density (up to 1500 μmol $m^{-2}s^{-1}$) and then decreased at 2000 μmol $m^{-2}s^{-1}$. In the field study, transpiration rates increased with temperature and irradiance in both species and they were much higher in *E. camaldulensis* than in *C. quadrangulare*. The relationships between transpiration rate, temperature and irradiance did not indicate any distinct effects caused by salinity. **Key words :** salinity, transpiration, water – use efficiency, *Eucalyptus camaldulensis*, *Combretum quadrangulare*.

INTRODUCTION

The physical laws defining the rate of evaporation as a function of solar energy, temperature and wind velocity, are not identical with the biological laws defining the rate of transpiration. Since transpiration is a physiological process, it is not bound by physical laws related to physical evaporation. This fact is particularly important in the case of woody plants (Gindel 1973).

A parallelism between fluctuations in transpiration and in photosynthesis to a greater or lesser extent has been shown by Schneider and Childers (1941), Shimshi (1963), Brawdo (1972), Gindel (1973) and others. At the leaf scale, stomatal control of transpiration can be either large or small, depending on how well the saturation deficit at leaf surface is coupled to that of the ambient air. The coupling is usually very strong for small well – ventilated leaves. When the stomata close, transpiration decreases and resistance to water flow increases.

Transpiration is a factor of water balance in plants. The water balance of a plant is given by the difference between the rates of water intake and water loss (Larcher 1983). It can be computed directly from quantitative determinations of water uptake and transpiration or indirectly from the water content or water potential of the plant. A negative balance always eventually produces a decrease in turgidity and water potential of the tissues. These changes appear first in the leaves, which are the sites of intensive evaporation and, moreover, are the furthest removed from the roots.

In many crop species, salinity induces physiological and morphological adjustments which assist in the maintenance of a favourable water balance. Such adjustments may also be effective in modifying the response of salinised plants to drought (Stark and Jarrell 1980). Plants under conditions of salinity have been considered as suffering from "physiological drought" (Gale 1975).

By this was meant a shortage of water within the plant even when growing under moist but saline soil conditions or in saline solutions. The lowered osmotic potential of the soil water, resulting from high concentrations of soluble salts, was thought to prevent uptake of water by the plant. A negative water balance is therefore considered to be the main factor in salinity damage, although specific toxic effects are also recognised.

Besides inducing osmotic adjustment, with the attendant effects on water relations and growth, salinity also causes structural changes which can improve the water balance of the plant (Gale 1975, Maas and Nieman 1978, Stark and Jarrell 1980). These changes vary with species and type of salinity but may include reductions in the size and number of leaves, fewer stomata per unit leaf area, earlier lignification of roots, increased leaf succulence, thickening of leaf cuticles and surface wax layers, and reduced water conduction due to impaired development of vascular tissue (Maas and Nieman 1978).

As a long-term response to salinity, prolonged transpiration brings large amounts of salt into the shoot, especially into the old leaves, thus killing them (Munns and Termaat 1986). Gale (1975) reported that there is a depression of transpiration under saline conditions. He also had further reports that the depression of transpiration is greater with the effect of chloride than sulphate type of salinity.

Aims of the present study. The aim of the present work was to investigate the transpiration rates in relation to salinity in two salt-tolerant tree species of which one is indigenous *(Combretum qudrangulare)* and the other exotic *(Eucalyptus camaldulensis)*.

An attempt was also made to identify criteria that could be useful in the selection of salt-tolerant species and genotypes.

MATERIAL AND METHODS

Greenhouse experiments

Experimental material and design

Eucalyptus camaldulensis Dehnh. seeds were obtained from Mt. Carmine, Queensland, Australia (CSIRO seedlot No. 0149, 16° 29'S, 144° 55'E, altitude of 380 m, average rainfall of 850 mm and minimum-maximum temperatures of 16° to 29°C). *Combretum quadrangulare* Kurz seeds were brought from Nong-Kai province, northeastern Thailand (latitude 18° 00'N, longitude 103° 30'E, altitude 150 m, average rainfall 1200 mm and minimum-maximum temperatures 20-33°C).

The seeds were germinated and the laboratory experiments carried out at the Hyytiälä Forestry Field Station, University of Helsinki, Finland, starting on 29 March 1986. The seedlings were transplanted from germination boxes to seedling tray pots containing a peat : sand medium (3 : 1) on 11 April 1986 and grown under glasshouse conditions (diurnal temperature 15-25°C, 40% to 70% humidity and minimum photon flux density about 300 μmol $m^{-2}s^{-1}$, at 14-h photoperiod).

When the seedlings were some two months old they were lifted from tray pots and their roots were washed. The seedlings were replanted into 10.0 × 7.5 cm black plastic pots containing 180 cm^3 of vermiculite No. 2 as growth medium. Each pot had a perforated bottom to allow the roots to grow through. Underneath each pot was a 1000 cm^3 plastic bottle containing 500 cm^3 of North Carolina State University (N.C.S.U.) Phytotron Nutrient Solution (Downs and Bonaminio 1976). The pot was connected to the nutrient bottle by means of a cotton wick. The treatment with sodium chloride began after the roots had grown through the pots and into the solution bottles.

Sodium chloride was added to the nutrient solution so as to produce 0, 0.5, 1.0, 1.5 or 2.0% salinity. The solution was replaced every week, when the pH, electrical conductivity and resistance of the remaining and replacement solutions were also measured. The seedlings were treated in this way for three months. The experiment consisted of 15 replications, with one seedling in each replication and treatment. Effort was made to select only uniform seedlings with respect to both the above-ground parts and roots.

Another batch of seedlings from the tray pots was transplanted individually into 12.5 l plastic containers with sand as medium. These seedlings were treated with the same nutrient solution of either 0 or 2.0% NaCl salinity. In this case there were seven replications. The treatments were applied by pouring 500 cm^3 of the solution to the surface of the sand once a week for the same three-month period.

Measurements of transpiration

Measurements of transpiration were made by enclosing a selected leaf inside a transparent plastic cuvette – the assimilation chamber – which was connected to a Hartmann – Braun IRGA model 2T analyser. Data acquisition was controlled by a data logger (Veko 771, Helsinki University of Technology) which sent on the data to a PDP 11/34 minicomputer for processing and storing. The system has been described in detail by Korpilahti (1988).

The cuvette was fitted around a selected leaf of each seedling for measurement in turn. The volume of the cuvette was 8 dm^3. The air inside the cuvette was mixed by means of a small fan so as to minimise boundary layer resistance. Temperature control in the system was achieved using a thermostat and a pump which circulated water through the water jacket of the gas exchange chamber. Air temperature within the assimilation chamber as well as water temperatures at different points in the cooling system were monitored using Cu – constantan thermocouples. The photon flux density from mercury sodium lamps was measured using a quantum meter (LI – 190S – 1, LI – COR Inc. instrument, U.S.A), which was attached to the cuvette at the same level as the leaf inside the cuvette. Different photon flux densities were achieved by adjusting the position of the lamps.

After achieving the set values for light and temperature, the recording of CO_2 exchange was started after a 30 minute stabilization period. The measuring interval was 120 seconds and all the sensors were measured simultaneously. The air temperature within the assimilation chamber was maintained within ±1°C of the desired temperature.

The flow rate of gas in the measuring system was adjusted to 60 l h^{-1}, which was controlled by a rotameter.

Transpiration rates per unit area (μmol $m^{-2}s^{-1}$) were simultaneously measured with IRGA analyser in the opened system was at temperatures of : 18°, 24°, 30° and 36°C and at photon flux densities of : 300, 500, 1000, 1500 and 2000 μmol $m^{-2}s^{-1}$.

Calculation of transpiration rates from porometer

Transpiration rates were also calculated using the porometer values of leaf resistance and thermohygrograph readings of ambient air humidity and temperature (transpiration = intercellular water vapour concentration minus ambient water vapour concentration divided by leaf resistance). These calculated transpiration rates were compared with those obtained by IRGA measurements.

Field studies

Site description and experimental design

E. camaldulensis and *C. quadrangulare* plantations located in Khon Kaen and Roi-et provinces of northeastern Thailand were selected for the study. The *E. camaldulensis* at Khon Kaen included both a local variety and the Australian variety (No. 0149) used in the greenhouse experiment. The plantations' had been established in June – July 1985 with a planting spacing of 3 × 3 m.

The Khon Kaen site (16° 30'N, 102° 30'E) is at an of altitude 165 m and has an average annual rainfall of 1000 – 1100 mm. The soil at the plantations of *C. quadrangulare* and the local variety of *E. camaldulensis* was saline and had a sandy – loam texture. The soil at the plantation of *E. camaldulensis* variety 0149 was non – saline and had a loamy – sand texture.

The Roi – et site (15° 30'N, 103° 30'E) is at an altitude of 130 m and has average annual rainfall of 1000 – 1500 m. The soil in plantation of *C. quadrangulare* and the local variety of *E. camaldulensis* was non.– saline and had a loamy – sand texture.

The field study thus consisted of five sites : *C. quadrangulare* on saline and non – saline soils, *E. camaldulensis* (local variety) on saline and non – saline soils, and *E. camaldulensis* (variety 0149) on non – saline soil only.

Measurements of transpiration

An LI – 6200 portable photosynthesis system and an LI – 6250 gas analyser (LI – COR Inc. U.S.A.) were used for measurements of gas exchange in the field study. The variation in transpiration rates (μmol $m^{-2}s^{-1}$), photon flux density (μmol $m^{-2}s^{-1}$), leaf temperature (°C), stomatal resistance (s cm^{-1}), and stomatal conductance (cm s^{-1}) were investigated.

On each occasion a single tree was randomly selected in one of the plots ; on the fifth occasion the same tree in the first plot was used again. At two – week intervals during the three month study period, five sample trees per site were made. Ten mature leaves were measured per tree per day between 07 : 00 and 17 : 00 h at one – hour measurement interval on the same leaf. Transpiration and stomatal conductance programming frequently resulted in a 10 – fold error ; but these data were later corrected to correspond to the appropriate level. This correction did not affect the comparison between treatments..

Numerical handling

All data were analysed using one-way analyses of variance (ANOVA). Treatment means were compared using the Duncan's multiple range test, and non-linear and linear regressions were applied to examine the relationships among treatments (SAS 1985). The significance levels of the F-test used in all statistical analyses as follows : ns = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, and *** = $p < 0.001$.

RESULTS

Greenhouse experiments – Measured transpiration rates tended to decrease with increasing salinity in culture solution experiment (Table 1). Transpiration rates were higher in *E. camaldulensis* than in *C. quadrangulare* at 18° ($p > 0.05$), 24° ($p < 0.05$), 30° ($p < 0.001$) and 36°C ($p < 0.01$). There were no statistically confirmed differences among effects of salinity levels in *C. quadrangulare* at any temperature, but in *E. camaldulensis* higher transpiration rates were found at a lower salinity level at higher temperatures (30° to 36°C) ($p < 0.001$). Similar results were also found in porometer measurements carried out on seedlings grown in culture solutions (Table 1).

In contrast to the results of the culture solution experiment, the transpiration rates of both species measured in the sand medium experiment were higher under the saline treatment than under the non-saline treatment, and at all temperatures. However, when the rates were measured using the porometer, on opposite trend was observed (Table 1).

Table 1. Means (±sd) of transpiration rate of Combretum quadrangulare and Eucalyptus camaldulensis variety 3149 measured with IRGA at a photon flux density of 1000 µmol $m^{-2}s^{-1}$ and different temperatures, and measured with porometer at variable irradiance and temperature in different salinity treatments in the solution (1) and sand medium (2) greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species and salinity (%)	Transpiration rate (IRGA, mmol $m^{-2}s^{-1}$) Temperature (°C) 18	24	30	36	(Porometer) (mmol $m^{-2}s^{-1}$)
(1)					
Com 0.0	0.55±0.23^{ab}	1.31±0.57^{bc}	2.11±1.07^{cde}	2.76±1.37^{bc}	1.81±0.55^{c}
Com 0.5	0.65±0.37^{ab}	1.22±0.72^{bc}	1.68±1.18^{de}	2.08±1.37^{c}	1.99±0.30^{c}
Com 1.0	0.55±0.27^{ab}	1.02±0.46^{bc}	1.26±0.56^{de}	1.53±0.55^{c}	1.29±0.12^{c}
Com 1.5	0.32±0.6^{b}	0.51±0.18^{c}	0.62±0.16^{e}	0.70±0.17^{c}	1.08±0.26^{c}
Com 2.0	0.91±0.61^{ab}	1.33±1.06^{bc}	1.57±1.36^{de}	1.59±1.19^{c}	0.73±0.17^{c}
Eu 0.0	1.17±0.95^{ab}	3.16±1.81^{ab}	5.03±2.06^{abc}	6.89±3.32^{ab}	5.28±1.98^{a}
Eu 0.5	0.82±0.63^{ab}	2.68±1.60^{abc}	5.46±3.56^{ab}	6.57±4.06^{ab}	4.13±2.43^{ab}
Eu 1.0	1.54±0.88^{ab}	5.08±2.52^{a}	6.53±5.89^{a}	7.35±4.56^{a}	3.99±1.80^{ab}
Eu 1.5	1.29±1.07^{ab}	3.48±2.97^{ab}	3.85±3.23^{abcd}	3.67±3.81^{abc}	2.47±1.46^{bc}
Eu 2.0	1.56±0.99^{a}	2.76±1.44^{abc}	2.86±1.27^{bcde}	2.62±1.30^{c}	1.46±0.29^{c}
F	1.52^{ns}	2.81*	4.45***	3.78**	7.75***
C	0.47	5.09	3.26	3.67	2.38
(2)					
Com 0.0	0.49±0.29^{a}	1.35±0.58^{a}	2.03±0.41^{b}	1.74±0.70^{c}	4.08±3.46^{a}
Com 2.0	0.32±0.19^{a}	1.33±0.57^{a}	2.19±0.51^{ab}	2.28±0.54^{bc}	3.97±2.71^{a}
Eu 0.0	0.46±0.37^{a}	1.72±0.44^{a}	2.87±0.50^{ab}	3.16±0.69^{ab}	6.07±4.81^{a}
Eu 2.0	0.70±0.41^{a}	2.19±1.08^{a}	5.08±1.11^{a}	3.71±1.28^{a}	3.76±3.20^{a}
F	0.61^{ns}	1.66^{ns}	2.56^{ns}	4.65*	0.50^{ns}
C	0.57	1.65	2.57	1.51	4.58

Transpiration rates were statistically significantly higher in *E. camaldulensis* than in *C. quadrangulare* at all photon flux densities and in both media. Transpiration rates always increased with temperature, regardless of species or growth medium (Figures 1, 2 and 3). Transpiration rates also increased with irradiance up to 1500 µmol $m^{-2}s^{-1}$ and then decreased at the 2000 µmol $m^{-2}s^{-1}$ (Table 2).

Field studies – Transpiration increased with temperature and irradiance in both species, and transpiration rates per unit leaf area were much higher in *E. camaldulensis* than in *C. quadrangulare* ($p < 0.001$; Figure 4). The relationship between transpiration rate and temperature did not indicate any distinct effects caused by salinity. Similarly, the measured values of transpiration rate did not indicate any clear effects caused by salinity in relation to photon flux density

Table 2. Means (±sd) of transpiration rate of Combretum quadrangulare and Eucalyptus camaldulensis variety 0149 measured with IRGA at 30°C and different photon flux densities in different salinity treatments in the solution (1) and sand medium (2) greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species and salinity (%)	Transpiration rate (Es, mmol $m^{-2}s^{-1}$) Irradiance (μmol $m^{-2}s^{-1}$) 300	500	1000	1500	2000
(1)					
Com 0.0	2.23±0.52^{bcd}	2.28±0.49^{bcd}	2.39±0.42^{abcd}	2.38±0.60^{abc}	1.94±0.70^{abc}
Com 0.5	1.61±0.83^{cd}	1.70±0.85^{cd}	1.84±0.91^{cd}	1.88±0.93^{bc}	1.63±0.80^{abc}
Com 1.0	1.67±1.09^{cd}	1.87±1.29^{bcd}	2.05±1.36^{bcd}	2.26±1.44^{abc}	2.35±1.80^{abc}
Com 1.5	1.03±0.66^{d}	1.06±0.68^{d}	1.13±0.65^{cd}	1.45±0.61^{c}	1.05±0.36^{bc}
Com 2.0	0.90±0.83^{d}	0.92±0.86^{d}	0.98±0.89^{d}	1.01±0.48^{c}	0.99±0.53^{c}
Eu 0.0	4.38±1.90^{ab}	4.55±1.97^{ab}	4.93±2.22^{ab}	4.70±2.09^{ab}	3.79±2.17^{a}
Eu 0.5	3.79±2.73^{abc}	3.89±2.65^{abc}	4.14±3.00^{abc}	3.77±2.56^{abc}	2.41±1.79^{abc}
Eu 1.0	5.01±3.05^{a}	5.18±3.15^{a}	5.30±3.56^{a}	4.99±3.63^{a}	3.53±2.51^{ab}
Eu 1.5	3.72±1.79^{abc}	4.06±1.69^{abc}	3.91±1.67^{abcd}	2.28±1.45^{abc}	2.57±1.25^{abc}
Eu 2.0	3.26±0.87^{abcd}	3.28±0.77^{abcd}	3.24±0.73^{abcd}	2.92±0.34^{abc}	2.64±0.50^{abc}
F	3.35**	3.52**	3.09**	2.74*	1.80^{ns}
$\bar{x}$	2.91	3.03	3.17	2.91	2.43
(2)					
Com 0.0	1.82±0.35^{ab}	1.85±0.35^{b}	1.83±0.36^{b}	1.69±0.39^{b}	1.25±0.41^{b}
Com 2.0	1.72±0.65^{b}	1.72±0.67^{b}	1.67±0.71^{b}	1.51±0.62^{b}	1.13±0.39^{b}
Eu 0.0	2.58±0.53^{ab}	2.63±0.49^{ab}	2.73±0.46^{ab}	2.61±0.46^{ab}	2.04±0.40^{ab}
Eu 2.0	2.80±0.88^{a}	2.91±0.88^{a}	3.08±1.00^{a}	3.14±1.13^{a}	2.53±1.15^{a}
F	2.92^{ns}	3.42^{ns}	4.03*	4.73*	3.96*
$\bar{x}$	2.23	2.28	2.33	2.24	1.74

Table 3. Temperature dependence of transpiration rate (mean±sd) of Combretum quadrangulare and Eucalyptus camaldulensis measured with LI-6250 on non-saline (normal) and saline soil types in the field study at 09:00 to 12:00 h (nonsignificant differences are indicated in the same column by same letters).

Species and soil type	Transpiration rate (Tr, mmol $m^{-2}s^{-1}$) Temperature (°C) 21	24	27	30	33	36	39
Com normal	-	1.14±0.261^{c}	1.15±0.28^{d}	1.47±0.56^{f}	2.28±0.47^{d}	2.86±0.49^{c}	3.01±0.65^{b}
Com saline	-	1.38±0.351^{b}	1.01±0.37^{e}	1.55±0.48^{e}	2.22±0.76^{a}	2.79±0.80^{c}	-
Eu0149 normal	-	1.45±0.13^{ab}	2.01±0.63^{a}	3.87±1.26^{a}	3.44±1.23^{a}	4.17±1.15^{b}	-
Eu normal	1.26±0.49^{a}	1.83±0.22^{a}	2.08±0.27^{a}	2.75±0.55^{b}	3.64±0.65^{a}	3.51±0.95^{a}	3.76±0.83^{a}
Eu saline	1.28±0.15^{a}	1.56±0.37^{ab}	1.97±0.49^{a}	2.57±0.50^{b}	3.78±1.50^{a}	4.21±1.11^{b}	-
F	0.16^{ns}	7.47***	56.65***	61.29***	35.16***	56.21***	15.71**
$\bar{x}$	1.27	1.49	1.77	2.21	3.00	3.71	3.32

Table 4. Irradiance dependence of transpiration rate (mean±sd) of Combretum quadrangulare and Eucalyptus camaldulensis measured with LI-6250 on non-saline (normal) and saline soil types in the field study at 09:00 to 12:00 h (nonsignificant differences in the same column are indicated by same letters).

Species and soil type	Transpiration rate (Tr, mmol $m^{-2}s^{-1}$) Irradiance (μmol $m^{-2}s^{-1}$) 300	500	700	1000	1300	1500	1700	2000
Com normal	2.00±3.18^{ab}	1.96±0.83^{a}	1.78±0.65^{b}	1.82±0.61^{c}	1.49±0.21^{b}	1.78±0.48^{b}	1.66±0.47^{c}	2.79±0.65^{b}
Com saline	8.47±8.00^{b}	2.85±0.63^{a}	2.27±0.66^{ab}	1.87±0.91^{bc}	1.65±0.58^{b}	1.68±0.62^{a}	1.83±0.98^{c}	3.21±0.46^{c}
Eu0149 normal	2.91±1.21^{a}	3.88±1.52^{a}	5.08±1.44^{a}	2.55±1.14^{a}	2.45±1.36^{a}	2.69±3.08^{a}	2.76±0.78^{a}	4.29±1.41^{ab}
Eu normal	-	-	5.47±1.68^{a}	2.85±1.10^{bc}	2.44±1.85^{a}	2.82±1.16^{a}	3.56±1.26^{a}	5.08±1.17^{a}
Eu saline	2.85±1.22^{a}	1.62±0.45^{a}	2.37±1.35^{ab}	2.31±1.10^{bc}	2.42±1.27^{a}	2.80±0.66^{a}	2.95±1.03^{ab}	4.28±1.35^{b}
F	1.69^{ns}	5.86**	2.96*	4.33**	7.98***	28.35***	28.77***	17.85***
$\bar{x}$	2.74	2.63	2.37	2.01	2.06	2.36	2.42	3.18

(Figure 5 and Tables 3 and 4).

The diurnal course of transpiration indicated a more rapid increase in the rate of transpiration in *E. camaldulensis* than in *C. quadrangulare*. In *C. quadrangulare*, a midday depression in the transpiration rate was observed on saline soil but not on non-saline soil (Figure 6).

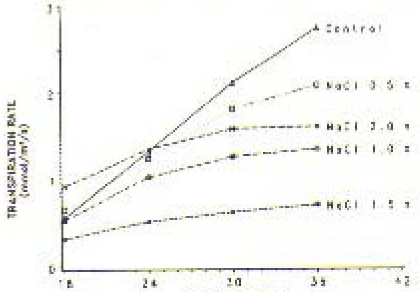

Figure 1. Relationship between transpiration rate and temperature for *Combretum quadrangulare* at photon flux density 1000 $\mu mol/m^2/s$ and different salinity levels. Mean values for seedlings grown in culture solution in the greenhouse.

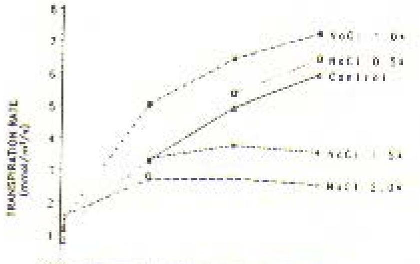

Figure 2. Relationship between transpiration rate and temperature for *Eucalyptus camaldulensis* at photon flux density 1000 $\mu mol/m^2/s$ and different salinity levels. Mean values for seedlings grown in culture solution in the greenhouse.

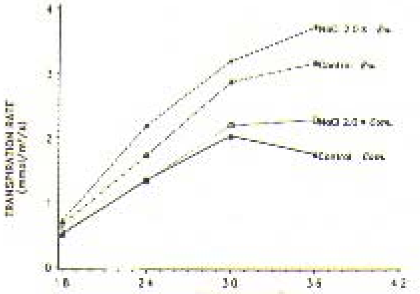

Figure 3. Relationship between transpiration rate and temperature for *Combretum quadrangulare* and *Eucalyptus camaldulensis* at photon flux density 1000 $\mu mol/m^2/s$ and different salinity levels. Mean values for seedlings grown in sand medium in the greenhouse.

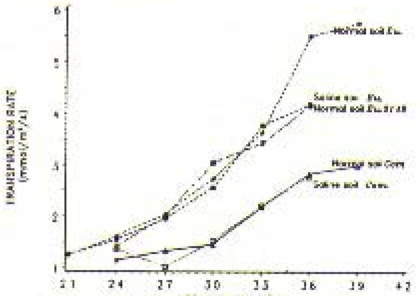

Figure 4. Relationship between transpiration rate and temperature for *Combretum quadrangulare* and *Eucalyptus camaldulensis* in the field (mean values).

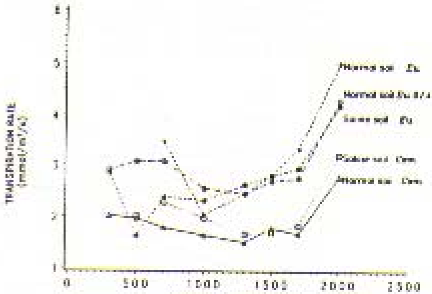

Figure 5. Relationship between transpiration rate and photon flux density for *Combretum quadrangulare* and *Eucalyptus camaldulensis* in the field study (mean values).

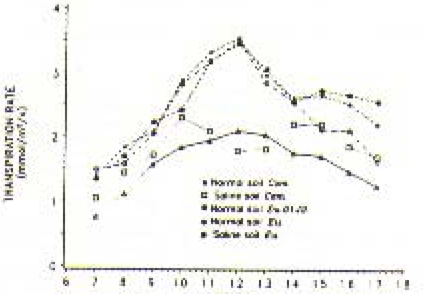

Figure 6. Average diurnal course of the transpiration rates for *Combretum quadrangulare* and *Eucalyptus camaldulensis* in the field study.

DISCUSSION

The **water balance** of leaves during the day is controlled by the **water potential** gradient along the soil – plant – atmosphere continuum (Morse 1990). For both *Eucalyptus camaldulensis* and *Combretum quadrangulare*, the water potential decreased with increasing salinity (see Luangjame 1990). Manohar (1977) found that the water potential and its components for *E. camaldulensis* decreased in the direction of the tip from the base of the leaf as well as from the midrib towards the margin. The highest values of water potential and its components were recorded towards the tip and the lowest towards the base of the seedlings and also decreased with leaf ageing because younger leaves are metabolically more active and may receive a larger proportion of the available water. The diurnal pattern of water potential in *E. marginata* has been shown to decrease through daylight hours, reaching a minimum in early afternoon, and then increase in late afternoon (Carbon *et al.* 1981). The readings at dusk were often lower than those at dawn, and were lower during summer than winter.

In theory, the lower the water potential is the higher the water deficit (Vu and Yelenosky 1988) and the lower the net photosynthetic rate (Adedeji 1984, Gupta and Berkowitz 1988). However, there is within a species genetic variation in this report (LaRosa *et al.* 1989). Results obtained by Grunwald and Karschon (1982) showed that *Eucalyptus camaldulensis* from a drought area maintained a higher production at lower water potentials with less reduction in water content than a seed source from a higher rainfall area during the dry season. They concluded that this was an adaptation to drought.

In saline environments, sufficient osmotic adjustment must occur for adequate water flux and growth. Insufficient osmotic adjustment would lead to growth reduction as a result of water deficits (Neumann *et al.* 1988, Naidoo and Rughunanan 1990). In *Eucalyptus camaldulensis* the **transpiration rate** was lower on the saline soil than on the non – saline soil over the observed temperature range (cf. Table 3).

High transpiration was limited to certain hours of the day, the peak being around 11 : 00 and 12 : 00 h (cf. Figure 6). Rapid transpiration can accentuate localized salinity stress by exacerbating the solute build – up in leaf cell walls. The results obtained by Gorham and Hardy (1990), showed that photosynthesis and transpiration of tef (*Eragrostis tef* Zucc.) were reduced in all salt solution culture treatments (100 – 300 mol m^{-3} or 0.59 – 1.76% NaCl).

Gindel (1973) found that transpiration was greater for dominant than for the suppressed leaves in *Eucalyptus* spp., *Quercus* spp. and *Acacia* spp.. A high transpiration rate is associated with a large number of stomata distributed over both leaf surfaces and extensive rooting (Pereira and Kozlowski 1976). Gale (1975) reported that in the case of *Atriplex halimus* L. (halophytic saltbush) grown in culture solution, transpiration was lower in saline treatment than control treatment. Further-more, transpiration was higher on the lower leaf surface than on the upper leaf surface in control treatments, while no difference between the lower and upper surfaces was found in the saline treatment.

Gindel (1973) found that while the rainless, hot season continued, *Eucalyptus camaldulensis* Dehnh. and *E. occidentalis* Endl. (both glycophytes) grown under water deficiency had a 43% smaller leaf area and a lower transpiration rate. Both *E. camaldulensis* and *E. occidentalis* showed an increase of 36% in transpiration after irrigation up to field capacity. The results presented by Carbon *et al.* (1981) showed that transpiration rates of *E. marginata* were generally higher at sites with a higher water table, and higher in the 1200 mm areas relative to the 700 mm rainfall areas in the late summer.

The results obtained by Pereira and Kozlowski (1976) showed that in pot experiments with a restricted soil volume, the transpiration rates of the two species, *Eucalyptus camaldulensis* and *E. globulus* varied depending on how they were expressed. When the soil was well watered, transpiration rate per seedling or per unit of the abaxial leaf surface area was higher in *E. camaldulensis* than in *E. globulus*. As the soil in the pots dried, plant water stress increased faster in *E. camaldulensis* than in *E. globulus*. The pot experiment results were misleading in suggesting that *E. globulus* was more drought resistant than *E. camaldulensis*. The higher transpiration rate and extensive rooting of *E. camaldulensis* in the restricted volume of soil in the pots induced greater water deficits than developed in *E. globulus*. When plants of both species were grown in long plastic tubes, with unrestricted soil volume, water stress did not develop faster in *E. camaldulensis* than in *E. globulus*. The tube experiments showed that a major factor in greater drought avoidance of *E. camaldulensis* over *E. globulus* was the capacity of the former to produce a deep and ramifying root system that could absorb water from deep soil layers after the surface soil dried. This advantage of *E. camaldulensis* over *E. globulus* was obscured in the pot experiments.

When a water shortage in the soil intensifies and physiological activities cease, the rate of transpiration falls, no matter what the strength of the wind. Under conditions of extreme water shortage, increased winds may further weaken transpiration and even hasten its cessation (Gindel 1973).

In rapidly – growing trees, a high rate of photosynthesis is generally accompanied by a high rate of transpiration. According to Gindel (1973), the rate of transpiration can be 2 – 3 times greater during the period of intense growth than towards the end of the season. There is no doubt that *Eucalyptus camaldulensis* is a fast – growing tree with high transpiration. However, in the present study, it was found to have a lower transpiration rate on saline soil than on non – saline soil. It is able to adapt very well to environmental extremes and is therefore suitable for improving saline soil areas where it can serve as a pioneer species to rehabilitate forest land.

The transpiration rates of *Eucalyptus camaldulensis* seedlings were also higher than those of *Combretum quadrangulare*. However, *E. camaldulensis* was found to have a much higher total dry weight than *C. quadrangulare* and it grew faster than seemed to be normal for fast-growing tree species. On fertile soil with enough water, *E. camaldulensis* may grow very quickly and transpire large amount of water because the stomata are open all the time.

This assumption was supported by the photosynthesis models applied under conditions of water deficit (see Luangjame 1990). In dry or in saline areas the stomata close in order to prevent the cells from wilting. The trees are able to survive and continue to grow, which non-tolerant species cannot. This is very useful when making a decision about choosing the right species for a particular site.

Water consumption is strongly related to growth. Species that consume more water generally make more efficient use of it since they produce a higher quantity of biomass per unit of water consumed. *Eucalyptus camaldulensis* had a higher consumption of water per plant and also had higher photosynthetic rates. Chaturvedi *et al.* (1984, 1988) concluded that *E. camaldulensis* produces the greatest biomass per unit volume of water consumed among the 10 species of forest trees studied. On the basis of above-ground productivity and transpiration data represented by Herwitz and Gutterman (1990), with consideration of some of the lesser-known eucalypt species, it was found that *Eucalyptus salubris* F. Muell. was the most efficient in its water use because it had the highest productivity (1169 kg ha^{-1}year^{-1}) and the lowest transpiration rates when compared with *E. torquata* Luehm., *E. grossa* F. Muell. ex Benth., *E. socialis* F. Muell. ex Miq. and *E. woodwardii* Maiden.

Luangjame (1990) found, when analysing the same material as used in the present study, that the **water-use efficiency** (WUE = NP/Tr in μmol CO_2/mmol H_2O) decreased with increasing salinity and was better in *Eucalyptus camaldulensis* variety 0149 than in *Combretum quadrangulare* in the greenhouse experiment. In the field study, the WUE tended to be lower under saline conditions as compared to the non-saline situation. The WUE decreased in the following order : *E. camaldulensis* local variety, *C. quadrangulare* and *E. camaldulensis* variety 0149. In both species, the WUE in the morning was better on non-saline than on saline soils.

Singh *et al.* (1987) investigated water-use efficiency by using the NP/ET (net photosynthesis/evapotranspiration) ratio. In the case of chickpea *(Cicer arietnum* L. cv. H-355) they found that water-use efficiency increased from the initial vegetative stage to full bloom and declined thereafter to maturity. A long period of slow growth after sowing tended to result in a low water-use efficiency, which was primarily due to low photosynthetic rates. The efficiency was highest during the period of highest photosynthetic activity.

Salinity induced changes in plant water status which led to reductions in leaf expansion.

Eucalyptus species from arid regions are able to maintain high growth rates by having thicker leaves, *i.e.* stacking their photosynthetic tissues into denser packages, which are potentially more efficient in water use (Mooney *et al.* 1978). As water stress increased, Attiwill and Clayton – Greene (1984) showed that water – use efficiency (NP/Tr) tended to increase in *Callitris columellaris* F. Muell. and to decrease in *Eucalyptus microcarpa* Maiden. A *Eucalyptus* hybrid was found to be the most efficient in water consumption among other fast growing tree species (Chaturvedi *et al.* 1988)

CONCLUSIONS

In the greenhouse experiments as well as in the field studies, transpiration increased with salinity (not significantly) and with temperature both at low (significantly) and high salinity (not significantly) in both species. Transpiration decreased at high light intensities in the greenhouse experiment. The decrease was more distinct in the case of *E. camaldulensis* than in the case of *C. quadrangulare*. In the field study, transpiration increased with light intensity. Transpiration rates were higher in *E. camaldulensis* than in *C. qudarangulare* in the greenhouse experiment and much higher on non – saline than on the saline soils in the field study.

Salinity affects transpiration and influences the growth of *E. camaldulensis* and *C. quadrangulare* via the effect on plant – water relations.

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