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JESADA LUANGJAME

SALINITY EFFECTS IN EUCALYPTUS CAMALDULENSIS AND COMBRETUM QUADRANGULARE: ECOPHYSIOLOGICAL AND MORPHOLOGICAL STUDIES

SUOLAISUUDEN VAIKUTUKSET EUCALYPTUS CAMALDULENSIKSEEN JA COMBRETUM QUADRANGULAREEN: EKOFYSIOLOGISIA JA MORFOLOGISIA TUTKIMUKSIA

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SALINITY EFFECTS IN *EUCALYPTUS CAMALDULENSIS* AND *COMBRETUM QUADRANGULARE:* ECOPHYSIOLOGICAL AND MORPHOLOGICAL STUDIES

Suolaisuuden vaikutukset *Eucalyptus camaldulensikseen* ja *Combretum quadrangulareen*: ekofysiologisia ja morfologisia tutkimuksia

Jesada Luangjame

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The aim of this study was to investigate the ecophysiological and morphological characteristics of two salt- tolerant tree species, *Combretum quadrangulare* Kurz and *Eucalyptus camaldulensis* Dehnh. 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. The determination of optimum gas exchange and the development and evaluation of photosynthetic models with and without water deficit were also included in this study.

Morphological characteristics under saline conditions showed that shoot height and diameter growth, shoot internode length, root length/biomass, leaf width and length, leaf area, number and biomass, and shoot/root and leaf/root ratios decreased with salinity, while leaf thickness increased with salinity. More growth was allocated to the roots than to the leaf canopy. Ecophysiological studies under laboratory conditions showed that photosynthesis, stomatal conductance and water potential decreased with salinity, while the CO_2 compensation point increased with salinity. Transpiration, dark respiration and photorespiration increased at low salinity but decreased at high salinity levels. In the field study, however, there were no significant differences in stomatal conductance and opening between saline and non-saline soils. Model predictions supported the results of the field measurements. Adaptation to salinity was reflected in an acclimatization of tree structure in the field study. There were both functioning and structural changes of seedlings in the greenhouse experiment.

In terms of ecophysiological and morphological characteristics, *E. camaldulensis* showed better salt tolerance than *C. quadrangulare* both in the greenhouse experiment and field study.

Tutkimuksen tarkoituksena oli tutkia suolankestävien puulajien *Eucalyptus camaldulensis* Dehnh. ja *Combretum quadrangulare* Kurz ekofysiologisia ja morfologisia ominaisuuksia. Kasvihuonekokeessa eri NaCl-pitoisuuksilla (0, 0,5, 1,0, 1,5 ja 2,0 %) saatuja tuloksia verrattiin kenttäkokeisiin suolattomilla ja suolaisilla mailla. Tutkimukseen liittyi optimaalisen kaasujenvaihdon määrittäminen ja fotosynteesimallien kehittäminen sekä niiden arviointi kuivuusstressin vaikuttaessa ja ilman sen vaikutusta.

Suolaisuuden lisääntyessä verson pituus, läpimitan kasvu, verson nivelvälin kasvu, juurten pituus/biomassa, lehtien leveys, pituus, pinta-ala, lukumäärä ja biomassa sekä verso-/juurisuhde ja lehti/juurisuhde pienenivät. Lehdet paksunivat suolaisuuden lisääntyessä. Puiden kasvu kohdentui enemmän juuriin kuin lehvästöön. Laboratorio-olosuhteissa tehdyt mittaukset osoittivat fotosynteesin, ilmarakojen konduktanssin ja vesipotentiaalin laskevan ja hiilidioksidin kompensaatiopisteen nousevan suolaisuuden lisääntyessä. Haihdunta, pimeähengitys ja valohengitys kasvoivat alhaisissa olosuhteissa, mutta vähenivät korkeissa suolapitoisuuksissa. Suolaisilla ja suolattomilla mailla kasvaneiden puiden ilmarakojen konduktanssin ja aukiolon välillä ei havaittu tilastollisesti merkitseviä eroja. Mallin antama ennuste tuki kenttämittauksen tuloksia. Kenttäkokeessa puiden sopeutuminen suolaisuuteen heijastui niiden rakenteen mutkautumisena. Kasvihuonekokeessa taimissa havaittiin toiminnallisia ja rakenteellisia muutoksia.

Ekofysiologisilta ja morfologisilta ominaisuuksiltaan *E. camaldulensis* osoitti *C. quadrangularea* parempaa suolansietokykyä sekä kasvihuone- että kenttäoloissa.

Keywords: salinity, photosynthesis, carbon dioxide compensation point, respiration, photorespiration, transpiration, water-use efficiency, water deficit, leaf resistance, stomatal resistance, stomatal movement, allocation, biomass, *Combretum quadrangulare, Eucalyptus camaldulensis.*
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List of main symbols

A	leaf area (m^2)
a	the diffusion constant of water vapour and CO_2 in the air (1.6)
Ca	ambient CO_2 concentration (ppm)
CE	carboxylation efficiency
Ci	intercellular CO_2 concentration (ppm)
Com	*Combretum quadrangulare*
cot γ	slope of total resistance to CO_2 diffusion
cot δ	slope of leaf resistance to CO_2 diffusion
cot ξ	slope of mesophyll resistance
D	water vapour diffusion coefficient
D'	CO_2 diffusion coefficient
Es	transpiration rate measured by Hartmann-Braun IRGA (mmol $m^{-2}s^{-1}$)
Eu	*Eucalyptus camaldulensis*
g	measured stomatal conductance (cm s^{-1})
g_0	predicted stomatal conductance of open stomata (cm s^{-1})
h	mean thickness of intercellular space (μm)
I	irradiance or photon flux density (μmol $m^{-2}s^{-1}$ equals $\mu Em^{-2}s^{-1}$)
NP	net photosynthetic rate (μmol $m^{-2}s^{-1}$)
P	total (gross) photosynthetic rate (μmol $m^{-2}s^{-1}$)
P_1	daily photosynthesis (g CO_2/day)
P_0	daily photosynthesis (g CO_2/g leaf dry weight/day)
Pr	extrapolated photorespiration rate (μmol $m^{-2}s^{-1}$)
qv	apparent (or net) photosynthetic rate (μmol $m^{-2}s^{-1}$)
R	photorespiration in the field (μmol $m^{-2}s^{-1}$)
Rl	correlated photorespiration (μmol $m^{-2}s^{-1}$)
Σr'	total resistance to CO_2 diffusion (s cm^{-1})
ra	boundary layer resistance to H_2O (s cm^{-1})
r'a	boundary layer resistance to CO_2 (s cm^{-1})
rg	leaf resistance to H_2O (s cm^{-1})
r'g	leaf resisrance to CO_2 (s cm^{-1})
r_{mx}	mesophyll resistance (s cm^{-1})
rs	stomatal resistance to H_2O (s cm^{-1})
r's	stomatal resistance to CO_2 (s cm^{-1})
sp.	species (one)
spp.	species (several)
t	time
tl	leaf temperature (°C)
Tr	transpiration rate measured by LI-COR IRGA and predicted by model (mmol $m^{-2}s^{-1}$)
u	stomatal opening coefficiency
u*	optimal degree of stomatal opening
wa	ambient water vapour concentration (g m^{-3})
wi	intercellular water vapour concentration (g m^{-3})
WUE	water-use efficiency (μmol CO_2/mmol H_2O)
X	amount of leaf dry weight (g)
α	coefficient relating of P, I and Ci ($cm^3\mu mol^{-1}$)
α_L	allocation of growth to leaf coefficient
λ	transpiration cost (g CO_2/g H_2O)
Γ	CO_2 compensation point (ppm)

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Helsinki, October 1990

Jesada Luangjame

1. Introduction

11. Background

Saline soils cover a substantial portion of the earth's surface; the global estimate is about 950 million hectares (Szabolcs 1979, Shannon 1984). In the northeastern part of Thailand, about 6 million ha or 12 % of the total area is considered saline (Keerati-Kasikorn 1984). The increase in the extent of saline soils has never been officially estimated. Undoubtedly, in the past 5—10 years salinisation has been widespread and has covered successively more land, presumably due to the rise in the ground water level as a result of deforestation and the construction of a large number of reservoirs without controlling the direction of flowing water. At least four large reservoir irrigation schemes in the Northeast Thailand have recently reported evidence of salinity as a consequence of continuous dry-season cropping, especially in rice paddies. It has been reported that the paddy yield in the salt-affected area of Tung Kula Rong-Hai (Roi-et, Mahasarakam, Surin, Srisaket and Yasothorn provinces) was only 65 % of the yield from non-saline land (Limpinuntana 1984).

Reclamation, drainage and water control can minimize the extent and spread of saline soils; however,the engineering and management costs involved are high. The increasing costs of water and energy accentuate the need for new strategies (Williamson 1984). One such new strategy is the selection and breeding of plants with increased salt tolerance (Shannon 1984). The selection and breeding of plants is a formidable challenge for researchers.

The adaptation of plants to saline environments is a complex process and plants in such environments are exposed to a variety of stresses (Coughlan and Wyn Jones 1980). Plants may be categorized as halophytes or glycophytes, as far as their responses to salinity are concerned. Halophytes are salt tolerant plants native to saline habitats. The glycophytes, or non-halophytes, to which most crop species belong, vary in response to salinity from being very salt-sensitive through moderately salt-resistant to being highly salt tolerant. The majority of plants are relatively salt-sensitive. Glycophytes adopt different strategies to deal with saline conditions. Many glycophytes respond to relatively low salt concentrations (below about 6,000 mg l^{-1}, or 100 mM) by exhibiting "salt exclusion". This is mainly carried out by lowering the rates of net transport of sodium or chloride, or both, from the root to the shoot (Läuchli and Epstein 1984, 1985). Most of these so-called salt-excluding glycophytes cannot adjust osmotically to the low external water potential by increasing the synthesis of organic solutes, as halophytes can, and therefore suffer from a decrease in turgor. Hence salinity may induce an osmotic stress in this kind of glycophyte. Salt-resistant glycophytes, on the other hand, adjust osmotically to saline conditions by increasing the rates of ion uptake and transport and, in particular, by increasing the synthesis of organic solutes for osmotic regulation. The additional expenditure of energy and carbon allocation required, which would otherwise support growth processes, may contribute substantially to the observed growth reduction.

Salt tolerance may be defined generally as the ability of a plant to sustain growth in an environment rich in NaCl or combinations of mixed salts (Larcher 1983, Shannon 1984). Levitt (1972) has associated salt tolerance with an absence of negative effects on growth in plants that accumulate salt within their tissues. He distinguishes between salt tolerance and salt avoidance mechanisms and uses the term "salt resistance" to refer to a combination of tolerance and avoidance strategies. In practice, the terms "salt tolerance" and "salt resistance" have been used interchangeably to define true cytoplasmic resistance to salinity or, in conjunction with salt avoidance, to describe all mechanisms that may give a plant a selective advantage during saline stress.

Salt tolerance can be measured by a number of criteria. Survival at high salt concentrations has been used as a criterion for the selection of tree species in plantation forestry (Luangjame *et al.* 1984, Luangjame and Bunbhakdee 1987). However, the mechanisms that trees employ to ensure survival may not be the same ones used to maintain high growth rates at moderate salinities. For example, many halophytes withstand high salinities by such strategies as temporary dormancy, increased succulence, or shortening the growing season (Levitt 1972). Dormancy is not compatible with high yields, and increasing succulence contributes nothing to dry weight yield. Moreover, dormancy may be important in contributing to survival during temporary periods of high osmotic stress due to low soil water potentials.

Another method of measuring salt tolerance is to determine the growth or yield response to saline conditions. This can be expressed as the relative reduction in yield as a function of increasing soil salinity (as in the present study). Relative salt tolerance is the fraction of growth (yield) under saline conditions compared to the growth under non-saline conditions. If the additional growth and water use of tolerant plants concentrate salts through exclusion processes, the salinity in the root zone soil may be higher than in the surrounding soil (Shannon 1984).

It may be possible to develop a screening technique based on physiological or morphological characteristics for identifying salt tolerant plants. Biochemical indicators, such as Na^+/K^+ ratios, however, have not yet shown any promise as selection criteria. This is probably because salt tolerance is related to many plant characteristics, both morphological and physiological.

Species selection for improving saline soils in Northeast Thailand have been carried out by Luangjame *et al.*(1984). These species trials included a comparison of indigenous and exotic tree species. Most indigenous species were dipterocarps which grow almost everywhere in northeastern Thailand, *e.g. Dipterocarpus alatus*, Roxb. *D. intricatus* Dyer, *D. obtusifolius* Teysm., *D. tuberculatus* Roxb., and *Anisoptera glaba* Kurz. Exotic species from Australia which have been found to grow in saline and dry areas before are *Eucalyptus brassiana* S.T. Blakely, *E. camaldulensis* Dehnh., *E. microtheca* Maiden, *E. resinifera* Smith and *E. sideroxylon* Cunn. ex Woolls. This screening test showed that among the exotic species which were adapted to saline soils better than the indigenous species were *E. camaldulensis* and *E. brassiana.*

A further step is the use of laboratory experiments based on solution culture. This technique is suitable for rapid screening of a large number of species for salt tolerance (Luangjame and Bunbhakdee 1987). Based on these earlier studies, the exotic species *Eucalyptus camaldulensis* and the indigenous species *Combretum quadrangulare* were suggested as materials for continued investigation. *Combretum quadrangulare* Kurz (Combretaceae) grows naturally widespread in Thailand, mostly in the central plains. However, *C. quadrangulare* is found on saline soils, both at the sea coast and inland in the northeastern Thailand. The species is an excellent source of fuelwood. *Eucalyptus camaldulensis* Dehnh. (Myrtaceae) is one of the best known species which is most widely planted outside its natural range. It is known to be a relatively salt tolerant tree, and has been considered suitable for the reclamation of saline areas. *E. camaldulensis* which can tolerance up to half the strength of sea-water (1.8 % w/v NaCl) (Hart 1972, El-Lakany 1986).

12. Plant physiological and nutrient-salinity interactions

Terrestrial plants that grow on saline soils are confronted with complex problems. The concentration of salts in the soil solution fluctuates because of changes in water supply, drainage, and evaporation and transpiration. Salinity is caused not only by NaCl but also by Na_2CO_3, $NaHCO_3$ and Na_2SO_4. The proportions of these salts to each other as well as to other nutrients, such as K^+, Ca^{2+} and Mg^{2+}, are important and may differ greatly at different sites (Kramer 1984).

Salinity is the occurrence of a high concentration of soluble salts in the soil or solution in which plants grow. In most instances the origin of the ions can be traced to an oceanic influence, be it past or present. The most important ions, as far as saline soils are concerned, are Na^+ and Cl^-, the dominant ions in sea waters. Although sea waters vary in their salt concentration, the relative proportions of dissolved salts differ very little. An ocean with an average chlorinity of 35 kg m^{-3} will contain sodium and chloride at 480 and 560 mol m^{-3}, respectively, and have an osmotic potential of —2.4 MPa. Many halophytes survive in seawater salt concentrations and higher; the salt concentration on a drying salt march may reach 1000 mol m^{-3} even in temperate regions (Flowers and Yeo 1986).

The most important ions as far as the osmotic adjustment of halophytes is concerned are sodium, potassium and chloride. Ion concentrations in dicotyledonous species can often reach 6—8 mmol Na^+ and Cl^- g^{-1} dry weight, which represents 30—50 % of the dry weight (Flowers and Yeo 1986). Sodium and Cl uptake has been shown to be directly related to the NaCl concentration of the substrate (Schröppel-Meier and Kaiser 1988a). In the halophyte *Sarcocornia natalensis* Bunge ex Ung.-Sternb., shoot and plant Na/K ratios and concentrations of total Na, K, Ca, Mg and Cl increased with increasing NaCl salinity (Naidoo and Rughunanan 1990). Na and Cl exclusion, particularly by cells in the growing regions of the shoot, has been implicated as the primary mechanism of salt tolerance in glycophytes (Binzel *et al.* 1988). Rains (1972) reported that Cl is actively transported into the cell and Na actively moved out of the cell. Aswathappa and Bachelard (1986) studied salt tolerance in *Casuarina* species and showed that the highly tolerant species (*C. equisetifolia* L. and *C. glauca* Sieber ex Sprengel) accumulated little Na and Cl in their shoots and that the concentrations of Na and Cl decreased from old to young growing needles. The concentrations of Na and Cl were much higher in shoots of the moderately tolerant species (*C. cunninghamiana* Miq.). The Na/K ratio was lower in the needles and stem of the highly tolerant species but Ca and Mg concentrations were higher than in the moderately tolerant species. In barley, even in the most tolerant varieties, growth was retarded at low NaCl concentrations, and a 50 % growth reduction occurred at about 100 mM NaCl in tolerant varieties (Jeschke 1984). The Na^+ content in rice (*Oryza sativa* L.) was higher in the older leaves than in the younger leaves (Yeo and Flowers 1982).

Calcium is an important factor in the resistance of plants to salinity (Greenway and Munns 1980). The protective effect of Ca in salinised plants is due to its role in maintaining membrane integrity. One of the primary effects of salinity is the displacement of Ca from the cell surface by Na which results in the disruption of membrane integrity. Salinity has been found to increase the Na influx, decrease the Ca influx and increase the Ca efflux from cells of corn (*Zea mays* L. cv. Pioneer 3377) root (Lynch and Läuchli 1988). Uptake and the translocation of nutrients such as K and Ca are greatly reduced by salinity stress and salt tolerance is reduced under conditions of low nutrient availability. The reaction of plant cells to salt stress is often to increase vesiculation of the plasma membrane and amounts of rough endoplasmic reticulum. These observations point to the importance of plant cell membranes in the regulation of internal ion fluxes under conditions of salt stress in order to maintain a favourable ionic composition in cells and tissues.

In salinity stress, Levitt (1972) distinguishes between primary specific ion stresses and secondary osmotic (water) and nutritional deficiencies. The high concentration of ions accumulating in the cell as a result of osmotic adjustment may exert an allosteric effect on the enzyme proteins and may affect the structure of membranes, thus changing the natural equilibria of permeability and rates of reactions. The effects of the high ionic concentration in the cell, are probably responsible for most of the observed changes in the biochemical pathways and enzyme activity induced by salinity (Kylin and Quatrano 1975). Wyn Jones (1980) has discussed the close interdependence of these stresses at the cellular level. The processes and metabolism by which salt stress becomes limiting for plant growth are not known. The stress affects many species osmotically, inducing a water deficiency (Bernstein 1975, Jennings 1976, Greenway and Munns 1980, Gupta and Berkowitz 1988, Nieman *et al.* 1988), but in some species ionic effects are also indicated. For the salt-excluder type of salt tolerance, absorption and lateral transport of nutrients have limited the degree of adaptation. But even for salt includers have the great importance because these plants also accumulate large amounts of K^+ against the electrochemical gradient (Kramer 1984). A great quantity of Na^+ is found in the vacuoles of leaf (Sacher and Staples 1984) and root cells (Munns and Termaat 1986). Na and K transport was expected to be mutually competitive (Rains 1972). There is a preference for K during influx selectivity (Jeschke 1984). In barley it was found that net K retranslocation was common in both control and salt treatment, so that no specific Na dependency for this K retranslocation occurred (Bogemans *et al.* 1990).

Biochemical reactions in all metabolic processes are activated by enzymes and high Na$^+$/K$^+$ ratios are known to inhibit many enzyme activities (cf. Flowers *et al.* 1977, van der Moezel *et al.* 1988). However, Wingstrand and Lindberg (1982) reported finding ATPase activity in sugar beet (*Beta vulgaris* L. cv. Monohill), which is a characteristic glycophyte, grown in saline conditions. Systems for active transport of sodium, biochemically traceable as Na$^+$ plus K$^+$ activated ATPases, play a role in salt tolerance (Kylin and Quatrano 1975, Kuiper 1984). In some cases ATPases require Mg-ATP as a substrate but in some cases Mg^{2+} inhibited stimulation of the ATPase by Na$^+$ plus K$^+$ as well as Ca-ATP can serve as a substrate for Na$^+$ plus K$^+$ stimulated hydrolytic activity. In the presence of Mg-ATP, ATPase activity was stimulated by Na$^+$ and by K$^+$ alone, but their combination reduced enzyme activity considerably in the glycophytes, English ryegrass (*Lolium* sp.) and soybean (*Glycine* sp.). In the presence of Ca-ATP, ATPase activity in *Plantago* sp., a halophytic species, was stimulated by the combined action of Na$^+$ plus K$^+$ (Kuiper 1984).

Na$^+$ stimulation of ATPase is suppressed when plants are exposed to salinity, indicating that long-term exposure to NaCl induces a conformational change of the Na$^+$ translocator of the ATPase complex. Also, the more general Ca^{2+}, Mg^{2+} stimulated ATPase activity is depressed in halophytic *Plantago* spp., when the plants are grown under extreme saline stress (Kuiper 1984). Therefore, the ATPases respond in a more complicated way among the plants and the ions. Kylin and Quatrano (1975) used a combined ecological and biochemical approach to trace a Cl$^-$ activated ATPases in the salt glands of *Limonium* spp., and they also found that the Rb$^+$ stimulated ATPase in roots of corn (*Zea mays* L.), wheat (*Triticum* sp.) and barley (*Hordeum vulgare* L.) is quantitatively sufficient to account for the transport of rubidium. Spinach (*Spinacia oleracea* var "Yates") grown in the absence of Mg^{2+} for about 10 days showed no visible deficiency symptoms or other anomalies (Schröppel-Meier and Kaiser 1988b). While Mg^{2+}-ATPase maintains an adequate supply of adenine nucleotide, a decrease in the content of or a change in the ratios of the adenine nucleotides reduces chloroplast photosynthesis (Fu and Gibbs 1988). Mg^{2+}-ATPase activity can be induced in the light in maize (*Zea mays* L. Pioneer hybrid No. 3747) mesophyll thylakoids (Cohen 1989).

High NaCl concentrations induces cell membrane depolarization, a decrease in the membrane resistance and an increase in the rate of Na$^+$ influx. These responses are prevented by including a combination of Ca^{2+} in the external medium and ATP in the cytoplasm. The results from Katsuhara and Tazawa (1990) indicated that both extracellular Ca^{2+} and intracellular ATP are necessary for completely preventing the Na$^+$ influx. While ATP cannot prevent the Na$^+$ influx without Ca^{2+}, neither can Ca^{2+} fully prevent the Na$^+$ influx in ATP-depleted cells. The large K$^+$ efflux occurring with the Na$^+$ influx is prevented only when both Ca^{2+} and ATP are present.

13. Leaf anatomy

131. Salinity effects on leaf anatomy

The first effect of salinity on plants is the induction of leaf succulence. The phenomenon does not occur if the plants were grown in non-salinised substrates, or in substrate which is specific for NaCl. The succulence is due to the development of larger cells in the spongy mesophyll and the presence of a multilayer palisade tissue which is absent in leaves of plants grown in non-saline substrate. Under NaCl and Na$_2$SO$_4$ salinities, the thickness of the spongy mesophyll and the palisade layers increased with increasing salinity, but Na$_2$SO$_4$ had more effect on the spongy mesophyll layer while NaCl had more effect on the palisade layer (Poljakoff-Mayber 1975).

132. Stomatal characteristics

Stomatal size, in general, is often correlated with density (Wilkinson 1979). The diploid plants usually have smaller stomata than their polyploid relatives. Related species often have stomata of similar size. Shade, a humid atmosphere, and moist soil conditions are all known to be coincidental with smaller stomata, while full sunlight and drier conditions seem to produce larger stomata. Stomatal dimensions decreased slightly at higher altitudes. In the literature, stomatal size is often designated such as 'small' or 'large', so that an actual comparison cannot be made. However, from experience, it appears that the term 'small' is generally applied to stomata the guard cells of which are less than 15 μm long and 'large' to stomata with guard cells of more than 38 μm long (Wilkinson 1979).

Guard cells offer favourable material to study the control of osmosis and ionic fluxes at the membrane level, and the control of cell surface activity during the deposition of extracellular macromolecules (MacRobbie 1981, Meidner 1981, Paleviz 1981, Zeiger 1981). The importance of ion movements in producing the turgor changes in guard cells responsible for the opening and closing of the stomatal pores in now clearly recognized, and the accumulation of potassium salts in guard cells in the opening process in implicated.

Measurements of stomatal aperture and their changes, can be done either by microscopic measurements or by estimates based on conductance methods (Meidner 1981). Only a microscopic measurements alone give precise information about the dimensions of stomatal pores and guard cells enclosing them.

133. Stomatal index

The stomatal density is a function of cell size (Schoch *et al.* 1980). Wilkinson (1979) defined the 'stomatal index' as percentage stomata out of the total number of epidermal cells plus stomata and is independent of cell size. By means of this index it can be shown that the number of stomata formed in the epidermis is no greater for sun-leaves than for shade-leaves. Stomatal frequency is greater on plants grown on dry soils as compared with those grown on wet soil, and a small leaves as compared with large leaves. Variations in the stomatal index that do occur are due to internal factors, mainly humidity and nutritional conditions (Wilkinson 1979) and the external factors. Schoch *et al.* (1980) showed that the number of stomata per unit area of a leaf increases as the light intensity received by the plant increases. The stomatal index does not vary significantly in different positions and parts of the same leaflet. Wilkinson (1979) further cited that stomata index is independent of leaf size and plant habitat, that it is the same for different varieties within a species, and that the stomatal index value is more uniform upon the lower than the upper surface, except in isobilateral leaves. By comparing winter and summer leaves a number of herbaceous species, demonstrated that stomata are more abundant in stem leaves than rosettes (Kumar and Rao 1985).

14. Ecophysiological effects of salinity on plants

141. Water balance

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 quantative determinations of water uptake and transpiration on 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, 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).

The relationship between plant water balance and salinity cannot be resolved by a study of osmotic adjustment alone, as was implicit in the original "physiological drought" concept. Reference must be made to the effect of salinity on each of the many factors governing the entry, passage and evaporation of water into, through and from the plant. Furthermore, no single parameter, such as osmotic potential or turgor potential, should be used alone for evaluating plant water status.

142. Water potential

Fluctuations in the water content necessarily affect the concentration of the cell sap and the water potential of the cells. The osmotic pressure, as a component of the water potential of the cell, provides an indication of changes in the water balance — it rises as long as the water balance is negative. Osmotic adjustment enables the plant to maintain turgor and tissue water content at lower tissue water potentials. In Hsiao's (1985) studies, water stress induced leaf-turgor pressure of cotton (*Gossypium* sp.) was found to be lower than salinity stress of similar levels. When the cotton plants were shifted from soil water stress to equivalent soil-salinity stress, leaf-turgor pressure recovered to levels expected of unstressed plants. Osmo-regulation in response to salinity may utilize ions from the soil, particularly those ions in excess, whereas under in the absence of salinity, the necessary solutes have to be supplied mostly from within the plant.

A water potential gradient from soil solution to plant maintained under saline conditions. Furthermore, there is an increase in the leaf resistance to water vapour loss which will tend to counteract the effect of any increase in resistance to water flow occuring in the roots. The results is both a high turgor and a high osmotic concentration in plants grown under saline conditions. This increase of osmotic concentration may in itself be detrimental and the overall rates of water turnover, uptake and transpiration are generally reduced.

143. Photosynthesis

Photosynthesis is closely related to the movement of water in plants. To facilitate the absorption of carbon dioxide for use in photosynthesis a leaf must have wet cell surfaces. As a consequence, transpiration accounts for nearly all of the water taken up by the roots. In effect, water is traded through the stomata for carbon dioxide. Although stomatal CO_2 conductance was believed to be a major factor limiting photosynthetic capacity (Farquhar and Sharkey 1982, Pearcy *et al.* 1987), leaf photosynthetic capacity is determined primarily by the amounts and catalytic activities of photosynthetic enzymes. There is a strong correlation between stomatal conductance and photosynthetic rate (Wong *et al.* 1979, Pearcy *et al.* 1987). According to a theoretical model for stomatal control, the stomata may minimize daily transpiration for a given daily carbon gain. In other words, if a certain amount of water can be acquired for transpiration, the stomata should act to maximize photosynthesis within this constraint (Cowan and Farquhar 1977, Pearcy *et al.* 1987). Because terrestrial plants must permit water loss (transpiration) in order to obtain CO_2 from atmosphere (Osmond *et al.* 1987).

Both theoretical and empirical evidence suggest that rising CO_2 levels in the atmosphere can increase plant photosynthetic rates differentially and alter other biochemical cycles in ways which may influence the productivity of trees and plants, as well as their competitive distribution in natural ecosystem (Shands and Wells 1987, Sanderburgh *et al.* 1987). Higher CO_2 concentrations appear to improve water-use efficiency by decreasing stomatal aperture (Sandenburgh *et al.* 1987) and transpiration (Kramer and Sionit 1987), but by how much, however, is far from definitive, especially for a particular species grown under actual field conditions.

The effect of salinity on photosynthesis is much complicated by the variety of methods and bases of calculation used by different researchers. The experimental conditions during measurement of gas exchanges may be very varied. The periods of exposure to salt, and age of leaf *etc.*, also varies greatly in different reports and frequently makes comparison of results difficult. A common effect of salinity is to decrease photosynthesis per unit leaf area. In general, photosynthesis is reduced in proportion to salt concentration. The percentage reduction varies greatly between different plant species and varieties. An exception to this general rule, however, is seen in halophytes, where low concentrations of salt do not always reduce, and may even enhance, photosynthesis (Gale 1975).

When salinity was increased by increments to moderate levels (150 mM NaCl), sugar beet (*Beta vulgaris* L.) exhibited no decline in rates of photosynthesis (Terry and Waldron 1985). This presumably because the plants modified their osmosis before serious water stress developed. Salinity had little effect on the photosynthetic rate until relatively high salinities were reached, at least 200 to 350 mM NaCl. Valencia orange (*Citrus sinensis* (L.) Osbeck) leaves, in contrast, reduced CO_2 assimilation rates in response to NaCl salinisation, even though the leaves maintaided turgor (Lloyd *et al.* 1987). Rawson (1986) suggested that comparisons of gas exchange amongst single leaves grown at varying salinity levels should only be made for leaves of equivalent age; an error of 1 week in leaf age could in an error in photosynthesis of 20 %. Descriptions of measured leaves as 'young' and fully expanded are often not precise enough.

Rates of photosynthesis are usually lower in NaCl treated plants (Longstreth and Nobel 1979) and may decrease with increasing exposure time to a given level of NaCl (Walker *et al.* 1982, Yeo *et al.* 1985). As salt concentrations in leaves typically increase with increasing exposure time, the reduction in photosynthesis may be interpreted in terms of salt toxicity alone (Yeo *et al.*) or interactions with the ageing pattern of the leaves and the typical decline in photosynthetic rate with leaf age (Rawson 1986). Additionally, there may be a negative feedback on photosynthesis by reduced sink activity (Munns and Termaat 1986).

144. Transpiration

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 stomata close, transpiration decreases and resistance to water flow increases.

As a long-term responses 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.

145. Stomatal conductance

The importance of stomatal conductance is related to the diffusion of gases during photosynthesis and transpiration (Squire and Black 1981). Many studies have concentrated on the stomatal response to dry conditions, stomatal closure regulates transpiration temporarily in well water canopies than the water vapour deficit in the ambient air increases. Canopies may respond to drought by reducing leaf area, and large decreases in stomatal conductance occur simultaneously.

The assumption that stomatal conductances are smaller than aerodynamic conductances is usually valid near the top of a canopy where turbulent mixing is most intense, and remains valid in the layers of foliage which contribute most of the water vapour. Leaves near the bottom of complete canopies contribute relatively little to transpiration because stomatal conductances are usually small. There are also differences in stomatal conductance between sun and shade leaves and between upper and lower leaf surfaces because of differences in stomatal frequency. Stomatal conductance varies with leaf age (Squire and Black 1981). Environmental factors that are known to have a major influence on stomatal conductance are irradiance, leaf water status, ambient humidity, leaf temperature and carbon dioxide concentration (Hall *et al.* 1976). These factors have direct and interactive effects.

Stomatal responses may be followed readily using a diffusion porometer or infrared gas analyser (IRGA). The stomatal resistances obtained may be used to estimate rates of transpiration from leaves provided boundary layer resistance, leaf temperature and atmospheric saturation deficit are also measured. Stomatal conductance, or reciprocal resistance, can be used as well. Canopy conductance can be estimated from canopy transpiration and leaf area. Estimates of canopy conductance derived from lysimeter studies or from synthesizing profiles of temperature, humidity and wind speed above a canopy can provide a good estimate of the influence of the environment on stomatal conductance (Squire and Black 1981). Canopy conductance can also be estimated from measurements of leaf conductance with a porometer and leaf area index. Canopy conductance is therefore the sum of the leaf conductance in each layer weighted by the corresponding leaf area index.

In amphistomatous species, such as *Eucalyptus* spp., stomatal resistance is usually higher on the upper, adaxial surface of leaf (cf. Kaarakka *et al.* 1985). Beadle *et al.* (1981) found that stomatal conductance of Sitka spruce (*Picea sitchensis* (Bong.) Carr. Queen Charlotte Islands provenance), varied little with height above the whorl where branches of neighbouring trees were in contact. The stomatal conductance of 2 and 3-year-old needles was 0.48 and 0.31 times that of 1-year-old needles, respectively.

In numerous studies, decreases in ambient humidity have resulted in increases in leaf resistance (e.g. Schulze *et al.* 1972, Camacho-B *et al.* 1974, Hall *et al.* 1976). With increasing vapour pressure differences between leaf and air, Schulze *et al.* (1972) and Hall *et al.* (1976) observed decreases in leaf conductance and transpiration, and increases in leaf relative water content. The overall resistance to loss of water vapour from the leaves, increases under conditions of salinity (Gale 1975). This can be related to an increase in stomatal resistance, for which there is much evidence, and to an increase in mesophyll resistance.

146. Stomatal opening

The guard cells are capable of considerable vacuolar salt accumulation during stomatal opening (MacRobbie 1981). Most plant cells regulate their salt accumulation, often in response to a pressure signal as turgor increases, and shut down net salt uptake at much lower levels of accumulation than in guard cells of open stomata. But although guard cells seem capable of accumulation to much higher levels than other cells, there is little indication that the processes involved are special, or in any way different from those of other cells (MacRobbie 1981).

In general, stomata close in response to water deficits and open in response to deficits of CO_2 (Coombs *et al.* 1983). The degree of stomatal opening, and thus stomatal diffusion resistance, can be adjusted in response to changes in the environment and within the plant (Larcher 1983). The stomata can only open only when the turgor potential is high (Coombs *et al.* 1983). But when plants are exposed to salinity, even with complete osmotic adjustment and high levels of turgor, leaf stomata are often partly closed (Gale *et al.* 1967, Meiri and Poljakoff-Mayber 1970, Gale and Zeroni 1984). A result of this partial closure is to lower the stomatal diffusion conductance for CO_2 gas and thus reduce photosynthesis.

Studies of stomatal response to temperature have yielded contradictory results. Stomatal opening with increasing temperature has been observed (e.g. Hofstra and Hesketh 1969, Drake *et al.* 1970, Drake and Salisbury 1972, Crookston *et al.* 1974, Hall *et al.* 1976), an optimum response curve to temperature with maximal values at intermediate temperatures observed by others (Hofstra and Hesketh 1969, Hall *et al.* 1976), and decreases in conductance with increasing temperature have also been reported (Hall *et al.* 1976).

There is abundant evidence that, in some conditions, stomata remain open until a threshold level of leaf water deficit is reached after which stomata close dramatically (Hsiao 1973, Hall *et al.* 1976). The value of this threshold level of leaf water deficit may be associated with a bulk leaf pressure potential of zero (Kanemasu and Tanner 1969, Hall *et al.* 1976). This indicates that leaves may be subjected to moderate water deficits before stomata respond to changes in bulk leaf water status. In field conditions, leaf water potentials may drop to very low levels without reaching the threshold value for stomatal closure (Jordan and Ritchie 1971, Schulze *et al.* 1975, Hall *et al.* 1976).

Optimal stomatal functioning reflects a compromise between the conflicting requirements of controlling water use and the development of plant water deficits, while maintaining adequate levels of photosynthesis and evaporative cooling. Optimal stomatal functioning will depend upon environmental conditions, physiological, morphological, anatomical and phenological properties, and the ecological strategies of plants. During the evolution of plant ecotypes, complex systems governing stomatal response to both the external and the internal leaf environment have probably developed, that can achieve optimal functioning with different plant and environmental conditions. Ecophysiological aspects of stomatal response to environment can be elucidated by combination of field and controlled environment studies and mathematical modeling (Hall *et al.* 1976).

Stomatal activity depends on both ion influx and efflux. Schwartz *et al.* (1988) found that a certain concentration of Ca^{2+} is an absolute requirement for salt efflux and stomatal closure. In general, stomatal apertures are modulated continuously in response to changes in the leaf environment and prevailing photosynthetic rates. Stomatal aperture depends on guard cell turgor, which is a function of solute content, particularly K^+ salts (influx). Braconnier and d' Auzac (1990) found that K^+ and Cl^- deficiency reduces stomatal opening and the osmoregulation capacity of oil palm and coconut. The energy required for such ion-uptake can be derived from photosynthesis, respiration or a blue light sensitive system. The quality of light has a marked influence on the stomatal function so that blue light causes much wider opening of stomata than red light (Raghavendra 1990). Photon flux density increases with stomatal opening and biochemical (RuBisco) activation (Fu and Gibbs 1988, Kirschbaum and Pearcy 1988).

Some hormones have also been found to affect stomatal movement. Stomatal opening in darkness was stimulated by increasing indole-3-acetic acid (IAA) concentrations but stomatal aperture did not reach saturation, *i.e.* IAA only affected the primary, initial opening (Gale 1975, Schwartz *et al.* 1988). Kinetin promoted but abscisic acid (ABA) was found to have a synergistic effect on the inhibition of stomatal opening.

One definite way in which salinity affects stomata is by reducing stomatal aperture and an increase in resistance (Gale 1975). As the partial closure of stomata are often found in plants exposed to salinity, even when there is a full adjustment of the internal osmotic concentration, and turgor is high.

147. Respiration

Respiration serves many important functions, including the supply of energy and the structural building blocks required for synthesis of new biomass. Additional respiration also is required for maintenance of membranes, proteins and ion gradients (Pearcy *et al.* 1987).

High concentrations of NaCl have often, but not always, increased respiration of roots and other tissues (Gale 1975). For example, the respiration of sorghum (*Sorghum bicolor* (L.) Moench) was about 6 % higher than normal when grown in the presence of Cl^- salts, mainly as NaCl (McCree 1986, Munns and Termaat 1986). The increased respiration of roots in the presence of high concentrations of mineral salts is often referred to as "salt respiration". There appears to be a large differences in respiration between species. For example, dark respiration increased in both pea (*Pisum sativum* L.) and corn (*Zea mays* L.) but decreased in tomatoes (*Lycopersicon* spp.) grown in the same environments and salt concentrations (Gale 1975). In lucerne (or alfalfa), (*Medicago* *sativa* L.) grown in culture solutions to which NaCl had been added, dark respiration of tissue samples increased by 40 % at NaCl concentrations of $5 g l^{-1}$ but at $12 g NaCl l^{-1}$ dark respiration was decreased by 10 %. Gale (1975) further mentioned that an increase in dark respiration in response to salt was greater in a salt resistant than in a salt sensitive species. And in both resistant and sensitive species, the efficiency of respiration was reduced under saline conditions.

Under saline conditions plants require more energy for pumping ions against electro-chemical gradients and for maintenance; this energy appears to be supplied by increase of respiration. The increase of respiration and use of energy derived directly from photosynthesis is correlated to a decrease in CO_2 fixation and in overall plant growth. At very high levels of salinity, respiration is reduced, this effect being more pronounced in salt sensitive species. As a result there may be a shortage of energy for maintenance at the very time when demand is greatest.

148. Photorespiration and dark respiration

Photorespiration connected with photosynthesis takes place in the chloroplast-containing plant cells. Like respiration, photorespiration takes up O_2 and releases CO_2 in the light, but contrary to respiration, ceases in the dark.

Photorespiratory activity is a major factor in reducing the productivity of many higher plants. In general, the magnitude of photorespiration is increased as the partial pressure of oxygen in the atmosphere is increased (Gates 1980, Coombs *et al.* 1983), as the concentration of carbon dioxide is decreased, and as the temperature or light intensity rises. However, precise measurements of the magnitude of either photorespiration or the extent of losses in productivity due to this phenomenon are more difficult to estimate. The problem arises from the fact that photorespiration is the exact opposite of photosynthesis and at the same time plant tissue also possesses the capacity for dark respiration. As a results of these complexities, a wide range of techniques have been used in order to estimate the magnitude of photorespiration.

More precise methods of analysis used in this dissertation were derived from measurements of the CO_2 compensation point (Γ) in laboratory and modification to be used a model in the field.

According to Gates (1980), dark respiration is independent of atmospheric concentrations of both CO_2 and O_2 concentrations but increases monotonically with increasing temperature. Gale (1975) reported that plants having the C_3-caboxylation pathway of CO_2 fixation also exhibit photorespiration which releases CO_2. Photorespiration may also be present in plants having the C_4-carboxylation pathway when it is more to detect.

15. Salinity effects on morphology

151. Morphological performances

Salinity is known to affect many aspects of plant morphology, *e.g.* leaf area, sizes, thickness, stem structure, diameter and root structure, *etc.* One of the most common effects of salinity is to stunt growth, often without any other sign of damage such as chlorosis or leaf burn. (Gale 1975, Poljakoff-Mayber 1975). These changes are often considered to be acclimatization which increase the changes of the plant to endure the stress imposed by salinity, alternatively, they may be considered to be signs of damage and disruption of the normal equilibrium of life processes. Increases in leaf thickness can be induced by exposure of roots to high concentrations of NaCl (Longstreth and Nobel 1979). Changes in leaf and stem thickness have long been used as indicators of water deficit (Bùrquez 1987).

The factors that influence the toxicity of sodium, both its initial uptake and any mitigating effects, are likely to be independent elements, incidental variation in a salt-sensitive glycophyte. It is fairly evident that an advantageous variation in one aspect (such as leaf-to-leaf distribution) may be confounded or completely masked by a poor performance in another. Poor control of sodium uptake can be lethal to the phenotype, will be rajected both on grounds of survival and its overall sodium content (Yeo and Flowers 1984).

Inhibition of leaf expansion under water or salt stress has a profound effect on field crop production, independent of any stomatal or biochemical effects (McCree 1986). The expansion of the leaf surface on an annual plant is initially exponential in an unconstrained environment. A period of water or salinity stress will first cause reduction in the rate of leaf surface addition, followed by a cessation of expansion as the stress intensifies and then resumption of growth when the stress is relieved. (Aspinall 1986). If the stress is not severe, growth resumption is rapid, suggesting a physical process, and compensatory growth may occur.

152. Salinity effects on growth

Salinity appears to affect growth either through the toxic effects of Na^+ or Cl^- accumulation or through the effects of a low soil or solution osmotic potentials. Plants can avoid or minimize toxic effects by excluding salts from the plant, excreting it from glands, or translocating it to leaves that then drop from the plant (Greenway and Munns 1980, Pitman 1984). In exclusing salts, however, the plant may lose the oppotunity of using NaCl as an osmotic solute in the leaves. Alternatively, plants may accumulate salts in the leaves to provide lower osmotic potentials but then exclude them from the cytoplasm in order to avoid ionic interactions with enzymatic reactions.

Growth and yield in crop plants are affected to varying degrees by salinity. Responses to salinity are also modified by other environmental factors (Rawson 1986). Because the growth of a plant is the sum of the growth patterns of its parts, each of which has dynamic responses to the environment and to the rest of the plant, it is often difficult to extrapolate from short-term, single-factor measurements of responses to salinity, to the performance of trees in the yield.

Gas exchange techniques can determine whether stomatal conductance or photosynthetic efficiency limits growth. This approach can also give information about the efficiency of carboxylation, by measuring the relationship between photosynthesis and internal CO_2 concentration (Pitman 1984). A growth cannot proceed for long without carbon, changes in patterns of photosynthesis and respiration should reflect the responses of growth to salinity. However, as photosynthesis, like growth, is dynamic, responding to other aspects of the environment besides salinity. Munns and Termaat (1986) have hypothesized that it is leaf water deficiency that limits the leaf growth of barley and wheat plants grown in saline soil. At first sight it would appear that leaves grow more slowly after exposure to salinity bacause of a water deficit: the response is very rapid, usually proportional to the osmotic potential of the external solution and rapidly reversible.

153. Shoot/root relations

According to Passioura (1986), the roots of a mature crop are often only 10 % of the weight of shoots. In droughted crops the proportion is typically much larger than this, and may exceed 30 %. There is mounting evidence that roots consume much more, perhaps twice as much, assimilate in producing unit dry matter as does the shoot.

The earliest response of a non-halophyte exposed to salinity is that its leaves grow more slowly. Root growth is almost always less affected than shoot growth, so the root/shoot ratio increases (Munns and Termaat 1986). At low salinity, root growth may not decrease at all while shoot growth declines, or it may even increase depending on species. Whether it is root water deficiency or a specific salt effect on th roots which triggers the reduction in shoot growth is not known.

There is no evidence for a specific salt effect on the shoot, at least within a few days of exposure, and there is indirect evidence against it. Munns *et al.* (1982) found that leaf expansion recovers rapidly after the removal of salt from the root medium. It is not salt toxicity within the shoot that is limiting growth, because the salt concentrations within the shoot do not increase rapidly (Munns and Termaat 1986). Somebody salinity causes a rapid decrease in the transpiration of essential nutrients to the shoot, and this limits cell expansion. NaCl-salinity decreases K^+ concentrations in many species.

NaCl may affect root metabolism by an osmotic effect, causing a water deficit, or by a specific ion effect, causing excessive accumulation of Na^+ or Cl^- or inadequate uptake of an essential nutrient (Munns and

Termaat 1986). The root system is growing continuously, and moreover there will be a higher root/shoot ratio than growing before the NaCl was added (Munns and Termaat 1986). The time-scale of the response varies inversely with the salinity level, and varies greatly between species.

154. Biomass production

The biomass of plants grown at increased represents an important and reliable criterion to classify a species as salt-tolerant or salt-sensitive. However, physiological analysis of the causes of growth reduction due to salt-induced water stress by (destructive) biomass measurements after short and long-term measurements is limited. Leaf elongation, as an expression of the extension of individual plant cells, is considered to be a rapid, sensitive and reliable indicator of various kinds of water stress and, therefore, of changes in the plant's water relations (Tyree and Jarvis 1982, Waldron *et al.* 1985, Rozema, *et al.* 1987). Leaf elongation can be measured in a non-destructive way, and allows repeated measurements of one single leaf of the plant over the course of time, thus avoiding between-leaves and between-plants sources of error.

Plant biomass production depends on the accumulation of carbon products in photosynthesis. This in turn is determined by two main components: the rate of photosynthesis per leaf area and of leaf surface available for photosynthesis. The effects of salinity on these two physiological components of yield can be used as an experimental approach to study the effects of salinity on growth.

16. Field-scale studies under saline soils

Salts become concentrated in soils and soil water by evaporation and selective removal of water by plant roots. Whereas evaporative concentration is usually restricted to the top few centimeters of the soil, plant transpiration can result in water extraction by the roots and concentration of salts in the remaining soil solution to depths of many meters. There is abundant evidence too of the precipitation of various salts in soils when concentrations reach critical levels. Changes in the groundwater hydrology at local or regional scale may result in the movement of saline groundwater towards the soil surface and hence into the plant root zone. Salts accumulated in the soil over hundreds or thousands of years may be dissolved and transported towards the soil surface by a rising water table.

Leaching, evaporation and percolation are related to rainfall; rainfall is therefore a major factor determining the soil salinity (Thomas *et al.* 1981). Rooting depth has been found to be a very important factor in determining the quantity of rainfall which becomes recharge. Where plant rooting depths are greater than about 2 m, there is marginal effect on reducing the quantity of recharge (Peck *et al.* 1987). The key to salinity control is the management of the water which redistributes the salt in the landscape. There is a need to manage the recharge areas for greater water use by crops, the important criteria being to maintain or improve the economic return using crops with a deeper rooting system.

For most researchers, the selection of salt-tolerant trees from saline fields or plots would seem a logical step. However, this procedure has not produced good results in the past. The most common problem is that soil salinities vary substantially with time, location and depth. Selection techniques in fields would be improved if proper precautions were taken to uniformly presalinise the soil profile and to maintain salinities by applying saline water at uniform rates. This often requires big investments for control and monitoring devices for salinity.

17. Photosynthesis models used in the field study

The behaviour and changes in the behaviour observed in organisms responding to the natural environment can clarify the means by which specific organisms survive in particular environments. Survival and success of an organism occurs when the individual manages to reasonably respond to information from the environment. To assess the response of plants to environmental factors, fairly elaborate tools are needed because much of plant behaviour takes place at the biochemical and cellular level. These tools involve conceptual formulations as well as actual instrumentation. The analytical model can describe the interaction of biological and environmental factors governing the gas diffusion and biochemical processes of photosynthesis carbon dioxide fixation in a single leaf. This analytical model is a suggested conceptual tool allowing investigation, and most importantly, integration of aspects of plant behaviour closely linked to survival. This description combined with the leaf energy budget, allows simultaneous calculation of transpiration and photosynthetis rates for a natural environmental conditions. These models applied to a leaf can examine a number of ecologically important relationships for a particular leaf by integrating the established steady-state rates over the time. The amount of photosynthate accumulated, the amount of water lost, and the efficiency of water utilization can be estimated for any time period.

Tool design must correspond to the intended application. The major environmental factors of importance are incident radiant flux, air temperature, wind speed, humidity, and gas composition of the atmosphere. The photosynthesis model structure differentiates the following subprocesses: regulation of stomatal conductance of the leaf, transport of carbon dioxide from the intercellular air space to the site of carbon dioxide fixation, photorespiration, the coefficient relating of irradiance which combination denotes the net CO_2 assimilation per unit leaf area and per unit of CO_2 concentration connection. This is the model for the photosynthesis in a non-water deficit situation. If there is a water deficit, the transpiration would have to be taken into account, together with different water vapour concentrations at different leaf temperature, the optimal degree of the stomatal opening and the amount of carbon consumed per water unit or the transpiration cost.

18. Aims of the present study

The aim of the present study is to investigate the ecophysiological, anatomical and morphological characteristics of two salt-tolerant tree species, one is indigenous (*Combretum qudrangulare*) and the other is exotic (*Eucalyptus camaldulensis*) in relation to salt tolerance. The long-term objective is to contribute to the economic utilization of saline soils in northeastern Thailand by improving the silvicultural practices and by finding suitable species and provenances of trees in particular.

Accordingly, growth experiments with different levels of salinity were carried out under laboratory conditions and the results compared to those of a field study. A combination of ecophysiological parameters, as well as stomatal characteristics and growth responses are used to evaluate and compare the salt-tolerance of *Combretum quadrangulare* and *Eucalyptus camaldulensis*. The ecophysiological parameters included are photosynthesis, transpiration, photorespiration and dark respiration rates, and components of water vapour and CO_2 diffusion resistance. Emphasis is also given to the importance of functioning and acclimatization of structural regularities the of trees as influenced by saline conditions. It was hoped to identify criteria that could be used in the future for selecting salt-tolerant genotypes.

In addition, models developed for describing the net photosynthetic rate in trees were used to test the sensitivity of trees to salinity. By using models it was hoped to perfect a useful tool to aid in the selection of salt-tolerant species and genotypes.

2. Materials and methods

21. Laboratory experiments

211. Experimental material and design

Combretum quadrangulare Kurz seeds were brought from the Nong-Kai Province, Northeast Thailand (latitude 18° 00'N, longitude 103° 30'E, altitude 150 m, average rainfall 1200 mm and minimum-maximum temperatures 20—33°C) and *Eucalyptus camaldulensis* Dehnh. seeds from Mt. Carmine, Queensland, Australia (16° 29'S, 144° 55'E, altitude of 380 m, average rainfall of 850 mm and minimum-maximum temperatures of 16°—29°C). The *E. camaldulensis* seeds were kindly provided by Commonwealth Scientific and Industrial Research Organisation (CSIRO), Australia, seedlot number 0149.

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

When the *E. camaldulensis* and *C. quadrangulare* seedlings were some two months-old they were lifted from the seedling tray pots and their roots washed. The seedlings were then replanted into black plastic pots (10.0 cm dia. x 7.5 cm depth) containing 180 cm^3 of vermiculite No. 2 growth medium. Each pot had a perforated bottom to allow the roots to grow through (Plate 1). Underneath each pot was a 1000 cm^3 plastic bottle containing 500 cm^3 of North Carolina University State (N.C.S.U.) Phytotron nutrient solution (Downs and Bonaminio 1976). The pot was connected to the nutrient solution bottle by means of a 30 cm long cotton wick along which the nutrient solution could rise into the pot. After the roots had grown through the pots and into the solution in the bottles, treatment with sodium chloride began.

Sodium chloride solution was added to the N.C.S.U. Phytotron nutrient solution so as to produce one of five concentrations: 0, 0.5, 1.0, 1.5 and 2.0 % salinity. The nutrient/saline solution was replaced every week, when the pH, electrical conductivity and resistance of the remaining and replacement solutions were measured for further determination. The seedlings were treated in this way for 3 months; *C. quadrangulare* from 15 October 1986 to 15 January 1987, and *E. camaldulensis* from 15 August to 15 November 1986. The treatment of the eucalypt seedlings started earlier than that of the *Combretum* seedlings because the eucalypt seedling roots had grown through the pots and reached the solution bottles earlier. The experiment consisted of 15 replications per treatment, with one seedling in each replication. Effort was made to select only uniform seedlings with respect to both the above ground parts and roots. Anatomical and ecophysiological measurements were started after the seedlings had been treated for 45 days. Each replication and treatment was measured at two-week intervals, *i.e.* 4 times for ecophysiological measurements and 7 times for growth measurement over the whole period.

Another part of the washed seedlings from the tray pots were transplanted individually into 12.5 L plastic pots containing sand as the growth medium. The seedlings were treated with N.C.S.U. Phytotron nutrient solution of either 0 and 2.0 % NaCl salinity. There were seven replications of each treatment for each species. The treatment solutions were applied by pouring the whole 500 cm^3 of nutrient/saline solution to the surface of the sand once a week for the same three month periods. The same anatomical and ecophysiological measurements were also performed on these seedlings and the results presented for comparison with those of the culture solution experiment.

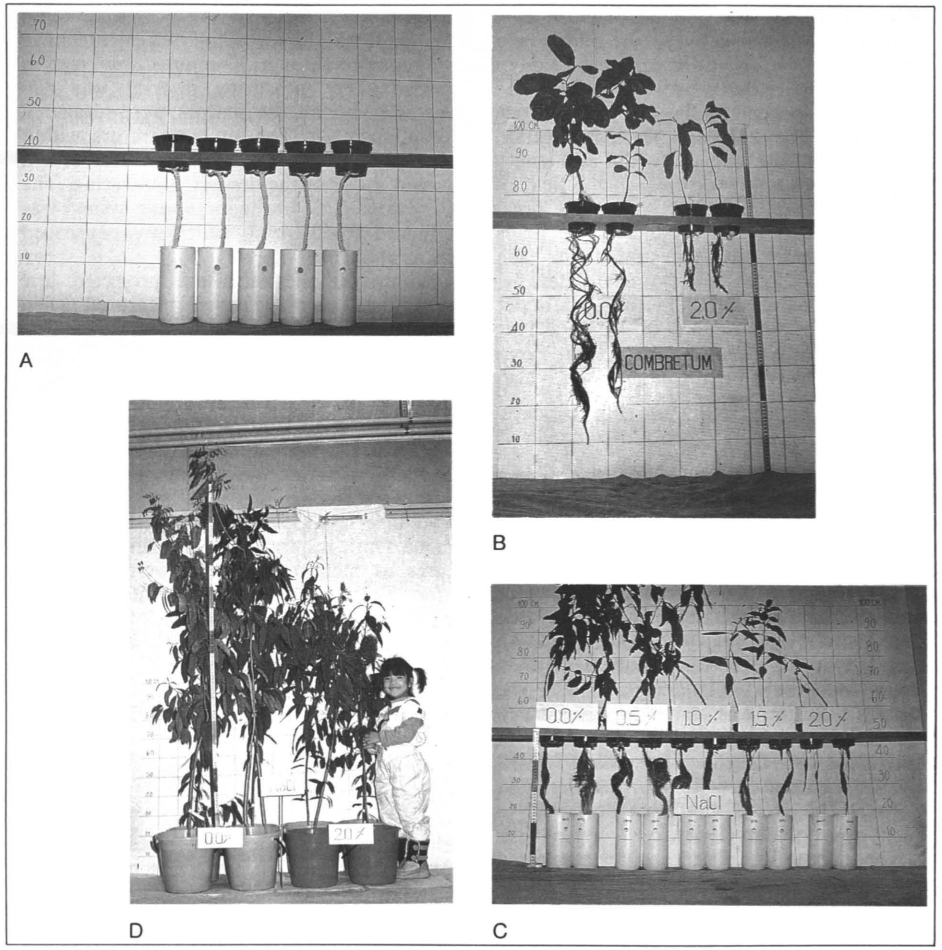


Plate 1. The greenhouse experiments. (A) The saline/nutrient solution experimental set-up. Underneath the black plastic pots are the 1L plastic bottles containing the saline/nutrient solutions and connected by cotton wicks, (B) control (left) and 2.0 % salinity (right) *Combretum quadrangulare* seedlings after 10 weeks, (C) the effect of different salinity levels on *Eucalyptus camaldulensis* and (D) *E. camaldulensis* seedlings grown in the sand medium pots, control treatment seedlings on the left and 2.0 % salinity treatment seedlings on the right.

212. Stomatal characteristics

The distribution, structure and size of stomata on sample leaves of the two species were determined using the glue imprint method. A 30 % solution of Mowiol (poly vinyl alcohol, 88 % hydrolyzed, melting point > 300°C and average molecular weight of a polymer 127,000, Merck Index) was spread onto the leaf surfaces and allowed to set. The imprints were then carefully peeled off the leaves and placed on slides for examination under a microscope. Imprints of on the abaxial and adaxial surfaces of a single sample leaf selected at random from four randomly selected seedlings in each treatment were made. The whole procedure was carried out on four occasions during the study period, at the two-week intervals. The imprints were always taken at 14:00 h.

The stomata on both leaf surfaces were observed and measured using an ocular and stage micrometer at four locations on each imprint at midway between the midrib and leaf margin: two locations from each side of midrib at the midway between leaf tip and base, one adjacent to the leaf tip and one adjacent to the leaf base. At each location the size of all the stomata (width and length of guard cells and apertures) in the field of view were examined by sampling the area. Four sampling areas of microscope fields were determined and ten stomata in each field were measured. The stomatal index, *i.e.* the proportion of the number of stomata per unit area to the number of stomata plus epidermal cells in the same unit area expressed as a percentage, was also determined.

213. Determination of ecophysiological parameters

2131. Measurements of CO_2 exchange

Measurements of CO_2 exchange were made by enclosing a selected leaf inside a transparent plastic cuvette — the assimilation chamber — which was connected to a Hartmann-Braun IRGA analyser model 3G. Data acquisition was controlled by a Veko 771 data logger of the 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.

Photosynthetic rates per projected leaf area (μmol $m^{-2}s^{-1}$) were measured when the equilibrium concentration of CO_2 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 $m^{-2}s^{-1}$. Transpiration rates per unit leaf area (mmol $m^{-2}s^{-1}$) were simultaneously measured with another IRGA analyser at the same temperature and irradiance levels as photosynthetic measurement. Dark respiration at the same temperatures as mentioned above, were measured after putting the seedlings into absolute darkness. For measurement of the CO_2 compensation points at 30°C and photon flux density 1000 μmol $m^{-2}s^{-1}$, the system was closed and the CO_2 concentration recorded when it has reached equilibrium.

2132. Calculation of gas exchange parameters

Photorespiration rates were calculated from the CO_2 compensation point values by extrapolation following the procedure described by Luukkanen (1978). By this method, photorespiration (Pr) is determined from the carboxylation efficiency (CE) and CO_2 compensation point (Γ) (Forrester *et al.* 1966, Luukkanen 1971, 1978 and Luaer *et al.* 1989):

$$\mathrm{Pr} = \mathrm{CE} \times \Gamma . \qquad (1)$$

Carboxylation efficiency is assumed to be the linear slope of increase in net photosynthesis with increasing ambient CO_2 concentrations (Ca). It is expressed as a function of both net photosynthesis (NP) and the difference between actual and compensation CO_2 concentrations:

$$\mathrm{CE} = \frac{\mathrm{NP}}{\mathrm{Ca} - \Gamma} . \qquad (2)$$

After determining photorespiration according to Equations (1) and (2), new values of the photorespiration rates had to be calculated because photorespiration rates obtained by this extrapolation method generally tend to underestimate the rates of the actual CO_2 output at the cellular level (cf. Luukkanen 1978). The recalculation procedure was carried out using a model of CO_2 diffusion into the leaf during photosynthesis (Jarvis 1971, Luukkanen 1978, Farquhar and Sharkey 1982):

$$\Sigma r' = \cot \gamma = r_{mx} + r's + r'a = \frac{\mathrm{Ca} - \Gamma}{\mathrm{qv}} , \qquad (3)$$

where $\Sigma r'$ is the total resistance to CO_2 diffusion, r_{mx} mesophyll (liquid diffusion and carboxylation) resistance, r's the stomatal resistance to CO_2 (including intercellular space resistance), r'a the boundary layer resistance to CO_2, Ca the ambient CO_2 concentration, and qv the CO_2 exchange. γ denotes the angle corresponding to the carboxylation efficiency line (solid line in Figures 22, 23 and 24).

Boundary layer resistance to CO_2 diffusion (r'a) was estimated from evaporation rates and using the equation given by Jarvis (1971):

$$r'a = ra \left[\frac{D}{D'} \right]^{2/3} \qquad (4)$$

where the ratio between diffusion coefficients for H_2O and CO_2 ,D/D', was assumed to equal 1.6 (Sesták *et al.* 1971, Luukkanen 1978, Hari *et al.* 1986, Korpilahti 1988, Hari and Berninger 1990), and where ra denotes boundary layer resistance to H_2O. The evaporation rates were measured by placing a Petri dish with a leaf image of green coloured paper in the bottom and filled with water close to the excised leaf in the cuvette. For the Petri dish, there is no stomatal resistance to water vapour diffusion (rs equals zero) because green paper acted as an artificial leaf. Since the stomatal resistance to water vapour diffusion (rs), in the equation for leaf resistance to H_2O (rg) equals:

$$rg = rs + ra , \qquad (5)$$

then rg = ra. Thus, ra can be replaced by rg in Equation (4) and calculated from the equation presented by Luukkanen (1978) as follows:

$$rg = \frac{wi\text{-}wa}{Es} , \qquad (6)$$

where wi and wa denote the concentrations of water vapour in the intercellular space (on the surface of mesophyll cells) and in the ambient atmosphere respectively, and Es the transpiration rate by IRGA in the laboratory. Similarly, in boundary layer resistance to H_2O (ra) calculations, the water vapour concentration gradient and evaporation rate were used. In order to apply the value of boundary layer resistance to CO_2 (r'a) obtained with the Petri dish method to an amphistomatous leaf, r'a was divided by 2.

The leaf resistance to CO_2 (r'g = r's + r'a) can be obtained using the standard coefficient (1.6) for conversion between CO_2 and H_2O diffusion which uses elsewhere:

$$r'g = rg \times 1.6 . \qquad (7)$$

The stomatal resistance to CO_2 (r's) is finally obtained from the equation r'g = r's + r'a.

If the apparent photosynthetic rate (qv) at a given value of ambient CO_2 concentration (Ca) is known, then the relationship between qv and the CO_2 concentration in the intercellular space (Ci), can be determined using the following equation (Luukkanen 1978):

$$r'g = \mathrm{Cot}\ \delta = \frac{\mathrm{Ca\text{-}Ci}}{\mathrm{qv}} , \qquad (8)$$

where δ equals the angle of the line corresponding to the effect of leaf resistance (dotted line in Figures 22, 23 and 24).

From parameters, Ci, Γ and qv, a line showing the response of qv to variations in Ci and running through Γ on X-axis can be drawn. The point where this line meets the Y-axis corresponds to the true photorespiration (Rl) and the reciprocal value of the slope of the line equals mesophyll resistance (r_{mx}) (Jarvis 1971, Luukkanen 1978):

$$r_{mx} = \cot \zeta = \frac{\mathrm{Ci} - \Gamma}{\mathrm{qv}} , \qquad (9)$$

where ζ denotes the angle corresponding to the true photorespiration line (dotted-broken line in Figures 22, 23 and 24).

Total photosynthesis rates (P,gross) were derived from net photosynthesis (NP) plus the new calculation of photorespiration (Rl).

2133. Measurements of water potential

A portable pressure bomb apparatus designed and built by Mr. Toivo Pohja, University of Helsinki, was used for leaf water potential determinations. The measurements were made on given days at 15:00 h. The samples were taken in the same way for both species after the seedlings treated 45 days. A leaf on each of four randomly selected seedlings in each treatment at each time was selected for measurement and repeated four times at two-week intervals. Only healthy and mature leaves were accepted. The portable pressure bomb was brought near to the selected leaf which was then excised and its water potential immediately measured. Measurements were made on four occasions per treatment.

2134. Porometer measurements of leaf resistance

Leaf resistance was measured with a portable Delta-T diffusion porometer which was described by Kaarakka *et al.* (1985). Only healthy and mature leaves were accepted. Both sides, abaxial and adaxial, of leaves were measured. Single leaves from four seedlings from each treatment in the greenhouse experiment were measured at 15:00 h on four occasions at two-week intervals during the study period. The average leaf resistance (rg) from adaxial and abaxial surfaces was calculated using the equation presented by Kanemasu *et al.* (1969), Kanemasu and Tanner (1969) and Pereira and Koslowski (1976) but modified for a single surface:

$$rg = \frac{rg(\text{adaxial}) \times rg(\text{abaxial})}{rg(\text{adaxial}) + rg(\text{abaxial})} . \qquad (10)$$

2135. 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 (Equation 6). These calculated transpiration rates were compared with those obtained by IRGA measurements.

214. Morphological measurements

At the same time as the establishment of the culture solution experiment, 20 of the seedlings of similar size and condition of both species, were used to determine the initial fresh and dry weight biomasses (separately for main stems, side branches, leaves and roots) and the leaf area/biomass relationship. Xerox images of the leaves were taken and weighed as well as intact paper sheets of known area. The actual seedling leaf area could then be calculated using the measured leaf biomass values and the above relationship between the paper leaf area and weight.

The growth development of the *C. quadrangulare* and *E. camaldulensis* seedlings in the culture solution and sand medium experiments were measured in 7 times at two-week intervals during the whole study period. The number of leaves and newly occurring leaves per seedling were recorded as well as that of the nodes and internodes. The stem diameter at ground level and the length of shoots and roots were also measured. The length of the root system prior to transplanting the seedlings was also measured.

At the end of the experiment, biomass determinations of the main stem, side branches, leaves and roots were determined for each seedling separately to compliment the biomass determinations made at the beginning of the experiment. The leaf area at the end of the experiment was determined using the paper leaf area/weight relationship determined as at the beginning of the experiment.

During the study period, the leaf area and leaf dry biomass at each occasion were estimated from the average leaf area and leaf dry weight at the end of experiment of each treatment multiplied with the amount of leaf numbers.

22. Field studies

221. Site description and experimental design

C. quadrangulare and *E. camaldulensis* plantations located in the Khon Kaen and Roi-et provinces of northeastern Thailand were selected for 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 situated at an of altitude 165 m and has an average annual rainfall of 1000—1100 mm and a high evaporation rate. The soil in the *C. quadrangulare* and local variety of *E. camaldulensis* was saline and had a sandy-loam texture. The soil at the *E. camaldulensis* variety 0149 was non-saline and had a loamy-sand texture.

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

The field study, therefore 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. The non-saline soil in used as the control treatment and the saline soil as the saline treatment.

In each site, 4 plots were established. Each plot was 15 × 15 trees in size. The ecophysiological measurements were made on 5 occasions during November 1987 to January 1988 at two-week intervals.

222. Stomatal characteristics

Imprints of on the abaxial and adaxial leaf surfaces were taken and stomatal measurements made in the same way as in the greenhouse experiment except that the imprints were taken at 10:00 h and 14:00 h. The four trees and the four sample leaves in each study site were selected randomly.

223. Determination of ecophysiological parameters

2231. Measurements of gas exchange

An LI-6200 portable photosynthesis system and an LI-6250 gas analyser (LI-COR Inc. instruments U.S.A.) were used for measurements of gas exchange in the field study. The variation in the net photosynthetic rates (μmol m^{-2}s^{-1}) transpiration rates (mmol 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 an hour measurement interval on the same leaf. Sometimes the transpiration and stomatal conductance programming resulted in a 10 fold error; but these data were later corrected correspondingly.

2232. Photosynthesis models

Mathematical models describing biological processes are written at a number of organizational levels and for a variety of reasons. The complexity of models varies enormously, being affected by the abilities and inclinations of the modellers, their philosophy and their objectives (McMurtrie *et al.* 1988). The models presented and discussed in the present study are a further development of the methods used by Gaastra (1959), Hari *et al.* (1986), Korpilahti (1988) and Hari and Berninger (1990), with the optimality hypothesis of gas exchange. The photosynthetic models are based on experimental results obtained by measuring photosynthetic responses in forest tree species. Interpretation of the data and the approach are aimed resolving the conflicts between observed data and the models in order to perfect a tool useful to investigations of specific ecophysiological problems.

For modelling purposes, a single leaf can be considered so small that environmental factors do not result in spatial variation within the model elements. The model elements consist of: A, the leaf area; h, the mean thickness of intercellular space; Ci, the intercellular CO_2 concentration; Ca, the ambient CO_2 concentration; NP, the net photosynthetic rate; Rl, the photorespiration rate in the laboratory; R, the photorespiration rate in the field; g, the stomatal conductance measured; g_0, the stomatal conductance predicted from stomatal opening; u, the stomatal opening; I, irradiance; and α, the coefficient relating photosynthetic rate, irradiance and intercellular CO_2 concentration; λ the transpiration cost. Models for non-water deficit did not take stomatal regulation and transpiration cost into account like models for water deficit.

2233. Photosynthesis models under non-water deficit conditions

Under non-water deficit conditions, Hari and Berninger (1990) assumed that total photosynthesis (P) is proportional to the product of the two limiting factors, irradiance and intercellular CO_2 concentration,

$$P = \alpha ICi \, . \qquad (11)$$

The amount of CO_2 in the intercellular space is the product of volume and concentration, *i.e.* h A Ci. If the volume of intercellular space is considered to be constant, inflow plus photorespiration minus photosynthetic consumption equals the change in intercellular CO_2 concentration. This can be described by differential equation of the time development of the intercellular CO_2 concentration:

$$hA = \frac{dCi}{dt} = A\,[g(Ca—Ci) — P+R] \, . \qquad (12)$$

The time constant of the intercellular CO_2 concentration seems to be a few seconds (Hari and Berninger 1990). For short time intervals it can be assumed that the intercellular CO_2 concentration is in steady state. The time derivative then equals zero and Equation (12) becomes:

$$A\,[g(Ca—Ci)—P+R] = 0 \, . \qquad (13)$$

The intercellular CO_2 concentration, Ci, can be solved as follows:

$$Ci = \frac{gCa+R}{g+\alpha I} \, . \qquad (14)$$

Photorespiration rate values at 30°C (Rl) from laboratory results is modified to achieve photorespiration in the field (R) according to respiration assumption of Korpilahti (1988) as follows:

$$R = Rl{*}10^{0.032(tl—30)}. \qquad (15)$$

The dependence of total photosynthetic rate, P, on irradiance and ambient CO_2 concentration can be determined using Equations (11), (14) and (15):

$$P = \frac{\alpha I(gCa+R)}{g+\alpha I} \, , \qquad (16)$$

where NP = P—R; then

$$NP = \frac{\alpha I(gCa+R)}{g+\alpha I} —R \, . \qquad (17)$$

2234. Photosynthesis models under water deficit conditions

Stomatal functioning is related to the degree of stomatal opening, u, which can be understood as a control signal that varies between 0 and 1. The stomatal conductance of stomata when fully open is denoted by g_0. The degree of stomatal opening is then defined as follows:

$$g = ug_0 \, . \qquad (18)$$

When g is replaced with u and g_0 in Equation (17), the model for photosynthetic rate now includes the functioning of the stomata.

Tr denotes transpiration rate, measured by the LI-6200 in the field, wi the intercellular water vapour concentration and wa the ambient water vapour concentration. Using the model for transpiration (Gaastra 1959), the transpiration rate can be written as follows:

$$Tr = aug_0(wi\text{-}wa), \qquad (19)$$

where a is constant for gas exchange (a = 1.6); the saturated water vapour concentration in the intercellular space (wi) depends on leaf temperature (tl). Hence, wi can be modified from the equations presented by Sesták *et al.* (1971) and Korpilahti (1988) as follows:

$$wi = 4.847{*}Exp(0.0626{*}tl) \, . \qquad (20)$$

The model for transpiration can now be written as:

$$Tr = 1.6ug_0(4.847{*}Exp(0.0626{*}tl)—wa). \qquad (21)$$

A transpiration cost, λ , for maintaining a sufficient water stream per unit amount of water can be assumed. The values of λ can be expressed as grams CO_2 consumed per gram water transpired. The control of stomata is considered to be optimal if the difference between photosynthesis and transpiration costs is maximized during the time interval under consideration,

$$\max_{u} \left[\int_{t_1} \frac{t_2 \alpha I(t)\,(ug_0Ca+R(tl)\,(t))}{ug_0+\alpha I\,(t)}\, dt— \lambda \int_{t_1}^{t_2} aug_0(wi(t)—wa)dt \right] , \qquad (22)$$

where t1 is the beginning instant, t2 the cessation instant of the period consideration and λ is the transpiration cost.

The maximization problem can be solved using standard procedures. The modification of the solution follows that by Hari *et al.* (1986), Korpilahti (1988) and Hari and Berninger (1990). The optimal degree of the stomata opening, u*, is:

$$u^* = \left[\sqrt{\frac{Ca—\frac{R}{\alpha I}}{\lambda a\,(wi—wa)}} \;—1 \right]_{0}^{1} \frac{\alpha I}{g_0} \, . \qquad (23)$$

When u equals 1, the stomata are fully open; when u equals 0, the stomata are closed; and when u is between 0 and 1, the stomata are partially closed. According to the solution, the stomata may also be fully open during limited available water. This occurs if environmental factors are favourable for photosynthesis but unfavourable for transpiration. The degree of stomatal opening depends on irradiance, water vapour pressure deficit and respiration rate.

The behaviour of photosynthesis is obtained by combining Equations (17), (18), (20) and (23). It depends on irradiance and temperature if the ambient water vapour concentration is constant. Dependence of photosynthesis on irradiance is linear at the constant temperature if the stomata are partially closed. When the stomata are fully open the dependence follows the Michaelis-Menten function (Equation 17).

2235. Measurements of water potential

The same apparatus as described for the greenhouse experiment was also used in the field study. A leaf from ten trees on each plot were measured. Measurements were made on five occasions in the field study at two-week intervals. The measurements were made at 10:00 h and 14:00 h.

2236. Measurements of stomatal resistance

Field measurements of stomatal resistance were done with the portable IRGA LI-COR apparatus only. The method and procedure were used the same as mentioned on chapter 223.

23. 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 *** = $p < 0.001$.

3. Results

31. Effects of salinity on stomatal characteristics

311. Effects on guard cell size

Greenhouse experiments — The width of the adaxial and abaxial guard cells for *Combretum quadrangulare* showed no difference among salinity treatments, ($p > 0.05$), but there was a difference in the case of the *Eucalyptus camaldulensis* seedlings (Appendix I, Table 1). *E. camaldulensis* guard cells were wider in salinity treatments than in the control treatment ($p > 0.05$). The width of the guard cells was wider in *E. camaldulensis* than in *C. quadrangulare* ($p > 0.001$). Abaxial guard cells were about the same on adaxial guard cells in *C. quadrangulare* and in *E. camaldulensis*. The widest adaxial and abaxial *E. camaldulensis* guard cells were 17.50 μm and 17.84 μm, respectively, and were associated with the 0.5 % salinity treatment.

The length of the adaxial guard cells showed no difference among treatments ($p > 0.05$) in *C. quadrangulare*, but treatment related differences ($p > 0.001$) were found in *E. camaldulensis* (Appendix I, Table 1). *E. camaldulensis* adaxial guard cells were relative long at low salinity and short at 2.0 % salinity treatment. *E. camaldulensis* adaxial guard cells were longer than those of *C. quadrangulare* ($p > 0.01$). The longest *E. camaldulensis* adaxial guard cell was 22.98 μm and associated with the 0.5 % salinity treatment. The length of the abaxial guard cells was different ($p > 0.001$) at various salinity levels and within species (Appendix I, Table 1). The length of abaxial guard cells were relative long at low salinity and short at 2.0 % salinity treatment in both species. *E. camaldulensis* had longer abaxial guard cells than *C. quadrangulare* ($p > 0.001$) and the longest was 22.49 μm (1.0 % salinity treatment). The length of adaxial and abaxial guard cells was similar in *C. quadrangulare* and *E. camaldulensis*.

Field studies — The width of the adaxial guard cells measured at both 10:00 h and 14:00 h was narrower in *C. quadrangulare* than *E. Camaldulensis* and non-saline soil than on saline soil ($p < 0.001$) (Appendix I, Tables 2 and 3). The width of *C. quadrangulare* abaxial guard cells was wider at 10:00 h but narrower at 14:00 h ($p > 0.05$) on the non-saline soil than on the saline soil ($p > 0.05$). In the case of *E. camaldulensis*, the width of the abaxial guard cells was narrower on the non-saline soil at both times ($p < 0.05$). *C. quadrangulare* had narrower abaxial guard cells than *E. camaldulensis* ($p < 0.001$) at both times.

The length of adaxial guard cells was greater on the non-saline soil in the case of *C. quadrangulare* but narrower in the case of *E. camaldulensis* at both 10:00 h and 14:00 h, compared to the saline soil ($p < 0.05$) (Appendix I, Tables 2 and 3). The length of the adaxial guard cells was narrower in *C. quadrangulare* than *E. camaldulensis* ($p < 0.001$) at both times. The length of the abaxial guard cells of *C. quadrangulare* showed the same trend on the non-saline and saline soils ($p > 0.05$). The length of the abaxial guard cells of *E. camaldulensis* was longer on the saline soil at both times ($p < 0.05$). *C. quadrangulare* had shorter abaxial guard cells than *E. camaldulensis* ($p < 0.001$) at both times.

312. Effects on stomatal aperture size

Greenhouse experiments — The width of the adaxial aperture was different ($p < 0.001$) among treatments, both within species and between species (Appendix I, Table 1). The salinity treatments showed wider apertures than the control ($p < 0.001$) in both species. The stomatal openings of both species, however, showed no systematic increase with salinity (Figure 1). The width of adaxial and abaxial apertures in *E. camaldulensis* increased with low salinity and decreased at 2.0 % salinity treatment. The width of adaxial and abaxial for *C. quadrangulare* fluctuated with salinity but increased. The stomatal openings in *C. quadrangulare* were wider on abaxial than adaxial surfaces at every salinity level, but were narrower in the case of *E. camaldulensis* (Figure 1).

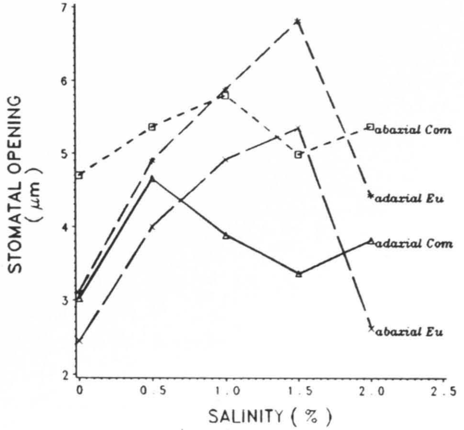


Figure 1. Relationship between stomatal opening on adaxial an abaxial surfaces and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown in culture solution in the greenhouse at 14:00 h.

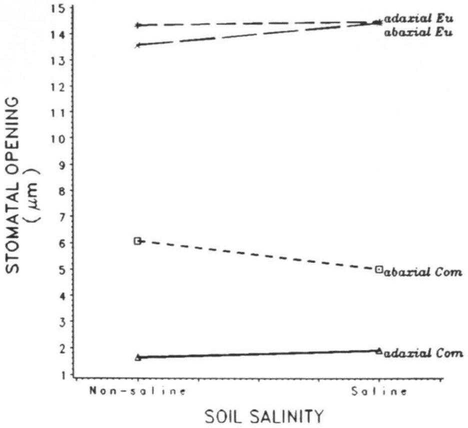


Figure 2. Relationship between stomatal opening on adaxial and abaxial surfaces and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown on non-saline (normal) and saline soil types in the field at 14:00 h.

The length of *C. quadrangulare* adaxial stomatal aperture increased with salinity ($p < 0.001$). In the case of *E. camaldulensis*, adaxial stomatal aperture length increased with salinity up to 1.5 % ($p < 0.001$) but in the 2.0 % salinity treatment, it was shorter ($p < 0.001$) than in the control (Appendix I, Table 1). The length of abaxial stomatal apertures in *C. quadrangulare* was greater in the 0.5 % to 1.5 % treatments, but smaller in the 2.0 % treatment, compared to the control ($p > 0.05$). For *E. camaldulensis*, however, the length of abaxial stomatal apertures was wider than the control at all salinity levels ($p < 0.001$) (Appendix I, Table 1).

Field studies — In both species, the stomatal apertures (opening) on the adaxial surfaces were narrower on the non-saline soils than on the saline soil, and at both 10:00 h and 14:00 h. On the abaxial surface, the apertures were wider on the non-saline soil in *C. quadrangulare* at 10:00 h ($p > 0.05$) and at 14:00 h ($p < 0.01$), but narrower at both times ($p < 0.01$) in *E. camaldulensis* (Figure 2). The apertures on both surfaces were wider in *E. camaldulensis* than *C. quadrangulare*, and at both times ($p < 0.001$).

The length of the adaxial stomatal aperture (opening) was greater on the non-saline soil than on the saline soil ($p < 0.05$), at both times, in the case of *C. quadrangulare* (Appendix I, Tables 2 and 3). In the case of the local variety of *E. camaldulensis*, the adaxial aperture was shorter on the non-saline soil than on the saline soils at 10:00 h ($p < 0.05$), but longer ($p > 0.05$) when measured at 14:00 h. For *E. camaldulensis* variety No. 0149 on the non-saline soil, the adaxial stomatal aperture remained shorter than *E. camaldulensis* of the local variety ($p < 0.01$) on the non-saline and saline soils at both times. The length of the abaxial stomatal aperture in the case of *C. quadrangulare* was shorter on the non-saline soils than on the saline soil at 10:00 h ($p > 0.05$), but longer at 14:00 h ($p > 0.05$). In the case of *E. camaldulensis*, the length of the abaxial aperture was shorter on the non-saline soil at both measurement times ($p < 0.001$). The length of the abaxial aperture was shorter in *C. quadrangulare* than *E. camaldulensis* at both times ($p < 0.001$) and sites ($p < 0.001$).

313. Effects on stomatal frequency and index

Greenhouse experiments — Stomatal numbers increased with salinity on adaxial surface (p > 0.05) in both species (Figure 3 and Appendix I, Table 4). Stomatal numbers were much more in *E. camaldulensis* than in *C. quadrangulare* (p < 0.001). Stomatal numbers on abaxial surface varied with treatment, but the differences were only significant (p < 0.001) in the case of *E. camaldulensis*. The stomatal numbers increase with salinity up to 1.5 % salinity treatment but in the 2.0 % salinity treatment, it was lower than control treatment. The highest number of stomata on the abaxial surface of *C. quadrangulare* leaves was 391 stomata mm^{-2} (0.5 % salinity treatment) and the lowest was 329 stomata mm^{-2} (1.0 % salinity treatment). In the case of *E. camaldulensis*, the corresponding values were 394 stomata mm^{-2} (0.5 % salinity treatment) and 271 stomata mm^{-2} (2.0 % salinity treatment), respectively (Figure 3). The abaxial surface had much greater stomatal numbers than the adaxial surface, especially in the case of *C. quadrangulare* (Appendix I, Table 4).

The stomatal index increased with salinity on adaxial surfaces of both *C. quadrangulare* (p > 0.05) and *E. camaldulensis* leaves (p < 0.05; Appendix I, Table 4). *E. camaldulensis* had a greater stomatal index than *C. quadrangulare* at all salinity levels (p < 0.001) (Figure 4 and Appendix I, Table 4). On abaxial surface, the stomatal index fluctuated in much the same way as stomatal frequencies, but only the differences in *E. camaldulensis* were significant (p < 0.001). The stomatal index increased with salinity on abaxial surface up to 1.5 % salinity treatment (p > 0.05) and decreased in the 2.0 % salinity treatment (p < 0.05) until lower than control treatment for *C. quadrangulare*. For *E. camaldulensis*, stomatal index had greater than control treatment at all salinity levels. The highest and lowest stomatal indices were 20.35 % (0.5 % salinity treatment) and 18.24 % (2.0 % salinity treatment), respectively, in *C. quadrangulare*, and for *E. camaldulensis* the corresponding values were 19.99 % (1.5 % salinity treatment) and 13.96 % (control) (Figure 4 and Appendix I, Table 4). The stomatal index was much higher on the abaxial than adaxial surfaces in both species at all salinity levels (Figure 4).

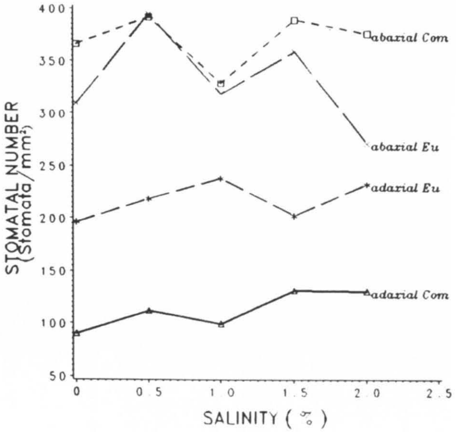


Figure 3. Relationship between stomatal frequency on adaxial and abaxial surfaces and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown in culture solution in the greenhouse at 14:00 h.

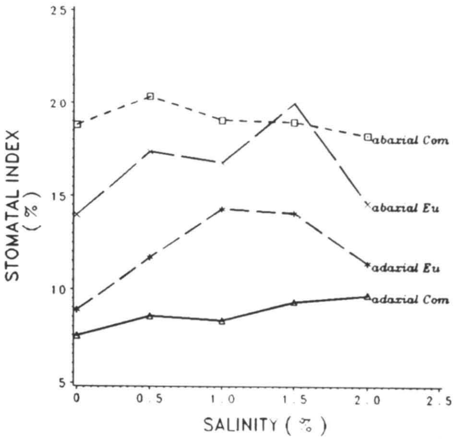


Figure 4. Relationship between stomatal index on adaxial and abaxial surfaces and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown in culture solution in the greenhouse at 14:00 h.

Field studies — Stomatal numbers on both leaf surfaces and in both species measured from the 10:00 h leaf imprints were higher on the non-saline soil than on the saline soil (p < 0.001) (Appendix I, Table 5). The imprints taken at 14:00 h, however, indicated that stomatal numbers on the abaxial surfaces of *C. quadrangulare* were less on the non-saline soil (p > 0.05; Figure 5). *C. quadrangulare*

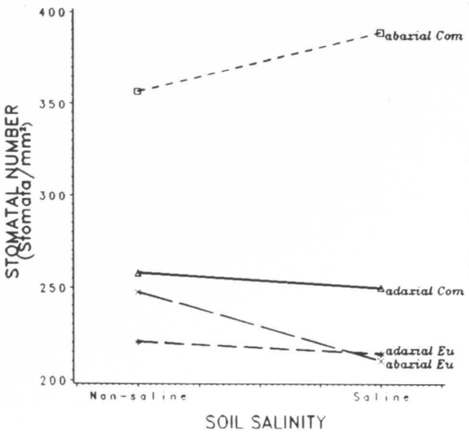


Figure 5. Relationship between stomatal frequency on adaxial and abaxial surfaces and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown on non-saline (normal) and saline soil types in the field at 14:00 h.

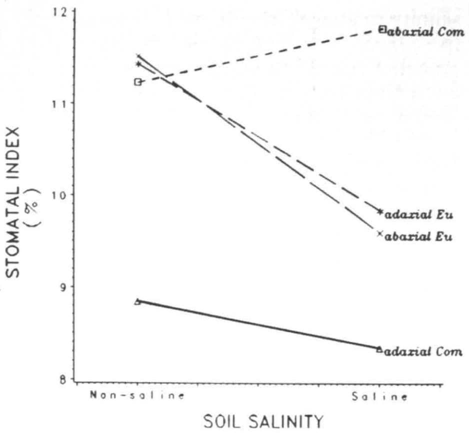


Figure 6. Relationship between stomatal index on adaxial and abaxial surfaces and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis* Mean values for seedlings grown on non-saline soil types in the field at 14:00 h.

abaxial leaf surface at 10:00 h had a greater number of stomata than adaxial surface, while at 14:00 h it was the reverse. Except on the saline soil, the same was also true for *E. camaldulensis*. For *E. camaldulensis* variety No. 0149 had greater stomatal numbers than for *E. camaldulensis* of local variety both saline and non-saline soils.

The stomatal index was higher on the non-saline soil than on the saline soil on the 10:00 h leaf imprints (p < 0.001). This was true for both leaf suefaces and for both species. The same was true for the imprints of the abaxial surface taken at 14:00 h, but the index for the adaxial surface was smaller on the saline soil than on the non-saline soil (Figure 6). In the case of the local variety of *E. camaldulensis* on non-saline soil had the highest stomatal index, was higher than for *E. camaldulensis* variety 0149 and *C. quadrangulare* both surfaces (adaxial and abaxial) and both sites (non-saline and saline line soils) (Appendix I, Table 5).

Table 1. Means (±sd) of afternoon leaf water potential of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) greenhouse experiments (nonsignificant differences are indicated by same letters).

Species and salinity (%)	Water potential (MPa) 13:30—15:30 h
(1)	
Com 0.0	-0.92 ± 0.25^{a}
Com 0.5	-1.18 ± 0.38^{b}
Com 1.0	-1.23 ± 0.26^{b}
Com 1.5	-1.58 ± 0.20^{c}
Com 2.0	-2.27 ± 0.47^{e}
Eu 0.0	-1.00 ± 0.35^{ab}
Eu 0.5	-1.16 ± 0.28^{ab}
Eu 1.0	-1.70 ± 0.41^{c}
Eu 1.5	-1.55 ± 0.29^{c}
Eu 2.0	-2.02 ± 0.24^{d}
F	31.73***
X	—1.42
(2)	
Com 0.0	-0.86 ± 0.39^{a}
Com 2.0	-1.26 ± 0.42^{b}
Eu 0.0	-0.92 ± 0.30^{a}
Eu 2.0	-1.22 ± 0.33^{b}
F	4.54**
X	—1.06

32. Effects of salinity on the water balance

321. Water potential

Greenhouse experiments — Leaf water potential decreased with increasing salinity in both species (p < 0.01) and growth media (Table 1). *C. quadrangulare* had a higher leaf water potential than *E. camaldulensis* in the control treatment (p > 0.05) but lower at the 2.0 %

salinity treatment in both media experiments ($p < 0.05$). For both species the leaf water potential started to significantly differ ($p < 0.05$) from control up to the 1.0 % salinity level in the culture solution experiment.

Field studies — Leaf water potential was higher on non-saline than saline soils for both species and at both measurement times (Table 2). The leaf water potential of *C. quadrangulare* was lower than that of *E. camaldulensis* and lower in the afternoon than in the morning.

Table 2. Means (±sd) of leaf water potential of *Combretum quadrangulare* and *Eucalyptus camaldulensis* in the morning and afternoon in the field study (non-significant differences in the same column are indicated by same letters).

Species and soil type	Water potential (MPa) 10:00 h	14:00
(1)		
Com normal	-1.92 ± 0.52^{b}	-2.25 ± 0.40^{b}
Com saline	-2.12 ± 0.51^{c}	-2.42 ± 0.43^{c}
Eu0149 normal	-1.73 ± 0.31^{a}	-1.97 ± 0.27^{a}
Eu normal	-1.70 ± 0.38^{b}	-1.96 ± 0.39^{a}
Eu saline	-1.78 ± 0.34^{ab}	-2.06 ± 0.35^{a}
F	11.55***	17.84***
$\bar{X}$	−1.84	−2.13

322. Measured transpiration

Greenhouse experiments — Measured transpiration rates tended to decrease with increasing salinity in culture solution experiment (Table 3). 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 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 3).

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 (Table 3). However, when the rates were measured using the porometer, the opposite trend was observed (Table 3).

Table 3. Means (±sd) of transpiration rate of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 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	0.56 ± 0.23^{ab}	1.31 ± 0.57^{bc}	2.11 ± 1.01^{cde}	2.74 ± 1.37^{bc}	1.81 ± 0.50^{c}
Com 0.5	0.65 ± 0.37^{ab}	1.22 ± 0.79^{bc}	1.80 ± 1.18^{de}	2.08 ± 1.37^{c}	1.59 ± 0.30^{c}
Com 1.0	0.53 ± 0.27^{ab}	1.02 ± 0.46^{bc}	1.24 ± 0.54^{de}	1.33 ± 0.55^{c}	1.29 ± 0.12^{c}
Com 1.5	0.32 ± 0.6^{b}	0.51 ± 0.10^{c}	0.62 ± 0.14^{e}	0.70 ± 0.17^{c}	1.02 ± 0.26^{c}
Com 2.0	0.91 ± 0.61^{ab}	1.33 ± 1.06^{bc}	1.57 ± 1.30^{de}	1.59 ± 1.19^{c}	0.73 ± 0.11^{c}
Eu 0.0	1.17 ± 0.95^{ab}	3.34 ± 1.81^{ab}	5.03 ± 2.04^{abc}	6.09 ± 3.32^{ab}	5.28 ± 1.91^{a}
Eu 0.5	0.82 ± 0.63^{ab}	2.86 ± 1.60^{abc}	5.46 ± 3.34^{ab}	6.57 ± 4.26^{ab}	4.13 ± 2.63^{ab}
Eu 1.0	1.44 ± 0.88^{ab}	5.09 ± 3.52^{a}	6.53 ± 3.09^{a}	7.35 ± 4.36^{a}	3.99 ± 1.90^{ab}
Eu 1.5	1.27 ± 1.07^{ab}	3.40 ± 2.97^{ab}	3.85 ± 3.23^{abcd}	3.67 ± 3.07^{abc}	2.47 ± 1.46^{bc}
Eu 2.0	1.58 ± 0.95^{a}	2.74 ± 1.44^{abc}	2.83 ± 1.27^{bcde}	2.67 ± 1.30^{c}	1.46 ± 0.29^{c}
F	1.50^{ns}	2.18*	4.43***	3.78**	7.15***
$\bar{X}$	0.97.	5.89	3.26	3.67	2.38
(2)					
Com 0.0	0.49 ± 0.29^{a}	1.35 ± 0.50^{a}	2.03 ± 0.41^{b}	1.74 ± 0.70^{c}	4.08 ± 3.46^{a}
Com 2.0	0.52 ± 0.13^{a}	1.33 ± 0.37^{a}	2.19 ± 0.51^{ab}	2.28 ± 0.54^{bc}	3.97 ± 2.71^{a}
Eu 0.0	0.64 ± 0.31^{a}	1.72 ± 0.44^{a}	2.87 ± 0.50^{ab}	3.16 ± 0.49^{ab}	6.22 ± 4.81^{a}
Eu 2.0	0.70 ± 0.41^{a}	2.19 ± 1.08^{a}	3.20 ± 1.11^{a}	3.71 ± 1.28^{a}	3.76 ± 3.20^{a}
F	0.41^{ns}	1.49^{ns}	2.56^{ns}	4.65*	0.50^{ns}
$\bar{X}$	0.59	1.65	2.57	1.51	4.50

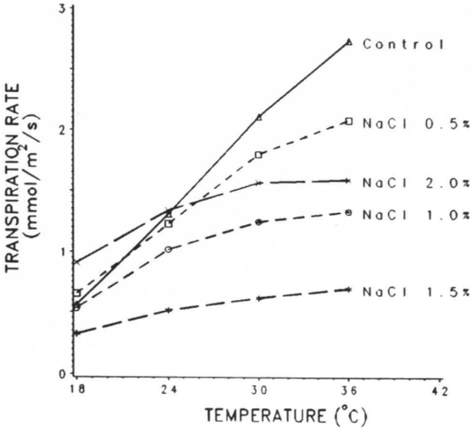


Figure 7. Relationship between transpiration and temperature for *Combretum quadrangulare* at a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and different salinity levels. Mean values for seedlings grown in culture solution in the greenhouse.

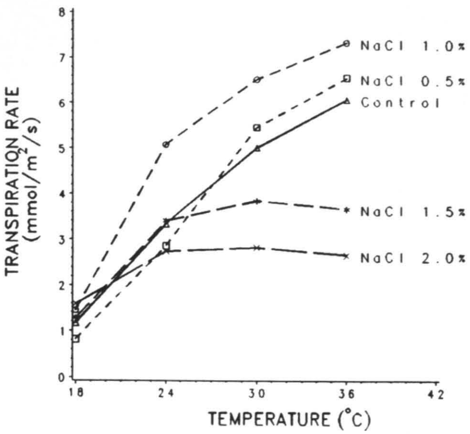


Figure 8. Relationship between transpiration rate and temperature for *E. camaldulensis* at a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and different salinity levels. Mean values for seedlings grown in culture solution in the greenhouse.

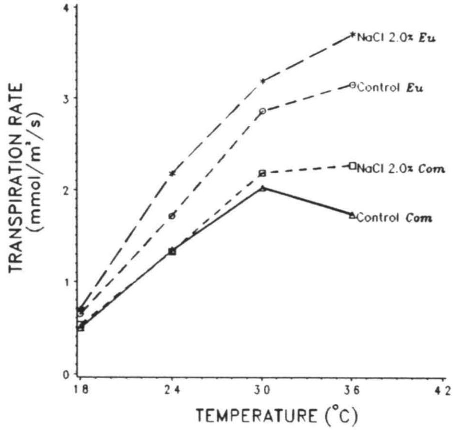


Figure 9. Relationship between transpiration rate and temperature for *Combretum quadrangulare* and *Eucalyptus camaldulensis* in sand medium at a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and different salinity levels. Mean values for seedlings grown in sand medium in the greenhouse.

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 media (Figures 7, 8 and 9). Transpiration rates also increased with irradiance up to 1500 μmol $m^{-2}s^{-1}$ and then decreased at the 2000 μmol $m^{-2}s^{-1}$ (Appendix I, Table 6).

Field studies — Transpiration increased with temperature and irradiance in both species, and transpiration rates were much higher in *E. camaldulensis* than in *C. quadrangulare* ($p < 0.001$; Figure 10). 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 (Figure 11 and Appendix I, Tables 7 and 8).

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 the saline soil but not on non-saline soil (Figure 12).

323. Modeled transpiration

Predicted values for transpiration rates in the field, calculated using Equation (21), are shown in Figures 13 and 14 (see also

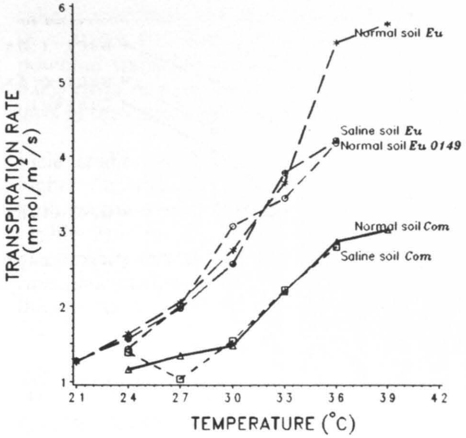


Figure 10. Relationship between transpiration rate and temperature for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (mean values).

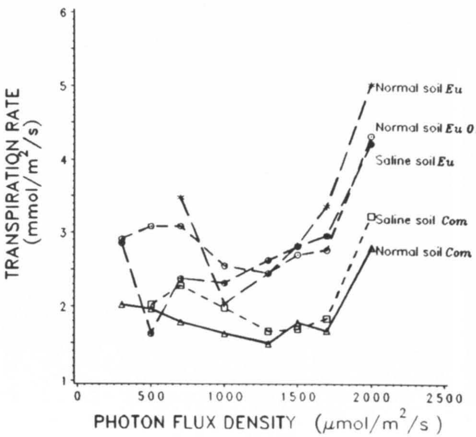


Figure 11. Relationship between transpiration rate and photon flux density for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (mean values).

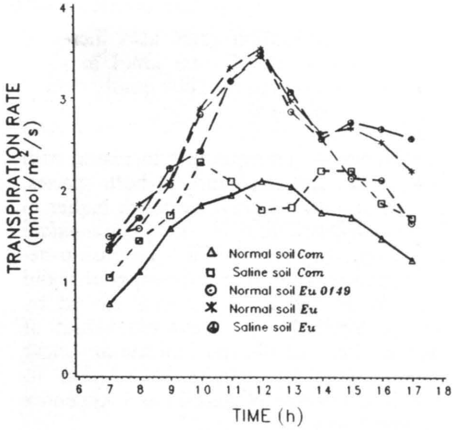


Figure 12. Average diurnal course of the transpiration rates for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

Appendix I, Tables 9 and 10). According to the model, the transpiration rates of both species increase with temperature on non-saline soil. However, transpiration decreases in the case of *E. camaldulensis* on saline soil when the temperature was over 30°C, while in *C. quadrangulare* it still increased. Model-based transpiration rates increased with irradiance for both species and on both non-saline and saline soils. The highest transpiration rate was for *E. camaldulensis* on non-saline soil (Figures 13 and 14).

The correlation between measured and predicted transpiration rates is illustrated by Figures 15 A—D, and the fitness of the two curves (based on measurements of individual trees) is shown in Appendix II (Figures 1 E—6 E).

According to the model, the diurnal course of the transpiration rate showed the highest level for *E. camaldulensis* on non-saline soil, whereas the lowest was associated with *C. quadrangulare* on saline soil. The rates for other treatments were intermediate between these extremes (Figure 16).

324. Water-use efficiency

Greenhouse experiments — The water-use efficiency (WUE, NP/Es) was decreased with increased salinity in both species (Table 8). The WUE of *E. camaldulensis* was better than *C. quadrangulare* at every level of salinities.

Field studies — The water-use efficiency of photosynthesis (WUE, NP/Tr), was at its peak in the morning from 08:00 to 11:00 h

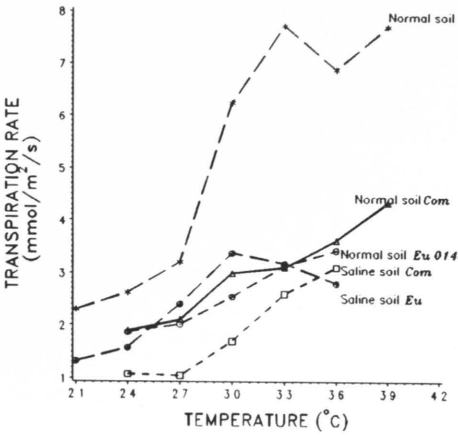


Figure 13. Relationship between the transpiration rate by the model (Eq. 21) and temperature for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (mean values).

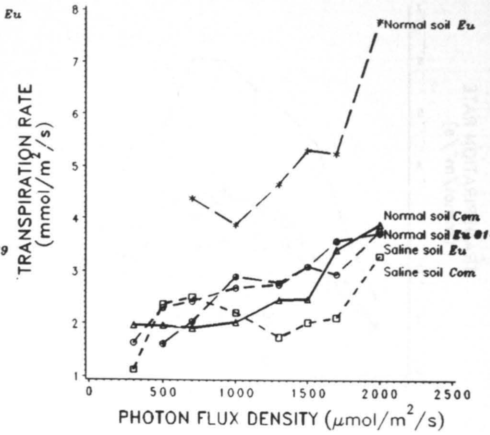


Figure 14. Relationship between the transpiration rate predicted by the model (Eq. 21) and photon flux density for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (mean values).

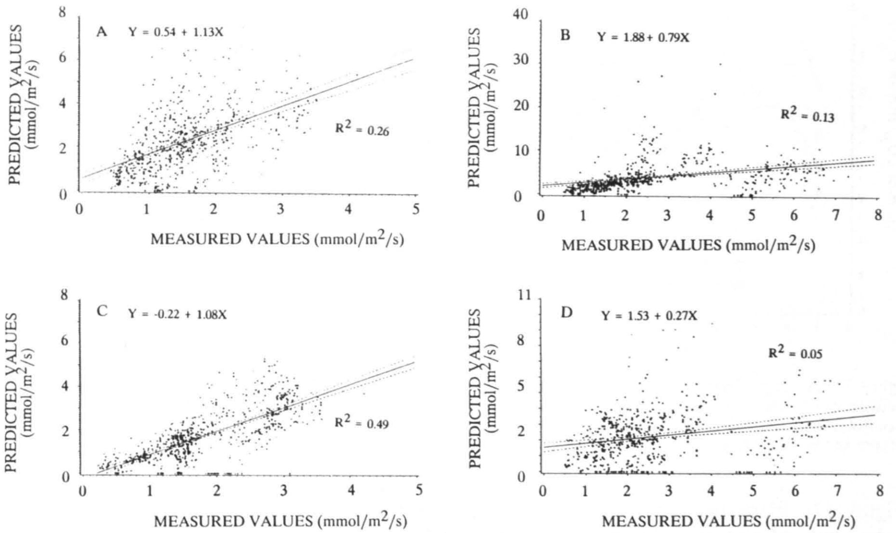


Figure 15. Relationship between predicted and measured transpiration rates in *Combretum quadrangulare* and *Eucalyptus camaldulensis* (local variety) on non-saline soils (A and B) and saline soils (C and D) respectively, in the field study.

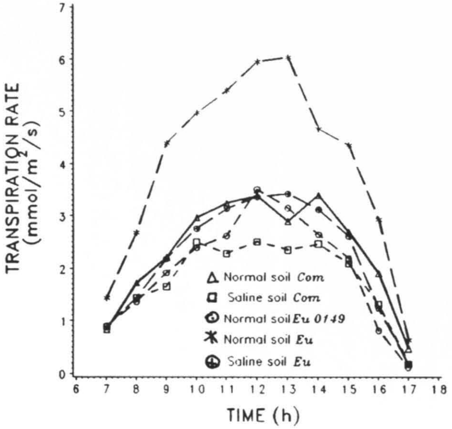


Figure 16. Average diurnal course of the transpiration rate as predicted by the model (Eq. 21) for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

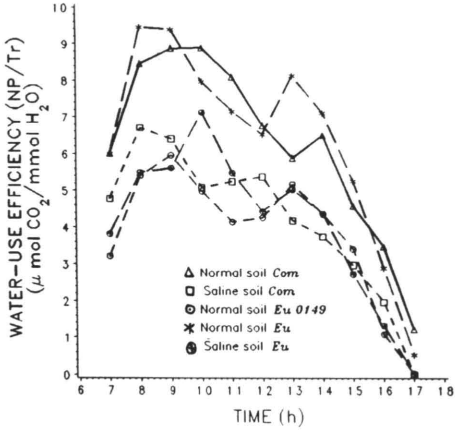


Figure 17. Average diurnal course of the water-use efficiency for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

(Figure 17). Water-use efficiency was higher in *E. camaldulensis* local variety than in *C. quadrangulare*, and higher on non-saline than on saline soils. The local variety of *E. camaldulensis* showed a higher efficiency than the one from Australian variety No. 0149 (Appendix I, Table 11). Furthermore, *C. quadrangulare* on saline soil showed a higher water-use efficiency than *E. camaldulensis* variety No. 0149 on the non-saline soil.

Water-use efficiency also varied significantly ($p < 0.001$) during the day. According to the model, the average water-use efficiency for *C. quadrangulare* was higher on saline than on non-saline soils from 07:00 to 12:00 h, except at 10:00 h but was lower on the saline than on the non-saline soils from 13:00 to 17:00 h except at 15:00 h. For *E. camaldulensis* (local variety), the average water-use efficiency was lower on the saline than on the non-saline soils from 07:00 to 17:00 h except only at 10:00 to 11:00 h (Appendix I, Table 12, and Appendix II, Figure 7). In the afternoon the average predicted water-use was more effective on non-saline than on saline soils in both species (Appendix II, Figure 7).

33. Effects of salinity on CO_2 exchange

331. Photosynthesis

Greenhouse experiments — Measurements of photosynthesis on greenhouse-grown seedlings indicated that, at each temperature and irradiance level, the net photosynthetic rate was higher ($p < 0.001$) in *E. camaldulensis* than in *C. quadrangulare* (Figures 18, 19 and 20). Within species, increasing salinity tended to decrease the photosynthetic rate. This effect was very distinct in seedlings grown in the culture solution (Appendix II, Figures 8, 9, 10 and 11). In contrast, no statistically confirmed differences within species were observed in seedlings grown in sand medium (Tables 4 and 5). In the greenhouse experiments, net photosynthesis saturation of control plants of both species occurred at a temperature of 27°C and irradiance of 700 μmol $m^{-2}s^{-1}$. Both the temperature and irradiance required for the maximal net photosynthetic rate decreased in both species with increasing salinity.

Field studies — The observed photosynthetic rates were higher in the field than in the greenhouse experiment. In the field, the rates of net photosynthesis increased up to temperatures of around 36°C (Table 6 and Appendix II, Figure 12). The light response of photosynthesis indicated that the net photosynthetic rates increased up to an irradiance level of 2000 μmol $m^{-2}s^{-1}$ in both species and on both soil types (Table 7 and Appendix II, Figure 13). Photosynthetic rates were higher on the non-saline than on the saline soils over the temperature and irradiance range studied and higher in *E. camaldulensis* (local variety) than in *C. quadrangulare* (Tables 6 and 7). The photosynthetic performance of *E. camaldulensis* variety No. 0149 on non-saline soil was poorer than that of the local variety of *E. camaldulensis* on the saline soil and *C. quadrangulare* on non-saline soil (Figure 21).

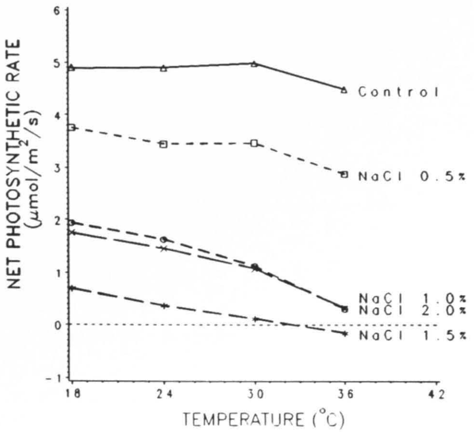


Figure 18. Relationship between net photosynthetic rate and temperature for *Combretum quadrangulare* at a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and different salinity levels. Mean values for seedlings grown in culture solution in the greenhouse.

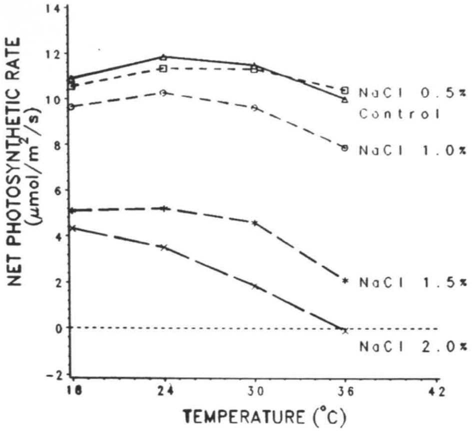


Figure 19. Relationship between net photosynthetic rate and temperature for *Eucalyptus camaldulensis* at a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and different salinity levels. Mean values for seedlings grown in culture solution in the greenhouse.

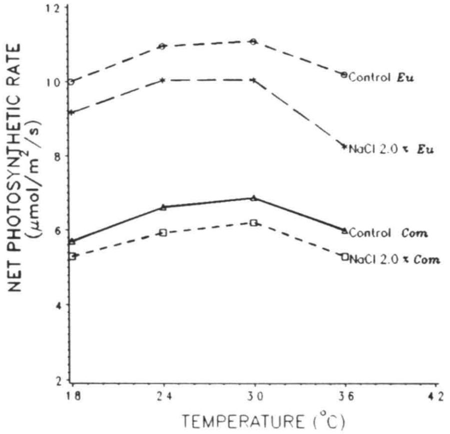


Figure 20. Relationship between net photosynthetic rate and temperature for *Combretum quadrangulare* and *Eucalyptus camaldulensis* at a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and different salinity levels. Mean values for seedlings grown in sand medium in the greenhouse.

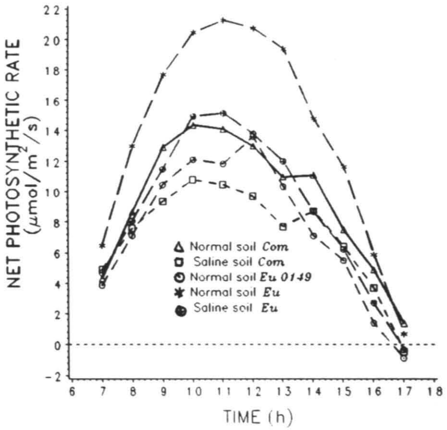


Figure 21. Diurnal course of the photosynthetic rate for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

Table 4. Means (±sd) of net photosynthesis of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 at a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and different temperatures 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 (%)	Net photosynthetic rate (NP, μmol $m^{-2}s^{-1}$) Temperature (°C) 18	24	30	36
(1)				
Com 0.0	4.90±1.91^{b}	4.91±2.79^{bc}	5.01±3.12^{b}	4.51±3.21^{b}
Com 0.5	3.75±1.41^{bc}	3.45±2.04^{bcd}	3.47±2.23^{bc}	2.89±2.23^{bc}
Com 1.0	1.93±0.75^{bc}	1.62±0.87^{cd}	1.13±0.73^{c}	0.30±0.41^{c}
Com 1.5	0.69±0.43	0.36±0.29^{d}	0.12±0.14^{c}	—0.16±0.17^{c}
Com 2.0	1.74±2.04^{bc}	1.45±1.88^{cd}	1.08±1.63^{c}	0.32±0.62^{c}
Eu 0.0	10.89±2.27^{a}	11.88±2.54^{a}	11.51±3.01^{a}	10.03±3.88^{a}
Eu 0.5	10.54±2.25^{a}	11.36±2.45^{a}	11.33±2.58^{a}	10.41±2.61^{a}
Eu 1.0	9.65±1.46^{a}	10.28±1.49^{a}	9.64±1.73^{a}	7.90±2.00^{a}
Eu 1.5	5.11±3.97^{b}	5.22±4.07^{b}	4.61±3.59^{b}	2.12±1.97^{bc}
Eu 2.0	4.32±2.59^{b}	3.53±1.89^{bcd}	1.86±1.29^{bc}	—0.10±0.36^{c}
F	14.65***	17.59***	17.88***	16.42***
$\bar{X}$	5.79	5.89	5.41	4.19
(2)				
Com 0.0	5.70±0.47^{b}	6.62±0.63^{b}	6.88±0.54^{b}	5.99±0.41^{b}
Com 2.0	5.29±0.94^{b}	5.92±1.21^{b}	6.20±1.54^{b}	5.30±1.75^{b}
Eu 0.0	9.99±1.54^{a}	10.95±1.63^{a}	11.08±1.66^{a}	10.19±1.32^{a}
Eu 2.0	9.15±2.00^{a}	10.32±2.06^{a}	10.05±1.91^{a}	8.25±1.62^{a}
F	12.12***	11.28***	10.00***	10.43***
$\bar{X}$	7.53	8.38	8.55	7.43

Table 5. Means (±sd) of net photosynthesis of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 at a temperature of 30°C and solution (1) and sand medium (2) greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species and salinity (%)	Net photosynthetic rate (NP, μmol $m^{-2}s^{-1}$) Irradiance (μmol $m^{-2}s^{-1}$) 300	500	1000	1500	2000
(1)					
Com 0.0	5.59±2.53^{bc}	5.54±2.23^{bc}	5.19±2.22^{cd}	4.63±2.34^{bcd}	3.23±2.34^{c}
Com 0.5	3.42±2.18^{cd}	3.69±2.25^{cd}	3.75±2.35^{cde}	3.61±2.42^{cd}	2.85±1.85^{c}
Com 1.0	1.61±1.74^{d}	2.08±2.10^{cd}	2.13±2.45^{de}	2.11±2.54^{cd}	1.79±2.45^{c}
Com 1.5	1.35±1.37^{d}	1.50±1.60^{d}	1.27±1.61^{e}	0.92±1.39^{cd}	0.60±0.84^{c}
Com 2.0	0.97±1.07^{d}	0.93±1.21^{d}	0.70±1.06^{e}	0.57±0.89^{d}	0.28±0.50^{c}
Eu 0.0	10.00±2.18^{a}	11.29±2.48^{a}	11.71±2.58^{a}	11.38±2.69^{a}	9.72±2.88^{a}
Eu 0.5	9.77±1.21^{a}	10.99±2.19^{a}	11.08±2.78^{a}	10.66±3.18^{a}	7.86±3.35^{ab}
Eu 1.0	9.79±2.66^{a}	10.32±3.47^{a}	9.63±3.96^{ab}	7.71±5.04^{ab}	4.34±5.36^{bc}
Eu 1.5	7.11±2.16^{ab}	8.02±2.65^{ab}	6.93±2.63^{bc}	5.00±2.66^{bc}	1.76±1.07^{c}
Eu 2.0	3.41±1.77^{cd}	3.50±2.06^{cd}	2.60±2.33^{de}	1.50±1.45^{cd}	0.34±0.50^{c}
F	15.98***	14.51***	13.24***	10.93***	8.62***
$\bar{X}$	7.73	6.28	6.06	5.41	3.86
(2)					
Com 0.0	4.75±0.72^{b}	5.11±1.14^{b}	4.90±1.09^{b}	4.16±0.99^{b}	3.11±0.63^{c}
Com 2.0	4.10±1.63^{b}	4.55±2.03^{b}	4.44±2.33^{b}	3.82±2.28^{b}	2.93±2.03^{c}
Eu 0.0	9.19±0.59^{a}	10.74±1.56^{a}	11.06±1.88^{a}	10.96±1.93^{a}	10.07±1.93^{a}
Eu 2.0	7.81±1.37^{a}	8.96±1.49^{a}	9.06±1.56^{a}	8.43±1.42^{a}	6.87±1.44^{b}
F	17.57***	14.21***	13.19***	16.05***	18.03***
$\bar{X}$	6.46	7.34	7.37	6.84	5.74

Table 6. Temperature dependence of net photosynthesis (mean±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (nonsignificant differences in the same column are indicated by same letters).

Species and soil type	Net photosynthetic rate (NP, μmol $m^{-2}s^{-1}$) Temperature (°C) 21	24	27	30	33	36	39
Com normal	—	13.51±2.39^{b}	13.05±2.50^{b}	13.44±3.01^{c}	13.70±4.59^{bc}	14.93±4.93^{b}	11.19±4.79^{a}
Com saline	—	11.09±3.12^{bc}	7.56±2.22^{d}	9.39±2.21^{e}	9.86±4.01^{d}	12.53±5.37^{b}	—
Eu0149 normal	—	11.28±3.92^{bc}	10.74±4.02^{c}	11.62±3.85^{d}	13.44±3.73^{c}	13.15±6.53^{b}	—
Eu normal	14.89±1.02^{a}	18.11±3.11^{a}	18.55±3.11^{a}	18.61±5.35^{a}	21.67±5.13^{a}	24.62±3.80^{a}	20.58±0.00^{a}
Eu saline	7.51±0.91^{b}	10.15±2.56^{c}	12.67±4.15^{b}	15.43±4.53^{b}	15.42±3.56^{b}	12.31±4.70^{b}	—
F	227.28***	21.64***	49.52***	38.71***	55.64***	31.18***	3.41^{ns}
$\bar{X}$	11.66	14.49	13.28	12.94	14.31	15.46	12.23

Table 7. Irradiance dependence of net photosynthesis (means±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (nonsignificant differences in the same column are indicated by same letters).

Species and soil type	Net photosynthetic rate (NP, μmol $m^{-2}s^{-1}$) Irradiance (μmol $m^{-2}s^{-1}$) 300	500	700	1000	1300	1500	1700	2000
Com normal	4.42±1.42^{a}	5.44±0.00^{b}	13.00±1.97^{ab}	11.83±3.15^{c}	13.02±2.54^{b}	13.11±1.88^{c}	14.33±3.42^{bc}	16.07±4.49^{b}
Com saline	3.10±0.00^{a}	8.67±2.63^{a}	9.17±2.29^{c}	10.09±3.31^{d}	9.60±2.19^{c}	9.89±4.27^{d}	8.90±4.01^{d}	15.78±5.04^{b}
Eu0149 normal	5.92±2.02^{a}	9.72±2.44^{a}	12.55±2.43^{ab}	12.92±3.75^{bc}	14.04±3.73^{b}	14.22±3.52^{bc}	13.77±4.54^{c}	16.56±6.06^{b}
Eu normal	—	—	14.65±6.88^{a}	16.32±3.00^{a}	18.91±3.96^{a}	20.75±4.52^{a}	21.50±4.27^{a}	24.44±4.25^{a}
Eu saline	6.33±1.52^{a}	9.13±2.57^{a}	11.29±2.59^{bc}	14.22±4.02^{b}	14.98±3.14^{b}	15.83±3.50^{b}	15.93±4.78^{b}	15.83±5.53^{b}
F	1.83^{ns}	2.34^{ns}	8.34***	22.00***	32.15***	56.05***	42.75***	13.56***
$\bar{X}$	5.89	9.37	11.18	12.78	14.50	15.09	15.33	17.63

The results derived from a single leaf, the photosynthetic rates of *C. quadrangulare* and *E. camaldulensis* (local variety) were the same on the non-saline as on the saline soils. Both species are shown in Appendix II, Figures 2D and 4D, respectively.

332. CO_2 compensation point, Γ

Greenhouse experiments — The results from the greenhouse experiment demonstrated some significant differences in CO_2 compensation points (Γ) between *C. quadrangulare* and *E. camaldulensis* and between the salinity treatments (Table 8). The values of Γ for the *C. quadrangulare* ($p < 0.001$) and *E. camaldulensis* seedlings ($p > 0.05$) increased with the salinity of the culture solution (Figures 22, 23 and 24). In these seedlings, Γ was also significantly higher for *C. quadrangulare* than for *E. camaldulensis*, at all salinity levels (Figure 25). For *C. quadrangulare*, salinity levels of 1.0 % or higher increased Γ to values near the ambient CO_2 concentration; this was also reflected in the very low net photosynthetic rates observed.
In contrast, no statistically confirmed differences in Γ were found between the species in the seedlings grown in sand medium. Neither did salinity cause any increase in Γ.

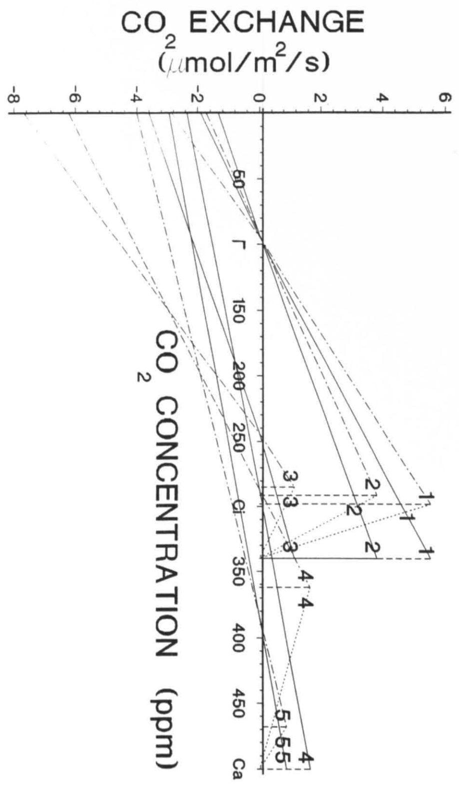
333. Photorespiration

Greenhouse experiments — Laboratory measurements of the photorespiration rate were extrapolated from the values of carboxylation efficiency and CO_2 compensation point (Γ), according to Equations (1) and (2). Due to the underestimation of the extrapolated photorespiration (Pr), corrected values (Rl) were calculated using the intercellular CO_2 concentrations (Ci) (Equations 3—9). Both sets of results are shown in Table 8 and Figures 22, 23 and 24.

The maximal corrected photorespiration rates (Rl) of the seedlings grown in culture solution, found at 30°C and a photon flux density of 1000 μmol $m^{-2}s^{-1}$, were 7.68 μmol $mm^{-2}s^{-1}$ for *C. quadrangulare* (at 1.0 % salinity) and 9.13 μmol $m^{-2}s^{-1}$ for *E. camaldulensis* (at 1.5 % salinity). In the case of *C. quadrangulare*, photorespiration rates tended to decrease with an increase in salinity from 0 % to 0.5 % and then increase

Table 8. Means (±sd) of total and net photosynthesis, photorespiration, dark respiration, transpiration, water-use efficiency (NP/Es) and CO_2 compensation point (Γ) of *combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 at 30°C and a photon flux density of 1000 μmol $m^{-2}s^{-1}$ 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 (%)	Total photosynthesis (μmol $m^{-2}s^{-1}$)	Net (photosynthesis (NP) (μmol $m^{-2}s^{-1}$)	Photorespiration (μmol $m^{-2}s^{-1}$) Extrapolated	Photorespiration (μmol $m^{-2}s^{-1}$) Corrected	Dark respiration (μmol $m^{-2}s^{-1}$)	Transpiration (Tr) (μmol $m^{-2}s^{-1}$)	Water-use efficiency (μmol CO_2/mmol H_2O)	CO_2 comp. point (Γ) (ppm)
(1)								
Com 0.0	7.86±1.92^{abc}	5.01±3.12^{b}	1.89±0.72^{ab}	2.85±2.15^{ab}	0.91±0.01^{ab}	2.11±1.01^{cde}	2.19±0.68^{ab}	94.25±56.76^{d}
Com 0.5	5.18±2.68^{c}	3.47±2.24^{bcd}	1.34±0.41^{b}	1.71±0.68^{b}	0.72±0.16^{b}	1.80±1.18^{de}	1.94±0.64^{abc}	92.75±24.85^{d}
Com 1.0	8.81±8.69^{abc}	1.13±0.73^{cd}	3.60±2.89^{a}	7.68±8.29^{ab}	1.37±0.10^{a}	1.24±0.55^{de}	0.79±0.49^{de}	244.25±49.52^{bc}
Com 1.5	6.33±8.45^{bc}	0.12±0.14^{d}	2.34±2.30^{ab}	6.21±8.41^{ab}	0.98±0.14^{ab}	0.62±0.14^{e}	0.22±0.22^{e}	286.75±178.52^{b}
Com 2.0	5.09±1.99^{c}	1.08±1.63^{cd}	2.93±0.60^{ab}	4.01±1.44^{ab}	0.73±0.20^{b}	1.57±1.30^{de}	0.48±0.42^{e}	383.75±107.95^{a}
Eu 0.0	14.71±3.71^{a}	11.51±3.01^{a}	2.72±0.82^{ab}	3.22±1.08^{ab}	1.16±0.36^{ab}	5.03±2.04^{abc}	2.48±0.90^{a}	77.00±9.70^{d}
Eu 0.5	15.43±3.66^{a}	11.33±2.58^{a}	2.73±0.46^{ab}	3.76±0.62^{ab}	1.07±0.28^{ab}	5.46±3.34^{ab}	2.43±0.92^{a}	72.75±10.14^{d}
Eu 1.0	13.19±1.94^{abc}	9.64±1.73^{a}	2.84±0.47^{ab}	3.55±0.36^{ab}	1.24±0.29^{a}	6.53±3.09^{a}	1.69±0.67^{abcd}	89.50±26.71^{d}
Eu 1.5	13.74±9.96^{ab}	4.61±3.59^{bc}	2.77±1.15^{ab}	9.13±7.26^{a}	1.02±0.46^{ab}	3.85±3.23^{abcd}	1.20±0.68^{bcde}	138.50±28.34^{d}
Eu 2.0	5.58±1.53^{c}	2.49±1.29^{bcd}	2.43±1.22^{ab}	2.90±1.44^{ab}	1.04±0.48^{ab}	2.83±1.27^{bcde}	0.90±0.99^{cde}	157.25±32.50^{cd}
F	3.00**	16.46***	0.88^{ns}	1.29^{ns}	1.86^{ns}	4.43***	5.90***	10.39***
$\bar{X}$	10.04	5.63	2.57	4.38	1.04	3.26	1.50	155.80
(2)								
Com 0.0	9.67±1.28^{b}	6.88±0.54^{b}	2.20±0.54^{b}	2.79±0.86^{b}	0.86±0.08^{c}	2.03±0.40^{b}	3.48±0.67^{a}	75.50±8.66^{a}
Com 2.0	8.57±2.24^{b}	6.20±1.53^{b}	1.99±0.73^{b}	2.38±0.98^{b}	0.92±0.13^{bc}	2.19±0.51^{ab}	2.91±0.82^{a}	74.00±7.39^{a}
Eu 0.0	16.02±2.22^{a}	11.08±1.66^{a}	4.00±0.63^{a}	4.94±0.93^{a}	1.11±0.14^{a}	2.87±0.50^{ab}	3.91±0.58^{a}	83.50±7.59^{a}
Eu 2.0	13.49±2.64^{a}	10.04±1.91^{a}	2.96±0.73^{b}	3.45±0.84^{b}	1.07±0.08^{ab}	3.20±1.11^{a}	3.33±0.78^{a}	85.25±10.40^{a}
F	10.20***	10.00***	7.54**	6.21**	4.82*	2.56^{ns}	1.32^{ns}	1.72^{ns}
$\bar{X}$	11.94	8.55	2.79	3.39	0.99	2.57	3.41	79.56



Figural 22. Principles used in recalculation of photorespiration rate and estimation of different components of CO_2 diffusion resistance, with actual mean values of net photosynthetic rate and CO_2 compensation point at 30°C in each treatment group (1 = control, 2 = 0.5 %, 3 = 1.0 %, 4 = 1.5 % and 5 = 2.0 % salinity) for *Combretum quadrangulare* seedlings grown in culture solution. Slopes of the lines correspond to the following resistance components: Σr' (solid line), r_{mx} (dotted-broken line) and r'_g (dotted line). Ca = ambient, Ci = intercellular CO_2 concentration; Γ = CO_2 compensation point.

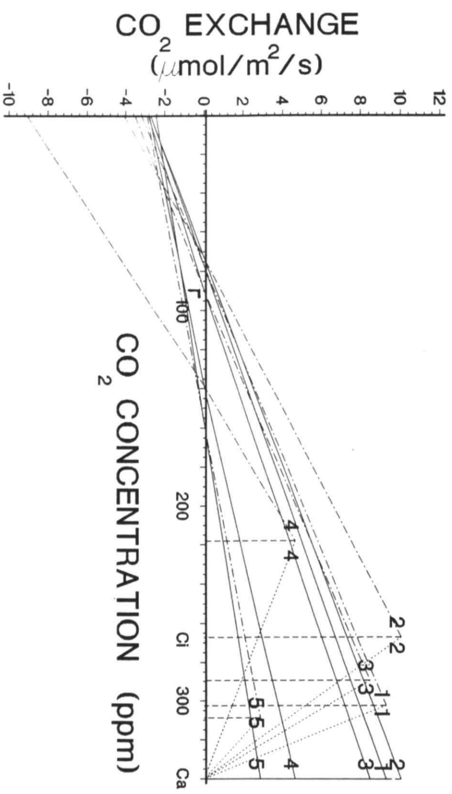


Figure 23. Principles used in recalculation of photorespiration rate and estimation of different components of CO_2 diffusion resistance, with actual mean values of net photosynthetic rate and CO_2 compensation point at 30°C in each treatment group (1 = control, 2 = 0.5 %, 3 = 1.0 %, 4 = 1.5 % and 5 = 2.0 % salinity) for *Eucalyptus camaldulensis* seedlings grown in culture solution. Slopes of the lines corresponding to the following resistance components: Σr' (solid line), r_{mx} (dotted-broken line) and r'_g (dotted line). Ca = ambient, Ci = intercellular CO_2 concentration; Γ = CO_2 compensation point.

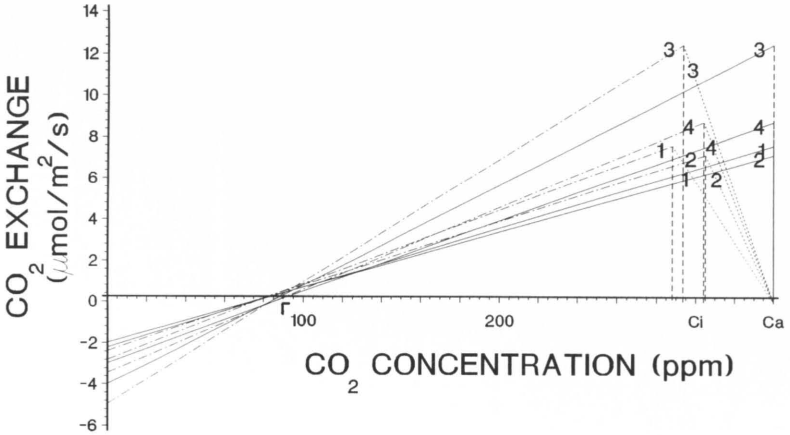


Figure 24. Principles used in recalculation of photorespiration rate and estimation of different components of CO_2 diffusion resistance, with actual mean values of net photosynthetic rate and CO_2 compensation point at 30°C in each treatment group (1 = Com/control, 2 = Com/2.0 % salinity, 3 = Eu/ control and 4 = Eu/2.0 % salinity) for *Combretum quadrangulare* and *Eucalyptus camaldulensis* seedlings grown in sand medium. Slopes of the lines correspond to the following resistance components: $\Sigma r'$ (solid line) r_{mx} (dotted-broken line) and r'_g (dotted line). Ca = ambient, Ci = intercellular CO_2 concentration; Γ = CO_2 compensation point.

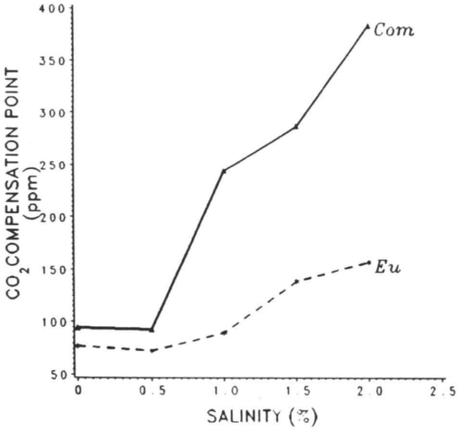


Figure 25. Relationship between CO_2 compensation point and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis* at temperature 30°C and photon flux density of 1000 μmol $m^{-2}s^{-1}$. Mean values for seedlings grown in culture solution in the greenhouse.

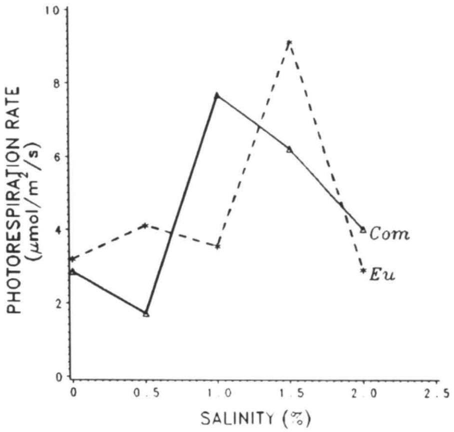


Figure 26. Relationship between photorespiration rate and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis* at temperature 30°C and photon flux density of 1000 μmol $m^{-2}s^{-1}$. Mean values for seedlings grown in culture solution in the greenhouse.

from 0.5 % to 1.0 % and finally decrease from 1.0 % to 2.0 % (Figure 26). In the case of *E. camaldulensis*, changes in Rl with salinity were irregular (Figure 26).

Of the seedlings grown in the sand medium, Rl seemed to be higher for *E. camaldulensis* than for *C. quadrangulare*, in both the non-saline and saline (2 %) sand: This variation, as well as the effect of salinity on Γ in sand-grown seedlings, was statistically confirmed ($p < 0.01$).

334. Modeled photorespiration rates from field data

Photorespiration rates in the field (R) for both species and different soil sites were estimated using the means of the corrected photorespiration values (Rl) observed in the laboratory measurements at 30°C and photon flux density 1000 μmol $m^{-2}s^{-1}$ (Table 8) and Equation (15). The results are shown in Appendix I, Tables 13 and 14.

The calculated photorespiration rates increased with temperature and irradiance. Photorespiration rates for both species were also higher on saline than non-saline soils over the temperature range 21°—36°C (Appendix I, Table 13). R values for *C. quadrangulare* and *E. camaldulensis* were similar on saline soil but higher for *E. camaldulensis* on non-saline soil (Figure 27). During the day, R gradually rose from 07:00 to 12:00 h and then remained quite constant until 15:00 h, after which it decreased (Figure 28).

335. Dark respiration

The results of the laboratory experiments indicated that dark respiration rates increased steadily with temperature over the range used (18° to 36°C). In both species and at each temperature, the highest dark respiration rates were found at 1.0 % salinity concentration, but only in the case of *C. quadrangulare* was the difference between the highest rate at 1.0 % and the lowest rate at 0.5 % and 2.0 % statistically confirmed. No difference in the dark respiration rate was found between the species in the culture solution seedling experiment (Figures 29, 30 and 31, Table 9).

In the sand medium experiment, dark respiration rates were somewhat higher for *E. camaldulensis* than for *C. quadrangulare*, both in non-saline (0 %) and saline (2.0 %) treatments. This difference was, however, statistically significant (Table 9 and Figure 31).

336. Components of H_2O and CO_2 diffusion resistance

Greenhouse experiments — Components of CO_2 and H_2O diffusion resistance were measured on greenhouse-grown seedlings using both IRGA and porometer measurements; the results are summarized in Table 10.

Salinity generally caused an increase in stomatal as well as in mesophyll resistance (the only exception being *C. quadrangulare* in sand medium in which the stomatal resis-

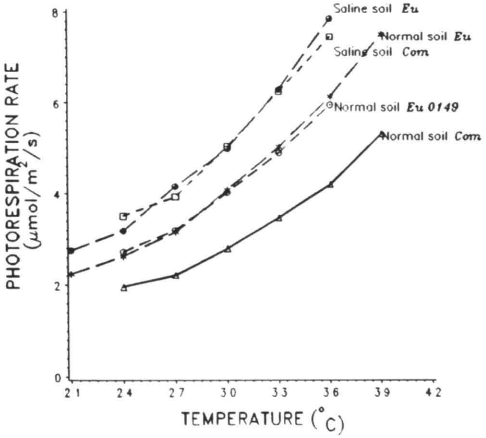


Figure 27. Relationship between the calculated photorespiration rate and temperature for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (mean values).

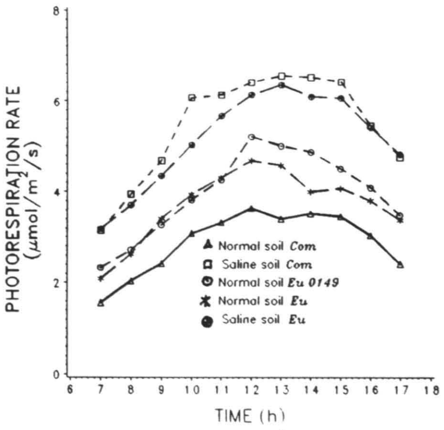


Figure 28. Average diurnal course of the calculated photorespiration rate for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

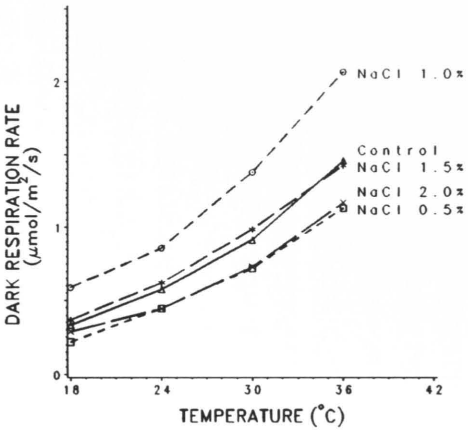


Figure 29. Relationship between dark respiration rate and temperature for *Combretum quadrangulare* at different salinity levels. Mean values for seedlings grown in culture solution in the greenhouse.

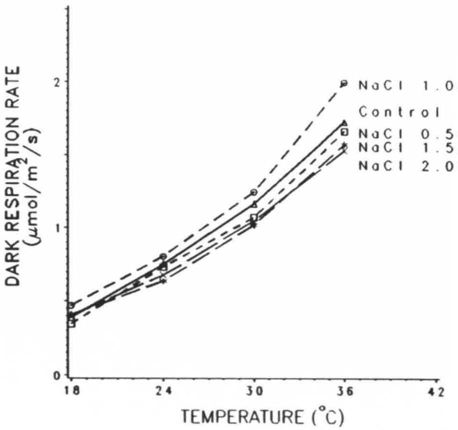


Figure 30. Relationship between dark respiration rate and temperature for *Eucalyptus camaldulensis* at different salinity levels. Mean values for seedlings grown in culture solution in the greenhouse.

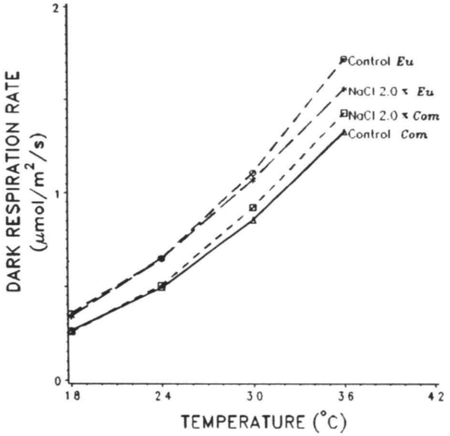


Figure 31. Relationship between dark respiration rate and temperature for *Combretum quadrangulare* and *Eucalyptus camaldulensis* at different salinity levels. Mean values for seedlings grown in culture solution in the greenhouse.

tance decreased as a result of higher salinity concentration). The mesophyll resistance to CO_2 diffusion (r_{mx}) was usually much higher than the corresponding stomatal resistance at every salinity level. On average, *C. quadrangulare* showed higher values for each resistance component than *E. camaldulensis*, $\Sigma r'$ ($p < 0.01$), r'g ($p < 0.01$), r_{mx} ($p < 0.05$), and r's ($p < 0.01$); both in IRGA and porometer measurements.

The leaf resistance to H_2O (rg) measured with the porometer under natural light and converted to the corresponding value for CO_2 resistance (r'g) was much higher than r'g measured with the IRGA under artificial light except for at the 1.0 % and 1.5 % salinity treatments for *C. quadrangulare* and at the 1.5 % salinity treatment for *E. camaldulensis*.

Of the seedlings grown in the sand medium, the salinity treatment (2 %) did not cause any statistically significant change in the resistance components in either of the two species. However, when measured with the porometer, the leaf resistance was again higher than when measured using IRGA (Table 10), and obviously for the same reason as in seedlings grown in culture solution, *i.e.* because of the different environmental conditions during IRGA and porometer measurements.

Field studies — The stomatal H_2O diffusion resistance (rs), as measured using the portable IRGA apparatus (LI-6250), was smaller than that observed in the greenhouse experiments by an order of magnitude. *C. quadrangulare* had higher values of rs than *E. camaldulensis* (Tables 11 and 12). Trees growing on the saline soil sites had, on an average, higher stomatal resistances than those growing on the non-saline control sites; this trend was observed in both species (Appendix II, Figures 14 and 15). Temperature and irradiance did not cause much distinct variation in the stomatal resistance (Tables 11 and 12).

The average diurnal course of measured stomatal conductance to CO_2 (g) in the field (Figure 32) also indicated differences related to site salinity and species, but these differences only occurred between 09:00 and 13:00 h. During this time the highest values of g were observed for *E. camaldulensis* growing on both the non-saline and saline soils, while g was higher on non-saline than saline soils, whereas for *C. quadrangulare* on both soil types, conductance reached only half of the maximum values and g was higher on saline than non-saline soils.

Table 9. Means (±sd) of dark respiration of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 at different temperatures 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 (%)	Dark respiration rate (µmol $m^{-2}s^{-1}$) Temperature (°C) 18	24	30	36
(1)				
Com 0.0	0.33 ± 0.05^{ab}	0.57 ± 0.10^{ab}	0.91 ± 0.11^{ab}	1.45 ± 0.18^{ab}
Com 0.5	0.22 ± 0.09^{b}	0.44 ± 0.09^{b}	0.72 ± 0.16^{b}	1.13 ± 0.27^{b}
Com 1.0	0.59 ± 0.25^{a}	0.86 ± 0.07^{a}	1.37 ± 0.10^{a}	2.06 ± 0.29^{a}
Com 1.5	0.37 ± 0.15^{ab}	0.62 ± 0.25^{ab}	0.98 ± 0.14^{ab}	1.42 ± 0.11^{ab}
Com 2.0	0.29 ± 0.13^{b}	0.44 ± 0.10^{b}	0.73 ± 0.20^{b}	1.16 ± 0.16^{b}
Eu 0.0	0.39 ± 0.16^{ab}	0.75 ± 0.23^{ab}	1.16 ± 0.36^{ab}	1.72 ± 0.36^{ab}
Eu 0.5	0.34 ± 0.09^{ab}	0.73 ± 0.18^{ab}	1.07 ± 0.28^{ab}	1.66 ± 0.52^{ab}
Eu 1.0	0.47 ± 0.25^{ab}	0.80 ± 0.37^{ab}	1.24 ± 0.29^{a}	1.99 ± 0.75^{a}
Eu 1.5	0.41 ± 0.23^{ab}	0.63 ± 0.26^{ab}	1.02 ± 0.46^{ab}	1.57 ± 0.51^{ab}
Eu 2.0	0.40 ± 0.17^{ab}	0.68 ± 0.35^{ab}	1.04 ± 0.48^{ab}	1.53 ± 0.76^{ab}
F	1.42^{ns}	1.52^{ns}	1.86^{ns}	1.81^{ns}
$\overline{X}$	0.38	0.66	1.03	1.58
(2)				
Com 0.0	0.26 ± 0.01^{b}	0.50 ± 0.03^{b}	0.86 ± 0.09^{c}	1.33 ± 0.10^{b}
Com 2.0	0.26 ± 0.03^{b}	0.51 ± 0.06^{b}	0.92 ± 0.13^{bc}	1.43 ± 0.17^{b}
Eu 0.0	0.35 ± 0.05^{a}	0.65 ± 0.07^{a}	1.11 ± 0.14^{a}	1.72 ± 0.19^{a}
Eu 2.0	0.34 ± 0.04^{a}	0.65 ± 0.05^{a}	1.07 ± 0.09^{ab}	1.56 ± 0.15^{ab}
F	8.10**	9.09**	4.82*	4.57*
$\overline{X}$	0.30	0.58	0.93	1.51

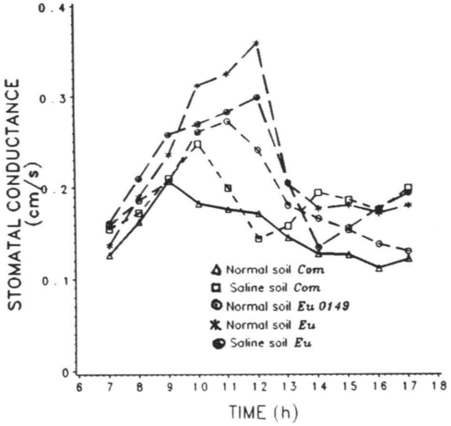


Figure 32. The average diurnal course of stomatal conductance for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non saline (normal) and saline soil types in the field study (IRGA measurements).

34. Modelling of photosynthesis without the effect of a water deficit

341. Model based on estimated α and measured g

The response of photosynthesis to irradiance is known to be non-linear. The parameter α is one of the essential factors for describing the photosynthetic rate (Equation 11) when using a non-linear equation. This parameter is associated with the biochemical reactions of photosynthesis and the regulation of

Table 10. Means (±sd) of the components of CO_2 diffusion resistance of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 measured with IRGA at a temperature of 30°C and a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and leaf resistances measured with porometer at varying temperature and irradiance in different salinity treatments of seedlings grown in the solution (1) and sand medium (2) greenhouse experiments (nonsignificant differences in the same column are indicated by same letters). $r'a = 0.70 \pm 0.28$ s cm^{-1} which is a constant value.

Species and salinity (%)	CO_2 resistance components (IRGA, s cm^{-1}) $\Sigma r'$	$r'g$	r_{mx}	$r's$	Leaf resistance (porometer, s cm^{-1}) rg (adaxial)	rg (abaxial)	rg (combined)	$r'g$ (combined)
(1)								
Com 0.0	19.56 ± 5.17^{cd}	4.64 ± 6.25^{bc}	14.91 ± 4.03^{b}	3.94 ± 6.25^{bc}	18.79 ± 5.25^{bcd}	5.90 ± 1.28^{cde}	4.49 ± 1.03^{cd}	7.18 ± 1.65^{cd}
Com 0.5	30.03 ± 11.56^{bcd}	5.27 ± 0.90^{bc}	24.75 ± 11.39^{b}	4.57 ± 0.90^{bc}	21.38 ± 4.23^{bc}	6.50 ± 1.08^{cd}	4.98 ± 0.86^{c}	7.97 ± 1.37^{c}
Com 1.0	48.57 ± 37.28^{abc}	11.68 ± 8.86^{abc}	36.88 ± 32.70^{ab}	10.98 ± 8.86^{abc}	26.27 ± 9.89^{b}	7.46 ± 0.21^{bc}	5.96 ± 0.45^{c}	9.10 ± 0.73^{c}
Com 1.5	79.50 ± 56.77^{a}	18.04 ± 9.77^{a}	61.11 ± 58.12^{a}	17.69 ± 58.12^{a}	35.81 ± 4.38^{a}	9.90 ± 2.01^{b}	7.67 ± 1.13^{b}	12.28 ± 1.81^{b}
Com 2.0	56.42 ± 23.89^{ab}	13.55 ± 8.90^{ab}	42.87 ± 22.16^{ab}	12.85 ± 8.90^{ab}	39.49 ± 6.44^{a}	14.32 ± 2.26^{a}	10.46 ± 1.42^{a}	16.73 ± 2.27^{a}
Eu 0.0	12.45 ± 4.33^{cd}	1.61 ± 0.62^{c}	10.84 ± 4.42^{b}	0.91 ± 0.62^{c}	6.37 ± 2.50^{e}	2.82 ± 1.09^{f}	1.95 ± 0.75^{e}	3.12 ± 1.20^{e}
Eu 0.5	10.92 ± 1.48^{d}	2.91 ± 0.81^{c}	8.01 ± 1.80^{b}	2.21 ± 0.81^{c}	10.49 ± 8.51^{de}	3.51 ± 1.82^{ef}	2.54 ± 1.47^{e}	4.06 ± 2.35^{e}
Eu 1.0	12.76 ± 3.24^{cd}	2.34 ± 1.46^{c}	10.42 ± 3.69^{b}	1.64 ± 1.45^{c}	13.22 ± 7.70^{cde}	4.18 ± 1.70^{def}	3.12 ± 1.50^{de}	4.99 ± 2.40^{de}
Eu 1.5	25.49 ± 17.35^{bcd}	16.47 ± 16.42^{a}	9.02 ± 4.89^{b}	15.76 ± 16.24^{a}	19.12 ± 6.49^{bcd}	8.70 ± 4.87^{bc}	5.74 ± 2.32^{c}	9.18 ± 3.71^{c}
Eu 2.0	32.83 ± 18.99^{bcd}	5.34 ± 3.84^{bc}	27.48 ± 15.49^{b}	4.64 ± 3.84^{bc}	24.72 ± 6.96^{b}	7.32 ± 1.19^{bc}	5.60 ± 0.98^{c}	8.95 ± 1.57^{c}
F	4.04**	3.40**	3.45*	3.40**	12.76***	13.02***	19.05***	19.05***
$\overline{X}$	31.00	7.62	23.38	6.92	21.57	7.06	5.22	8.36
(2)								
Com 0.0	14.27 ± 2.23^{ab}	2.75 ± 1.31^{a}	11.52 ± 2.64^{ab}	2.05 ± 1.31^{a}	12.51 ± 14.22^{a}	6.00 ± 7.27^{a}	4.05 ± 4.81^{a}	6.47 ± 7.70^{a}
Com 2.0	17.07 ± 7.86^{a}	2.01 ± 2.09^{a}	15.06 ± 8.55^{a}	1.31 ± 2.09^{a}	8.77 ± 7.62^{a}	4.07 ± 2.59^{a}	2.75 ± 1.95^{a}	4.41 ± 3.13^{a}
Eu 0.0	8.66 ± 1.76^{b}	1.63 ± 1.15^{a}	7.02 ± 1.47^{b}	0.93 ± 1.15^{a}	9.26 ± 8.29^{a}	3.49 ± 3.13^{a}	2.25 ± 1.71^{a}	3.60 ± 2.73^{a}
Eu 2.0	11.97 ± 1.90^{ab}	1.71 ± 0.76^{a}	10.26 ± 1.51^{ab}	1.01 ± 0.76^{a}	16.27 ± 10.44^{a}	5.56 ± 3.48^{a}	4.09 ± 2.53^{a}	6.55 ± 4.06^{a}
F	2.77^{ns}	0.52^{ns}	2.45^{ns}	0.52^{ns}	0.55^{ns}	0.35^{ns}	0.47^{ns}	0.47^{ns}
$\overline{X}$	12.99	2.03	10.96	1.32	11.70	4.78	3.29	5.26

Table 11. Temperature dependence of stomatal resistance (means±sd) to H_2O of *Combretum quadrangulare* and *Eucalyptus camaldulensis* 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	Stomatal resistance (rs, s cm^{-1}) Temperature (°C) 21	24	27	30	33	36	39
Com normal	—	4.28 ± 1.40^{a}	4.11 ± 1.20^{b}	5.57 ± 2.40^{a}	3.62 ± 2.50^{ab}	2.64 ± 1.20^{ab}	3.72 ± 2.00^{a}
Com saline	—	4.34 ± 4.70^{a}	8.63 ± 7.40^{a}	5.91 ± 3.80^{a}	4.63 ± 3.90^{a}	3.55 ± 3.80^{a}	—
Eu0149 normal	—	3.67 ± 0.60^{a}	3.11 ± 0.80^{bc}	2.74 ± 0.80^{b}	2.60 ± 1.10^{bc}	2.47 ± 1.40^{ab}	—
Eu normal	3.28 ± 0.20^{a}	2.83 ± 0.80^{a}	2.37 ± 0.70^{c}	1.97 ± 1.10^{b}	1.85 ± 0.60^{c}	2.05 ± 0.40^{b}	1.65 ± 0.00^{a}
Eu saline	4.05 ± 1.10^{a}	3.49 ± 1.50^{a}	3.26 ± 1.50^{bc}	2.29 ± 0.90^{b}	2.93 ± 3.00^{bc}	2.15 ± 0.40^{b}	—
F	4.40^{ns}	2.11^{ns}	24.49***	38.20***	10.06***	2.66*	0.99^{ns}
$\overline{X}$	3.62	3.43	3.69	3.97	3.27	2.71	3.49

Table 12. Irradiance dependence of stomatal resistance (means±sd) to H_2O of *Combretum quadrangulare* and *Eucalyptus camaldulensis* with LI-6250 on non-saline (normal) and saline soil types in the field study at 09:00 to 12:00 h (nonsignificant differenses in the same column are indicated by same letters).

Species and soil type	Stomatal resistance (rs, s cm^{-1}) Irradiance (μmol $m^{-2}s^{-1}$) 300	500	700	1000	1300	1500	1700	2000
Com normal	3.92 ± 1.50^{b}	3.28 ± 0.00^{a}	3.39 ± 1.00^{a}	3.86 ± 1.90^{b}	3.72 ± 0.90^{b}	3.76 ± 1.10^{b}	5.71 ± 2.90^{a}	3.01 ± 1.50^{a}
Com saline	16.72 ± 0.00^{a}	3.06 ± 1.20^{a}	2.67 ± 1.80^{ab}	5.52 ± 6.20^{a}	5.25 ± 2.10^{a}	6.37 ± 3.50^{a}	7.01 ± 4.70^{a}	2.07 ± 0.70^{bc}
Eu0149 normal	3.05 ± 1.00^{b}	2.71 ± 0.80^{a}	2.39 ± 0.80^{ab}	2.92 ± 0.90^{bc}	2.98 ± 0.90^{bc}	2.97 ± 1.10^{bc}	3.18 ± 1.30^{b}	2.64 ± 0.60^{ab}
Eu normal	—	—	1.59 ± 0.10^{b}	2.78 ± 0.90^{b}	2.49 ± 1.10^{c}	2.15 ± 0.70^{c}	1.98 ± 0.50^{b}	1.82 ± 0.50^{c}
Eu saline	2.32 ± 1.20^{b}	3.34 ± 1.00^{a}	3.22 ± 1.80^{a}	2.94 ± 1.30^{b}	2.81 ± 1.00^{c}	2.39 ± 0.80^{c}	3.25 ± 3.40^{b}	2.17 ± 0.60^{bc}
F	52.95***	2.08^{ns}	1.77^{ns}	5.16***	18.19***	36.55***	18.94***	6.72***
$\overline{X}$	3.20	2.88	2.73	3.84	3.45	3.62	4.33	2.37

Table 13. Means ($\pm$sd) of the estimated parameters of the photosynthesis model of *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (nonsignificant differences in the same column are indicated by same letters).

Species and soil type	Parameters						
	Measured	Estimated α and g_0		Estimated g_0	Estimated α	Estimated λ	
	g (correlated)(cm s^{-1})	α ($cm^3 \mu mol^{-1}$)	g0 (cm s^{-1})	g0 (cm s^{-1})	α ($cm^3 \mu mol^{-1}$)	λ	u*
Com normal	0.16 ± 0.06^{d}	1.73 ± 0.70^{c}	0.18 ± 0.07^{bc}	0.18 ± 0.08^{d}	1.89 ± 0.62^{bc}	0.003 ± 0.002^{a}	0.82 ± 0.11^{a}
Com saline	0.18 ± 0.10^{cd}	2.16 ± 0.44^{b}	0.13 ± 0.07^{c}	0.17 ± 0.10^{cd}	1.59 ± 0.37^{d}	0.003 ± 0.002^{b}	0.84 ± 0.11^{a}
Eu0149 normal	0.19 ± 0.07^{bc}	2.29 ± 0.55^{ab}	0.18 ± 0.10^{bc}	0.21 ± 0.12^{bc}	2.08 ± 0.69^{b}	0.004 ± 0.002^{a}	0.70 ± 0.10^{b}
Eu normal	0.22 ± 0.03^{a}	2.44 ± 0.55^{a}	0.33 ± 0.21^{a}	0.27 ± 0.07^{a}	2.58 ± 0.69^{a}	0.002 ± 0.002^{b}	0.83 ± 0.10^{a}
Eu saline	0.21 ± 0.06^{ab}	2.47 ± 0.77^{a}	0.19 ± 0.10^{b}	0.24 ± 0.13^{ab}	1.74 ± 0.51^{cd}	0.004 ± 0.002^{a}	0.74 ± 0.12^{b}
F	7.92***	11.84***	17.95***	8.87***	21.11***	4.17**	15.32***
$\bar{X}$	0.19	2.22	0.20	0.21	1.98	0.003	0.79

Table 14. Means ($\pm$sd) of the residual mean squares from estimation of the different values of the parameters of the photosynthesis model of *combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (nonsignificant differences in the same column are indicated by same letters).

Species and soil type	Residual mean square			
	α & g_0	g_0	α	λ
Com normal	8.21E—09$\pm$1.0E—08^{b}	9.90E—09$\pm$1.0E—08^{ab}	1.27E—08$\pm$1.0E—08^{bc}	9.76E—09$\pm$1.0E—08^{a}
Com saline	7.77E—09$\pm$1.0E—08^{b}	8.35E—09$\pm$1.0E—08^{b}	9.27E—08$\pm$1.0E—08^{c}	6.93E—09$\pm$1.0E—08^{a}
Eu 0149 normal	1.03E—08$\pm$1.0E—08^{ab}	1.12E—08$\pm$1.0E—08^{ab}	1.21E—08$\pm$1.0E—08^{ab}	1.03E—08$\pm$1.0E—08^{a}
Eu normal	1.26E—08$\pm$1.0E—08^{a}	1.31E—08$\pm$1.0E—08^{a}	2.41E—08$\pm$1.0E—08^{a}	1.11E—08$\pm$1.0E—08^{a}
Eu saline	9.60E—09$\pm$1.0E—08^{ab}	1.22E—08$\pm$1.0E—08^{ab}	1.63E—08$\pm$1.0E—08^{b}	7.84E—09$\pm$1.0E—08^{a}
F	2.05^{ns}	1.70^{ns}	13.43***	1.34^{ns}
$\bar{X}$	9.70E—09	1.09E—08	1.49E—08	9.18E—09

metabolic processes. The higher the value of α is, the higher the photosynthetic rate.

With estimated α and measured g, α was higher ($p < 0.001$) on non-saline than on saline soils, for both species (Table 13). The goodness of the model fit, described by R^2, is shown in Table 15. The model yielded a better fit when used for *E. camaldulensis* than for *C. quadrangulare*. The fit was also better for a saline soil than for a non-saline soil.

342. Model based on estimated g_0 and given α

Stomatal conductance was also used for comparing the net photosynthetic rates derived from different models because it is of central importance for the primary regulation of gas exchange. Stomatal conductance was determined when the stomata were fully open, since no water deficit was assumed.

The model based on fully open stomata yielded a better fit with the observed variation than the model in which the measured stomatal conductance was included. The results were supported by R^2 values (Table 15) and the least residual mean squares (Table 14). The correlation for photosynthesis from the estimated stomatal conductance was higher than the measured one for saline and non-saline soils in the case of *E. camaldulensis* but only for non-saline soil in the case of *C. quadrangulare* (Table 13).

343. Model based on estimated α and given g_0

Because the fitness of the model for net photosynthesis based on estimated α and measured g was poorer than that of the model in which estimated g_0 and given α were used, a new estimation of α from g_0 was attempted. The result was a slight improvement of the model for *E. camaldulensis* but there was little difference for *C. quadrangulare* (Table 15).

Table 15. Correlation between measured and estimated parameters of *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

Species and soil type	Parameters (R^2)												
	Estimated α, g measured	Estimated g_0 fixed α			Estimated α, fixed g_0			Estimated α, fixed g_0			Estimated α and g_0 with		
	NP	NP	Tr	g	NP	Tr	g	NP	Tr	g	NP	Tr	g
Com normal	0.79	0.84	0.53	0.29	0.84	0.53	0.29	0.87	0.20	0.02	0.89	0.26	0.02
Com saline	0.83	0.85	0.66	0.60	0.85	0.66	0.60	0.87	0.60	0.58	0.86	0.49	0.58
Eu0149 normal	0.83	0.83	0.15	0.16	0.84	0.15	0.16	0.86	0.02	0.03	0.86	0.13	0.07
Eu normal	0.83	0.90	0.14	0.08	0.91	0.14	0.08	0.91	0.07	0.03	0.92	0.13	0.03
Eu saline	0.85	0.87	0.12	0.13	0.88	0.12	0.13	0.90	0.03	0.06	0.91	0.05	0.06

Table 16. Temperature dependence of the predicted stomatal conductance (means$\pm$sd) to CO_2 of *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (nonsignificant differences in the same column are indicated by same letters).

Species and soil type	Stomatal conductance (g_0, cm s^{-1}) Temperature (°C)						
	21	24	27	30	33	36	39
Com normal	—	0.19 ± 0.09^{b}	0.18 ± 0.06^{b}	0.18 ± 0.07^{b}	0.18 ± 0.07^{b}	0.18 ± 0.06^{b}	0.17 ± 0.07^{b}
Com saline	—	0.10 ± 0.02^{c}	0.09 ± 0.04^{c}	0.11 ± 0.05^{c}	0.17 ± 0.09^{b}	0.17 ± 0.06^{bc}	—
Eu0149 normal	—	0.17 ± 0.06^{b}	0.18 ± 0.10^{b}	0.19 ± 0.11^{b}	0.17 ± 0.09^{b}	0.16 ± 0.07^{bc}	—
Eu normal	0.24 ± 0.02^{a}	0.24 ± 0.06^{a}	0.25 ± 0.08^{a}	0.41 ± 0.27^{a}	0.42 ± 0.31^{a}	0.35 ± 0.10^{a}	0.35 ± 0.00^{a}
Eu saline	0.14 ± 0.02^{b}	0.13 ± 0.03^{bc}	0.19 ± 0.10^{b}	0.22 ± 0.11^{b}	0.20 ± 0.10^{b}	0.13 ± 0.09^{c}	—
F	75.43***	12.87***	13.72***	30.43***	26.20***	36.29***	7.31*
$\bar{X}$	0.19	0.19	0.19	0.20	0.22	0.20	0.19

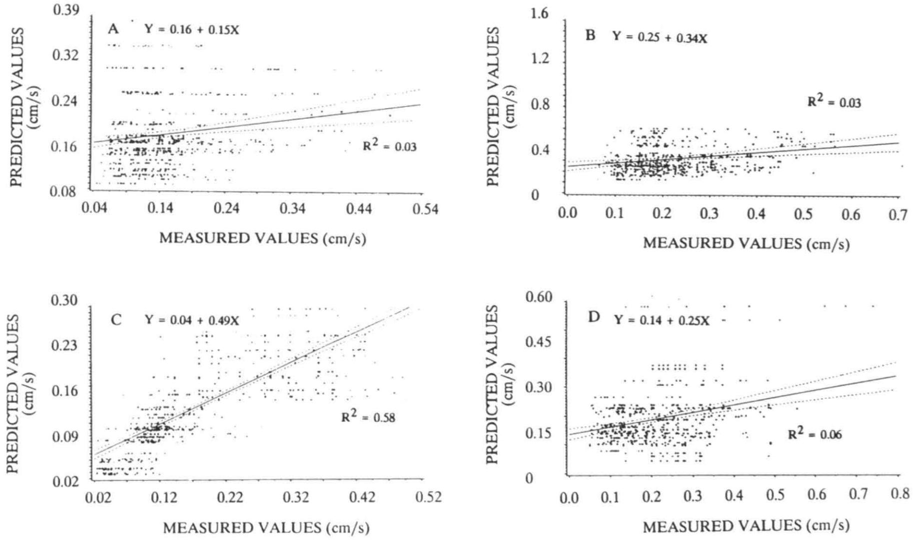


Figure 33. Relationship between predicted and measured stomatal conductance in *Combretum quadrangulare* and *Eucalyptus camaldulensis* (local variety) on non-saline soils (A and B) and saline soils (C and D) respectively, in the field study.

344. Model based on estimated α and g_0

Since only the results on modelling the net photosynthetic rate using estimated g_0 or α showed a good fit, a new model based on the estimation of both α and g_0 was applied. The results were better than with any of the other models for describing photosynthesis under a no-water deficit situation (Tables 14 and 15). The model was still better for *E. camaldulensis* than for *C. quadrangulare*, but the models were equally good for saline and non-saline soils.

The predicted stomatal conductance to CO_2 and H_2O showed the same trends as above as far as differences between species and soil salinity were concerned (Tables 16 and 17, Appendix I, Tables 17 and 18). In the case of *C. quadrangulare*, the predicted stomatal conductance (g_0) was the same at all temperature levels for a non-saline soil but increased with temperature between 24° and 36°C for a saline soil. In the case of the local variety of *E. camaldulensis*, the conductance increased with temperature on both soil types. The lowest values of g_0 were obtained for *C. quadrangulare* growing on saline soil (Table 16). The predicted stomatal conductance also varied with irradiance (Table 17) and reached the highest values in the local variety *E. camaldulensis* at high irradiance (Table 17).

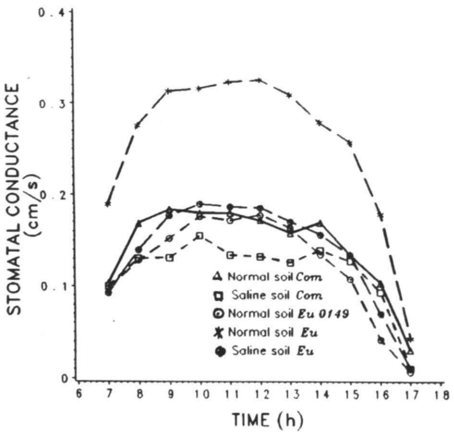


Figure 34. Average diurnal course of the stomatal conductance according to the model for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

Table 17. Irradiance dependence of the predicted stomatal conductance (means±sd) to CO_2 of *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (nonsignificant differences in the same column are indicated by same letters).

Species and soil type	Stomatal conductance (g_0, cm s^{-1}) Irradiance (μmol m^{-2}s^{-1}) 300	500	700	1000	1300	1500	1700	2000
Com normal	0.17 ± 0.07^a	0.19 ± 0.03^a	0.14 ± 0.03^b	0.16 ± 0.04^c	0.20 ± 0.08^b	0.16 ± 0.05^{bc}	0.20 ± 0.08^b	0.19 ± 0.07^b
Com saline	0.08 ± 0.00^a	0.18 ± 0.08^a	0.19 ± 0.07^{ab}	0.15 ± 0.08^c	0.10 ± 0.04^b	0.11 ± 0.06^c	0.11 ± 0.07^c	0.18 ± 0.03^b
Eu0149 normal	0.23 ± 0.15^a	0.19 ± 0.10^a	0.19 ± 0.11^{ab}	0.17 ± 0.10^c	0.16 ± 0.05^b	0.16 ± 0.05^{bc}	0.15 ± 0.05^c	0.18 ± 0.06^b
Eu normal	—	—	0.25 ± 0.04^a	0.30 ± 0.14^a	0.32 ± 0.24^a	0.35 ± 0.26^a	0.31 ± 0.12^a	0.39 ± 0.27^a
Eu saline	0.14 ± 0.05^a	0.14 ± 0.03^a	0.14 ± 0.04^b	0.21 ± 0.12^b	0.19 ± 0.07^b	0.20 ± 0.10^b	0.22 ± 0.13^b	0.20 ± 0.13^b
F	1.78^{ns}	1.14^{ns}	2.35^{ns}	16.11***	8.63***	18.63***	21.05***	9.32***
$\bar{X}$	0.18	0.18	0.18	0.19	0.21	0.21	0.21	0.23

The match between the measured photosynthetic rate and the one predicted after estimation of α and g_0 (Equation 17) was quite good for the different sets of conditions in the field. The values of conductance estimated with the model were similar to the measured ones (after taking into account to correction for instrument calibration; Table 13). The correlation between measured and predicted values of stomatal conductance is shown in Figures 33A—D, was not good. But the correlation of photosynthetic rates was very good (Table 15). The least residual mean square was a good indicator of the estimated values (Table 14). R^2 was also found to be a good indicator (Table 15).

The diurnal course of stomatal conductance, as determined by the model, was higher on non-saline than saline soil in both species (*E. Camaldulensis* of local variety and *C. quadrangulare*) and reached the highest peak for *E. Camaldulensis* on non-saline soil and the lowest values were for *C. quadrangulare* on saline soils; the remaining treatments were scattered between these two estremes (Figure 34).

35. Modelling of photosynthesis with the effect of water deficit

351. Model for estimating λ

The models for photosynthesis without a water deficit, as presented above, were based on maximal stomatal conductance (g_0) without a control signal. The next step was to use u* as the optimal degree of stomatal opening for model under water deficit. A combination of Equations 17, 18 20 and 23 for estimating λ, when $u = 1$, yielded estimates of net photosynthetic rates which equalled the values obtained with the model for photosynthesis without a water deficit. It was thus not possible to use the model of water describing the net photosynthetic rate during a water deficit. So the model under water deficit when the transpiration cost (λ) was nearly zero then no water deficit. At $u = 0$, with the stomata completely closed, no net photosynthesis or transpiration occurs and only respiration is assumed to take place. When the stomata were partially closed in the early morning and late afternoon, then $0 < u^* < 1$ and $0 < \lambda < 1$. However, λ was

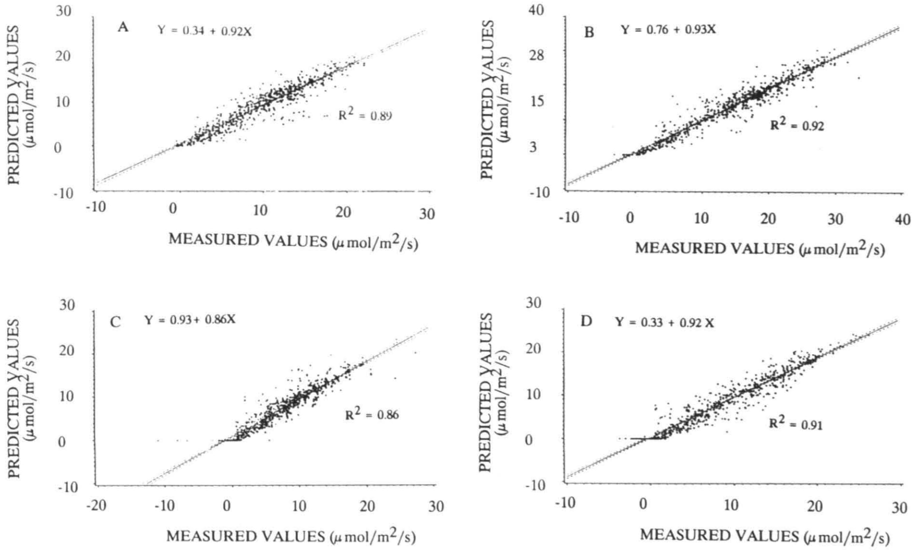


Figure 35. Relationship between predicted and measured photosynthetic rates for *Combretum quadrangulare* and *Eucalyptus camaldulensis* (local variety) on non-saline soils (A and B) and saline soils (C and D) respectively, in the field study.

still low and u* was quite high (Table 13). This model for the estimation of λ yielded the best fit for net photosynthesis among the all models for photosynthesis, even in the case where no water deficit was found (Appendix II, Figures 1D—6D). The residual mean squares of the estimation of λ supported the fit; for both species and sites, $\lambda < g_0 < \alpha$. The values of residual mean squares was lower (Table 14) and the correlation (R^2) was higher (Table 15) than found with any other model. The correlation coefficients (R^2) for the relationship between measured and predicted net photosynthesis in *C. quadrangulare* on non-saline and saline soils, and *E. camaldulensis* of local variety on non-saline and saline soils, were 0.89, 0.86, 0.92, and 0.91 respectively (Figure 35A—D). Again, R^2 was a good indicator for the best choice of model.

36. The effect of salinity on photosynthesis

361. Dependence of α on salinity

For comparison of α between saline and non-saline soils, only the model based on estimated values of α and g_0 was used since this model yielded the best fit. The values of α for saline soil were higher than those for a non-saline soil. For *C. quadrangulare*, α equalled 2.16 cm^3 μmol^{-1} on saline and 1.73 cm^3 μmol^{-1} on non-saline soil; for *E. camaldulensis* (local variety) the corresponding values were 2.47 and 2.44 cm^3 μmol^{-1} (Table 13). The values of α for *E. camaldulensis* were significantly higher than those for *C. quadrangulare* ($P < 0.001$). A higher value of α was interpreted as indicating a lower sensitivity to salinity.

362. Dependence of g_0 on salinity

For comparison of g_0 between saline and non-saline soils, the model based on the estimation of α was applied. The parameter, g_0 was smaller on saline soil than on non-saline soil, both in the case of *C. quadrangulare* ($p > 0.05$) and *E. camaldulensis* of local variety ($p < 0.001$) (Table 13). The variation in g_0 statistically significant ($p < 0.001$) between species. Under saline conditions, a high stomatal conductance was interpreted as indicating a lower sensitivity to salinity, since it was associated with a high rate of photosynthesis.

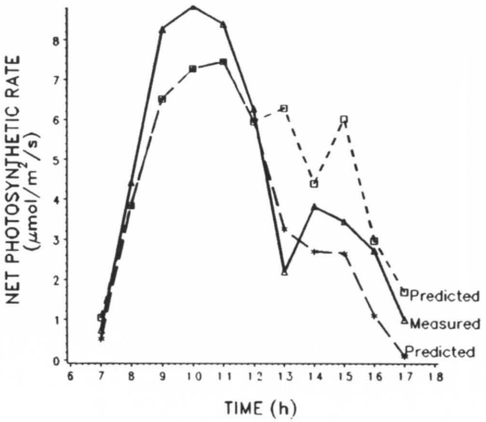


Figure 36. Diurnal course of the photosynthetic rate for *Combretum quadrangulare* during water deficit in the field study (15 Jan 1988). Symbols: Δ, measured; □, calculated according to Eq. 17 and *, calculated according to Eqs. 17, 18, 20, and 23.

363. Effect of salinity and water deficit on photosynthesis

Based on the low values of the indicator (λ) produced by the model, almost no water deficit effect was revealed in the field data (Table 13). The reason for this, trees may have been sufficient soil moisture and a low sensitivity to salinity for both species. However, on 15 January 1988, a slightly water deficit effect on the diurnal course of net photosynthetic rate was indicated for *C. quadrangulare* on the saline soil in the afternoon (Figure 36).

37. Effects of salinity on seedling growth in the greenhouse

371. Height growth

The development of seedling height during the greenhouse experiments is shown in Table 18. Seedlings of the two species differed in height before the onset of the salinity treatment, *E. camaldulensis* being taller ($p < 0.001$; Table 18). In culture solution experiment, the height growth of

Table 18. Seedlings height (means±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at two-week intervals from the beginning of salinity treatments at each measurement of the greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species		Height (cm)						
and		Measurement						
salinity (%)		1st	2nd	3rd	4th	5th	6th	7th
(1)								
Com	0.0^{0}	17.20 ± 2.07^{g}	—	—	—	—	—	—
Com	0.0	32.51 ± 6.33^{e}	34.27 ± 7.05^{c}	37.85 ± 8.30^{e}	43.37 ± 11.38^{e}	44.19 ± 11.39^{e}	44.93 ± 11.26^{e}	45.69 ± 11.25^{e}
Com	0.5	29.73 ± 5.72^{ef}	31.15 ± 5.80^{cd}	32.69 ± 6.25^{ef}	35.61 ± 5.97^{f}	36.37 ± 6.46^{f}	36.86 ± 6.54^{f}	37.29 ± 6.70^{f}
Com	1.0	26.08 ± 7.23^{f}	26.79 ± 7.23^{d}	27.41 ± 7.06^{f}	28.73 ± 7.02^{f}	29.07 ± 7.13^{g}	29.40 ± 7.09^{g}	29.63 ± 7.25^{g}
Com	1.5	29.66 ± 6.46^{ef}	30.45 ± 6.63^{cd}	30.87 ± 6.60^{f}	31.19 ± 6.66^{f}	31.53 ± 6.80^{fg}	31.75 ± 6.77^{fg}	31.76 ± 6.76^{fg}
Com	2.0	28.60 ± 5.01^{ef}	29.09 ± 4.94^{cd}	29.36 ± 5.05^{f}	29.61 ± 5.02^{f}	29.73 ± 5.03^{fg}	29.85 ± 5.06^{fg}	29.86 ± 5.06^{g}
Eu	0.0^{0}	41.39 ± 4.29^{d}	—	—	—	—	—	—
Eu	0.0	62.35 ± 8.37^{b}	71.07 ± 9.75^{a}	74.69 ± 10.02^{a}	77.83 ± 10.75^{a}	81.37 ± 11.63^{a}	83.33 ± 12.24^{a}	83.58 ± 12.30^{a}
Eu	0.5	56.71 ± 8.92^{c}	64.93 ± 8.86^{a}	67.09 ± 9.21^{b}	69.95 ± 8.99^{b}	72.32 ± 9.12^{b}	74.71 ± 9.31^{b}	74.91 ± 9.31^{b}
Eu	1.0	53.60 ± 7.36^{c}	58.43 ± 6.98^{b}	60.43 ± 6.90^{c}	62.20 ± 7.35^{c}	63.41 ± 7.05^{c}	64.25 ± 6.50^{c}	64.31 ± 6.49^{c}
Eu	1.5	51.83 ± 8.42^{c}	53.11 ± 7.85^{b}	55.77 ± 7.88^{d}	55.12 ± 8.02^{d}	55.83 ± 8.06^{d}	56.06 ± 8.02^{d}	56.13 ± 8.06^{d}
Eu	2.0	70.60 ± 5.61^{a}	70.78 ± 5.78^{a}	71.64 ± 7.00^{ab}	72.32 ± 6.92^{ab}	72.70 ± 7.18^{b}	74.04 ± 8.08^{b}	74.26 ± 8.05^{b}
F		91.01***	86.47***	86.86***	79.75***	83.65***	87.44***	86.65***
$\bar{X}$		40.01	46.20	47.89	50.03	51.23	52.10	52.32
(2)								
Com	0.0	37.40 ± 5.03^{c}	40.03 ± 4.95^{c}	46.92 ± 0.88^{c}	49.45 ± 9.80^{c}	52.07 ± 10.47^{c}	54.78 ± 12.36^{c}	56.32 ± 13.23^{c}
Com	2.0	37.62 ± 5.64^{c}	39.47 ± 5.48^{c}	43.35 ± 5.22^{c}	47.98 ± 5.66^{c}	50.17 ± 3.91^{c}	51.80 ± 4.23^{c}	52.28 ± 4.20^{c}
Eu	0.0	99.67 ± 20.56^{a}	111.63 ± 20.40^{a}	125.33 ± 19.61^{a}	141.18 ± 19.35^{a}	154.65 ± 13.72^{a}	161.42 ± 12.07^{a}	165.58 ± 14.42^{a}
Eu	2.0	83.30 ± 9.20^{b}	93.92 ± 7.65^{b}	107.08 ± 6.19^{b}	116.22 ± 6.08^{b}	124.25 ± 8.69^{b}	128.77 ± 9.55^{b}	134.42 ± 10.99^{b}
F		43.20***	64.41***	73.50***	99.55***	170.21***	175.97***	148.10***
$\bar{X}$		64.50	71.26	80.67	88.71	95.28	99.19	102.15

0, Before giving nutrient solution

Table 19. Seedling height increment (means±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at two-week intervals from the beginning of salinity treatments at each measurement of the greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species	Two-weekly height (cm)						Total increament (cm) (3 months)
	Measurement						
and salinity (%)	2nd	3rd	4th	5th	6th	7th	
(1)							
Com 0.0^{0}	—	—	—	—	—	—	—
Com 0.0	1.77±1.36^{c}	3.58±2.34^{a}	5.52±3.60^{a}	0.81±0.58^{c}	0.74±0.58^{cd}	0.76±0.53^{a}	13.18±5.66^{b}
Com 0.5	1.43±1.15^{c}	1.54±1.58^{bcd}	2.91±1.81^{b}	0.77±1.10^{c}	0.49±0.43^{cd}	0.43±0.40^{b}	7.56±2.79^{cd}
Com 1.0	0.71±0.67^{c}	0.62±0.44^{cd}	1.32±0.90^{cd}	0.35±0.38^{c}	0.33±0.28^{d}	0.23±0.32^{bc}	3.55±1.53^{e}
Com 1.5	0.79±0.73^{c}	0.42±0.36^{d}	0.31±0.31^{d}	0.34±0.67^{c}	0.22±0.20^{d}	0.01±0.04^{c}	2.10±1.01^{e}
Com 2.0	0.49±0.53^{c}	0.27±0.28^{d}	0.25±0.24^{d}	0.11±0.19^{c}	0.13±0.21^{d}	0.01±0.03^{c}	1.26±0.54^{e}
Eu 0.0^{0}	—	—	—	—	—	—	—
Eu 0.0	8.72±5.94^{a}	3.63±2.99^{a}	3.14±2.12^{b}	3.54±2.48^{a}	1.96±1.75^{ab}	0.26±0.25^{bc}	20.98±8.04^{a}
Eu 0.5	8.22±3.74^{a}	2.15±1.21^{b}	2.87±2.20^{bc}	2.37±1.83^{b}	2.39±1.70^{a}	0.19±0.19^{bc}	18.00±6.04^{a}
Eu 1.0	4.83±3.02^{b}	1.99±0.93^{bc}	1.77±1.56^{bcd}	1.21±0.90^{c}	0.85±1.04^{cd}	0.05±0.14^{c}	10.65±4.52^{bc}
Eu 1.5	1.28±1.11^{c}	0.66±0.91^{cd}	1.35±1.17^{cd}	0.73±0.85^{c}	0.21±0.43^{d}	0.07±0.12^{c}	4.23±2.84^{de}
Eu 2.0	0.18±0.19^{c}	0.86±1.49^{bcd}	0.68±0.63^{d}	0.38±0.41^{c}	1.34±2.73^{bc}	0.22±0.20^{bc}	3.44±3.37^{e}
F	20.88***	9.89***	11.49***	12.58***	8.45***	10.73***	37.89***
$\bar{X}$	3.23	1.69	2.14	1.19	0.87	0.22	9.35
(2)							
Com 0.0	2.63±0.91^{b}	6.88±6.46^{ab}	2.53±1.41^{c}	2.62±1.75^{b}	2.72±2.23^{b}	1.53±0.99^{b}	18.92±9.08^{c}
Com 2.0	1.85±1.11^{b}	3.88±1.70^{b}	4.63±1.26^{c}	2.18±2.33^{b}	1.63±1.50^{b}	0.48±0.48^{b}	14.67±2.15^{c}
Eu 0.0	11.97±2.97^{a}	13.70±6.60^{a}	15.85±3.44^{a}	13.47±9.10^{a}	6.77±2.48^{a}	4.17±4.99^{ab}	65.92±14.04^{a}
Eu 2.0	10.62±3.86^{a}	13.17±5.67^{a}	9.13±2.38^{b}	8.03±3.38^{ab}	4.52±3.00^{ab}	5.65±3.82^{a}	51.12±10.02^{b}
F	25.73***	4.61*	39.46***	6.59**	5.40**	3.32*	38.67***
$\bar{X}$	6.77	9.41	8.04	6.58	3.91	2.96	37.65

0, Before giving nutrient solution

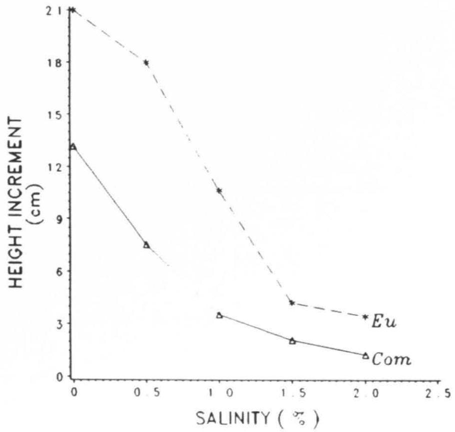


Figure 37. Relationship between height growth increment and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis* for 3 month study period. Mean values for seedlings grown in culture solution in the greenhouse experiments.

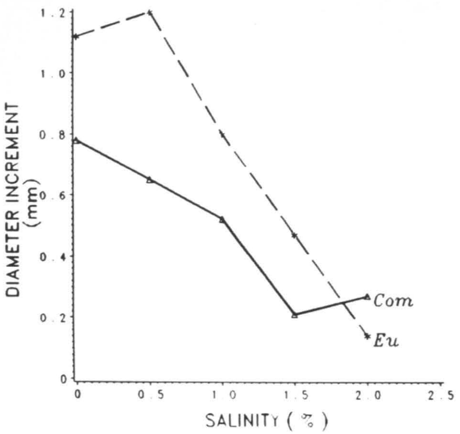


Figure 38. Relationship between diameter growth increment and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis* for 3 month study period. Mean values for seedlings grown in culture solution in the greenhouse experiments.

both species was negatively affected by salinity ($p < 0.001$) at every measurement occasion (Figure 37). In sand medium experiment, seedling height growth was also grown faster under the non-saline treatment than under the saline treatment, but this difference could only be statistically confirmed for *E. camaldulensis*.

The height increment consistently decreased with increased salinity and time. The increment was, however, greater for *E. camaldulensis* than for *C. quadrangulare*, and at each salinity level (Table 19; Figure 37 and Appendix II, Figures 16 and 17).

372. Diameter growth

At each time of measurement, *C. quadrangulare* stem diameter growth was not significantly reduced by salinity, while for *E. camaldulensis* there was a significant reduction ($p < 0.001$; Tables 20 and 21).

In the seedlings grown in the culture solution, the biweekly *E. camaldulensis* stem diameter increment also showed a more distinct inhibition due to salinity than was the case for *C. quadrangulare* (Table 21). In both species, however, the total diameter increment correlated negatively with salinity (Figure 38). The total diameter increment was higher in *C. quadrangulare* than in *E. camaldulensis* at the highest (2 %) salinity level, whereas the difference between species showed the opposite trend at lower salinity levels.

Of the sand medium grown seedlings, the total diameter increment was also statistically significantly greater under the non-saline treatment than under the saline treatment. In general, the height and the diameter of the seedlings grown in the sand medium were much greater than those of the seedlings grown in the culture solution medium.

373. Shoot internode length

Salinity significantly shortened the final internode length in both species (Table 22). The internode increment was also slower at higher salinity levels (Figure 39).

374. Root growth

The root growth characteristics of the seedlings grown in the nutrient solution are shown in Table 23 and Appendix II, Figures 18 and 19. Root length in both species

Table 20. Stem diameter of the seedlings (means±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at two-week intervals from the beginning of salinity treatments at each measurement of the greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species and salinity (%)	Stem diameter (mm) Measurement 1st	2nd	3rd	4th	5th	6th	7th
(1)							
Com 0.0^{0}	3.52 ± 0.38^{d}	—	—	—	—	—	—
Com 0.0	4.79 ± 0.79^{ab}	4.93 ± 0.85^{a}	5.09 ± 0.90^{ab}	5.20 ± 0.94^{a}	5.29 ± 0.98^{a}	5.43 ± 0.94^{a}	5.57 ± 1.00^{a}
Com 0.5	4.48 ± 0.76^{ab}	5.08 ± 0.87^{a}	5.14 ± 0.88^{a}	5.23 ± 0.93^{a}	5.25 ± 0.93^{a}	5.41 ± 1.01^{a}	5.49 ± 0.97^{a}
Com 1.0	4.56 ± 0.89^{ab}	4.67 ± 0.92^{ab}	4.76 ± 0.91^{abcd}	4.84 ± 0.91^{abcd}	4.91 ± 0.95^{ab}	5.01 ± 0.95^{abc}	5.08 ± 0.96^{abc}
Com 1.5	5.01 ± 0.61^{a}	5.11 ± 0.63^{a}	5.12 ± 0.62^{a}	5.15 ± 0.63^{ab}	5.16 ± 0.63^{ab}	5.21 ± 0.64^{ab}	5.23 ± 0.64^{ab}
Com 2.0	4.84 ± 0.66^{ab}	5.02 ± 0.60^{a}	5.05 ± 0.60^{ab}	5.06 ± 0.60^{abc}	5.08 ± 0.58^{ab}	5.11 ± 0.57^{abc}	5.12 ± 0.57^{abc}
Eu 0.0^{0}	2.75 ± 0.37^{e}	—	—	—	—	—	—
Eu 0.0	4.48 ± 0.69^{abc}	4.99 ± 0.85^{a}	5.31 ± 0.85^{a}	5.43 ± 0.82^{a}	5.55 ± 0.81^{a}	5.57 ± 0.80^{a}	5.60 ± 0.80^{a}
Eu 0.5	4.01 ± 0.68^{cd}	4.77 ± 0.95^{a}	4.96 ± 1.00^{abc}	5.09 ± 0.95^{abc}	5.18 ± 0.91^{ab}	5.20 ± 0.90^{ab}	5.21 ± 0.90^{ab}
Eu 1.0	3.73 ± 0.56^{d}	4.09 ± 0.63^{bc}	4.32 ± 0.68^{cd}	4.44 ± 0.70^{cd}	4.52 ± 0.72^{bc}	4.53 ± 0.73^{bcd}	4.54 ± 0.73^{bcd}
Eu 1.5	3.75 ± 0.58^{d}	3.98 ± 0.62^{c}	4.12 ± 0.61^{d}	4.19 ± 0.60^{d}	4.22 ± 0.60^{c}	4.22 ± 0.60^{d}	4.22 ± 0.60^{d}
Eu 2.0	4.34 ± 0.72^{bc}	4.40 ± 0.76^{abc}	4.41 ± 0.76^{bcd}	4.46 ± 0.71^{bcd}	4.47 ± 0.69^{bc}	4.48 ± 0.69^{cd}	4.48 ± 0.69^{cd}
F	19.62***	4.07***	3.73***	3.77***	4.01***	4.51***	4.97***
$\bar{X}$	4.16	4.73	4.87	4.96	5.02	5.07	5.11
(2)							
Com 0.0	7.52 ± 0.90^{a}	8.31 ± 0.87^{a}	9.40 ± 1.28^{a}	10.33 ± 1.03^{a}	11.18 ± 1.48^{ab}	11.70 ± 1.67^{a}	11.78 ± 1.61^{a}
Com 2.0	8.23 ± 0.78^{a}	8.77 ± 0.87^{a}	9.17 ± 1.06^{a}	10.13 ± 1.24^{a}	10.90 ± 1.36^{ab}	11.30 ± 1.61^{a}	11.43 ± 1.73^{a}
Eu 0.0	7.50 ± 1.60^{a}	8.20 ± 1.39^{a}	9.28 ± 1.05^{a}	10.57 ± 1.89^{a}	11.67 ± 1.70^{a}	11.87 ± 1.58^{a}	12.00 ± 1.62^{a}
Eu 2.0	7.65 ± 1.18^{a}	8.10 ± 1.36^{a}	8.50 ± 0.99^{a}	9.22 ± 0.59^{a}	9.78 ± 1.06^{b}	10.13 ± 0.81^{a}	10.30 ± 0.81^{a}
F	0.53^{ns}	0.39^{ns}	0.80^{ns}	1.29^{ns}	1.90^{ns}	1.71^{ns}	1.49^{ns}
$\bar{X}$	0.53	8.35	9.09	10.06	10.88	11.25	11.38

0, Before giving nutrient solution.

Table 21. Stem diameter increment of the seedlings (means±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at two-week intervals from the beginning of salinity treatments at each measurement of the greenhouse experiments (non-significant differences in the same column are indicated by same letters).

Species and salinity (%)	Two-weekly increment (mm) Measurement 2nd	3rd	4th	5th	6th	7th	Total increment (mm) (3 months)
(1)							
Com 0.0^{0}	—	—	—	—	—	—	—
Com 0.0	0.14 ± 0.12^{cd}	0.17 ± 0.18^{bc}	0.11 ± 0.11^{ab}	0.09 ± 0.12^{abc}	0.14 ± 0.12^{a}	0.15 ± 0.13^{a}	0.78 ± 0.37^{b}
Com 0.5	0.24 ± 0.23^{cd}	0.06 ± 0.07^{cde}	0.09 ± 0.11^{abc}	0.02 ± 0.06^{cd}	0.17 ± 0.24^{a}	0.08 ± 0.12^{b}	0.65 ± 0.39^{b}
Com 1.0	0.11 ± 0.10^{cd}	0.08 ± 0.07^{cde}	0.09 ± 0.12^{abc}	0.07 ± 0.09^{abcd}	0.10 ± 0.12^{ab}	0.07 ± 0.07^{b}	0.52 ± 0.20^{bc}
Com 1.5	0.09 ± 0.10^{cd}	0.01 ± 0.02^{de}	0.03 ± 0.06^{bc}	0.01 ± 0.03^{d}	0.04 ± 0.11^{bc}	0.02 ± 0.05^{c}	0.21 ± 0.24^{cd}
Com 2.0	0.18 ± 0.28^{cd}	0.03 ± 0.04^{de}	0.01 ± 0.02^{c}	0.02 ± 0.03^{cd}	0.04 ± 0.05^{bc}	0.00 ± 0.02^{c}	0.27 ± 0.30^{cd}
Eu 0.0^{0}	—	—	—	—	—	—	—
Eu 0.0	0.52 ± 0.45^{b}	0.32 ± 0.27^{a}	0.12 ± 0.12^{a}	0.12 ± 0.12^{a}	0.02 ± 0.02^{bc}	0.02 ± 0.02^{c}	1.12 ± 0.57^{a}
Eu 0.5	0.77 ± 0.51^{a}	0.18 ± 0.20^{bc}	0.13 ± 0.10^{a}	0.10 ± 0.11^{ab}	0.01 ± 0.02^{bc}	0.01 ± 0.03^{c}	1.20 ± 0.52^{a}
Eu 1.0	0.36 ± 0.28^{bc}	0.23 ± 0.16^{ab}	0.12 ± 0.08^{a}	0.08 ± 0.08^{abcd}	0.01 ± 0.01^{bc}	0.01 ± 0.00^{c}	0.80 ± 0.46^{b}
Eu 1.5	0.23 ± 0.28^{cd}	0.14 ± 0.15^{bcd}	0.07 ± 0.05^{abc}	0.03 ± 0.03^{cd}	0.00 ± 0.01^{c}	0.00 ± 0.01^{c}	0.47 ± 0.33^{bcd}
Eu 2.0	0.06 ± 0.07^{d}	0.00 ± 0.01^{e}	0.06 ± 0.06^{abc}	0.01 ± 0.03^{d}	0.00 ± 0.01^{c}	0.00 ± 0.00^{c}	0.14 ± 0.11^{d}
F	8.11***	6.54***	2.80**	3.98***	4.76***	7.92***	11.80***
$\bar{X}$	0.29	0.14	0.08	0.06	0.06	0.04	0.67
(2)							
Com 0.0	0.80 ± 0.37^{a}	1.08 ± 0.50^{a}	0.93 ± 0.45^{a}	0.85 ± 0.50^{a}	0.52 ± 0.45^{a}	0.08 ± 0.16^{a}	4.27 ± 0.97^{a}
Com 2.0	0.53 ± 0.41^{a}	0.40 ± 0.23^{b}	0.97 ± 0.64^{a}	0.77 ± 0.46^{a}	0.40 ± 0.50^{a}	0.13 ± 0.22^{a}	3.20 ± 1.53^{ab}
Eu 0.0	0.70 ± 0.37^{a}	1.08 ± 0.79^{a}	1.28 ± 0.88^{a}	1.10 ± 0.81^{a}	0.20 ± 0.32^{a}	0.13 ± 0.24^{a}	4.50 ± 1.18^{b}
Eu 2.0	0.45 ± 0.29^{a}	0.40 ± 0.40^{b}	0.72 ± 0.69^{a}	0.57 ± 0.61^{a}	0.35 ± 0.52^{a}	0.17 ± 0.32^{a}	2.65 ± 0.69^{b}
F	1.13^{ns}	3.46*	0.70^{ns}	0.79^{ns}	0.50^{ns}	0.12^{ns}	3.56*
$\bar{X}$	0.62	0.74	0.98	0.82	0.37	0.13	3.65

0, Before giving nutrient solution.

Table 22. Shoot internode length and the total increment of the seedlings (means±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at two-week intervals from the beginning of salinity treatments at each measurement of the greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species and salinity (%)	Shoot internode length (cm) Measurement 1st	2nd	3rd	4th	5th	6th	7th	Total increment (cm) (3 months)
(1)								
Com 0.0	1.23 ± 0.61^{a}	1.89 ± 1.02^{a}	1.92 ± 1.02^{a}	1.93 ± 1.03^{a}	1.93 ± 1.03^{a}	1.93 ± 1.03^{a}	1.93 ± 1.03^{a}	0.70 ± 0.72^{ab}
Com 0.5	0.88 ± 0.37^{ab}	1.24 ± 0.56^{b}	1.27 ± 0.37^{bc}	1.29 ± 0.58^{bc}	1.29 ± 0.58^{bc}	1.29 ± 0.58^{bc}	1.29 ± 0.58^{bc}	0.41 ± 0.38^{bcde}
Com 1.0	0.65 ± 0.31^{bc}	0.81 ± 0.40^{bc}	0.85 ± 0.39^{bcd}	0.86 ± 0.39^{cd}	0.86 ± 0.39^{cd}	0.86 ± 0.39^{cd}	0.86 ± 0.39^{cd}	0.21 ± 0.13^{cde}
Com 1.5	1.12 ± 0.87^{a}	1.27 ± 0.87^{b}	1.31 ± 0.87^{bc}	1.32 ± 0.87^{bc}	1.33 ± 0.86^{bc}	1.33 ± 0.86^{bc}	1.33 ± 0.86^{bc}	0.21 ± 0.16^{cde}
Com 2.0	0.66 ± 0.24^{bc}	0.71 ± 0.28^{bc}	0.73 ± 0.27^{cd}	0.74 ± 0.27^{cd}	0.77 ± 0.31^{cd}	0.77 ± 0.31^{cd}	0.77 ± 0.31^{cd}	0.11 ± 0.14^{e}
Eu 0.0	0.64 ± 0.70^{bc}	1.32 ± 0.99^{b}	1.43 ± 0.95^{ab}	1.48 ± 0.94^{ab}	1.51 ± 0.93^{ab}	1.51 ± 0.93^{ab}	1.51 ± 0.93^{ab}	0.87 ± 0.55^{a}
Eu 0.5	0.44 ± 0.18^{c}	0.93 ± 0.68^{bc}	0.95 ± 0.67^{bcd}	0.96 ± 0.68^{bcd}	0.96 ± 0.68^{bcd}	0.96 ± 0.68^{bcd}	0.96 ± 0.68^{bcd}	0.52 ± 0.58^{abcd}
Eu 1.0	0.44 ± 0.16^{c}	0.93 ± 0.45^{bc}	0.98 ± 0.51^{bcd}	0.98 ± 0.50^{bcd}	0.99 ± 0.50^{bcd}	0.99 ± 0.50^{bcd}	0.99 ± 0.50^{bcd}	0.55 ± 0.47^{abc}
Eu 1.5	0.52 ± 0.25^{bc}	0.71 ± 0.36^{bc}	0.72 ± 0.36^{cd}	0.74 ± 0.36^{cd}	0.74 ± 0.36^{cd}	0.74 ± 0.36^{cd}	0.74 ± 0.36^{cd}	0.22 ± 0.21^{cde}
Eu 2.0	0.40 ± 0.16^{c}	0.48 ± 0.16^{c}	0.52 ± 0.20^{d}	0.56 ± 0.23^{d}	0.56 ± 0.23^{d}	0.56 ± 0.23^{d}	0.56 ± 0.23^{d}	0.16 ± 0.21^{de}
F	5.04***	4.68***	4.99***	5.12***	5.14***	5.14***	5.14***	5.78***
$\bar{X}$	0.72	1.08	1.12	1.14	1.14	1.14	1.14	0.43
(2)								
Com 0.0	1.63 ± 0.89^{a}	2.53 ± 0.92^{a}	2.57 ± 0.95^{a}	2.60 ± 0.95^{a}	2.60 ± 0.95^{a}	2.60 ± 0.95^{a}	2.60 ± 0.95^{a}	0.97 ± 0.71^{a}
Com 2.0	1.23 ± 0.29^{a}	1.90 ± 0.38^{ab}	2.08 ± 0.50^{a}	2.12 ± 0.54^{a}	2.12 ± 0.54^{a}	2.12 ± 0.54^{a}	2.12 ± 0.54^{a}	0.88 ± 0.73^{a}
Eu 0.0	0.53 ± 0.14^{b}	1.50 ± 0.32^{b}	2.08 ± 0.61^{a}	2.10 ± 0.60^{a}	2.12 ± 0.62^{a}	2.13 ± 0.59^{a}	2.13 ± 0.59^{a}	1.60 ± 0.54^{a}
Eu 2.0	0.50 ± 0.13^{b}	1.60 ± 0.32^{b}	2.05 ± 0.37^{a}	2.07 ± 0.37^{a}	2.07 ± 0.37^{a}	2.07 ± 0.37^{a}	2.07 ± 0.37^{a}	1.57 ± 0.36^{a}
F	8.01**	4.34*	0.89^{ns}	0.92^{ns}	0.89^{ns}	0.89^{ns}	0.89^{ns}	2.39^{ns}
$\bar{X}$	0.97	1.88	2.20	2.22	2.23	2.23	2.23	1.25

Table 23. Root length and the total increment of the seedlings (mean±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at two-week intervals from the beginning of salinity treatments at each measurement of the greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species	Root length (cm)							Total increment (cm) (3 months)
	Measurement							
and salinity (%)	1st	2nd	3rd	4th	5th	6th	7th	
(1)								
Com 0.0^{0}	21.39±8.67^{de}	—	—	—	—	—	—	—
Com 0.0	37.83±14.82^{abc}	49.45±18.07^{abc}	63.69±22.83^{ab}	81.93±26.02^{a}	87.23±27.21^{a}	90.79±25.80^{a}	92.35±26.39^{a}	54.52±17.41^{a}
Com 0.5	32.94±7.50^{abc}	45.08±8.97^{bcd}	56.98±12.99^{abc}	74.89±20.26^{ab}	79.63±21.88^{ab}	82.43±21.78^{ab}	85.22±22.63^{abc}	52.28±22.06^{a}
Com 1.0	31.65±11.60^{bc}	39.22±11.94^{cde}	46.64±15.44^{cd}	57.07±21.99^{c}	62.42±24.92^{bc}	65.15±26.47^{bc}	66.67±27.99^{cd}	35.03±26.46^{bc}
Com 1.5	39.08±9.42^{ab}	45.57±12.62^{bcd}	50.62±15.85^{bc}	55.03±18.83^{c}	56.62±20.28^{c}	57.91±21.59^{c}	58.15±21.64^{d}	19.07±13.68^{cd}
Com 2.0	33.24±7.99^{abc}	34.19±8.27^{de}	34.91±8.01^{de}	37.55±8.89^{de}	38.00±9.21^{de}	38.62±9.25^{de}	38.71±9.24^{e}	5.47±4.31^{d}
Eu 0.0^{0}	14.59±0.39^{e}	—	—	—	—	—	—	—
Eu 0.0	42.28±13.44^{a}	59.65±21.59^{a}	69.04±24.03^{a}	74.05±26.36^{ab}	79.63±28.64^{ab}	83.73±29.99^{ab}	88.50±34.36^{ab}	46.22±27.60^{ab}
Eu 0.5	40.60±12.03^{ab}	55.27±16.20^{ab}	59.80±17.26^{abc}	64.47±16.76^{bc}	69.55±18.71^{abc}	71.50±19.25^{bc}	76.52±17.59^{abcd}	35.92±17.31^{bc}
Eu 1.0	41.60±14.24^{a}	52.60±16.50^{ab}	57.13±18.46^{abc}	59.87±18.76^{bc}	63.67±19.28^{bc}	65.65±21.88^{bc}	68.78±22.54^{bcd}	27.18±23.59^{c}
Eu 1.5	38.67±7.09^{ab}	44.07±5.71^{bcde}	47.53±7.24^{cd}	51.23±10.51^{cd}	52.85±12.29^{cd}	53.83±12.41^{cd}	58.63±14.57^{d}	19.97±13.70^{cd}
Eu 2.0	29.40±6.63^{cd}	32.04±6.56^{e}	32.70±6.48^{e}	33.50±6.68^{e}	34.20±7.60^{e}	34.38±7.79^{e}	34.48±7.76^{e}	5.08±1.94^{d}
F	11.96***	5.11***	6.30***	7.89***	8.46***	9.08***	9.01***	10.61***
$\bar{X}$	33.22	47.14	53.82	61.24	64.92	67.14	69.78	32.35
(2)								
Com 0.0	16.70±4.56^{ab}	—	—	—	—	—	51.87±7.57^{a}	35.17±9.82^{a}
Com 2.0	20.68±3.24^{a}	—	—	—	—	—	51.12±3.78^{a}	30.43±4.73^{a}
Eu 0.0	14.45±5.50^{b}	—	—	—	—	—	47.00±6.13^{a}	32.55±7.32^{a}
Eu 2.0	15.38±5.24^{ab}	—	—	—	—	—	49.33±6.38^{a}	33.95±5.23^{a}
F	2.03^{ns}						0.75^{ns}	0.50^{ns}
$\bar{X}$	16.80						49.83	33.03

0, Before giving nutrient solution.

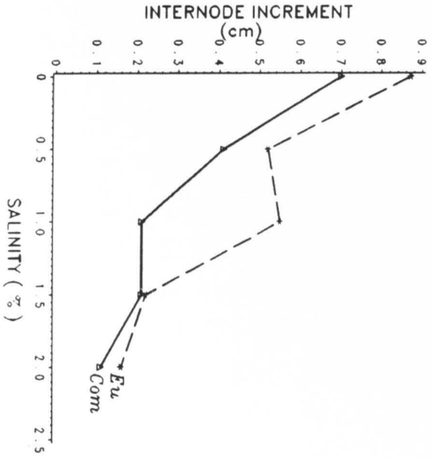


Figure 39. Relationship between stem internode increment and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis* for 3 month study period. Mean values for seedlings grown in culture solution in the greenhouse experiments.

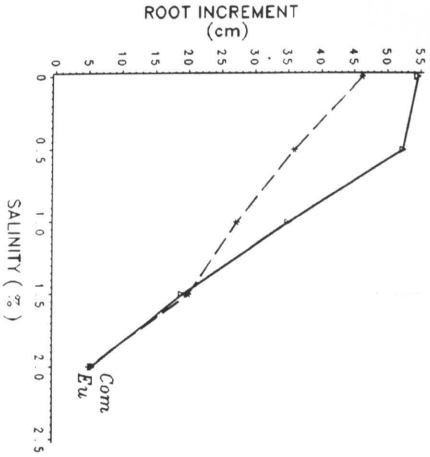


Figure 40. Relationship between root growth increment and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis* for 3 month study period. Mean values for seedlings grown in culture solution in the greenhouse experiments.

decreased with increasing salinity ($p < 0.001$). The root length increment in all treatments generally slowed down with time (Figure 40).

375. Estimated leaf biomass

In the case of both species, total leaf dry weight per seedling decreased with time and increasing salinity. The absolute leaf biomass of the seedlings grown in the culture solution decreased with increased salinity (Table 24). In sand medium experiment the reduction of leaf biomass was observed for *C. quadrangulare* ($p > 0.05$) and *E. camaldulensis* ($p < 0.05$). The saline treatment affected the increment of leaf biomass and did have effect of slowing down the development of new leaves.

376. Leaf area characteristics

The trend in total area was similar to that of leaf biomass and was generally negatively correlated with salinity. In the case of *C. quadrangulare*, the highest absolute decrease in area with time was found at 1.5 % salinity (Table 25). The total leaf area per plant was higher in those seedlings grown in the sand medium. While in sand medium experiment, the 2 % salinity treatment reduced total leaf area by about 15 % in the case of *C. quadrangulare* and by 45 % in the case of *E. camaldulensis* compared to that of the non-saline treatment at the end of the experiment, the corresponding reduction caused by the 2 % salinity treatment in the culture solution experiment was 70 % and 80 % (Table 26).

Table 26 shows the leaf area and dry biomass values at the end of the experiment. The leaf area per plant, for both species, was reduced by salinity (Figure 41). The mean area of a single leaf was decreased among the salinity treatments both for *C. quadrangulare* and *E. camaldulensis* (Figure 42). Leaf dry weight per unit area (g dm^{-2}) also tended to increase with salinity (Figure 43).

In sand medium experiment, the leaf area per plant (cm^{2}/plant) was higher under the non-saline treatment than under saline treatment, and also higher for *E. camaldulensis* than for *C. quadrangulare* ($p < 0.001$) (Table 26). The mean area per single leaf (cm^{2}/leaf) was smaller under non-saline condition than under 2 % saline condition in the case of *C. quadrangulare*. The trend was the opposite in the case of *E. Camaldulensis*. However, in the case of *C. quadrangulare* and *E. camaldulensis* were not the difference between saline and non-saline conditions, but there was different

Table 24. The estimated leaf and the total increment of leaf dry weight of the seedlings (mean±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at two-week intervals from the beginning of salinity treatments at each measurement of the greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species and salinity (%)	Leaf dry weight/plant (g)							Total increament (cm) (3 months)
	1st	2nd	3rd	Measurement 4th	5th	6th	7th	
(1)								
Com 0.0^{0}	0.57±0.07^{d}	—	—	—	—	—	—	—
Com 0.0	3.39±1.04^{a}	3.46±1.09^{a}	3.90±1.30^{a}	4.39±1.56^{a}	3.97±1.26^{a}	3.74±1.46^{a}	3.86±2.22^{ab}	0.47±1.73^{bc}
Com 0.5	2.12±0.69^{b}	2.38±0.80^{b}	2.47±0.84^{b}	2.63±1.04^{bc}	2.48±0.85^{c}	2.51±0.88^{bc}	2.42±0.94^{cd}	0.29±0.42^{cd}
Com 1.0	2.14±0.64^{b}	2.24±0.68^{b}	2.22±0.73^{bc}	2.27±0.76^{bcd}	2.26±0.80^{cd}	2.01±0.95^{cd}	1.81±0.93^{cde}	—0.33±0.62^{cde}
Com 1.5	2.59±1.23^{b}	2.67±1.20^{b}	2.65±1.25^{b}	2.45±1.08^{bc}	2.53±1.25^{c}	1.98±1.05^{cd}	1.51±1.19^{def}	—1.08±1.55^{e}
Com 2.0	2.26±0.78^{b}	2.05±0.57^{bc}	2.12±0.89^{bc}	1.92±0.78^{cde}	1.86±0.76^{cd}	1.40±1.00^{def}	1.23±1.03^{def}	—1.03±0.82^{e}
Eu 0.0^{0}	0.74±0.07^{d}	—	—	—	—	—	—	—
Eu 0.0	1.58±0.45^{c}	2.06±0.80^{bc}	2.45±0.86^{b}	3.04±1.08^{b}	3.46±1.47^{ab}	3.78±1.71^{a}	4.48±2.54^{a}	2.90±2.49^{a}
Eu 0.5	1.53±0.61^{c}	2.04±0.76^{bc}	2.15±0.70^{bc}	2.53±1.02^{bc}	2.70±0.93^{bc}	2.91±1.12^{ab}	2.91±1.12^{bc}	1.38±0.81^{b}
Eu 1.0	1.46±0.50^{c}	1.52±0.61^{cd}	1.69±0.66^{cd}	1.55±0.81^{def}	1.54±0.79^{de}	1.53±0.72^{de}	1.70±0.83^{def}	0.24±0.75^{cd}
Eu 1.5	1.58±0.50^{c}	1.04±0.66^{de}	1.03±0.70^{de}	1.17±0.78^{ef}	0.97±0.87^{ef}	0.84±0.76^{ef}	0.82±0.81^{ef}	—0.76±0.96^{de}
Eu 2.0	1.30±0.92^{c}	0.68±0.32^{e}	0.79±0.38^{e}	0.84±0.34^{f}	0.58±0.48^{f}	0.53±0.51^{f}	0.57±0.54^{f}	—0.73±1.00^{de}
F	22.42***	11.98***	12.18***	13.58***	13.69***	13.97***	11.94***	14.70***
$\bar{X}$	1.73	2.09	2.23	2.38	2.37	2.27	2.30	0.28
(2)								
Com 0.0	5.75±1.71^{a}	5.91±1.60^{a}	7.48±2.50^{a}	8.50±2.80^{b}	8.83±2.95^{b}	8.69±3.44^{b}	10.70±3.39^{b}	4.95±2.73^{b}
Com 2.0	6.47±2.34^{a}	6.70±2.57^{a}	8.21±2.49^{a}	9.34±2.61^{ab}	9.77±2.62^{b}	9.37±2.75^{b}	9.05±2.93^{b}	2.58±2.65^{b}
Eu 0.0	6.19±2.58^{a}	8.98±3.88^{a}	9.07±4.11^{a}	14.04±6.52^{ab}	16.74±8.54^{a}	18.51±8.55^{a}	19.95±7.47^{a}	13.76±6.75^{a}
Eu 2.0	5.19±2.11^{a}	6.66±3.15^{a}	8.02±3.35^{a}	9.75±4.05^{b}	11.35±4.98^{ab}	12.38±4.97^{b}	12.41±5.39^{b}	7.22±3.70^{b}
F	0.44^{ns}	1.25^{ns}	0.26^{ns}	2.10^{ns}	2.80^{ns}	4.38*	5.64**	8.23***
$\bar{X}$	5.89	7.03	8.19	10.34	11.59	12.13	12.85	6.96

0, Before giving nutrient solution.

Table 25. The estimated leaf and the total increment of leaf area of the seedlings (mean±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at two-week intervals from the beginning of salinity treatments at each measurement of the greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species and salinity (%)	Leaf area/plant (cm^{2})							Total increament (cm^{2}) (3 months)
	1st	2nd	3rd	Measurement 4th	5th	6th	7th	
(1)								
Com 0.0^{0}	104.53±12.35^{h}	—	—	—	—	—	—	—
Com 0.0	618.89±190.91^{a}	632.85±199.99^{a}	711.96±237.73^{a}	802.70±285.06^{a}	725.92±229.69^{a}	684.04±266.71^{a}	704.98±404.90^{a}	86.09±317.92^{c}
Com 0.5	400.30±130.87^{bc}	448.92^{a}150.10^{b}	465.13±157.78^{b}	495.92±195.73^{bc}	466.75±160.26^{bcd}	473.23±165.87^{bc}	455.41±177.33^{bc}	55.10±79.29^{c}
Com 1.0	345.27±103.85^{cd}	361.52±109.16^{bcd}	357.46±118.13^{bc}	365.58±123.30^{cd}	364.23±128.79^{de}	323.61±153.43^{cd}	292.46±150.39^{cde}	—52.81±99.14^{cd}
Com 1.5	442.89±211.17^{b}	456.57±205.93^{b}	453.15±212.99^{b}	418.95±184.63^{bcd}	432.63±214.14^{cd}	338.58±178.82^{cd}	258.21±203.00^{cde}	—184.68±264.65^{d}
Com 2.0	336.02±115.40^{cd}	304.32±84.45^{cd}	315.73±131.74^{c}	285.30±116.36^{de}	276.42±113.41^{e}	207.95±148.63^{de}	182.59±152.63^{de}	—153.43±122.31^{d}
Eu 0.0^{0}	164.78±15.74^{gh}	—	—	—	—	—	—	—
Eu 0.0	277.55±79.61^{def}	362.70±140.71^{bcd}	429.65±151.75^{bc}	533.65±190.34^{b}	607.10±257.60^{ab}	663.65±300.96^{a}	787.15±446.24^{a}	509.60±438.09^{a}
Eu 0.5	308.73±123.75^{cde}	411.29±154.05^{bc}	433.05^{a}140.58^{bc}	510.75±206.15^{bc}	544.94±188.46^{bc}	587.41±226.81^{ab}	586.38±226.68^{ab}	277.65±163.18^{b}
Eu 1.0	271.34±92.28^{def}	283.14±113.74^{d}	314.31±123.09^{c}	289.03±149.70^{de}	285.66±147.70^{e}	284.82±134.61^{d}	316.84±153.51^{cd}	45.50±139.43^{c}
Eu 1.5	221.36±70.00^{efg}	145.51±92.97^{e}	143.96±98.10^{d}	164.09±109.25^{ef}	136.22±121.17^{f}	116.87±106.45^{e}	115.33±112.77^{de}	—106.04±134.10^{cd}
Eu 2.0	203.36±144.73^{fg}	107.13±50.23^{e}	123.47±59.03^{d}	132.55±53.85^{f}	90.79±74.99^{f}	83.52±80.00^{e}	88.97±84.63^{e}	—114.39±156.70^{cd}
F	22.47***	14.80***	15.47***	16.85***	16.96***	17.06***	13.74***	14.50***
$\bar{X}$	302.31	365.07	390.33	418.95	416.80	402.08	408.49	60.56
(2)								
Com 0.0	1097.95±327.21^{a}	1129.47±305.22^{b}	1428.91±478.30^{b}	1623.28±534.45^{b}	1686.32±564.11^{b}	1660.05±658.06^{b}	2043.55±647.63^{b}	945.60±520.61^{b}
Com 2.0	1177.12±425.82^{a}	1219.35±467.38^{b}	1493.84±453.48^{b}	1699.70±475.11^{b}	1778.86±477.70^{b}	1704.98±500.95^{b}	1646.91±533.27^{b}	469.79±483.05^{b}
Eu 0.0	1633.28±680.79^{a}	2369.85±1025.13^{a}	2392.73±1084.39^{a}	3705.75±1720.66^{a}	4419.45±2259.97^{a}	4886.10±2256.72^{a}	5265.83±1972.62^{a}	3632.55±1781.22^{a}
Eu 2.0	1196.57±488.02^{a}	1536.00±727.96^{b}	1851.43±773.16^{ab}	2249.14±934.84^{b}	2619.43±1149.62^{b}	2856.00±1146.57^{b}	2862.86±1234.28^{b}	1666.29±853.14^{b}
F	1.46^{ns}	4.21*	2.23^{ns}	5.51**	5.98**	8.36***	11.04***	11.58***
$\bar{X}$	1269.35	1549.36	1782.56	2292.93	2593.18	2738.61	2900.95	1631.59

0. Before giving nutrient solution.

Table 26. Leaf area and weight characteristics of the seedlings (mean±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at the end of the experiment in the greenhouse (nonsignificant differences in the same column are indicated by same letters).

Species	Leaf area		Leaf weight	
salinity (%)	cm²/plant	cm²/leaf	g/leaf	g/dm²
(1)				
Com 0.0^{0}	104.36 ± 22.69^{g}	12.37 ± 2.38^{f}	0.07 ± 0.01^{c}	0.57 ± 0.12^{cde}
Com 0.0	640.98 ± 265.74^{ab}	34.90 ± 13.81^{a}	0.19 ± 0.07^{a}	0.56 ± 0.07^{cde}
Com 0.5	446.05 ± 186.38^{cd}	24.31 ± 5.13^{bc}	0.13 ± 0.03^{b}	0.53 ± 0.09^{def}
Com 1.0	272.34 ± 136.00^{ef}	20.31 ± 12.91^{bcd}	0.13 ± 0.08^{b}	0.64 ± 0.11^{abc}
Com 1.5	260.75 ± 136.13^{efg}	25.65 ± 13.14^{b}	0.15 ± 0.07^{b}	0.63 ± 0.12^{bcd}
Com 2.0	192.61 ± 64.05^{efg}	19.02 ± 7.06^{cde}	0.13 ± 0.05^{b}	0.68 ± 0.11^{ab}
Eu 0.0^{0}	161.87 ± 27.12^{a}	11.77 ± 2.40^{f}	0.05 ± 0.02^{c}	0.45 ± 0.10^{f}
Eu 0.0	717.81 ± 383.53^{bc}	13.00 ± 5.10^{ef}	0.07 ± 0.05^{c}	0.54 ± 0.15^{cdef}
Eu 0.5	565.43 ± 189.81^{de}	15.54 ± 4.45^{def}	0.08 ± 0.03^{c}	0.49 ± 0.07^{ef}
Eu 1.0	303.15 ± 136.81^{fg}	12.64 ± 3.48^{ef}	0.07 ± 0.02^{c}	0.54 ± 0.10^{cdef}
Eu 1.5	125.28 ± 66.67^{efg}	11.61 ± 3.81^{f}	0.08 ± 0.03^{c}	0.72 ± 0.19^{a}
Eu 2.0	146.49 ± 14.95^{efg}	12.71 ± 0.85^{ef}	0.08 ± 0.01^{c}	0.64 ± 0.06^{abc}
F	21.36***	13.93***	13.40***	6.23***
$\bar{X}$	343.09	17.58	0.10	0.57
(2)				
Com 0.0	1928.30 ± 312.43^{b}	31.5 ± 27.88^{ab}	0.17 ± 0.05^{a}	0.52 ± 0.04^{a}
Com 2.0	1638.20 ± 696.13^{b}	36.95 ± 12.08^{a}	0.20 ± 0.07^{a}	0.55 ± 0.03^{a}
Eu 0.0	5189.48 ± 1751.83^{a}	27.45 ± 4.25^{ab}	0.10 ± 0.03^{b}	0.38 ± 0.06^{b}
Eu 2.0	2865.21 ± 856.04^{b}	24.00 ± 4.48^{b}	0.10 ± 0.02^{b}	0.43 ± 0.06^{b}
F	14.20***	3.02*	6.95**	16.03***
$\bar{X}$	2905.30	29.98	0.14	0.47

0, Before giving nutrient solution.

Table 27. Biomass characteristics of the seedling (means±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at the end of the experiment in the greenhouse (nonsignificant differences in the same column are indicated by same letters).

Species and salinity (%)	Dry weight (g)					
	Leaves	Main shoot	Branch shoots	Roots	Above ground	Total plant
(1)						
Com 0.0^{0}	0.58 ± 0.11^{g}	0.26 ± 0.06^{f}	0.00 ± 0.00^{c}	0.30 ± 0.08^{c}	0.84 ± 0.16^{e}	1.14 ± 0.21^{d}
Com 0.0	3.50 ± 1.44^{ab}	2.13 ± 1.24^{cd}	0.08 ± 0.14^{bc}	2.87 ± 1.46^{a}	5.70 ± 2.29^{b}	8.44 ± 3.39^{a}
Com 0.5	2.28 ± 0.78^{cd}	1.38 ± 0.50^{e}	0.08 ± 0.14^{bc}	1.93 ± 0.86^{b}	3.75 ± 1.29^{c}	5.51 ± 1.82^{bc}
Com 1.0	1.67 ± 0.74^{de}	1.10 ± 0.58^{e}	0.13 ± 0.20^{bc}	1.74 ± 0.90^{b}	1.90 ± 1.36^{c}	4.64 ± 2.21^{bc}
Com 1.5	1.56 ± 0.84^{def}	1.33 ± 0.54^{e}	0.05 ± 0.08^{bc}	1.86 ± 0.78^{b}	2.95 ± 1.31^{c}	4.81 ± 1.96^{bc}
Com 2.0	1.27 ± 0.34^{efg}	1.16 ± 0.23^{e}	0.02 ± 0.04^{c}	1.68 ± 0.48^{b}	2.45 ± 0.48^{cd}	4.13 ± 0.84^{bc}
Eu 0.0^{0}	0.74 ± 0.22^{fg}	0.44 ± 0.13^{f}	0.00 ± 0.00^{c}	0.34 ± 0.11^{c}	1.18 ± 0.34^{de}	1.51 ± 0.45^{d}
Eu 0.0	3.66 ± 1.93^{a}	3.88 ± 1.28^{a}	0.44 ± 0.38^{a}	2.27 ± 0.90^{ab}	7.98 ± 2.96^{a}	9.89 ± 3.39^{a}
Eu 0.5	2.79 ± 0.96^{bc}	3.06 ± 1.36^{b}	0.22 ± 0.43^{b}	2.32 ± 1.51^{ab}	6.07 ± 2.19^{b}	8.27 ± 3.73^{a}
Eu 1.0	1.67 ± 0.80^{de}	2.07 ± 0.58^{cd}	0.05 ± 0.06^{bc}	2.17 ± 1.16^{ab}	3.79 ± 1.25^{c}	5.96 ± 2.12^{b}
Eu 1.5	0.93 ± 0.65^{efg}	1.52 ± 0.49^{de}	0.01 ± 0.02^{c}	1.58 ± 0.70^{b}	2.44 ± 1.06^{cd}	3.85 ± 1.67^{c}
Eu 2.0	0.94 ± 0.14^{efg}	2.44 ± 0.49^{c}	0.03 ± 0.04^{c}	1.55 ± 0.60^{b}	3.41 ± 0.63^{c}	4.96 ± 1.17^{bc}
F	19.56***	32.87***	7.46***	12.74***	30.75***	25.04***
$\bar{X}$	1.86	1.69	0.10	1.66	3.66	5.21
(2)						
Com 0.0	9.93 ± 0.99^{b}	4.00 ± 0.85^{c}	3.00 ± 1.46^{ab}	9.65 ± 4.31^{a}	16.93 ± 1.48^{c}	26.57 ± 5.05^{b}
Com 2.0	9.01 ± 3.93^{b}	4.25 ± 2.02^{c}	2.74 ± 1.25^{ab}	8.85 ± 3.47^{a}	16.00 ± 6.36^{c}	24.68 ± 9.29^{b}
Eu 0.0	19.08 ± 5.49^{a}	22.39 ± 5.38^{a}	3.74 ± 1.88^{a}	14.52 ± 7.29^{a}	45.20 ± 12.15^{a}	59.73 ± 18.97^{a}
Eu 2.0	12.13 ± 2.81^{b}	13.98 ± 2.99^{b}	1.52 ± 1.00^{b}	11.34 ± 4.95^{a}	27.63 ± 5.74^{b}	38.96 ± 10.35^{b}
F	9.14***	46.65***	2.51^{ns}	1.40^{ns}	19.82***	10.78***
$\bar{X}$	12.54	11.15	2.75	11.09	26.44	37.49

0, Before giving nutrient solution.

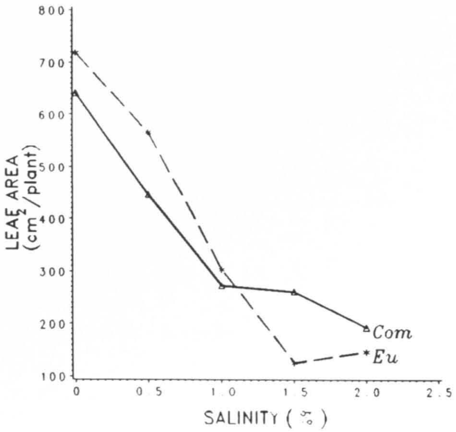


Figure 41. Relationship between area and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown in culture solution in the greenhouse experiments.

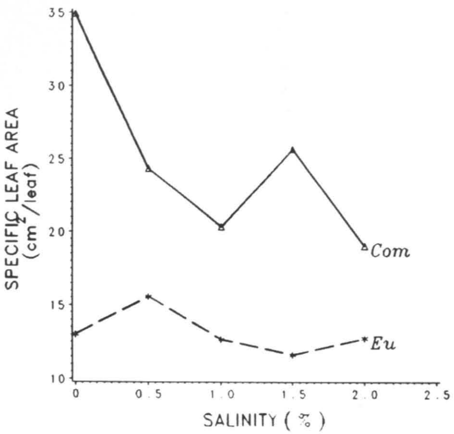


Figure 42. Relationship between specific leaf area and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown in culture solution in the greenhouse experiments.

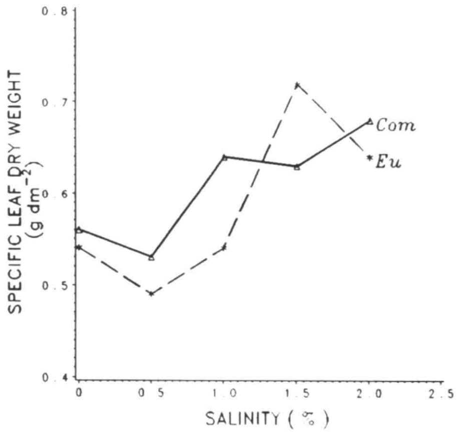


Figure 43. Relationship between specific leaf dry weight and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown in culture solution in the greenhouse experiments.

between species ($p < 0.05$). Leaf dry weight per unit area (g dm^{-2}) was not different within species but was between species ($p < 0.001$). Leaf dry weight per unit area seemed to be smaller in the sand medium experiment than in the nutrient solution experiment although this difference was not statistically tested.

377. Biomass characteristics

The biomass of the seedlings at the end of the greenhouse experiments is shown in Table 27. The total dry weight of the different components, *i.e.* leaves, shoots, branch-shoots, roots as well as their sums, decreased somewhat irregularly with increasing salinity, but the general trend was clear.

The total plant dry biomass of *C. quadrangulare* was smaller than that of *E. camaldulensis* at each treatment of the culture solution experiment, except for 1.5 %; this difference was not, however, statistically significant (Table 27). In sand medium experiment, the leaf, shoot, branch, root, total above-ground plant and total plant dry biomasses were higher under the non-saline treatment than under the saline treatment; for both species. Of the two species, *C. quadrangulare* had a lower total seedling biomass in both non-saline and saline conditions ($p < 0.001$).

378. Shoot:root ratio

The shoot:root ratio based on length decreased with time in both species (Table 28). In the culture solution experiment, shoots were shorter than roots in the case of *C.*

Table 28. Allocation of growth of the seedlings (mean±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution (1) and sand medium (2) at two-week intervals from the beginning of salinity treatments at each measurement of the greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species and salinity (%)	Shoot: root ratio (by length) 1st	2nd	3rd	4th	5th	6th	7th	Shoot: root ratio (by length) Total increment	Shoot: root ratio (by dry weight) final result	Leaf: root ratio (by dry weight) final result
(1)										
Com 0.0^{0}	0.91 ± 0.32^{d}	—	—	—	—	—	—	—	2.82 ± 0.55^{bc}	1.94 ± 0.35^{ab}
Com 0.0	0.98 ± 0.43^{d}	0.78 ± 0.32^{c}	0.67 ± 0.30^{c}	0.58 ± 0.25^{cd}	0.56 ± 0.23^{d}	0.53 ± 0.21^{e}	0.53 ± 0.21^{e}	0.27 ± 0.13^{b}	2.16 ± 0.63^{de}	1.37 ± 0.56^{cd}
Com 0.5	0.94 ± 0.25^{d}	0.71 ± 0.17^{c}	0.61 ± 0.19^{c}	0.52 ± 0.18^{d}	0.50 ± 0.18^{d}	0.48 ± 0.18^{e}	0.48 ± 0.17^{e}	0.30 ± 0.50^{b}	2.08 ± 0.51^{def}	1.27 ± 0.32^{de}
Com 1.0	0.89 ± 0.34^{d}	0.73 ± 0.28^{c}	0.65 ± 0.30^{c}	0.58 ± 0.27^{cd}	0.54 ± 0.25^{d}	0.53 ± 0.24^{e}	0.52 ± 0.24^{e}	0.54 ± 1.23^{ab}	1.75 ± 0.44^{ef}	1.02 ± 0.30^{ef}
Com 1.5	8.82 ± 0.31^{d}	0.73 ± 0.31^{c}	0.68 ± 0.28^{c}	0.64 ± 0.28^{cd}	0.64 ± 0.29^{cd}	0.63 ± 0.30^{de}	0.63 ± 0.30^{de}	0.20 ± 0.24^{b}	1.64 ± 0.66^{ef}	0.86 ± 0.45^{fg}
Com 2.0	0.91 ± 0.27^{d}	0.89 ± 0.25^{c}	0.88 ± 0.24^{c}	0.83 ± 0.24^{c}	0.82 ± 0.24^{c}	0.81 ± 0.25^{cd}	0.81 ± 0.25^{cd}	0.49 ± 0.52^{ab}	1.53 ± 0.37^{f}	0.78 ± 0.18^{fg}
Eu 0.0^{0}	3.18 ± 0.89^{a}	—	—	—	—	—	—	—	3.57 ± 0.59^{a}	2.23 ± 0.40^{a}
Eu 0.0	1.65 ± 0.77^{c}	1.35 ± 0.58^{b}	1.22 ± 0.54^{b}	1.21 ± 0.58^{b}	1.17 ± 0.56^{b}	1.14 ± 0.53^{b}	1.11 ± 0.55^{b}	0.59 ± 0.36^{ab}	3.65 ± 1.05^{a}	1.64 ± 0.70^{bc}
Eu 0.5	1.48 ± 0.40^{c}	1.25 ± 0.29^{b}	1.18 ± 0.26^{b}	1.14 ± 0.26^{b}	1.10 ± 0.28^{b}	1.11 ± 0.31^{b}	1.03 ± 0.26^{bc}	0.66 ± 0.45^{ab}	3.03 ± 0.89^{b}	1.40 ± 0.38^{cd}
Eu 1.0	1.40 ± 0.41^{c}	1.21 ± 0.37^{b}	1.16 ± 0.36^{b}	1.13 ± 0.35^{b}	1.08 ± 0.31^{b}	1.07 ± 0.32^{bc}	1.03 ± 0.31^{bc}	0.75 ± 0.72^{ab}	2.01 ± 0.74^{def}	0.86 ± 0.43^{fg}
Eu 1.5	1.36 ± 0.19^{c}	1.21 ± 0.15^{b}	1.15 ± 0.18^{b}	1.10 ± 0.21^{b}	1.09 ± 0.21^{b}	1.08 ± 0.22^{bc}	1.00 ± 0.25^{bc}	0.32 ± 0.24^{b}	1.56 ± 0.20^{f}	0.53 ± 0.14^{g}
Eu 2.0	2.48 ± 0.48^{b}	2.27 ± 0.41^{a}	2.25 ± 0.38^{a}	2.21 ± 0.37^{a}	2.19 ± 0.39^{a}	2.23 ± 0.44^{a}	$2.23.\pm0.45^{a}$	0.90 ± 1.12^{a}	2.34 ± 0.49^{cd}	0.66 ± 0.18^{g}
F	35.17***	16.01***	18.00***	19.86***	20.48***	21.44***	19.93***	1.72^{ns}	21.49***	24.01***
$\bar{X}$	1.40	1.04	0.97	0.92	0.89	0.88	0.85	0.48	2.46	1.33
(2)										
Com 0.0	2.39 ± 0.77^{b}	—	—	—	—	—	1.11 ± 0.33^{c}	0.60 ± 0.35^{c}	1.97 ± 0.62^{bc}	1.15 ± 0.38^{a}
Com 2.0	1.86 ± 0.42^{b}	—	—	—	—	—	1.03 ± 0.12^{c}	0.49 ± 0.12^{c}	1.86 ± 0.36^{c}	1.04 ± 0.22^{a}
Eu 0.0	7.76 ± 3.36^{a}	—	—	—	—	—	3.58 ± 0.62^{a}	2.16 ± 0.82^{a}	3.45 ± 0.83^{a}	1.45 ± 0.37^{a}
Eu 2.0	5.78 ± 1.53^{a}	—	—	—	—	—	2.76 ± 0.37^{b}	1.51 ± 0.27^{b}	2.71 ± 0.78^{ab}	1.18 ± 0.34^{a}
F	13.13***						58.45***	17.13***	7.25**	1.60^{ns}
$\bar{X}$	4.44						2.12	1.19	2.50	1.21

0, Before giving nutrient solution.

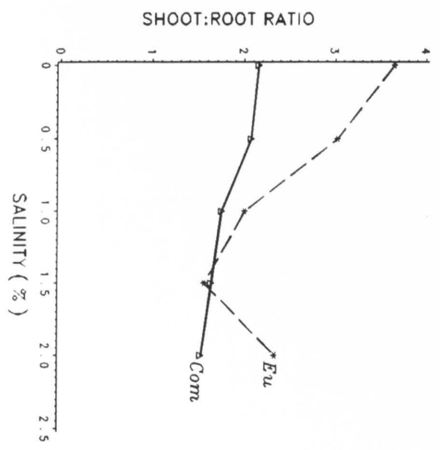


Figure 44. Relationship allocation of growth of the above ground shoots to roots and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown in culture solution in the greenhouse experiments.

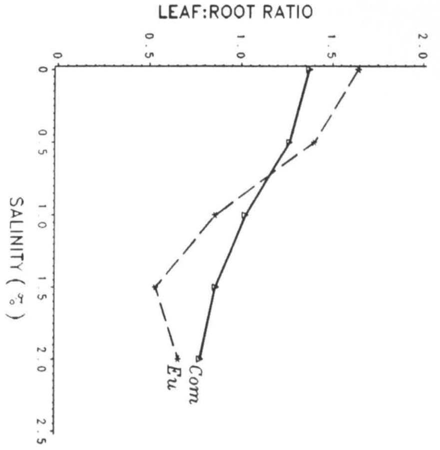


Figure 45. Relationship between allocation of growth of the leaves to roots and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown in culture solution in the greenhouse experiments.

quadrangulare (shoot:root < 1), but longer in the case of *E. Camaldulensis* (shoot:root > 1). The shoot:root ratios were less than 1 both *C. quadrangulare* and *E. Camaldulensis* when calculated from the increment of shoot and root in three months. In sand medium experiment, the shoots were as always longer than the root (shoot:root > 1) in both species, but the total increment, the roots were longer in *C. quadrangulare* both control (0 %) and saline (2 %) treatments.

The shoot:root ratio based on weight was negatively affected by solution salinity (Figure 44). The dry weight based shoot:root ratio was also higher in non-saline than in saline sand, for both species. This difference was only statistically significant in the case of between species but was not within species. The shoot:root weight ratio for *E. camaldulensis* was higher than that for *C. quadrangulare* at all salinity levels, and in both experiments (Table 28).

379. Leaf:root ratio

In both experiments, the leaf:root biomass ratio for both species decreased with salinity (Table 28). In the solution experiment, the leaf:root ratio of *C. quadrangulare* decreased from 1.37 to 0.78 over the salinity treatments: 0 % to 2.0 %, and of *E. camaldulensis* from 1.64 to 0.53 over the salinity treatments: 0 % to 1.5 % (Figure 45). The effect of salinity on the allocation of growth between leaves and roots indicates that salinity results in more of the trees structure being put into roots than leaves (Appendix II, Figure 20).

4. Discussion

41. Plant responses to genetic and site factors

The existence of a large number of species and varieties of *Eucalyptus* growing in many diverse habitats enables the selection of species and seed sources for almost any environmental conditions, including high soil salinity. Blake (1981) screened 52 species and subspecies of *Eucalyptus* for salt tolerance in solution culture. Eleven species survived NaCl concentrations of 300 mol m^{-3} (1.75 % w/v NaCl) or higher. Differences in salt resistance among provenances (seed sources) of *Eucalyptus camaldulensis* Dehnh. have been demonstrated and attributed to differences in tissue tolerance to sodium and/or chloride (Sands 1981, El-Lakany 1986). This intraspecific variability in salt tolerance suggests that salt tolerance is likely to be under genetic control (El-Lakany 1986, Midley *et al.* 1987). The results from the present study support this suggestion. In the field study, it was found that the local variety of *E. camaldulensis* had higher salt tolerance than the Australian variety (0149).

The plantations at Khon Kaen and Roi-et were 130 km apart and there were differences in precipitation and soil moisture conditions. The saline soils at Khon Kaen were more moist than the non-saline soils at Roi-et. Based on my observations, it would appear that the NaCl in the soil surface absorbs moisture from the air due to the higher temperature and humidity. The higher humidity also caused higher photosynthetic rates (cf. *Combretum quadrangulare* Kurz in Appendix II, Figures 2D and 3D; *Eucalyptus camaldulensis* Dehnh. in Appendix II, Figure 4D). However, the increase in ambient humidity to near saturation has two possible effects on the plant; one is to reduce water flow in the plant and the other is to reduce water stress (Pitman 1984).

42. Ecophysiological responses to salinity

Stomatal frequencies of the Australian variety *Eucalyptus camaldulensis* (No. 0149) and local variety were found to be higher on the abaxial leaf surface than on the adaxial surface (cf. Appendix I, Table 5). Pereira and Kozlowski (1976) also found a similar difference for *E. camaldulensis*. Moreshet (1981) reported the same difference for two Australian provenances of *E. camaldulensis*, Albacutya and Katherine. However, Jarvis and McNaughton (1986) reported that stomatal density was more on adaxial than abaxial surface of tobacco (*Nicotiana* sp.) leaves.

The leaf imprints taken at 10:00 h and 14:00 h came from different leaves. The differences in stomatal frequencies determined at 10:00 h and 14:00 h (cf. Appendix I, Table 5) are thus largely due to sampling variation. Adult leaves are known to have more stomatal numbers than juvenile and intermediate leaves (Cameron 1970). Even the same leaf, on different projected sampling area of the microscope determination is also different densities. Jarvis and McNaughton (1986) also reported that the stomatal densities almost double from the tip to the base while stomatal lengths decrease by about one-quater in the same direction. The differences are variations in both shading by other leaves in a canopy and in orientation of parts of an irregularly shaped leaf with respect to the solar beam.

Stomatal characteristics in relation to environmental factors/salinity: In the most successfully acclimatized exotic tree species, morphological and anatomical modifications are usually observed. Gindel (1973) reports that of the 300 species found to have adapted to more arid conditions, stomata were greater in number and present on both the upper and lower leaf surfaces, particularly in the case of the Myrtaceae family which includes *Eucalyptus* species. Such modifications were more evident, the greater the differences in climatic and edaphic conditions between their native and new habitats. Moreover, in some species, leaves that grew during the hottest months had a denser net of stomata on the adaxial leaf surface than leaves that grew during the spring months (Gindel 1973). Stomatal frequency in *Eucalyptus* species has been found to vary in relation to environment, *e.g. E. fastigata* Deane & Maiden (Camaron 1970); *Eucalyptus camaldulensis* Dehnh. and *E. globulus* Labill. (Pereira and Kozlowski 1976); *E. calophylla* R. Br., *E. globulus* Labill., *E. maculata* Hook., *E. marginata* Donn ex Smith, *E. resinifera* Smith, *E. saligna* Smith and *E. wandoo* Blakely (Ridge *et al.* (1984); *E. citriodora* Hook. and *E. tereticornis* Smith (Kumar and Rao 1985) and *Eucalyptus* hybrid (Nautiyal and Reynold 1988). Kumar and Rao (1985) found that a *E. tereticornis* Hook. exhibited a higher stomatal frequency and index on both leaf surfaces than *E. citriodora*.

Combretum quadrangulare and *Eucalyptus camaldulensis* grown in the culture solution experiment, in the greenhouse, did have a higher stomatal frequency and stomatal index in the higher salinity treatments. In contrast, however, the stomatal frequency and stomatal index were higher on the non-saline soil than the saline soil in the field study. Maas and Nieman (1978) found that chloride induces larger epidermis cells, and fewer stomata per unit surface area on barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.). Sulphate salinity, on the other hand, resulted in smaller cells and an increase number of stomata per unit surface area. They further reported that SO_4 inhibits cell expansion more than cell division, whereas Cl inhibits cell division while stimulating cell enlargement. Therefore, the stomatal changes caused by salinity depend very much on plant species and kind of salts.

For both species studied, the higher the CO_2 resistance components (Σ'r, r'g, r_{mx} and r's) were, the lower the photosynthetic rates and salt tolerance (cf. Tables 8 and 10). The **stomatal resistance** (r's) results for *Combretum quadrangulare* at 1.5 % salinity (cf. Table 10) are higher than at the 2 % salinity level. This result may have been because of the extremely low outside temperatures (less than —32°C) at the time of measurement. The IRGA system had difficulty when taking in such cold and dry air from outside. However, the trend in the results from the porometer measurements showed a gradual increase in stomatal resistance with salinity.

It is more convenient to use **stomatal conductance** than stomatal resistance. Stomatal conductance was found to be lower on the saline soil than on non-saline soil for *Eucalyptus camaldulensis* (cf. Table 16 and 17; Appendix I, Tables 15 and 16). However, the stomatal conductance of *Combretum quadrangulare* measured in the field studies was quite the same in non-saline and saline conditions at temperatures from 30° to 36°C (cf. Appendix I, Table 15). The stomatal conductance of *Eucalyptus camaldulensis* trees in both varieties increased over the temperature range 21° to 30°C in the non-saline and saline treatments, and then decreased (cf. Appendix I, Table 15). The dependence of stomatal conductance on irradiance in the case of both species was not regular. However, stomatal conductance did tend to increase over the photon flux density range 1000 to 2000 μmol m^{-2}s^{-1} (cf. Table 17 and Appendix I, Table 16). Stomatal conductance was thus shown to vary with species, seed source, temperature and irradiance (cf. Appendix I, Tables 15 and 16).

Stomatal conductance increased from 06:00 to 12:00 h, then decreased until 14:00 h and then stayed at a constant level from 14:00 to 17:00 h (cf. Figure 32). Davis (1987) found that stomatal conductance of *Chrysothamnus nauseosus* spp. *albicaulis* was the highest during the morning and decreased by about 30% by the afternoon, even though the plants were well-watered. Stomatal conductance of the subalpine conifers obtained by Kaufmann (1985) decreased downward through the canopy. The stomatal conductance also depends on which side of the leaf is exposed to irradiation. Vos and Oyarzun (1987) found that stomatal conductance of potato leaves (*Solanum tuberosum* L. cv. Bintje) showed a decline with leaf age but without a clear relationship to leaf numbers. Beadle *et al.* (1979) discovered that stomatal conductance of Sitka spruce (*Picea sitchenensis* (Bong.) Carr.) decreased with decreased xylem water potential while cuticular conductance stayed constant.

In the greenhouse experiment it was generally found that *Combretum quadrangulare* had a lower stomatal conductance (high resistance) and lower photosynthetic rates than was the case for *Eucalyptus camaldulensis* variety 0149. The results from the field study, however, showed that while the Australian variety of *E. camaldulensis* variety 0149 had lower photosynthetic rates than *C. quadrangulare* (cf. Tables 6 and 7), it had a higher stomatal conductance (cf. Table 13 and Appendix I, Tables 15 and 16). The difference was not statistically significant though (cf. Tables 6 and 7). Furthermore, *E. camaldulensis* variety 0149, had a relatively low water-use efficiency when compared with the local variety of *E. camaldulensis* (cf. Appendix I, Tables 11 and 12). Therefore, within a species, much of its acclimatization and adaptation ability is dependent on the source of the seeds.

The width and length of the guard cells in the greenhouse experiment increased with salinity treatment. In the field, guard cells were also found to be bigger on the saline soil than on the non-saline soil. In the case of non-saline conditions, the average size of the guard cells of *Combretum quadrangulare* was the same in the greenhouse and field experiments. *Eucalyptus camaldulensis* of the Australian variety 0149 had larger guard cells than *C. quadrangulare*. The average size guard cells in the case of the local variety of *E. camaldulensis* grown in the field study was greater than that of the Australian variety grown in the greenhouse. The Australian variety of *E. camaldulensis* grown in the field had larger guard cells than that grown in the greenhouse (cf. Appendix I, Tables 1, 2 and 3). For both varieties of the *Eucalyptus*, the photosynthetic and transpiration rates were higher when the guard cell size was greater. However, *C. quadrangulare* had the same guard cell sizes in the greenhouse and field studies, but the photosynthetic and transpiration rates were greater in the field study. In the field, *C. quadrangulare* also had greater net photosynthetic rates but the transpiration rates were lower than in the Australian variety of *E. camaldulensis*. In the case of saline conditions in the field, the local variety of *E. camaldulensis* had lower photosynthetic and transpiration rates than the non-saline soil, even though there were the bigger guard cell size, but not for *C. quadrangulare*.

The length of the stomatal aperture varies with the length guard cell, the bigger the guard cell is, the longer the length of aperture. The stomata regulate the guard cell aperture during the day. A longer aperture will be able to consume more CO_2 but at the same time may lose more water. However, the sampling was only taken two different time in the morning (10:00 h) and in the afternoon (14:00 h) in the field and a time in the afternoon (14:00) in the greenhouse, the variation was determined only taken time.

The size of the **stomatal opening** in the greenhouse experiment initially increased with increasing salinity but then decreased at higher salinity treatments. The wider the stomatal opening were, the higher the transpiration rates. Stomatal opening was found to be wider on abaxial than on adaxial surfaces in the case of *Combretum quadrangulare*, both in the greenhouse and in the field study. For *Eucalyptus camaldulensis* stomatal opening were slightly bigger on the adaxial surfaces, in most cases (cf. Appendix I, Tables 1, 2 and 3). This may be because of the vertical orientational of the leaves, the isobilateral structure of the *E. camaldulensis*, since the size of the stomatal opening depends very much on radiation interception. The differences of the structure caused the size of the stomatal opening in the adaxial and abaxial surfaces in *C. quadrangulare* but not in *E. camaldulensis*. *E. camaldulensis*, which has greatly thickened cuticles and many sunken stomata (Cameron 1970).

The direct response of stomata to atmospheric humidity has recently received much attention. Stomata were found to be more open on days with low vapour pressure deficit (VPD), leading to greater transpiration and lower xylem water-potentials, than on drier days (cf. Schulze *et al.* 1972). The kinetic parameters of the conductance response appear to be more closely related to leaf-air vapour pressure difference (VPD) than to relative humidity or transpiration. Increasing the VPD significantly accelerated stomatal opening in both sugarcane (*Saccharum* spp. hybrid clone H65—7052) and soybean (*Glycine max* cv. Prize) (Assmann and Grantz 1990, Grantz and Meinzer 1990). In tobacco (*Nicotiana tabacum* var Havana), the quantum yield of CO_2 fixation was reduced by 20 % when increasing the mean VPD from 9.2 to 18.6 mbars. While the transpiration rate increased with increasing VPD, net photosynthesis decreased (Peterson 1990) as well as Grieu *et al.* (1988) found in 2-year-old seedlings of *Pseudotsuga menziesii* (provenance Ashford), *P. macrocarpa* (Torr.) Mayr and *Cedrus atlanta* (provenance Ventoux). Farquhar (1978) found that stomatal closure responds to an increase in the difference in humidity between the inside of the leaf and the ambient air. Nautiyal and Reynold (1988) showed that while there was a significant difference in the width of stomatal opening between various *Eucalyptus* hybrids, there was no such difference between leaf age, surfaces or regions. The stomata of *Eucalyptus fasciculosa* F. Muell. were found to open soon after dawn but partially close by 10:00 h, evidently in response to a falling water potential, and reopened slightly at 03:00 h before closing fully at sunset (Whittington and Sinclair 1988).

In the present study, the stomatal openings on the adaxial surface of *Combretum quadrangulare* were found to be wider in the morning (10:00 h) than in the afternoon (14:00 h). The photosynthesis and transpiration measurements of the adaxial surface were also found to be higher in the morning than in the afternoon (cf. Figures 12 and 21), when there was a better water-use efficiency, too (cf. Figure 17). However, stomatal opening was smaller on the adaxial surface than on abaxial surfaces. This may have been because the adaxial surfaces were directly exposed to the sun and thus regulated stomata size. With the isobilateral leaf structure of *Eucalyptus camaldulensis*, stomatal opening were about the same size on the abaxial and adaxial surfaces (cf. Appendix I, Tables 2 and 3). However, they were wider in the afternoon than in the morning, while the transpiration rates were lower. Presumably, the stomata were fully open at level where transpiration was equal to water flow into the leaf from the xylem pathway. Whittington and Sinclair (1988) also found that *E. fasciculosa* did not close its stomata completely during periods of increasing water stress, but only enough to prevent further dehydration.

Concerning the **CO_2 compensation point,** Γ the higher the Γ was the higher the photorespiration rates as well as salinity but the lower the photosynthetic rates. The temperature-induced increase in Γ showed a steeper trend at high temperatures (Slatyer 1977b and Luukkanen 1978). Γ was related to growth temperatures; the highest temperature optimum had significantly higher rates of net photosynthesis at the highest growth temperature at the lowest-elevation and warmest site (Slatyer 1977a, Slatyer and Ferrar 1977a). High values of Γ were also associated with low soil water contents (Luukkanen 1978). An increase in Γ decreased net photosynthesis (cf. Table 8). An increase in Γ has also been associated with a decrease in net photosynthetic efficiency in different genotypes (Luukkanen 1978, Grierson and Covey 1988). The Γ was higher in *C. quadrangulare* than *E. camaldulensis* (cf. Figure 25) but the trends in the **photorespiration** rate fluctuated, initially increasing with salinity at low levels and then lowering at higher salinity (cf. Figures 25 and 26) (Macler 1988). As far as photorespiration rates determined with the IRGA in the laboratory, changes in the ambient CO_2 (Ca), the intercellular CO_2 (Ci) changed. Ca had no affect on the photorespiration rates. Similar results were found by Gupta and Berkowitz (1988) and Mott (1988). While Sharkey (1988) stated that the rate of photorespiration in C_3 plants will fall to one half the current rate when the CO_2 level in the atmosphere doubles. Furthermore, he stated that the resistance to CO_2 diffusion through the mesophyll is less than the resistance of the stomata, often one third the stomatal resistance. In this study, however, it was found that the mesophyll resistance (r_{mx}) was very much higher than stomatal resistance (r's) (cf. Table 10).

The **photorespiration** model at different leaf temperatures used a constant photon flux density at 1000 μmol m^{-2}s^{-1} (cf. Figure 26). Therefore, only photorespiration rates at irradiance around 1000 μmol m^{-2} s^{-1} can be considered reliable, rates at other irradiance levels may not. However, since the temperature treatment was parallel with irradiance, the photorespiration rates may be considered reasonable values. Furthermore, photorespiration rates were assumed from dark respiration rates by using exponential as a temperature dependence modification (cf. Korpilahti 1988, Hari and Berninger 1990). This might be very useful and convenient way in which to achieve respiration rates. Photorespiration is a very difficult parameter to determine, especially for stressed plants. It takes time to achieve the CO_2 compensation point and there are many procedures in the calculation which may be subject to error.

Within a species, variation in photorespiration and the CO_2 compensation point have been suggested as criteria for the selection of trees with a potentially high photosynthetic performance (Decker 1970, Luukkanen *et al.* 1976). In some cases, both the photorespiration rate and the CO_2 compensation point correlated (inversely) with net photosynthetic rates per unit of foliage (Luukkanen *et al.* 1976).

According to determined photorespiration rates, the photosynthetic efficiency of *Combretum quadrangulare* was better than that of *Eucalyptus camaldulensis* on non-saline soil but was worse on saline soil (cf. Figure 28). It therefore might be better to grow *E. camaldulensis* on saline soil and *C. quadrangulare* on non-saline soil. The lower the photorespiration rates will be, the higher the net photosynthesis rates (Macler 1988). This situation is a goal in plant improvement programmes (Grierson and Covey 1988).

Dark respiration was affected by temperature and by salinity but only in the case of *Combretum quadrangulare* (cf. Table 8). However, dark respiration tended to be higher at lower salinities in the case of both species (Macler 1988). According to the results obtained by Luukkanen (1978) for different clones of spruce, dark respiration rates varied significantly among the clones with temperature. Hellmuth (1967) found the same effect in *Eucalyptus marginata* Donn ex Smith.

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 *Combretum quadrangulare* and *Eucalyptus camaldulensis*, the water potential decreased with increasing salinity (cf. Tables 1 and 2). 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. 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.

Water potential decreased with leaf ageing because younger leaves are metabolically more active and may receive a larger proportion of the available water. Therefore, the younger leaves near tip of the seedlings display higher levels of water potential, osmotic potential and pressure potential, whereas significantly lower values of water potential and its components may be recorded in the older leaves towards the base of the plant (Manohar 1977). Morse (1990) found that rosette leaves of the high polysaccharide subspecies of *Hemizonia luzulifolia* DC. had greater leaf specific weight, water weight at full hydration, transpiration rates and higher water potential than low polysaccharide subspecies.

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 species genetic variation (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). For *Eucalyptus camaldulensis* according to temperature dependence, the **transpiration rate** was lower on the saline soil than on the non-saline soil (cf. Appendix I in Table 7).

Correspondence between **transpiration** and stomatal conductance has parallelism to that between photosynthesis and stomatal conductance. There are optimum and the higher limits for stomatal conductance, for higher transpiration rates and the lower photosynthetic rates. Transpiration was limited to certain hours of the day, the peak being around 11:00 and 12:00 h (cf. Figure 12). K^+/Na^+ selectivity diminishes with faster transpiration even in plants with intact root systems (Jeschke 1984, Kriedemann 1986), so that the Na^+ load on transpiring leaves will be increased accordingly. The effect of such a solute load on leaf physiology would be alleviated if transpiration were to diminish relative to photosynthesis (Kriedemann 1986). 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, 200 and 300 mol m^{-3} 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. Furthermore, transpiration was higher on lower leaf surface than upper leaf surface in control treatment while the lower and upper surfaces were the same in saline treatment.

Gindel (1973) found that while the rainless, hot season continued, *Eucalyptus camaldulensis* Dehnh. and *E. occidentalis* Endl. (glycophytes) grown under water deficiency had a 43 % smaller leaf area and a lower transpiration rate. Both *E. camaldulensis* and *E. occidentalis* were showed an increase of 36 % in transpiration after irrigation up to field capacity. The results presented by Carbon *et al.* (1981) showed 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 experiment 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 *E. globulus*. As the soil in the pots dried, plant water stress increased faster in *E. camaldulensis* than *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 *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).

For 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 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 respiration. However, in the present study, it was found to have a lower transpiration on saline soil than on non-saline soil. It is able to adapt very well to environmental extreme and is therefore suitable for improving saline soil areas where it can serve as a pioneer species to produce forest land.

The transpiration rates of the *Eucalyptus camaldulensis* seedlings was also higher than of *Combretum quadrangulare*. However, *E. camaldulensis* was found to have a much higher total dry weight than *C. quadrangulare* and 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 effect was supported by the photosynthesis models under condition of a water deficit (cf. Table 13). In dry or in saline areas the stomata close in order to prevent the cell 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 a consideration of some of the lesser-known eucalupt 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.

The **water-use efficiency** (WUE = NP/Tr in μmol CO_2/mmol H_2O) in the present study decreased with increasing salinity and was better in *Eucalyptus camaldulensis* variety 0149 than *Combretum quadrangulare* on the greenhouse experiment (cf. Table 8). In the field study, the WUE tended to be lower in the saline condition compared to the non-saline condition. The WUE decreased in the order *E. camaldulensis* local variety, *C. quadrangulare* and *E. camaldulensis* variety 0149 (cf. Appendix I, Tables 11 and 12). Furthermore, from Figure 17 and Appendix II, Figure 7, it can be seen that the WUE in the morning by both species was better on the non-saline than 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 arietinum* 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. 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).

Photosynthesis in the seedlings grown in the sand medium showed less effects related to salinity than the seedlings grown directly in the salt culture solution. This was probably because of the leaching of the salts through the bottom of the sand medium pots. Therefore, there were no differences $(P > 0.05)$ in photosynthesis related to the salinity treatment. (cf. Tables 4 and 5). Macler (1988) found that stress responses to altered salinities directly affected photosynthesis in the case of red alga (*Gelidium coulteri* Harv.). A similar effect was shown by *Combretum quadrangulare* in the culture solution experiment. The net photosynthetic rates at the salinity level of 1.5 % were lower than at 2.0 % (cf. Appendix II, Figure 8). The temperature outside during measurements was —32°C and temperatures in the greenhouse could not be controlled so efficiently. The seedlings were therefore chilled resulting in an inhibition of net photosynthesis (cf. Larcher 1983, Öquist 1987). Bunce (1984) found that net CO_2 uptake rates of sunflower (*Helianthus annuus* L. cv. Mammoth and *Chenopodium album* L.) decreased linearly with increasing vapour pressure difference, even in cases where transpiration rates were highest at intermediate values of vapour pressure difference. Slatyer and Ferrar (1977b) studied on snow gum (*Eucalyptus pauciflora* Sieb. ex Spreng.) and found that the rate of acclimatization was affected as well. The temperature optimum for photosynthesis also changes markedly during the season (Slatyer and Morrow 1977) and different day and night temperatures have an effect too (Slatyer 1977b). Moreshet (1981) studied the physiological activity of two provenances of *Eucalyptus camaldulensis* in a semi-arid environment and found that activity during the summer was very low, but CO_2 uptake and stomatal conductance after winter rains returned to normal levels. Diurnal trends of CO_2 uptake and stomatal conductance change during the season. Warner and Edwards (1989) found that the C_4 dicot *Atriplex confertifolia* (Torr. & Frem.) S. Wats. increased photosynthetic rates per unit leaf area with increasing polyploidy from the diploid (2x) to the decaploid (10x). Furthermore, the photosynthetic rate per leaf area was highly correlated with the DNA content per leaf area. Larger cells in polyploid plants have higher photosynthetic capacity than smaller cells with lower chromosome numbers. It will be a criteria for further breeding salt-tolerant tree species in the future.

The light saturation of photosynthesis was found to be lower in the greenhouse experiment than in the field study, because the plants acclimatized to lower light intensity in the greenhouse. Wong and Dunin (1987) found that the light saturation of shade leaves in the lower stratum of a *Eucalyptus maculata* Hook. canopy was similar to that of young leaves and was lower than that of sun leaves. Furthermore, the light climate under which *Eucalyptus* seedlings are grown has a significant effect on photosynthetic behaviour, moderate shade producing plants which utilize light more effectively than plants grown in either full sunlight or deeper shade (Brittain and Cameron 1973). Doley (1978) found that high-light treatment resulted in light saturation of *E. grandis* Hill ex Maiden photosynthesis at about 120 nE $cm^{-2}s^{-1}$ (1200 μmol $m^{-2}s^{-1}$, and the low light treatment at about 80 nE $cm^{-2}s^{-1}$ (800 μ mol $m^{-2}s^{-1}$).

Photosynthetic rates for the adaxial and abaxial leaf surfaces of *Eucalyptus camaldulensis* (glycophyte) in the field study were the same. Gale (1975) reported that the photosynthesis of *Atriplex halimus* L. (halophyte) was lower in saline treatment than control treatment and lower on lower leaf (abaxial) than upper leaf (adaxial) surfaces.

Photosynthesis and leaf growth are involved in the common function of radiation interception and utilization. Interception is dictated by size, shape, pose and spatial distribution, while utilization depends upon leaf area duration and the photosynthetic effectiveness of individual organs. The dynamics of leaf growth depend on current assimilation. Schröppel-Meier and Kaiser (1988a) found that extremely high external CO_2 concentrations were required to saturate photosynthesis and to overcome the very high stomatal resistance of salt-treated spinach (*Spinacia oleracea* var "Yates").

Photosynthetic capacity showed a continuous decline with leaf age of potato (*Solanum tuberosum* L., cv. Bintje) (Vos and Oyarzun 1987). Trees from higher latitudes may photosynthesize at a faster rate per unit of foliage than trees of a more southern origin but of the same species (Pelkonen and Luukkanen 1974, Luukkanen *et al.* 1976).

The physiological basis of salt tolerance is regarded as the productive capacity at a given level of salinity. The highest yielding species may be designated as the most salt tolerant. It is the capacity to persist in the presence of increasingly saline soils regardless of growth (Shrivastava *et al.* 1988). Salinity can damage the plant through an osmotic effect, which is equivalent to a decrease in water activity, through the specific toxic effects of ions and by disturbing the uptake of essential nutrients.

43. The empirical model

The application of the photosynthesis model to the control of CO_2 exchange in relation to salinity in the field produced a very good fit when compared with actual measurements. In the single leaf determination of photosynthetic rates, salinity had no effects on photosynthesis. The sampled *Eucalyptus camaldulensis* trees had very high photosynthetic rates, which might reflect genetic variation in salt tolerance. The acclimatization may be taking place by the replacement of old root with root tips of increasing salt tolerance. According to the model, the stomata remained opening during the day and therefore, there were no symptoms of water deficiency. Plants growing in saline conditions will have a water deficiency, even though water is available, unless they are salt tolerant. CO_2 exchange is an outcome of two processes, photosynthesis and transpiration in a no water deficit situation. These two processes cannot be measured separately in field conditions (Korpilahti 1988, Hari and Berninger 1990). Consequently, when analysing CO_2 exchange data, the combined effects of both processes are included in the models.

The model of optimal stomatal behaviour depends on the underlying mesophyll metabolism (Farquhar and Wong 1984). In the models, the photosynthetic rates were assumed from intercellular CO_2 concentrations (Gupta and Berkowitz 1988, Mott 1988). The inflow of ambient CO_2 into intercellular space is accompanied by the outflow of water vapour from the leaves. The intercellular concentration of water is considered to be saturated. The difference in pressure between the saturated and ambient water vapour causes stomatal regulation. According to the estimated α and g_0 model was the best among the models for photosynthesis without water deficit. It used g_0 (stomatal conductance fully opened) and assumed u=1 and λ=0. The advantage in estimating α and g_0 is that the value of g_0 affects the estimation of the value of α and vice versa. The values of α and g_0 compensated each other until optimum values. When the separated estimation of α or g_0 was found different in photosynthesis because the values of α and g_0 were no compensation and the fitness of the models showed differences. The higher value of α of between species is good but not within species. For the value of g_0 is better in a higher one as well because it is associated with a rate of photosynthesis.

The response of photosynthesis to water deficit — The effect of water deficit on gas exchange is brought about by the internal state of the plant. It is assumed that the internal state changes slowly. Stomatal regulation depends on the state of the plant and the ambient temperature at the moment. The threshold temperature decreases with an increasing deficit of soil water (Korpilahti 1988). The effect of stomatal regulation on the rate of the photosynthesis becomes very important under conditions of water deficit. In the present study, u always had a value of 1. However, there was a slight water deficit between November 1987 and January 1988. A leaf of *Combretum quadrangulare* measured on the 15th January 1988 was found to have the greatest deficit (cf. Figure 36). The model for water deficit improved in the afternoon, when the predicted photosynthesis without water deficit was higher than the measured value. When the predicted photosynthesis with water deficit had improved, the predicted photosynthetic rate was lower than the measured value and the transpiration cost, λ, was 0.008 (g CO_2/g H_2O). When u=1 and λ =0, it was impossible to predict photosynthesis during water deficit. A water deficit is only possible when $\lambda >> 0 < 1$ in this model. The fitness of models with and without a water deficit were almost the same, but the model with a water deficit was slightly better than the others. The stomata were partially closed, $0 < u^* < 1$, in the early morning because of irradiance and in the late afternoon because of a slight water deficiency.

44. Morphological responses to salinity

The growth form of the seedlings changed markedly along the salinity gradient (cf. Tables 18—23). Similar results were found by El-Lakany and Luard (1982) in some *Casuarina* spp. which were also studied in culture solution. The longer the duration of the treatment was, the smaller the growth increment, including that of height, diameter, internode length, root length, and leaf dry weight, number and area. The main cause was the salinity but the seedlings may have also been stressed by the rooting conditions in the containers (Pereira and Kozlowski 1976). The leaf width and length showed no further increment on the later measurement occasions because of leaf maturation.

Van der Moezel *et al.* (1988) formulated a tolerance index to saline (waterlogging) conditions by multiplying percentage survival by relative growth. With this index they obtained values for *Casuarina obesa* Miq., *Eucalyptus camaldulensis* Dehnh., *E. platycorys* Maiden et Blakely, *E. lesouefii* Maiden, *E. spathulata* Hook., *E. comitae-vallis* Maiden and *E. kondininensis* Maiden et Blakely of 7730, 2205, 1190, 911, 669, 443 and 247.

In the sand medium experiment, the 2 % salinity treatment did not have an effect on seedling growth. This was most probably because of leaching of the salt through the holes in the bottom of the pots. The grand means of the total leaf number increment were almost constant over the study period because the fall and emergence of leaves were equal. The stem leaf dry weight at higher salinity levels did not change because the seedlings were already stunted and leaf fall was equal to or more than leaf emergence. The later measurements (6th or 7th) of total seedling leaf dry weight were still high because the new leaves came from the branches when there were no more stem leaves.

In the control treatment, the seedlings had sufficient nutrients and the leaves could continue to expand and new leaves were always flushing. With the high salinity treatment the period of leaf expansion was shorter than in control. Leaf growth response to root-zone salinisation varies according to ion species and can be alleviated to an extent depending upon the initial exclusion by the roots, the subsequent distribution via the vascular network, migration within the apoplast, and osmotic adjustment within photosynthetic tissues and growth centres (Kriedemann 1986). The maturation and the expansion of the stem leaves of bean (*Phaseolus vulgaris* L.) continued later at lower salinity treatments than at higher salinity because of the suitable conditions for development (Neumann *et al.* 1988).

The estimated leaf biomass and leaf area at each occasion from amount of number of leaves were reasonable results. The total leaf area increment per seedling showed negative values at the higher salinity treatments because leaf fall was greater than leaf emergence. The leaf area per leaf decreased in response to increasing salinity. It generally follows that plants that produce a smaller leaf area and allocate more to roots have lower growth rate (Mooney *et al.* 1978).

Leaf size and specific weight clearly changed with increasing salinity. Specific weight increased while leaf area decreased with salinity (cf. Figure 43 and Table 26). Salinity symptoms can be compared to drought symptoms. In a study by Mooney *et al.* (1978), leaves of the *Eucalyptus* spp. from the driest region averaged about one-third the size of those of the wettest habitat studied, and their specific weight was about three times as great.

Leaf thickness was less in the sand medium experiment than in the culture solution experiment because the seedlings were less stressed in the sand experiment because of leaching, as previously mentioned. The pots size in two experiments were also different and this could have had an effect on rooting, resulting in differences in of leaf thickness (Pereira and Kozowski 1976).

As mentioned, the greenhouse was not properly controlled. Diurnal variation in shoot growth changes with increasing day/night temperatures. In the case of *Eucalyptus obliqua* L'Hér., Blake (1977) showed that stem-elongation occurred predominantly during the day with a 20°C constant day/night temperature, with night growth accounting for only one-third of the total daily elongation. *E. grandis* Hill ex Maiden seedlings grown under conditions of high (12.6) and low (2.8 E $m^{-2}day^{-1}$) daily integrals of photon flux density exhibited a greater allocation of dry matter to leaves, stems and roots. Leaf area and thickness were greater in the high daily light treatment (Doley 1978). In the halophyte, *Sarcocornia natalensis* Bunge ex Ung.-Sternb., an increase in salinity from 0 to 300 mol m^{-3} NaCl stimulated the production of biomass, increased succulence and shifted resource allocation from the roots to shoots (Naidoo and Rughunanan 1990). Growth was optimal at 300 mol m^{-3} and decreased with any further increase in salinity. The results from this study showed that leaf, shoot, branch and root biomass decreased with salinities over the range 0.5 % to 2.0 % in the case of *Combretum quadrangulare* and *Eucalyptus camaldulensis* (cf. Table 27).

Both shoot and root biomasses decreased with increasing salinity, but the decrease was greater in the case of the shoots. On the other hand, the higher the salinity was, the greater the root increment when compared to the shoot increment (cf. Table 24). This effect is due to vigorus rooting. Sands (1981) also concluded that *E. camaldulensis* from a moderately saline and dry site (Port Lincoln, South Australia) had the lowest shoot:root ratios when compared with seed sources from a moderately saline site (Lake Albacutya, Western Australia) and a non-saline site (Shepparton in Victoria, Australia). Therefore, it appears that *E. camaldulensis* has both drought resistance and salt resistance. However, the salt treatments reduced the amount of roots in the Port Lincoln seedlings more than in seedlings from the other seed sources and thereby effectively removing much of the advantage they had in this regard. El-Lakany and Luard (1982) found that the shoot:root ratios of the most salt-tolerant species, *Casuarina* spp., showed no general trend and were close to control treatment values or higher. The moderately and less salt-tolerant species had lower shoot:root ratios in the salt treatments than in the controls because of the restricted root growth at higher levels of salinity. Pereira and Kozlowski (1976) found that the dry weight increment of shoots and roots was greater in *E. globulus* than in *E. camaldulensis* during the first two weeks because rooting restrictions imposed by the volume of the pots. Seedlings with longer roots or rapid root growth were more drought resistant than seedlings with shallow roots or slower growing ones (Levitt 1972, Pereira and Kozlowski 1976). On the other hand, increased availability of water, and particularly of nutrients, has been shown to increase the shoot:root ratio (Bröms and Azelsson 1985). The absence of K markedly suppresses plant growth and reduces the biomass of the roots more than that of the shoots (Houman *et al.* 1990).

When considering the leaf:root ratio, the allocation of biomass to the leaves decreased with salinity more so than to the roots (cf. Appendix II, Figure 20). The allocation of growth is different among site types of differing productivity. The allocation to roots is greater if the specific nutrient uptake rate is lower (Mäkelä 1988). Improved soil nutrient availability increases allocation to the leaves and decreases allocation to the roots and indirectly implies increasing allocation to the stem (Hari *et al.* 1990).

45. Laboratory based studies

Problems of environmental interaction can be alleviated by screening under controlled conditions in the greenhouse or laboratory. Such methods are popular because screening can be accomplished in smaller spaces and shorter times. However, most methods are distinctly different from field conditions and may not be useful in selecting factors associated with interactions. Generally, a wide variety of media and criteria can be used for such screening, including the use of culture solutions and salinity solutions. The application of saline solutions directly to the pots in the sand medium experiment is not to be recommended, however, because of the possibility of leaching. The photosynthetic rates were still high and the values of Γ were the same as control in the present sand medium experiment (cf. Figure 20 and 24).

It was convenient to choose growth developmental and eco-physiological characteristics as markers for salt-tolerant trees. This is because salt tolerance is reflected in many characteristics of a plant-anatomical, morphological, eco-physiological and genetic. Proper evaluation of such characteristics, however, should be developed if this approach is to become a valuable tool to study mechanisms of salt tolerance.

Even though *Eucalyptus camaldulensis* was found to be resistant to salinity, the Australian variety used in the culture solution experiment was probably not the best one. This was made evident when it was compared to local variety in the field study. Seed sources of the more tolerant varieties were, unfortunately, not available at the time of this study.

Salinity resulted in thicker leaves being produced. In many other studies a thickening of the leaf surface resulted in higher rates of photosynthesis per unit leaf area. However, whole plant photosynthesis decreased with salinity because salinity produced less leaves with a smaller total leaf area. The dynamics of leaf growth reveal a similar dependence on current assimilation. Leaf growth rates have been shown to be highly dependent on small changes in turgor pressure (Kriedemann 1986). The potential area of leaves is set by the cell population within each expanding lamina. Since cell division depends more closely on the photo-assimilate supply than on the availability of water and nutrients, the final leaf size can be limited by photosynthetic activity.

The importance of changes in functioning and structure can be analysed by using a simple model. Firstly, I assume that photosynthesis is proportional to the amount of leaves. Secondly, photosynthetic products are immediately used for growth. Finally, the proportion of growth (α_L) is allocated for leaves. The model based on these assumptions is as follows:

$$P_1 = X P_0,$$

$$\frac{dX}{dt} = \alpha_L P_0 X,$$

where P_1 denotes daily photosynthetic production (g CO_2/day), X amount of leaves (g dry weight), t time and P_0 daily photosynthetic production of 1 g of leaves (g CO_2/g of leaf dry weight/day). The values of α_L are calculated from amount of measured leaf mass divided by total seedling biomasses during salinity treatment. The daily photosynthetic production (P_0) is estimated from the final biomass of control treatment seedlings.

The greenhouse experiments showed that salinity may regulate changes in the functions of carbon allocated to leaves (cf. Figures 46A and 47A) photosynthesis per leaf area (cf.

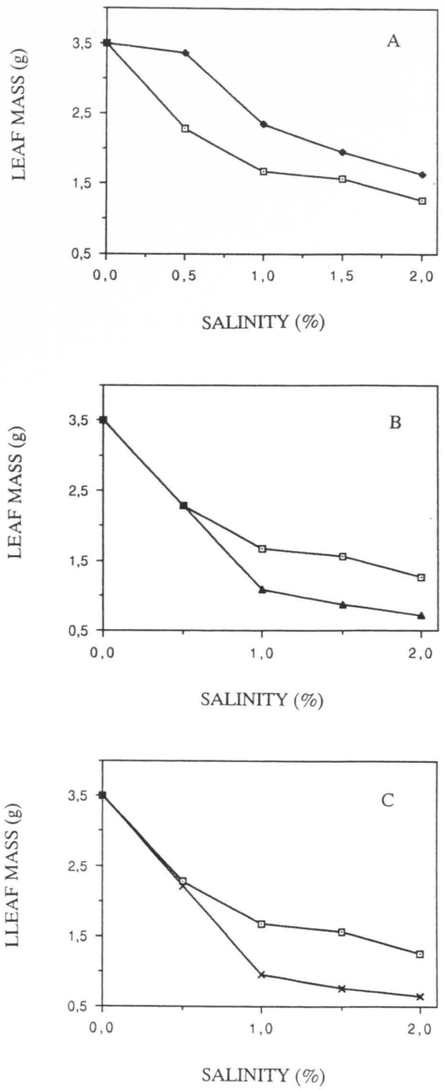


Figure 46. Measured and calculated relationship between leaf mass and salinity for *Combretum quadrangulare* for 3 month study period in the greenhouse experiments. A, the leaf mass measured (⊡) and calculated using in allocation (◆), B, using change in photosynthesis (▲) and C, using changes both in allocation and photosynthesis (×).

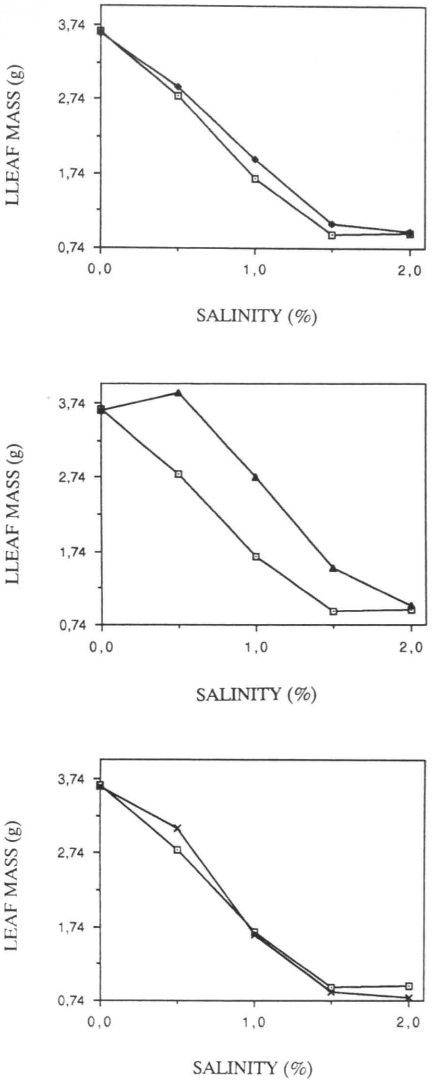


Figure 47. Measured and calculated relationship between leaf mass and salinity for *Eucalyptus camaldulensis* for 3 month study period in the greenhouse experiments. A, the leaf mass measured (⊡) and calculated using in allocation (◆), B, using change in photosynthesis (▲) and C, using changes both in allocation and photosynthesis (×).

Figures 46B and 47B) and specific leaf area changed (cf. Figures 46C and 47C). The effect of these changes on final growth can be estimated using the above simple model. These alternatives were analysed in some details: Firstly change in allocation; secondly, change in photosynthesis per unit of leaf area and finally, changes in allocation and photosynthesis per unit leaf area.

For *Combretum quadrangulare*, when allocation is taken in consideration, the calculated leaf mass was higher than the measured ones. The changes in photosynthesis clearly over estimate the growth reduction at high salinity levels. The changes in allocation and photosynthesis result still more pronounced over estimation of growth reduction.

For *Eucalyptus camaldulensis* the matches between the measured and the calculated values both the growth allocation itself (cf. Figure 47A) and allocation combined with photosynthesis (cf. Figure 47C) were very good. Only the changes in photosynthesis clearly under estimate the growth reduction (cf. Figure 47B). The leaf mass of *E. camaldulensis* stunts at salinity over 1.5 %. While *C. quadrangulare* seedlings had only minimal growth at salinity over 1.0 %. Thus, *E. camaldulensis* is higher tolerant than *C. quadrangulare* when determined from leaf mass allocation.

In conclusion the observed changes in functions result in too large growth reduction. This may be caused by some abnormal behaviour during the extreme experimental conditions. However, the exact fit in *Eucalyptus camaldulensis* when allocation was taken in consideration, stresses the role of changes in allocation. From methodological point of view it is promising that the simple model applied can explain most of the growth changes observed.

46. Field based studies

Research into the effects of soil salinity has made great strides in the past few decades. There is, however, a general lack of conceptual knowledge on how best to monitor and analyse ecophysiological characteristics of trees and soil salinity in the field. Field screening for increased yields under saline conditions is slow, costly, and subject to many edaphic, environmental, and biological stresses. Tree response to spatial and temporal soil-salinity distributions has not been dequately investigated or understood. Several quantitative techniques are available or are being proposed in order to predict the salinity of the root-zone and the carbon allocation required to maintain an optimum yield of *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Field verification of the photosynthesis models is required in order to improve our ability to relate salinity tolerance to the allocation of growth to the fine root structures in saline soils.

In the present field study, only functional measurements were available. The analysis proved that the salinity had only minor effects on photosynthesis. In fact the leaves on saline soil were slightly more effective than on non-saline soil. This functional change is unable to explain the clear growth reduction commonly observed on saline soil (Maas and Nieman 1978). Thus, the reason must be found somewhere else. In the greenhouse the changes in allocation in *Eucalyptus camaldulensis* seemed to be the major factor causing growth reduction. Thus, the possibility that changes in allocation on saline soil are the reason of growth reduction should be studied in more details.

5. Summary

Salinity affects growth by either the toxic effects of Na^+ or Cl^- accumulation or by the lowering of the osmotic potential of the soil solution. A plant can avoid or minimize toxic effects by excluding salt from the plant either by excreting it from glands or by translocating it to leaves which then drop off. In excluding salts, however, the plant may lose the opportunity of using NaCl as an osmotic solute in the leaves. Alternatively, plants may accumulate salts in the leaves, producing lower osmotic potentials, but then they may need to exclude salts from the cytoplasm in order to avoid ionic interactions with enzymatic reactions.

Ecophysiological and morphological characteristics were used to study the effect of endogenous NaCl contents on the rates of photosynthesis of *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Some progress was made by using gas exchange techniques in determining whether stomatal conductance or photosynthetic efficiency limits growth. This approach also provided information about the efficiency of carboxylation by measuring the relationship between photosynthesis and internal CO_2 concentration. The reduction in growth in salt tolerant plants is due to the small sink for photosynthetic products. On the other hand, the stress in plants is due to the inhibitory effects of NaCl on photosynthesis.

Stomata in *C. quadrangulare* and *E. camaldulensis* have an anomocytic arrangement with hypoamphistomates. Stomatal sizes were greater in *E. camaldulensis* than *C. quadrangulare*. The size of the guard cells and the stomatal opening in *E. camaldulensis* were bigger in the field study than in the greenhouse experiment. In the case of *C. quadrangulare*, only the stomatal opening was bigger in the field than in the greenhouse experiment. In both species the size of the stomatal opening increased with salinity. The openings were wider on abaxial than adaxial surfaces at all salinity levels in the case of *C. quadrangulare* but were narrower on the abaxial than on the adaxial surfaces in the case of *E. camaldulensis*. Stomatal openings were wider at 10:00 h than 14:00 h on the adaxial surface but about the same on the abaxial surface in the case of *C. quadrangulare*. In *E. camaldulensis*, stomatal openings were slightly wider at 14:00 h than 10:00 h on both surfaces and more open on saline than on non-saline soils.

Stomatal frequency only slightly increased with salinity treatment in the greenhouse culture solution experiment, but was higher on the non-saline soil than on saline soil in the field study. Stomata were more frequent on the abaxial leaf surfaces of *E. camaldulensis*, in both the greenhouse seedlings and the field study trees. In contrast, the stomatal frequency of *C. quadrangulare*, was greater on the adaxial surface in the case of the greenhouse seedlings, but about the same on both surfaces in the case of the field study trees. For both species, the stomatal frequency on the adaxial and abaxial leaf surfaces the greenhouse seedlings was, respectively, lesser and greater in comparison to the trees of the field study.

The stomatal index was higher for non-saline than saline soils, on abaxial than adaxial surfaces, and for *E. camaldulensis* than for *C. quadrangulare* on adaxial but about the same on abaxial surfaces in both the culture solution experiment and field study.

The water potential of both species decreased with salinity in the greenhouse experiment. In the field study, the water potential was lower on the saline than on non-saline soils, for *C. quadrangulare* than for *E. camaldulensis*, and at 14:00 h than at 10:00 h. There was no difference in the water potential of *E. camaldulensis* between the non-saline and saline soils but there was different in the case of *C. quadrangulare*. All growth reductions associated with salinity were reflected in a decrease in total leaf-water potentials.

Transpiration increased with salinity (not significantly) and temperature at low salinity (significantly) and at high salinity (not significantly) in both species and in the greenhouse experiment and field study.

Transpiration was not affected by low light intensities but decreased at high light intensities in the greenhouse experiment. The decrease was more 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 *C. quadrangulare* in the greenhouse experiment and much higher on non-saline soil than on the saline soil in the field study.

Water-use efficiency was better in *E. camaldulensis* local variety than *C. quadrangulare*, in non-saline than saline soils, and in the morning than in the afternoon. However, *E. camaldulensis* variety 0149 had the lowest water-use efficiency, lower than *C. quadrangulare* on the saline soil.

Photosynthesis of both species decreased with salinity in the greenhouse experiment. The decrease varied with both temperature and irradiance. Photosynthesis showed no differences at 0 % and 0.5 % salinity in the case of *C. quadrangulare* and at 0 %, 0.5 % and 1.0 % salinity in the case of *E. camaldulensis* at temperatures of 18° to 30°C. Photosynthesis of both species did not decrease at 36°C, and at the higher salinity treatments already at 18°C. Photosynthetic rates showed no differences at 0 %, 0.5 % salinity and 1.0 % salinity levels in the case of *C. quadrangulare* and at 0 % and 0.5 % in the case of *E. camaldulensis* at photon flux densities of 300 µmol m^{-2}s^{-1} to 1500 µmol m^{-2}s^{-1}, but decreased at 2000 µmol m^{-2}s^{-1}. Photosynthetic rates of *E. camaldulensis* were higher than of *C. quadrangulare*. In the field, photosynthetic rates increased (not significantly) at temperatures from 21° to 36°C but decreased at 39°C on both the non-saline and saline soils. The dependence of the photosynthetic rates on irradiance increased at photon flux densities from 300 µmol m^{-2}s^{-1} to 2000 µmol m^{-2}s^{-1} on both the non-saline and saline soils. The photosynthetic rates of *E. camaldulensis* were higher than those of *C. quadrangulare*.

The CO$_2$ compensation point increased with the level of salinity, especially in the case of *C. quadrangulare*. Photorespiration rates followed the net photosynthetic rates which increased at low salinity levels but decreased at high salinity levels. In the field, the predicted photorespiration rates were higher on the saline than non-saline soils over the studied temperature range. Within the non-saline and saline soils, there was no difference in photorespiration rate between the two species. Photorespiration rates increased with temperature and irradiance in both non-saline and saline soils. The irradiance dependence of the predicted photorespiration rates were higher for *C. quadrangulare* than for *E. camaldulensis* and on the saline soil than non-saline soil. Dark respiration rates of both species increased at low salinity level (not significantly) and temperature (significantly).

The total resistance to CO$_2$ (Σr'), mesophyll resistance (r$_{mx}$) and stomatal resistance (r's) of both species and measured with both IRGA and the porometer all increased with salinity in both species in the greenhouse experiment. In the field study, measured stomatal resistance of both species was unaffected by temperature over the range 21° to 39°C on the non-saline soil, but showed fluctuation on the saline soil. While there was no difference in the irradiance dependence of the stomatal resistance between non-saline and saline soils for *E. camaldulensis*, there was a fluctuation at photon flux densities 300 µmol m^{-2}s^{-1} to 2000 µmol m^{-2}s^{-1} for *C. quadrangulare*. Stomatal resistance was higher in *C. quadrangulare* than *E. camaldulensis* and on the saline than the non-saline soils at all temperature and irradiance levels. The diurnal course of the stomatal conductance was higher on the non-saline than the saline soils in the case of *E. camaldulensis*, but was higher on the saline than the non-saline soils in the case of *C. quadrangulare*.

The photosynthesis models indicated the optimum stomatal regulation and interaction of stomatal responses, particularly with regard to intercellular carbon dioxide, irradiance and α. The value of α for the saline soil was much greater than for the non-saline soil. According to the photosynthesis model, the predicted photosynthetic rates matched the measured ones very well. The predicted stomatal conductance on the saline soil was lower than on the non-saline soil. Generally, salinity caused lower photosynthesis, although for some leaves it had no effect and photosynthesis was higher. The trees had higher photorespiration rates on the saline soil than on the non-saline soil. According to the estimated λ, there was a slight water deficit on the saline soil during November 1987 to January 1988. This may have been due to transpiration by salt-tolerant trees, which were able to osmotically adjust to maintain turgor. The degree of stomatal opening remained almost constant all day long. The degree of the stomatal opening was related to irradiance.

Height growth decreased with salinity. *C. quadrangulare* had a lower height qrowth increment, diameter growth increment and shoot internode increment than *E. camaldulensis*. The stem leaf area per leaf was bigger in the case of *C. quadrangulare* than *E. camaldulensis* development earlier. Leaf development cessation was more rapid with increasing salinity. The total leaf dry weight per plant decreased with salinity but the leaf dry weight per area increased with salinity, which meant the leaf increased its thickness. The thickness increment increased with salinity more than in the case of *E. camaldulensis* than in the case of *C. quadrangulare*. Shoot:root and leaf:root ratios decreased with increasing salinity. The root biomass increased more than the leaf and shoot biomasses in the saline treatments.

The main conclusion emanating from the morphological studies is that salinity affects growth primarily through the expansion of the surface and not via photosynthesis per leaf area (or whole plant). Growth may be impaired at salinity levels as low as 1.0 % salinity. The results showed that the height, diameter, shoot internode, root, leaf width and length, leaf area, leaf number, leaf dry weight growth, biomass and shoot:root ratio decreased with increasing salinity, while leaf thickness increased with salinity. The ecophysiological studies showed that photosynthesis decreased with salinity. The result are consistent with the view that salinity influences the growth of *C. quadrangulare* and *E. camaldulensis* via the effect on plant-water relations.

Comparing the responses of the ecophysiological and morphological characteristics studied it is concluded that salinity result both in the functioning and structural changes of seedlings in the greenhouse experiment. While there is more in the structural changes than in ecophysiological functioning of trees in the field study. A comparison of salinity tolerance between *C. quadrangulare* and *E. camaldulensis* showed that, on the basis of morphological and ecophysiological (of gas exhange) considerations *C. quadrangulare* was less tolerant than *E. camaldulensis*. Further investigations should be made into the intraspecific variation in salt tolerance of *E. camaldulensis*.

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Appendix I

Table 1. Seedling leaf stomatal size (mean±sd) *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species	Stomatal size (µm) 14:00 h							
and	adaxial guard cell		adaxial aperture		abaxial guard cell		abaxial aperture	
salinity (%)	width	length	width	length	width	length	width	length
Com 0.0	13.87 ± 1.83^{bc}	20.53 ± 2.58^{d}	3.02 ± 1.38^{e}	13.71 ± 1.98^{bc}	16.12 ± 1.88^{cd}	19.77 ± 1.99^{de}	4.70 ± 1.33^{bc}	12.84 ± 1.39^{cd}
Com 0.5	13.79 ± 1.75^{bc}	20.99 ± 2.41^{cd}	4.66 ± 2.95^{c}	14.66 ± 2.12^{ab}	15.51 ± 1.53^{cd}	19.68 ± 1.72^{de}	5.36 ± 1.77^{ab}	12.92 ± 1.51^{cd}
Com 1.0	14.45 ± 1.71^{bc}	20.53 ± 1.85^{d}	3.89 ± 1.96^{cde}	13.64 ± 1.55^{bc}	16.47 ± 2.12^{bc}	20.86 ± 1.95^{bcd}	5.80 ± 2.25^{a}	13.46 ± 1.74^{bc}
Com 1.5	14.51 ± 2.16^{bc}	21.05 ± 2.29^{cd}	3.37 ± 1.72^{de}	14.93 ± 2.24^{a}	16.35 ± 1.83^{bcd}	20.14 ± 2.55^{cde}	4.99 ± 1.40^{ab}	13.28 ± 1.58^{bc}
Com 2.0	13.44 ± 2.11^{c}	20.20 ± 2.45^{d}	3.82 ± 2.41^{cde}	14.21 ± 2.53^{abc}	15.66 ± 1.79^{cd}	19.01 ± 2.01^{e}	5.37 ± 1.56^{ab}	12.59 ± 1.83^{cd}
Eu 0.0	14.86 ± 2.50^{b}	21.46 ± 2.57^{bcd}	3.11 ± 2.53^{e}	13.17 ± 1.66^{c}	15.32 ± 2.74^{d}	20.87 ± 3.06^{bcd}	2.44 ± 2.04^{d}	12.50 ± 1.94^{cd}
Eu 0.5	17.50 ± 2.30^{a}	22.98 ± 2.45^{a}	4.90 ± 2.45^{bc}	13.88 ± 2.62^{abc}	17.84 ± 1.76^{a}	21.48 ± 2.11^{ab}	4.00 ± 2.01^{c}	12.02 ± 1.70^{d}
Eu 1.0	16.75 ± 1.85^{a}	21.91 ± 2.41^{abc}	5.88 ± 1.73^{ab}	13.59 ± 1.75^{bc}	16.54 ± 2.16^{bc}	22.49 ± 2.88^{a}	4.92 ± 3.14^{abc}	14.66 ± 1.47^{a}
Eu 1.5	17.21 ± 1.74^{a}	22.52 ± 1.34^{ab}	6.82 ± 1.48^{a}	14.40 ± 2.28^{ab}	17.27 ± 2.15^{ab}	22.40 ± 3.07^{a}	5.35 ± 1.82^{ab}	14.20 ± 2.49^{ab}
Eu 2.0	17.40 ± 2.99^{a}	20.67 ± 3.60^{cd}	4.43 ± 2.82^{cd}	12.06 ± 2.33^{d}	16.58 ± 2.43^{bc}	21.06 ± 3.61^{bc}	2.62 ± 2.01^{d}	13.31 ± 2.85^{bc}
F	20.95^{***}	4.53^{***}	9.70^{***}	5.40^{***}	4.96^{***}	9.97^{***}	11.68^{***}	5.38^{***}
$\bar{X}$	14.56	20.91	4.01	14.07	16.16	20.25	4.97	13.08

Table 2. Tree leaf stomatal size (mean±sd) *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study at 10:00 h (nonsignificant differences in the same column are indicated by same letters).

Species	Stomatal size (µm) 10:00 h							
and	adaxial guard cell		adaxial aperture		abaxial guard cell		abaxial aperture	
soil type	width	length	width	length	width	length	width	length
Com normal	13.79 ± 1.67^{d}	20.03 ± 2.09^{c}	2.77 ± 1.92^{d}	15.09 ± 1.54^{d}	16.21 ± 1.23^{d}	20.03 ± 1.49^{d}	5.61 ± 1.56^{c}	13.87 ± 1.93^{d}
Com saline	14.28 ± 1.13^{d}	18.34 ± 1.51^{d}	4.84 ± 2.56^{c}	13.14 ± 1.79^{e}	15.87 ± 1.48^{d}	19.31 ± 1.64^{d}	5.57 ± 2.18^{c}	14.27 ± 1.93^{d}
Eu0149 normal	23.73 ± 2.05^{c}	30.16 ± 2.07^{b}	11.88 ± 1.63^{b}	18.18 ± 1.86^{c}	23.05 ± 1.87^{c}	29.76 ± 2.27^{c}	12.04 ± 1.88^{b}	18.60 ± 2.74^{c}
Eu normal	26.47 ± 1.74^{b}	34.62 ± 2.09^{a}	13.42 ± 1.22^{a}	21.14 ± 1.51^{b}	25.18 ± 2.65^{b}	32.57 ± 3.05^{b}	12.94 ± 2.06^{a}	20.20 ± 2.81^{b}
Eu saline	27.87 ± 2.46^{a}	35.46 ± 3.43^{a}	13.94 ± 1.47^{a}	22.92 ± 2.69^{a}	27.78 ± 2.86^{a}	35.29 ± 3.79^{a}	13.50 ± 1.42^{a}	21.83 ± 2.57^{a}
F	521.45^{***}	480.41^{***}	324.98^{***}	178.35^{***}	256.34^{***}	318.25^{***}	188.15^{***}	85.84^{***}
$\bar{X}$	21.23	27.72	9.37	18.09	21.62	27.39	9.93	17.75

Table 3. Tree leaf stomatal size (mean±sd) *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal and saline soil types in the field study at 14:00 h (nonsignificant differences in the same column are indicated by same letters).

Species	Stomatal size (µm) 14:00 h							
and	adaxial guard cell		adaxial aperture		abaxial guard cell		abaxial aperture	
soil type	width	length	width	length	width	length	width	length
Com normal	14.53±1.53^{c}	20.72±1.44^{c}	1.65±1.40^{c}	15.81±3.24^{c}	16.52±1.82^{d}	20.61±1.84^{d}	6.07±1.59^{c}	13.74±1.79^{d}
Com saline	14.87±1.23^{c}	20.29±2.05^{c}	1.91±1.21^{c}	14.19±2.39^{d}	17.35±1.47^{d}	21.04±1.76^{d}	5.01±1.46^{d}	13.20±1.69^{d}
Eu0149 normal	22.72±2.22^{b}	29.85±2.80^{b}	11.08±2.02^{b}	18.40±2.45^{b}	22.31±1.93^{c}	30.03±2.47^{c}	11.28±1.76^{b}	18.94±2.34^{c}
Eu normal	27.23±2.28^{a}	35.06±3.17^{a}	14.33±1.92^{a}	22.50±2.50^{a}	25.63±3.37^{b}	33.70±3.47^{b}	13.57±2.76^{a}	21.56±3.46^{b}
Eu saline	27.87±2.30^{a}	36.25±3.68^{a}	14.46±2.02^{a}	22.32±3.39^{a}	27.78±1.94^{a}	36.18±2.80^{a}	14.41±2.13^{a}	22.82±2.97^{a}
F	433.41***	309.18***	544.27***	70.54***	202.48***	317.71***	185.97***	120.19***
$\bar{X}$	21.44	28.43	8.68	18.65	21.92	28.31	10.07	18.05

Table 4. Seedling leaf stomatal frequencies (mean±sd) *Combretum quadrangulare* and *Eucalyptus camaldulensis* variety 0149 in different salinity treatments in the solution greenhouse experiments (nonsignificant differences in the same column are indicated by same letters).

Species	Stomatal number (stomata/mm^2)		Stomatal index (%)	
and	adaxial	abaxial	adaxial	abaxial
salinity (%)	(14:00-15:00 h)		(14:00-15:00 h)	
Com 0.0	89.83±3684^{b}	365.92±7375^{abc}	7.49±3.23^{d}	18.80±3.09^{ab}
Com 0.5	111.57±52.08^{b}	391.45±77.31^{a}	8.54±3.65^{d}	20.35±2.68^{a}
Com 1.0	99.28±35.36^{b}	329.05±42.97^{abcd}	8.30±2.84^{d}	19.07±2.74^{ab}
Com 1.5	131.43±45.79^{b}	389.56±69.33^{a}	9.32±2.71^{bcd}	18.97±3.00^{ab}
Com 2.0	130.48±62.22^{b}	376.32±114.93^{ab}	9.69±3.75^{bcd}	18.24±2.83^{ab}
Eu 0.0	195.73±49.35^{a}	309.19±60.76^{cd}	8.86±2.61^{cd}	13.96±3.44^{d}
Eu 0.5	218.42±44.18^{a}	394.29±105.61^{a}	11.68±2.49^{b}	17.35±4.30^{b}
Eu 1.0	238.28±98.12^{a}	318.65±87.78^{bcd}	14.29±4.45^{a}	16.77±3.47^{bc}
Eu 1.5	202.35±57.64^{a}	359.30±77.44^{abc}	14.07±2.93^{a}	19.99±3.44^{a}
Eu 2.0	232.60±132.22^{a}	271.37±79.76^{d}	11.39±4.21^{bc}	14.60±3.42^{cd}
F	11.67***	4.18***	8.16***	6.91***
$\bar{X}$	165.00	350.51	10.36	17.81

Table 5. Tree leaf stomatal frequencies (mean±sd) *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (nonsignificant differences in the same column are indicated by same letters.

Species	Stomatal number (/mm^2)				Stomatal index (%)			
and	adaxial	abaxial	adaxial	abaxial	adaxial	abaxial	adaxial	abaxial
soil type	10:00 h		14:00 h		10:00 h		14:00 h	
Com normal	273.37±44.15^{a}	373.16±145.89^{a}	258.00±28.39^{a}	356.75±49.73^{a}	8.82±1.32^{b}	11.04±3.67^{ab}	8.84±0.88^{c}	11.23±0.97^{a}
Com saline	218.70±24.56^{bc}	222.34±40.20^{cd}	250.14±51.11^{ab}	389.22±128.57^{a}	6.99±0.70^{c}	7.23±1.40^{c}	8.34±1.54^{c}	11.81±3.35^{a}
Eu0149 normal	224.17±35.03^{bc}	294.22±35.33^{b}	235.79±39.67^{abc}	263.12±33.10^{b}	8.65±1.29^{b}	10.74±1.32^{ab}	8.52±1.04^{c}	8.99±1.13^{b}
Eu normal	235.79±28.51^{b}	248.77±37.08^{bc}	220.41±34.39^{bc}	247.40±51.19^{bc}	10.65±1.07^{a}	11.34±1.63^{a}	11.43±1.23^{a}	11.51±1.22^{a}
Eu saline	200.25±58.51^{c}	187.26±57.33^{d}	214.26±48.21^{c}	210.50±25.80^{c}	9.82±2.60^{ab}	9.39±2.01^{b}	9.83±1.39^{b}	9.59±1.18^{b}
F	7.05***	13.47***	3.29*	19.76***	10.62***	7.72***	17.05***	7.75***
$\bar{X}$	231.07	267.40	235.72	293.40	9.09	10.09	9.39	10.62

Table 6. 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	Transpiration rate (Es, mmol m^{-2}s^{-1})				
and	Irradiance (µmol m^{-2}s^{-1})				
salinity (%)	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±0.98^{bc}	1.63±0.80^{abc}
Com 1.0	1.67±1.09^{cd}	1.87±1.20^{bcd}	2.03±1.36^{bcd}	2.26±1.64^{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}	1.06±0.56^{bc}
Com 2.0	0.90±0.83^{d}	0.92±0.86^{d}	0.98±0.89^{d}	1.01±0.88^{c}	0.99±0.83^{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±2.70^{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±1.26^{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±0.30^{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±0.33^{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*	3.94*
$\bar{X}$	2.23	2.28	2.33	2.24	1.74

Table 7. Temperature dependence of transpiration rate (mean±sd) *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	Transpiration rate (Tr, mmol m^{-2}s^{-1})						
and	Temperature (°C)						
soil type	21	24	27	30	33	36	39
Com normal	-	1.16±0.2.63^{c}	1.35±0.20^{b}	1.47±0.36^{c}	2.20±0.47^{b}	2.86±0.49^{c}	3.01±0.65^{b}
Com saline	-	1.38±0.3.51^{b}	1.03±0.37^{c}	1.53±0.48^{c}	2.22±0.76^{b}	2.79±0.80^{c}	-
Eu0149 normal	-	1.43±0.13^{ab}	2.01±0.63^{a}	3.07±1.20^{a}	3.44±1.23^{a}	4.17±1.15^{b}	-
Eu normal	1.26±0.49^{a}	1.63±0.22^{a}	2.05±0.27^{a}	2.75±0.556^{b}	3.64±0.69^{a}	5.51±0.83^{a}	5.76±0.00^{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±1.17^{b}	-
F	0.10^{ns}	7.67***	38.65***	64.29***	35.16***	56.21***	15.71**
$\bar{X}$	1.27	1.49	1.77	2.21	3.00	3.71	3.32

Table 8. Irradiance dependence of transpiration rate (mean±sd) *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	Transpiration rate (Tr, mmol $m^{-2}s^{-1}$)							
and	Irradiance (µmol $m^{-2}s^{-1}$)							
soil type	300	500	700	1000	1300	1500	1700	2000
Com normal	2.02±0.18^{ab}	1.96±0.00^{a}	1.78±0.68^{b}	1.62±0.67^{c}	1.49±0.27^{b}	1.78±0.40^{b}	1.66±0.67^{c}	2.79±0.65^{c}
Com saline	0.47±0.00^{b}	2.03±0.60^{a}	2.27±0.66^{ab}	1.97±0.93^{bc}	1.65±0.58^{b}	1.68±0.62^{b}	1.83±0.90^{c}	3.21±0.48^{c}
Eu0149 normal	2.91±1.27^{a}	3.08±1.52^{a}	3.08±1.44^{a}	2.55±1.14^{a}	2.45±1.06^{a}	2.69±0.88^{a}	2.76±0.70^{b}	4.29±1.47^{ab}
Eu normal	-	-	3.47±1.60^{a}	2.03±1.10^{bc}	2.44±1.06^{a}	2.82±1.16^{a}	3.34±1.24^{a}	5.00±1.17^{a}
Eu saline	2.85±1.22^{a}	1.62±0.45^{a}	2.37±1.35^{ab}	2.31±1.10^{ab}	2.62±1.27^{a}	2.80±0.60^{a}	2.95±1.03^{ab}	4.20±1.55^{b}
F	1.69^{ns}	5.84**	2.94*	4.33**	7.96***	20.53***	28.77***	17.03***
$\bar{X}$	2.74	2.65	2.57	2.07	2.08	2.34	2.42	3.78

Table 9. Temperature dependence of the predicted transpiration rate (mean±sd) *Combretum quadrangulare* and *Eucalyptus camaldulensis* 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	Transpiration rate (Tr, mmol $m^{-2}s^{-1}$)						
and	Temperature (°C)						
soil type	21	24	27	30	33	36	39
Com normal	-	1.88±0.79^{b}	2.10±0.72^{b}	2.99±1.28^{bc}	3.11±1.22^{b}	3.62±1.20^{b}	4.34±1.31^{b}
Com saline	-	1.07±0.17^{c}	1.04±0.35^{c}	1.69±0.59^{d}	2.59±1.11^{b}	3.10±0.89^{bc}	-
Eu0149 normal	-	1.86±0.55^{b}	2.01±0.76^{b}	2.54±0.15^{c}	3.13±1.36^{b}	3.42±1.22^{bc}	-
Eu normal	2.29±0.22^{a}	2.62±0.62^{a}	3.20±1.15^{a}	6.24±3.75^{a}	7.72±5.43^{a}	6.89±1.68^{a}	7.71±0.00^{a}
Eu saline	1.32±0.22^{b}	1.57±0.34^{b}	2.40±1.22^{b}	3.38±1.76^{b}	3.18±1.61^{b}	2.80±1.65^{c}	-
F	78.99***	16.57***	20.72***	37.46***	35.64***	47.02***	5.87*
$\bar{X}$	1.87	2.08	2.32	2.95	3.83	3.94	4.71

Table 10. Irradiance dependence of the predicted transpiration rate (mean±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* 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	Transpiration rate (Tr, mmol $m^{-2}s^{-1}$)							
and	Irradiance (µmol $m^{-2}s^{-1}$)							
soil type	300	500	700	1000	1300	1500	1700	2000
Com normal	1.96±2.24^{a}	1.95±0.70^{a}	1.91±0.59^{b}	2.03±0.77^{c}	2.46±0.80^{b}	2.47±0.76^{b}	3.43†1.31^{b}	3.90±1.25^{b}
Com saline	1.13±0.00^{a}	2.37±1.13^{a}	2.50±1.09^{b}	2.21±1.32^{bc}	1.74±0.66^{b}	2.02±0.86^{b}	2.12†1.09^{c}	3.30±0.52^{b}
Eu0149 normal	1.63±0.83^{a}	2.30±0.93^{a}	2.43±1.26^{b}	2.68±1.66^{bc}	2.74±0.87^{b}	3.10±1.07^{b}	2.95±0.97^{b}	3.77±0.97^{b}
Eu normal	-	-	4.38±2.34^{a}	3.88±2.50^{a}	4.67±3.84^{a}	5.32±4.39^{a}	5.26±2.57^{a}	7.80±5.26^{a}
Eu saline	0.94±0.25^{a}	1.62±0.41^{a}	2.03±0.46^{b}	2.90±1.28^{b}	2.78±0.85^{b}	3.10±1.28^{b}	3.58±1.74^{b}	3.73±2.09^{b}
F	2.41^{ns}	2.41^{ns}	3.65**	8.44***	7.31***	13.30***	16.63***	11.06***
$\bar{X}$	1.35	2.18	2.39	2.70	3.07	3.36	3.60	4.51

Table 11. Means (±sd) of the observed water-use efficiency (NP/Tr) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* in the field study in relation to time and soil types (nonsignificant differences in the same row and column are indicated by same capital and small letters respectively).

Species			Water-use efficiency (µmol CO_2/mmol H_2O)										
and			Time (h)										
soil type	F	$\bar{X}$	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700
Com normal	32.96***	6.42	^{B}6.01±3.41^{a}	^{A}8.46±2.76^{a}	^{A}8.88±2.88^{a}	^{A}8.89±3.55^{a}	^{A}8.10±3.16^{a}	^{B}6.76±3.13^{a}	^{B}5.89±2.87^{b}	^{B}6.49±2.23^{a}	^{C}4.59±2.35^{a}	^{C}3.47±1.66^{c}	^{D}1.22±1.85^{a}
Com saline	61.75***	4.14	^{BC}4.77±2.77^{b}	^{A}6.70±2.98^{a}	^{A}6.39±2.56^{b}	^{B}5.08±1.66^{c}	^{B}5.24±1.32^{c}	^{B}5.37±1.62^{b}	^{CD}4.18±1.85^{c}	^{D}3.74±1.75^{b}	^{E}2.97±1.31^{b}	^{F}1.96±0.92^{c}	^{G}-0.17±1.13^{cd}
Eu0149 normal	30.84***	3.76	^{E}3.21±2.13^{c}	^{AB}5.40±3.18^{b}	^{A}5.96±2.91^{b}	^{ABC}4.98±2.32^{c}	^{CDE}4.13±1.89^{d}	^{CDE}4.25±1.75^{c}	^{ABC}5.16±3.38^{bc}	^{BCD}4.35±3.18^{b}	^{DE}3.40±2.63^{b}	^{F}1.08±1.60^{d}	^{G}-0.52±0.95^{d}
Eu normal	43.44***	6.45	^{CD}6.00±4.13^{a}	^{A}9.44±4.61^{a}	^{A}9.38±2.67^{a}	^{B}7.96±2.69^{ab}	^{BC}7.16±2.26^{b}	^{C}6.51±2.03^{a}	^{B}8.12±3.03^{a}	^{BC}7.11±3.02^{a}	^{D}5.25±2.47^{a}	^{E}2.89±1.42^{b}	^{F}0.52±0.75^{b}
Eu saline	34.01***	4.13	^{E}3.81±2.32^{bc}	^{BC}5.49±3.34^{b}	^{B}5.61±2.62^{b}	^{A}7.12±4.71^{b}	^{BC}5.47±2.18^{c}	^{CDE}4.44±1.81^{c}	^{BCD}5.02±2.54^{bc}	^{DE}4.36±2.09^{b}	^{F}2.72±1.53^{b}	^{G}1.31±1.32^{d}	^{H}0.03±0.57^{c}
	F		9.68***	14.41***	21.36***	17.44***	25.01***	14.51***	14.47***	20.63***	13.83***	24.47***	16.86***
		$\bar{X}$	4.96	7.19	7.31	6.68	6.02	5.47	5.67	5.27	3.75	2.09	0.16

Table 12. Means (±sd) of the predicted water-use efficiency (NP/Tr) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* in the field study in relation to time and soil types (nonsignificant differences in the same row and column are indicated by same capital and small letters respectively).

Species			Water-use efficiency (µmol CO_2/mmol H_2O)										
and			Time (h)										
soil type	F	$\bar{X}$	0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700
Com normal	22.24***	4.25	^{BC}4.72±1.62^{ab}	^{AB}5.29±1.81^{ab}	^{A}5.76±1.58^{a}	^{BC}4.82±1.37^{ab}	^{CD}4.41±1.11^{ab}	^{DE}3.93±1.22^{a}	^{EF}3.76±1.27^{ab}	^{EFG}3.56±1.10^{ab}	^{FGH}3.25±1.06^{a}	^{GH}3.13±1.22^{a}	^{H}2.83±1.29
Com saline	34.95***	4.29	^{BC}5.25±2.11^{a}	^{A}5.94±2.13^{a}	^{AB}5.79±1.94^{a}	^{CD}4.78±1.19^{ab}	^{D}4.65±0.87^{a}	^{E}4.02±0.93^{a}	^{EF}3.51±1.06^{b}	^{EF}3.53±0.86^{abc}	^{EF}3.45±0.93^{a}	^{F}3.01±1.03^{a}	^{G}1.63±0.82
Eu0149 normal	21.87***	3.66	^{A}4.14±1.69^{b}	^{A}4.45±1.73^{c}	^{A}4.50±1.59^{c}	^{A}4.43±1.18^{b}	^{A}4.07±0.94^{b}	^{A}3.98±0.73^{a}	^{B}3.30±0.88^{b}	^{B}3.08±1.05^{c}	^{BC}2.77±0.82^{b}	^{C}2.44±0.80^{b}	^{D}1.81±0.83
Eu normal	18.63***	4.22	^{CDE}4.44±1.82^{b}	^{A}5.52±2.11^{ab}	^{AB}5.24±2.12^{ab}	^{ABC}5.09±1.88^{a}	^{BCD}4.75±1.64^{a}	^{CDE}4.45±1.75^{a}	^{DE}4.06±1.77^{a}	^{EF}3.97±1.67^{a}	^{FG}3.31±1.46^{a}	^{G}2.73±1.12^{ab}	^{H}2.00±0.97
Eu saline	31.35***	4.05	^{C}4.01±1.92^{b}	^{AB}4.91±1.32^{bc}	^{AB}4.94±1.14^{bc}	^{A}5.12±1.08^{a}	^{AB}4.87±0.96^{a}	^{BC}4.36±1.11^{a}	^{C}3.84±1.13^{ab}	^{D}3.15±0.95^{bc}	^{D}3.01±0.93^{ab}	^{E}2.45±0.88^{b}	^{F}1.36±0.96
	F		4.04**	4.83***	5.41***	2.02^{ns}	3.85**	1.97^{ns}	2.78*	5.23***	3.38**	3.93**	6.55***
		$\bar{X}$	4.55	5.23	5.26	4.84	4.55	4.15	3.69	3.48	3.17	2.76	2.07

Table 13. Temperature dependence of the calculated photorespiration rate (mean±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* 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	Photorespiration rate (R, μmol $m^{-2}s^{-1}$)						
and	Temperature (°C)						
soil type	21	24	27	30	33	36	39
Com normal	-	1.96 ± 0.04^{d}	2.22 ± 0.14^{d}	2.80 ± 0.16^{c}	3.48 ± 0.20^{c}	4.22 ± 0.24^{d}	5.34 ± 0.44^{b}
Com saline	-	3.52 ± 1.08^{a}	3.94 ± 0.28^{b}	5.04 ± 0.34^{a}	6.24 ± 0.36^{a}	7.46 ± 0.36^{b}	-
Eu0149 normal	-	2.72 ± 0.10^{c}	3.22 ± 0.18^{c}	4.02 ± 0.22^{b}	4.90 ± 0.32^{b}	5.96 ± 0.30^{c}	-
Eu normal	2.24 ± 0.04^{b}	2.64 ± 0.12^{c}	3.16 ± 0.18^{c}	4.08 ± 0.26^{b}	5.04 ± 0.32^{b}	6.14 ± 0.42^{c}	7.52 ± 0.00^{a}
Eu saline	2.76 ± 0.08^{a}	3.20 ± 0.26^{b}	4.16 ± 0.22^{a}	5.00 ± 0.30^{a}	6.30 ± 0.40^{a}	7.86 ± 0.48^{a}	-
F	335.12^{***}	16.57^{***}	673.06^{***}	816.16^{***}	595.80^{***}	504.93^{***}	22.26^{**}
$\bar{X}$	2.46	4.06	3.28	4.16	5.38	6.36	5.58

Table. 14 Irradiance dependence of the calculated photorespiration rate (mean±sd) of *Combretum quadrangulare* and *Eucalyptus camaldulensis* 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	Photorespiration (R, μmol $m^{-2}s^{-1}$)							
and	Irradiance (μmol $m^{-2}s^{-1}$)							
soil type	300	500	700	1000	1300	1500	1700	2000
Com normal	3.64 ± 0.46^{b}	3.20 ± 0.00^{b}	2.76 ± 0.76^{c}	2.64 ± 0.86^{e}	2.38 ± 0.42^{c}	2.92 ± 0.62^{e}	3.08 ± 0.52^{d}	4.24 ± 0.74^{d}
Com saline	3.24 ± 0.00^{b}	5.36 ± 1.02^{a}	5.48 ± 0.88^{a}	5.36 ± 1.30^{a}	5.46 ± 1.06^{a}	5.94 ± 0.82^{a}	6.44 ± 0.96^{a}	7.56 ± 0.48^{a}
Eu0149 normal	3.24 ± 0.46^{b}	3.76 ± 0.56^{b}	3.86 ± 0.74^{b}	4.06 ± 0.94^{c}	4.16 ± 0.78^{b}	4.62 ± 0.88^{c}	4.88 ± 0.58^{c}	5.84 ± 0.48^{c}
Eu normal	-	-	4.76 ± 1.64^{ab}	3.20 ± 1.00^{d}	3.68 ± 1.20^{b}	3.90 ± 1.10^{d}	4.54 ± 1.04^{c}	5.78 ± 0.70^{c}
Eu saline	4.58 ± 1.12^{a}	3.50 ± 1.04^{b}	4.64 ± 1.02^{ab}	4.76 ± 1.22^{b}	4.98 ± 1.00^{a}	5.50 ± 0.98^{b}	5.74 ± 1.04^{b}	6.86 ± 1.04^{b}
F	7.18^{***}	15.86^{***}	17.07^{***}	45.37^{***}	37.68^{***}	71.64^{***}	99.01^{***}	68.63^{***}
$\bar{X}$	3.86	3.90	4.58	4.14	3.96	4.58	4.60	5.92

Table 15. Temperature dependence of the measured stomatal conductance (means±sd) to CO_2 of *Combretum quadrangulare* and *Eucalyptus camaldulensis* with LI-6250 on non-saline (normal) and 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	Stomatal conductance (g, cm s^{-1})						
and	Temperature (°C)						
soil type	21	24	27	30	33	36	39
Com normal	-	0.16 ± 0.06^{b}	0.17 ± 0.05^{c}	0.14 ± 0.06^{d}	0.22 ± 0.10^{c}	0.28 ± 0.10^{a}	0.22 ± 0.11^{a}
Com saline	-	0.21 ± 0.07^{ab}	0.12 ± 0.006^{d}	0.14 ± 0.09^{d}	0.23 ± 0.13^{c}	0.28 ± 0.13^{a}	-
Eu0149 normal	-	0.18 ± 0.03^{b}	0.22 ± 0.06^{b}	0.24 ± 0.06^{c}	0.28 ± 0.10^{b}	0.30 ± 0.11^{a}	-
Eu normal	0.19 ± 0.01^{a}	0.23 ± 0.05^{a}	0.28 ± 0.07^{a}	0.36 ± 0.11^{a}	0.37 ± 0.11^{a}	0.31 ± 0.07^{a}	0.38 ± 0.00^{a}
Eu saline	0.16 ± 0.03^{b}	0.21 ± 0.08^{ab}	0.24 ± 0.11^{b}	0.32 ± 0.13^{b}	0.29 ± 0.07^{b}	0.30 ± 0.06^{a}	-
F	5.56^{*}	4.79^{**}	23.41^{***}	62.79^{***}	16.58^{***}	0.75^{ns}	1.88^{ns}
$\bar{X}$	0.18	0.21	0.22	0.22	0.27	0.29	0.23

Table 16. Irradiance dependence of the measured stomatal conductance (means±sd) to CO_2 of *Combretum quadrangulare* and *Eucalyptus camaldulensis* 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	Stomatal conductance (g, cm s^{-1})							
and	Irradiance (μmol $m^{-2}s^{-1}$)							
soil type	300	500	700	1000	1300	1500	1700	2000
Com normal	0.17 ± 0.05^{a}	0.19 ± 0.00^{a}	0.20 ± 0.09^{b}	0.20 ± 0.10^{a}	0.18 ± 0.05^{b}	0.19 ± 0.05^{c}	0.15 ± 0.10^{c}	0.24 ± 0.10^{b}
Com saline	0.04 ± 0.00^{b}	0.23 ± 0.09^{a}	0.29 ± 0.11^{ab}	0.22 ± 0.12^{a}	0.15 ± 0.10^{b}	0.14 ± 0.09^{c}	0.16 ± 0.13^{c}	0.33 ± 0.08^{a}
Eu0149 normal	0.22 ± 0.06^{a}	0.25 ± 0.07^{a}	0.29 ± 0.09^{ab}	0.24 ± 0.08^{a}	0.23 ± 0.08^{a}	0.24 ± 0.11^{b}	0.23 ± 0.10^{b}	0.25 ± 0.05^{b}
Eu normal	-	-	0.39 ± 0.02^{a}	0.24 ± 0.07^{a}	0.29 ± 0.60^{a}	0.32 ± 0.55^{a}	0.33 ± 0.08^{a}	0.36 ± 0.09^{a}
Eu saline	0.31 ± 0.10^{a}	0.21 ± 0.09^{a}	0.25 ± 0.11^{b}	0.25 ± 0.10^{a}	0.25 ± 0.09^{a}	0.29 ± 0.11^{a}	0.30 ± 0.13^{a}	0.31 ± 0.08^{a}
F	7.58^{***}	1.34^{ns}	2.19^{ns}	1.43^{ns}	11.05^{***}	29.38^{***}	26.10^{***}	7.83^{***}
$\bar{X}$	0.25	0.24	0.28	0.23	0.22	0.24	0.23	0.30

Table 17. Temperature dependence of the predicted stomatal conductance (mean±sd) to H_2O *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and 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	Stomatal conductance (1/rs, cm s^{-1})						
and	Temperature (°C)						
soil type	21	24	27	30	33	36	39
Com normal	-	0.30 ± 0.14^{b}	0.28 ± 0.10^{b}	0.29 ± 0.12^{b}	0.29 ± 0.11^{b}	0.29 ± 0.10^{b}	0.26 ± 0.11^{b}
Com saline	-	0.16 ± 0.03^{c}	0.14 ± 0.06^{c}	0.18 ± 0.08^{c}	0.27 ± 0.14^{b}	0.27 ± 0.09^{bc}	-
Eu0149 normal	-	0.28 ± 0.09^{b}	0.29 ± 0.16^{b}	0.30 ± 0.17^{b}	0.28 ± 0.14^{b}	0.25 ± 0.11^{bc}	-
Eu normal	0.39 ± 0.04^{a}	0.38 ± 0.10^{a}	0.40 ± 0.13^{a}	0.66 ± 0.44^{a}	0.67 ± 0.50^{a}	0.56 ± 0.17^{a}	0.57 ± 0.00^{a}
Eu saline	0.23 ± 0.04^{b}	0.21 ± 0.05^{bc}	0.30 ± 0.17^{b}	0.35 ± 0.18^{b}	0.32 ± 0.16^{b}	0.21 ± 0.14^{c}	-
F	75.43^{***}	12.87^{***}	13.75^{***}	30.44^{***}	26.21^{***}	36.29^{***}	7.31^{*}
$\bar{X}$	0.32	0.31	0.31	0.31	0.36	0.32	0.30

Table 18. Irradiance dependence of the predicted stomatal conductance (mean±sd) to H_2O *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types field study at 09:00 to 12:00 h (nonsignificant differences in the same column are indicated by same letters).

Species	Stomatal conductance (1/rs, cm s^{-1})							
and	Irradiance ($\mu^{-2}s^{-1}$)							
soil type	300	500	700	1000	1300	1500	1700	2000
Com normal	0.28 ± 0.12^{a}	0.31 ± 0.05^{a}	0.22 ± 0.05^{b}	0.25 ± 0.07^{c}	0.32 ± 0.13^{b}	0.26 ± 0.07^{bc}	0.31 ± 0.13^{b}	$0.30\dagger10.12^{b}$
Com saline	0.13 ± 0.00^{a}	0.29 ± 0.12^{a}	0.31 ± 0.11^{ab}	0.24 ± 0.13^{c}	0.17 ± 0.07^{b}	0.18 ± 0.10^{c}	0.17 ± 0.11^{c}	0.29 ± 0.04^{b}
Eu0149 normal	0.36 ± 0.23^{a}	0.31 ± 0.16^{a}	0.30 ± 0.18^{ab}	0.27 ± 0.16^{c}	0.26 ± 0.08^{b}	0.26 ± 0.09^{bc}	0.23 ± 0.09^{c}	0.29 ± 0.10^{b}
Eu normal	-	-	0.40 ± 0.06^{a}	0.48 ± 0.22^{a}	0.51 ± 0.39^{a}	0.56 ± 0.41^{a}	0.49 ± 0.19^{a}	0.63 ± 0.43^{a}
Eu saline	0.23 ± 0.08^{a}	0.23 ± 0.05^{a}	0.23 ± 0.07^{b}	0.34 ± 0.19^{b}	0.30 ± 0.12^{b}	0.32 ± 0.16^{b}	0.35 ± 0.20^{b}	0.32 ± 0.20^{b}
F	1.78^{ns}	1.14^{ns}	2.35^{ns}	16.11^{***}	8.63^{***}	18.63^{***}	21.05^{***}	9.32^{***}
$\bar{X}$	0.29	0.29	0.28	0.31	0.34	0.33	0.33	0.37

Appendix II

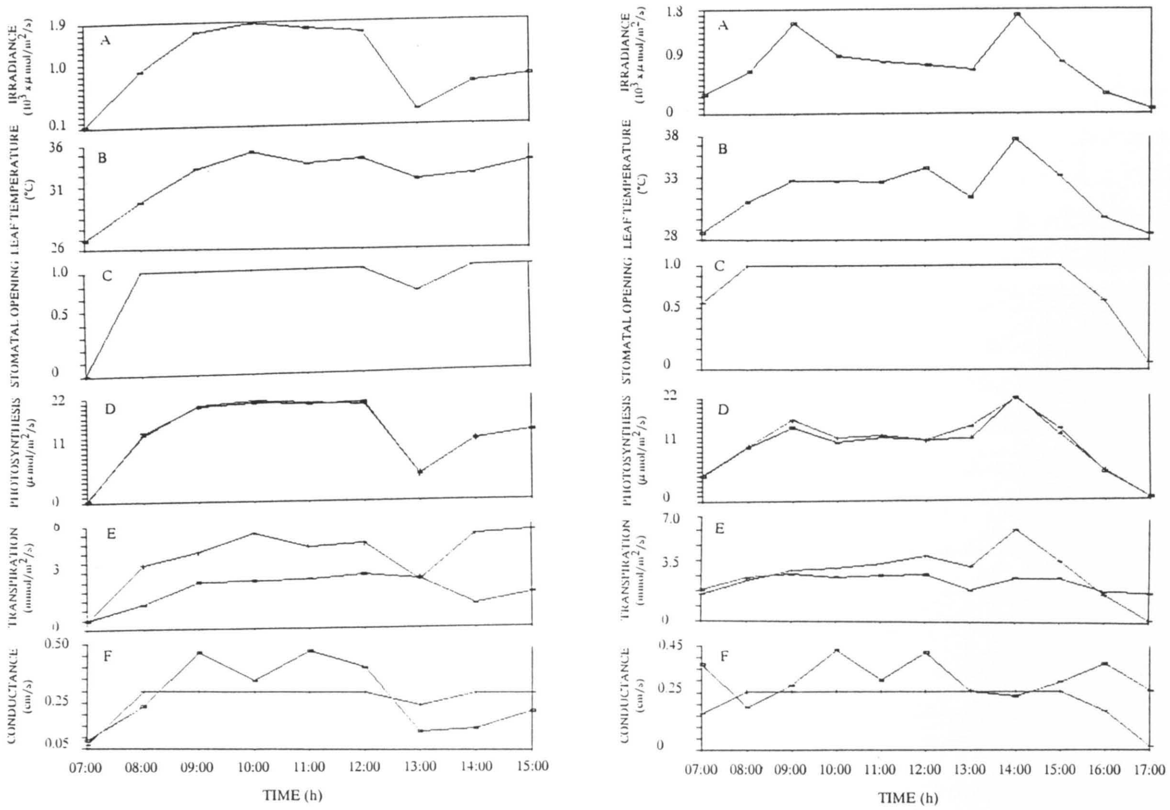

Figure 1. Time course of (A) the irradiance, (B) leaf temperature, (C) degree of stomatal regulation, (D) net photosynthetic rate, (E) transpiration rate and (F) stomatal conductance for one *Combretum quadrangulare* tree grown on non-saline soil (left-hand curves) or saline soil (right-hand curves) in November 1987. Symbols: ■, measured and +, estimated.

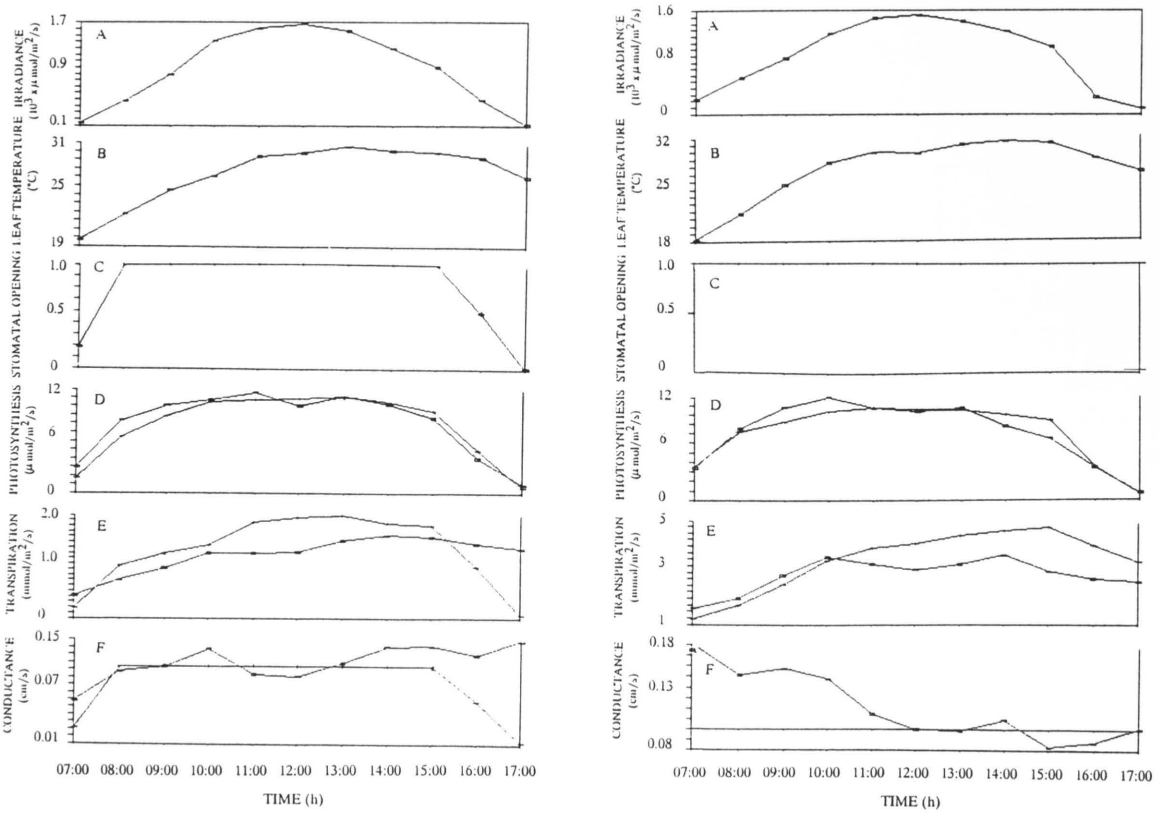

Figure 2. Time course of (A) the irradiance, (B) leaf temperature, (C) degree of stomatal regulation, (D) net photosynthetic rate, (E) transpiration rate and (F) stomatal conductance for one *Combretum quadrangulare* tree grown on non-saline soil (left-hand curves) or saline soil (right-hand curves) in December 1987. Symbols: ■, measured and +, estimated.

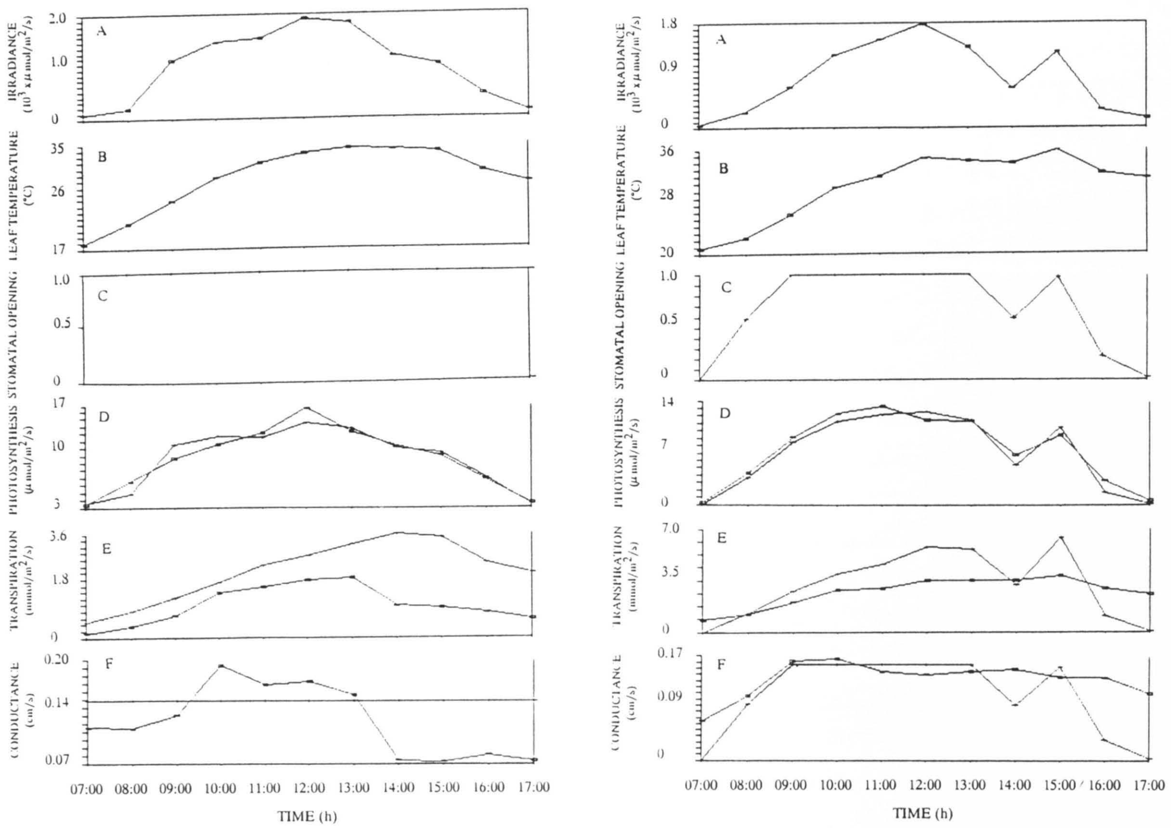

Figure 3. Time course of (A) the irradiance, (B) leaf temperature, (C) degree of stomatal regulation, (D) net photosynthetic rate, (E) transpiration rate and (F) stomatal conductance for one *Combretum quadrangulare* tree grown on non-saline soil (left-hand curves) or saline soil (right-hand curves) in January 1988. Symbols: ■, measured and +, estimated.

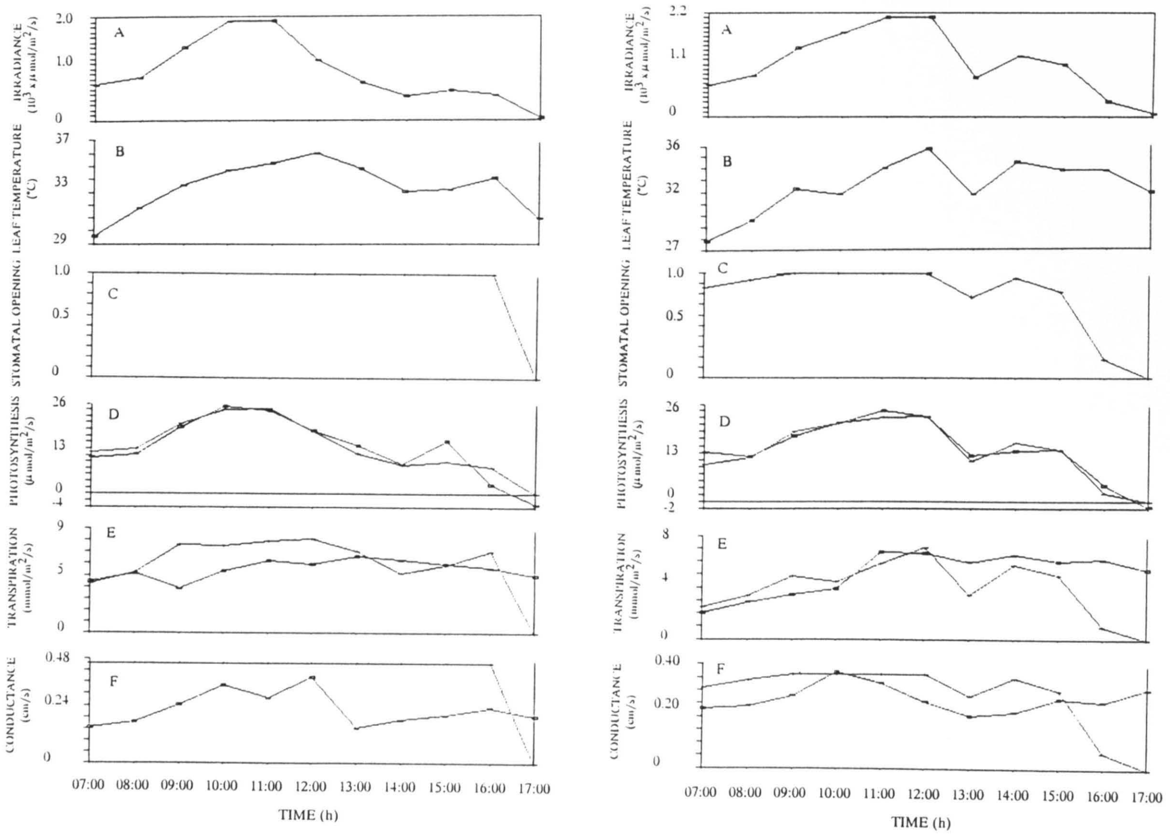

Figure 4. Time course of (A) the irradiance, (B) leaf temperature, (C) degree of stomatal regulation, (D) net photosynthetic rate, (E) transpiration rate and (F) stomatal conductance for one *Eucalyptus camaldulensis* (local variety) tree grown on non-saline soil (left-hand curves) or saline soil (right-hand curves) in November 1987. Symbols: ■, measured and +, estimated.

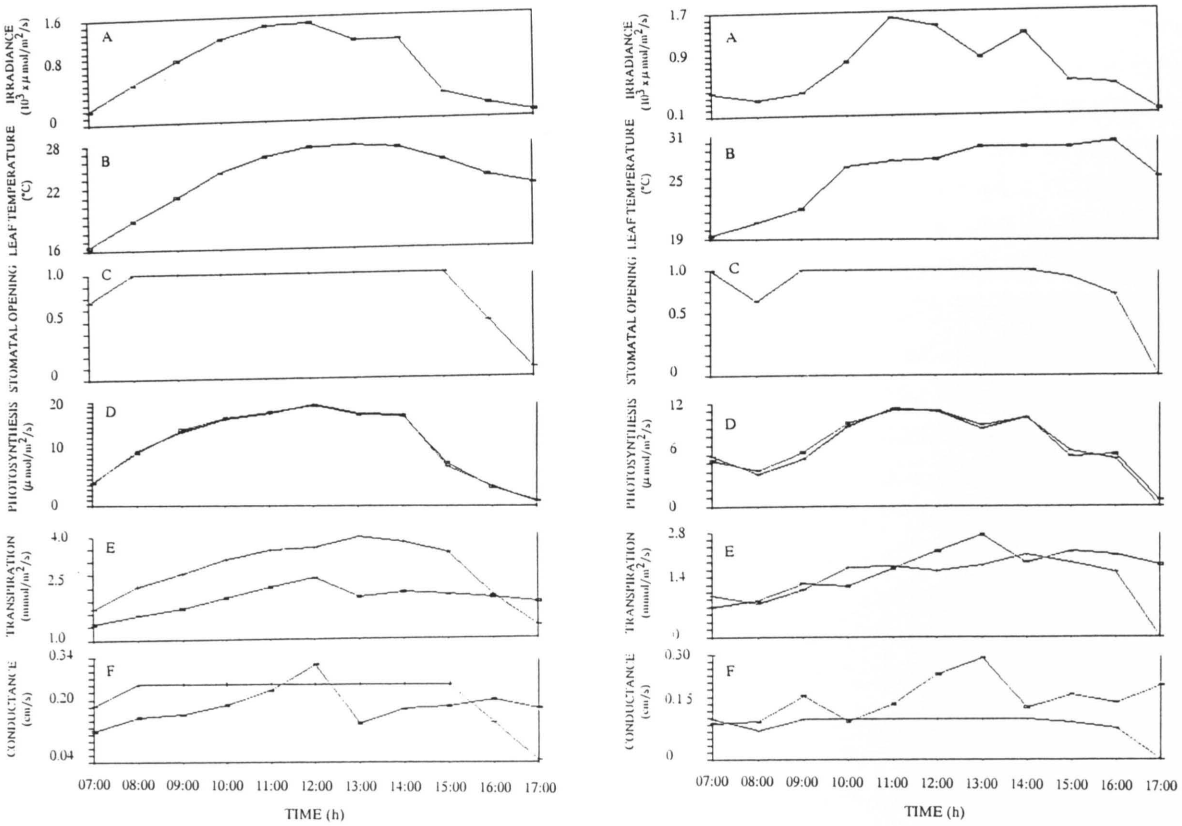

Figure 5. Time course of (A) the irradiance, (B) leaf temperature, (C) degree of stomatal regulation, (D) net photosynthetic rate, (E) transpiration rate and (F) stomatal conductance for one *Eucalyptus camaldulensis* (local variety) tree grown on non-saline soil (left-hand curves) or saline soil (right-hand curves) in December 1987. Symbols: ■, measured and +, estimated.

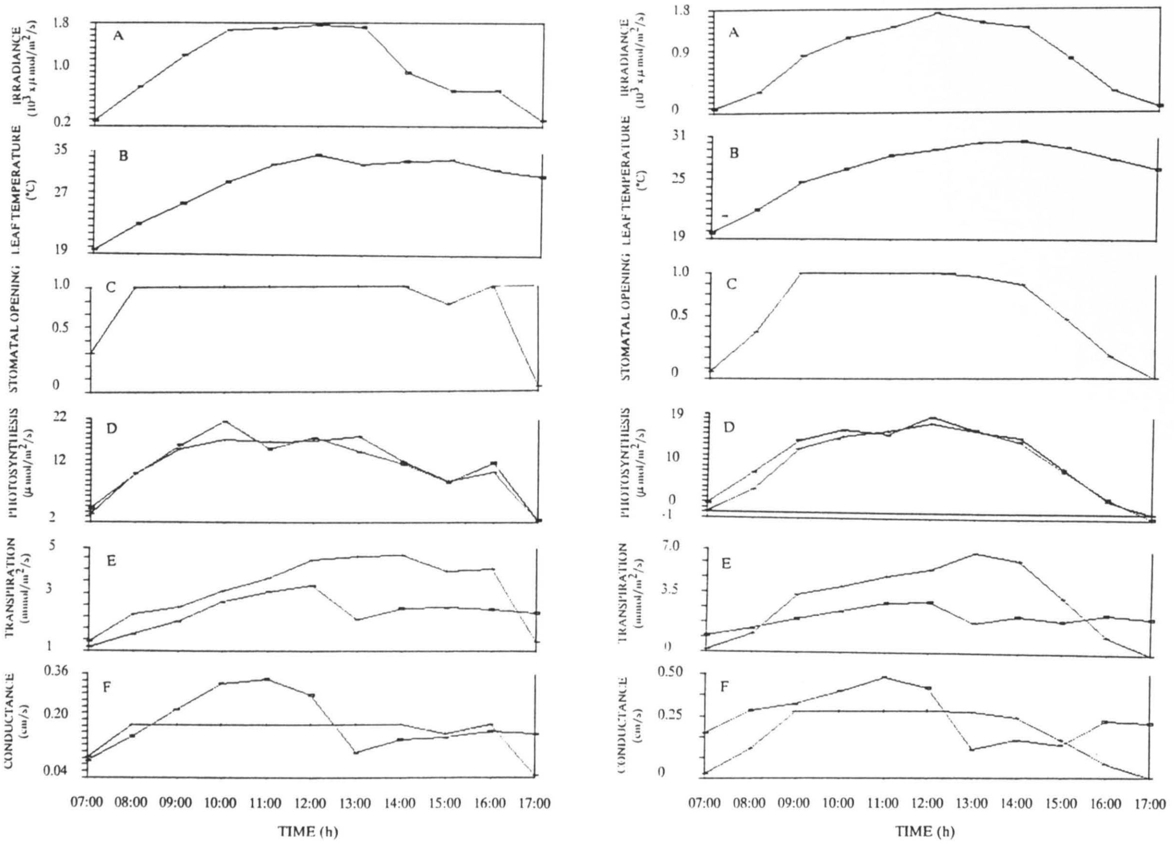

Figure 6. Time course of (A) the irradiance, (B) leaf temperature, (C) degree of stomatal regulation, (D) net photosynthetic rate, (E) transpiration rate and (F) stomatal conductance for one *Eucalyptus camaldulensis* (local variety) tree grown on non-saline soil (left-hand curves) or saline soil (right-hand curves) in January 1988. Symbols: ■, measured and +, estimated.

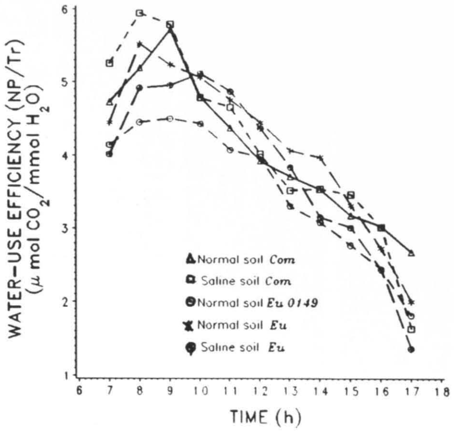

Figure 7. Average diurnal course of water-use efficiency resulted in the modelling values for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

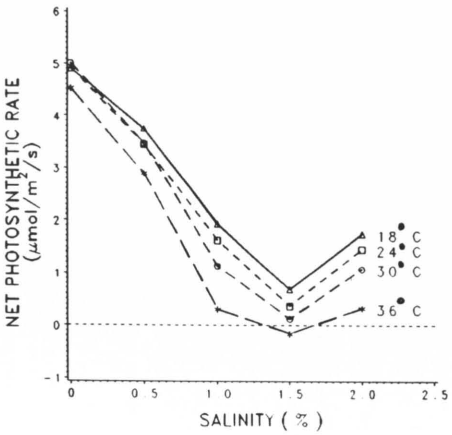

Figure 8. Relationship between net photosynthetic rate and salinity for *Combretum quadrangulare* at a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and different temperatures. Mean values for seedlings grown in culture solution in the greenhouse experiments.

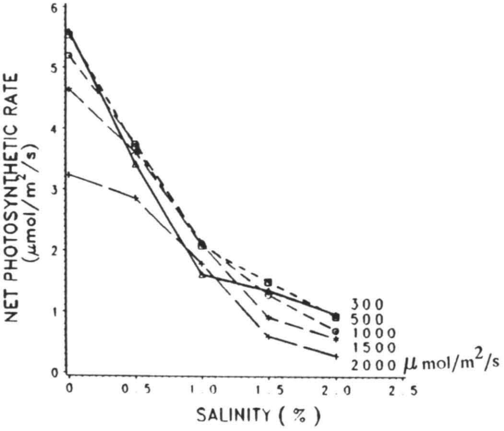

Figure 9. Relationship between net photosynthetic rate and salinity for *Combretum quadrangulare* at 30°C at different photon flux densities. Mean values for seedlings grown in culture solution in the greenhouse experiments.

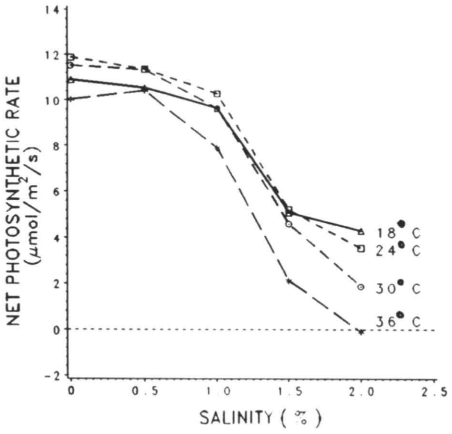

Figure 10. Relationship between net photosynthetic rate and salinity for *Eucalyptus camaldulensis* at a photon flux density of 1000 μmol $m^{-2}s^{-1}$ and different temperatures. Mean values for seedlings grown in culture solution in the greenhouse experiments.

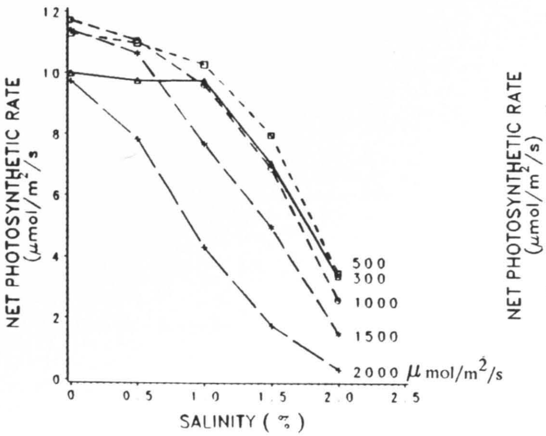

Figure 11. Relationship between net photosynthetic rate and salinity for *Eucalyptus camaldulensis* at temperature 30°C at different photon flux densities. Mean values for seedlings grown in culture solution in the greenhouse experiments.

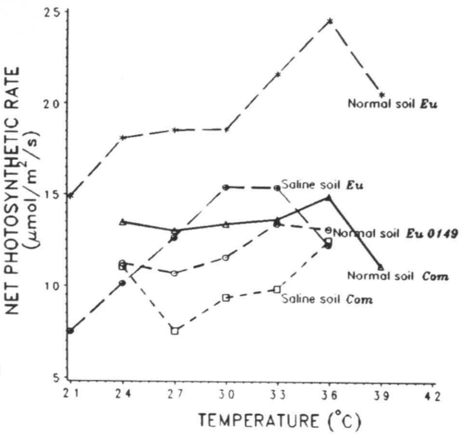

Figure 12. Relationship between net photosynthetic rate and temperature for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

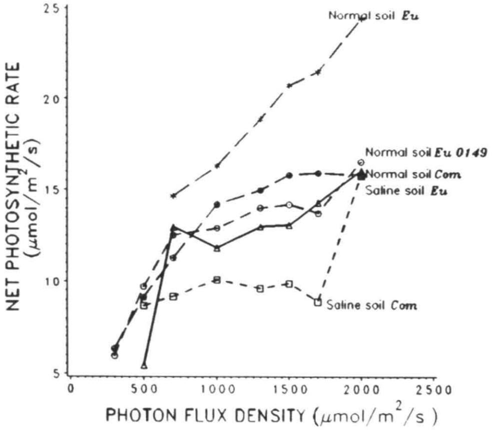

Figure 13. Relationship between net photosynthetic rate and photon flux density for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study.

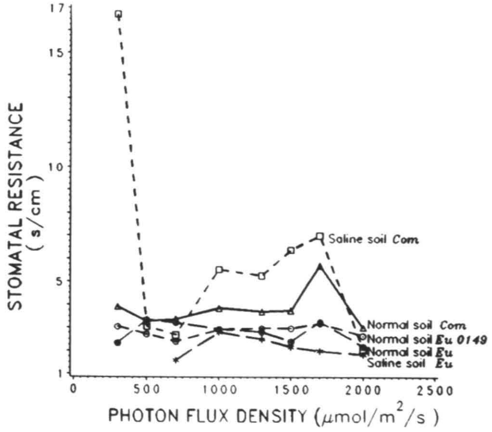

Figure 14. Relationship between stomatal resistance to H_2O and photon flux density for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (IRGA measurements, mean values).

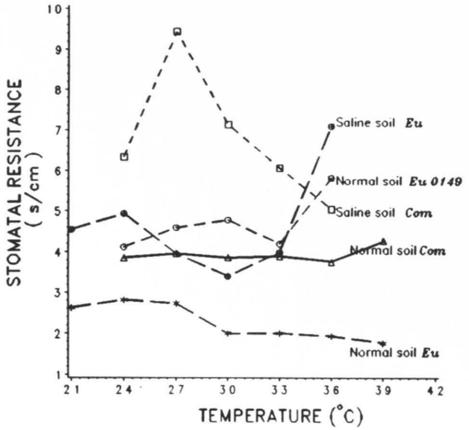

Figure 15. Relationship between stomatal resistance to H_2O and temperature according to the model for *Combretum quadrangulare* and *Eucalyptus camaldulensis* on non-saline (normal) and saline soil types in the field study (mean values).

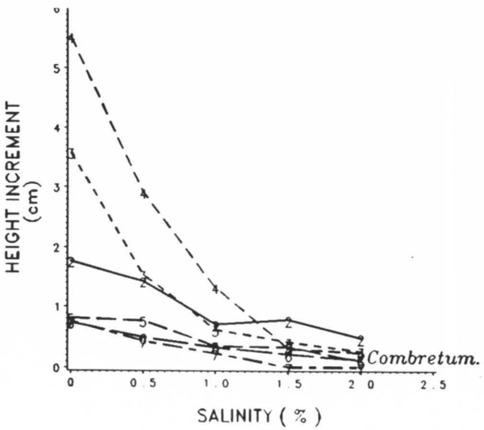

Figure 16. Relationship between height growth increment and salinity for *Combretum quadrangulare* on biweekly intervals for 3 month study period. Mean values for seedlings grown in culture solution in the greenhouse experiments. Symbols: 2 = the second, 3 = the third, 4 = the fourth measurements, respectively, etc.

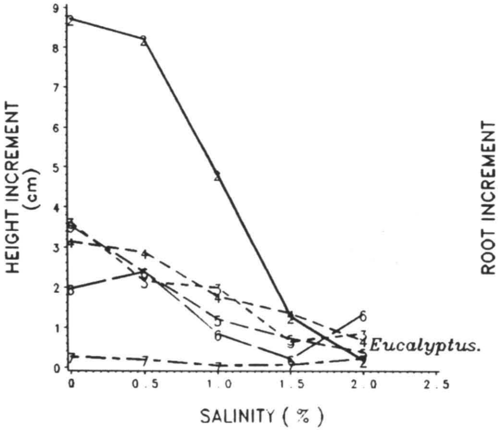

Figure 17. Relationship between height growth increment and salinity for *Eucalyptus camaldulensis* on biweekly intervals for 3 month study period. Mean values for seedlings grown in culture solution in the greenhouse experiments. Symbols: 2 = the second, 3 = the third, 4 = the fourth measurements, respectively, etc.

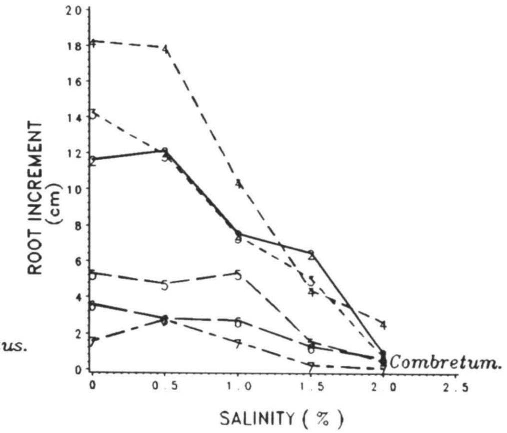

Figure 18. Relationship between root growth increment and salinity for *Combretum quadrangulare* on biweekly intervals for 3 month study period. Mean values for seedlings grown in culture solution in the greenhouse experiments. Symbols: 2 = the second, 3 = the third, 4 = the fourth measurements, respectively, etc.

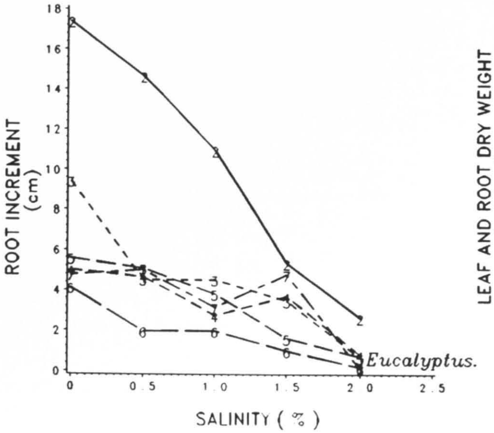

Figure 19. Relationship between height root increment and salinity for *Eucalyptus camaldulensis* on biweekly intervals for 3 month study period. Mean values for seedlings grown in culture solution in the greenhouse experiments. Symbols: 2 = the second, 3 = the third, 4 = the fourth measurements, respectively, etc.

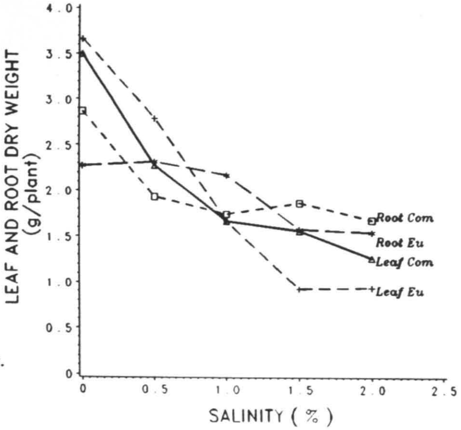

Figure 20. Relationship among leaf and root dry weight and salinity for *Combretum quadrangulare* and *Eucalyptus camaldulensis*. Mean values for seedlings grown in culture solution in the greenhouse experiments.

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ACTA FORESTALIA FENNICA

214 **Luangjame, Jesada.** Salinity effects in *Eucalyptus camaldulensis* and *Combretum quadrangulare*: ecophysiological and morphological studies. Tiivistelmä: Suolaisuuden vaikutukset *Eucalyptus camaldulensikseen* ja *Combretum quadrangulareen*: ekofysiologisia ja morfologisia tutkimuksia.

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