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University of Alberta

MODELLING STRATEGIES OF THE SOIL PLANT ATMOSPHERE CONTINUUM IN WATER LIMITED ENVIRONMENTS AND ELEVATED ATMOSPHERIC CO_2

BY

PAOLO MANUNTA ©

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

IN

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled MODELLING STRATEGIES OF THE SOIL PLANT ATMOSPHERE CONTINUUM IN WATER LIMITED ENVIRONMENTS AND ELEVATED ATMOSPHERIC CO_2 in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in WATER AND LAND RESOURCES.

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ABSTRACT

The rationale for this study is found in the probable higher temperatures and changes in rainfall patterns that are expected in the future as a result from increasing levels of CO_2 in the atmosphere. In particular, higher air temperatures may cause an increase in evapotranspiration (ET) demand while a reduction in rainfall could increase the severity and duration of drought in arid and semi-arid regions. Representation of the water transfer scheme includes water uptake by roots and the interaction between ET and CO_2 enrichment. The predicted response of a plant canopy, in terms of energy exchange processes to elevated atmospheric CO_2 level, was tested against measurements collected in the field. Simulated and measured canopy conductances were reduced by about 30% under elevated [CO_2] under optimum conditions of water supply. Reductions in latent heat fluxes under elevated vs. ambient [CO_2] caused reductions in both simulated and measured seasonal water use of 6% under optimum and 2% under suboptimum irrigation. This modelling framework was extended to explore adaptation and functioning of root system of woody plant canopies. A theoretical analysis of a recently observed phenomenon called "hydraulic lift" was conducted. Simulated results support the hypothesis that the water relocated via hydraulic lift prevents the upper soil layers from becoming extremely dry. In particular the soil layers close to the surface maintained soil water potential between −1.0 and −1.3 MPa during the drought period and under two different rainfall regimes. Conversely the absence of hydraulic lift caused the soil layer close to the surface (0.0-0.1 m) to drop to -20 MPa and -28 MPa. Water relocated via hydraulic lift did not provide a significant additional amount of water for plant transpiration. In conclusion, modelling of CO_2 and transpiration interactions may produce more accurate estimates of canopy water use under predicted climate change. Hydraulic lift was simulated to be more important for soil moisture re-distribution than for canopy transpiration.

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GLOSSARY OF SYMBOLS

A_n	CO_2 uptake
BD	Bulk Density
C_a	Atmospheric [CO_2]
$[C_i]$	Liquid concentration of CO_2 in the stroma
D	Soil hydraulic diffusivity
DOY	Day of the year
Ei	Exponential integral function
ET	Evapotranspiration
I	Absorbed photosynthetically active radiation
IRT	Infrared Thermometer
J	Potential electron transport rate
Jc	Dark reaction rate in CO_2 fixation
Je	Light reaction rate in CO_2 fixation
J_{max}	Maximum rate of electron transport
K	Proportionality factor designated as hydraulic conductivity
K_{EFF}	Effective mean hydraulic conductivity
K_{FC}	Hydraulic conductivity at field capacity
K_{SAT}	Saturated hydraulic conductivity
K_{WP}	Hydraulic conductivity at wilting point
K_z	Soil hydraulic conductivity
LAI	Leaf Area Index

L_z	Root length density
O	Outward water flux in soil layer 1
$[O_i]$	Liquid concentration of O_2 in the stroma
Q	Ratio of CO_2 fixation to electron transport
R_{bl}	Boundary layer resistance
R_l	Leaf canopy hydraulic resistance
R_{r1}	Root hydraulic resistance in soil layer 1
R_{r2}	Root hydraulic resistance in soil layer 2
R_{s1}	Hydraulic resistance in soil layer 1
R_{s2}	Hydraulic resistance in soil layer 2
R_{st}	Stem hydraulic resistance
T	Canopy transpiration
Tc	Canopy temperature
U_z	Soil water uptake
V_{cmax}	Maximum dark reaction rate at ambient temperature and saturating CO_2 in the absence of oxygen
V_{omax}	Maximum rate of oxygenation under conditions of saturating O_2 and absence of CO_2
X	Distance
Z	Gravitational potential
a	Radius of the root
b	Intercept parameter of the conductance model
b_z	Path length for water uptake
e^-	Electron transport requirement for CO_2 fixation

g_s	Stomatal conductance
l	Soil layer
k_c	Michaelis-Menten constant for CO_2
k_o	Michaelis-Menten constant for O_2
m	Slope parameter of the conductance model
q	Water flux in unsaturated soils
q_r	Water flux per unit root length
r	Radial distance from the center of the root
$\bar{\mathrm{r}}$	Mean radial distance
rr_z	Root resistance
rs_z	Soil resistance
z	Number of soil layers
Δz	Soil depth increment
Ψ	Matric potential
Ψ_c	Critical water potential at which conductance becomes half of the maximum
Ψ_l	Leaf water potential
Ψ_{sz}	Soil water potential for a given layer
α	Quantum efficiency
β	Curvature factor for transition of J from maximum quantum yield to light saturated rate.
θ	Water content
ρ	Density of water
ρr	Root radial resistivity

ψ_a	Air water potential
ψ_l	Leaf canopy water potential
ψ_r	Roots water potential
ψ_s	Soil water potential
ψ_{st}	Stem water potential
$\Delta\theta$	Water content gradient
Γ^*	Compensation point for gross photosynthesis

Chapter 1

Introduction

Plants constitute an important part of the earth's hydrological system. On average, approximately 70 % of the water that falls on vegetated continental regions is returned to the atmosphere by means of evapotranspiration (Molz, 1981). An immediate goal of ecologists and hydrologists is to develop an improved understanding of the hydrological processes involved in the transport of water from soil through vegetation, to the atmosphere. Incorporating accurate quantitative descriptions of water transport processes in the soil-plant system is a long-term goal that will lead to improvements in our ability to predict ecosystem responses to changes in global climate, as well as to changes resulting from local land management. There is a growing recognition that terrestrial ecosystems are dynamically linked to global climate. An improved representation of biophysical ecosystem processes, particularly the dynamic links between ecosystem and climate, must be included in models used to predict how climate will respond to human perturbation. During the last decade a wide variety of ecosystem models have been used to represent terrestrial processes (Foley, 1995; Parton *et al.*, 1993; Prentice *et al.*, 1992). Soil-vegetation-atmosphere transfer models (SVAT) supply the Atmospheric General Circulation Models (AGCMs) with surface boundary conditions such as energy flux, water and momentum transfer using geographically referenced vegetation and soil characteristics. Coupled SVAT - AGCMs may be extended to simulate the effects of climate change on terrestrial ecosystem productivity.

Surface hydrological processes (e.g., sensible heat and latent heat transfer, runoff) have been indicated by Garratt (1993) to be key components of SVATs. The geographic distribution of vegetation is important in the parameterization of SVATs due to its influence upon surface albedo (radiative energy transfer), canopy conductance (transpiration) and surface roughness (aerodynamic resistance to water vapor and heat transfer) used in the simulation of surface hydrology. Vegetation plays important roles in controlling surface hydrological process through canopy stomatal conductance and uptake of soil water by roots. Response of stomatal conductance to environmental conditions influences surface water and energy transfer processes. Possible roles that plant root systems may have in influencing the distribution of moisture in soil profile may also have important implications for surface water balance.

The rationale for this study is found in the probable higher temperatures and changes in rainfall patterns that might result from increasing CO_2 concentration (i.e.,[CO_2] hereafter) in the atmosphere. A combination of an increase in atmospheric [CO_2] and water limitations has been suggested as an important example of interactions which are expected to either magnify or limit the effect of higher [CO_2] (Lavorel *et al.*, 1998). For example, the doubling of the [CO_2] in the atmosphere is predicted to cause an increase in air temperature, as well as a some regional decrease in rainfall (Cubash *et al.*, 1996). Therefore, in areas where potential evapotranspiration already exceeds precipitation it is crucial to understand the main mechanisms that would minimize plant water stress and stomatal closure. These include reductions in transpiration induced by elevated [CO_2] and plant features that could enhance the amount of soil water available for transpiration, e.g. hydraulic lift (see section 1.2).

While looking at the general issue of plant water I narrowed the scope of my research to two main questions:

1) How does increased [CO_2] in the atmosphere influence the water and energy balance of a crop canopy?

2) What are the fundamental aspects of hydraulic lift? And how significant is this phenomenon in plant water balance?

The two cases studied, the first one carried on a wheat canopy and the second one on a shrub stand, offer the possibilities to examine two of the processes that play important roles in plant water relations: first, the expected reductions in transpiration rates of C_3 plants when exposed to increased level of CO_2, and secondly, the vertical relocation of water in the soil profile via hydraulic lift.

1.1 Canopy conductance

Canopy stomatal conductance is a key component of SVATs because it affects energy and mass exchange between terrestrial ecosystems and the atmosphere. Stomatal conductance depends upon several interacting environmental conditions, such as soil water availability, solar radiation, air temperature, atmospheric humidity and [CO_2]. New insights into the biochemical mechanisms governing stomatal conductance were provided by plant physiologists in the 1980s and early 1990s (Farquhar *et al.*, 1980; Ball, 1988; Collatz *et al.*, 1991).

Wong *et al.*, (1979) concluded that stomatal conductance is determined by the CO_2 fixation rate of the mesophyll. When net CO_2 fixation was altered by applying inhibitor of photosynthetic electron transport or abscisic acid (ABA), changes in the stomatal conductance were found to be proportional to changes in CO_2 fixation rate. Such observations led to the suggestion that a signal from the mesophyll controls stomatal opening. The conflicting role of stomata in allowing CO_2 diffusion in support of photosynthesis and restriction of water vapor diffusion out of the leaf, has to reach a balance so that no failure in one of the two roles occur (Collatz *et al.*, 1991). Despite the lack of mechanistic evidence in support of this hypothesis, it has been argued that a regulatory system must achieve compromise between providing CO_2 for assimilation and restricting water loss (Raschke, 1979).

Previous studies report that when [CO_2] was raised from ambient (i.e. about 370 μmol mol^{-1}) to 530 μmol mol^{-1}, wheat photosynthetic rate increased by about 12% (Sicher and Bunce, 1997). Other authors reported an increase of about 50% when [CO_2] was elevated from ambient to about 600 μmol mol^{-1} in light saturated conditions (Miglietta *et al.*, 1996). Although the absolute increase could be affected by plant nutrition status and perhaps by acclimation, Guehl *et al.* (1994) reported that higher [CO_2] produces a higher biomass accumulation. Although reduced stomatal conductance of water vapor leads to a decrease in transpiration (Kimball and Idso, 1983; Senock, 1996), the extent of this decrease is a balance between the higher CO_2 fixation and the reduced stomatal aperture induced by higher $[CO_2]$.

Water stress reduces stomatal conductance by decreasing plant water potentials and by inhibiting mesophyll fixation (Chaves, 1991). Foley *et al.*, (1996) represented heuristically the effect of water stress on CO_2 fixation by calculating a stress factor based on plant available water. Nevertheless, new modelling strategies that include a more realistic representation of the soil-plant hydraulic system are needed. For example, the ability of Mediterranean vegetation to fix carbon decreases as the drought season develops, and carbon assimilation becomes more a function of environmental conditions and time of the day. In particular, during the summer drought, the highest photosynthetic rate occurs during periods of low incident photon flux density and relatively low temperature found in the early part of the day (Tenhunen *et al.*, 1985), leading to important implications in terms of seasonal water use. A combination of factors such as characteristic diurnal patterns in leaf gas exchange at different drought stages, structural adjustment such as decreasing leaf area, and root activity permit these plants to functionally adjust to specific site environmental conditions. Detailed representation of diurnal plant water status and the response of stomatal conductance are needed to accurately predict the ecosystem behavior, which cannot be easily obtained by applying simple stress factors.

Past ecophysiological studies in Mediterranean ecosystem have been confined to repeated observations of leaf level gas exchange over extended periods of time (Turner *et al.*, 1984; Tenhunen *et al.*, 1985; Tenhunen *et al.*, 1987). The analysis of the results indicated the need for interpreted responses that would help investigators to understand physiological adaptation in specific environments, and that in turn could explain the results of gas exchange measurements. While attempting to represent the complexity of factors that influence carbon fixation and water use of Mediterranean sclerophyll shrubs, new modelling strategies have been adopted. For example, Tenhunen *et al.*, (1990) used a proportionality factor to express the relationship of stomatal conductance to net photosynthesis rate. Numerical values of such a parameter vary in accordance to the water stress experienced by the vegetation which alters the degree of stomatal opening for a given rate of carbon fixation. Interpretation of this parameter in terms of physiological mechanisms that control leaf gas exchange during drought could be possible. However, the understanding of the coupling mechanisms between gas exchange behavior and physiological changes occurring in the root environment during soil drying, is still missing.

1.2 Hydraulic lift

Roots traverse soil layers that have different levels of moisture. In drier soils, the water potential could be lower than the root water potential, and if water is lost from the root into drier soil it is because the root apparatus works as a bridge for water transport between soil layers. It is hypothesized that movement of water by such a bridge would be more rapid than either liquid or vapor phase movement of water within the soil. This process in which soil water is transferred from moist to drier regions of the soil through plant root systems, has been termed “hydraulic lift” by Richards and Caldwell (1987). In terms of water use strategy, the release of water resources in shallow soils surrounding the root mat region might constitute a storage mechanism, that when combined with the water extracted from other portion of the profile, can potentially extend the productive period of the plant. The possibility for such water transport has been observed under certain circumstances and species, including a native tree of the Atacama desert of Chile, *Prosopis tamaguro* (Moony *et al.*, 1980); *Phaseolus vulgaris* in a laboratory experiment (Schippers *et al.*, 1967); and *Sorghum bicolor* planted in the field (van Bavel *et al.*, 1984). Deep roots of trees and woody plants undergoing hydraulic lift, uptake water at night from deep, moist soil layers and re-locate this water to the upper soil layers. Subsequently, the water lifted and stored is used the following day by the plant and is hypothesized to aid different species in meeting their transpirational requirements (Dawson, 1993b). There is growing evidence that many deep-rooted shrubs and trees found in arid, semi-arid and even mesic environments conduct hydraulic lift (Dawson, 1993b). This water use strategy not only helps plants to meet their demand for water, but also improves the soil water status underneath the canopy (Richards and Caldwell, 1987). This may be important for the development of understory vegetation and it may lead to improved nutrient status in the surface horizon of the soil. Some authors have collected evidence of improved soil development (greater porosity and higher percentage of organic matter) under woody canopies as opposed to open grassland, and of greater water storage and soil nutrient concentrations (Joffre and Ramball, 1988). In particular some of the woody canopies found in the Mediterranean area, where trees are embedded in a matrix of grassland and other herbaceous species (e.g., dehesa), offer the possibility to determine if the heterogeneity in the canopy cover reflects a peculiarity of the water balance. Joffre and Ramball, (1988) reported that the measured transpiration of the tree-grass component of the (dehesa) ecosystem was about 20-50 % more than that computed by the water balance equation, suggesting that the hypothesis that evergreen oak trees perform hydraulic lift remains valid.

Earlier work carried out on alfalfa by Dirksen and Raats (1985) suggested that although water potential must have been higher in the roots than in the dry soil satisfying the condition for leakage of water, gamma ray measurements of soil water content only occasionally show a slight increase in water content due to water released by the roots. However, this may partly be due to the methods used in the study. The small amount of water released by the roots into a soil would only cause a slight increase of soil water content, which is difficult to measure because the accuracy of the instrument.

In an attempt to assess the relative extent of resistance to uptake and exudation, Baker and van Bavel (1986) conducted an experiment on bermudagrass, *Cynodon dactylon*, and showed that water was transferred through the stolons from the wet to the dry portion of the sod. About one half of the total transferred water occurred at nighttime, and furthermore, the transpiration of the plants in the dry sod was equal to the amount of water re-located by stolons.

Based on this evidence, it is hypothesized that deep-rooted shrubs and trees found in arid, semi-arid and even mesic environments may exhibit hydraulic lift. The latter consists of an uptake of water from moist deep soil. Water is relocated at nighttime into the upper portion of the profile, via outward flux of water from hydrated roots into the dry soil and driven by water potential gradients. During the daytime, transpiration demand increases so that water uptake will occur. Hydraulic lift has implications not only at the plant level, but also at the hydrological scale. This is because more water resources are made available to the plants so that carbon fixation is not inhibited, thus promoting the transfer of water from the soil into the atmosphere in vapor form.

Higher temperatures and changes in precipitation regimes will affect water availability to canopies, thus affecting evapotranspiration rates. In particular, higher air temperatures lead to increases in vapor pressure deficit, thus creating the conditions for higher transpiration demand while changes in rainfall pattern could shorten even more the seasonal period of water supply in the arid and semi-arid regions around the globe. Southern Europe for example is predicted to be especially vulnerable to climate change, as it lies on the border between the temperate climate of the mid-latitudes and the desert conditions of the subtropical belt. Computer simulations forecast a decrease in rainfall precipitation under a doubling of the [CO_2] (Cubash *et al.*, 1996). Predictive tools such as computer models are currently used to quantify water use by plants under different boundary conditions. However, most current models may produce inaccurate predictions because they do not take in account the effect of [CO_2] upon transpiration and the water relocated through hydraulic lift. The rooting system of *Pistacia lentiscus*, a Mediterranean shrub expands downward, reaching rock interstice and producing fine roots in the presence of moist soil. This type of rooting system allows water to be relocated closer to the surface and be either utilized by other plant species or by the same plant species that is performing the lifting. Finally, because the root system allows exploitation of water resources, its proper representation is of paramount importance for surface hydrology and in particular to stomatal conductance.

1.3 Thesis content

This thesis includes 5 chapters. Chapter 2 describes thedevelopment of two major model components, the plant atmosphere continuum and the plant carbon balance and growth. Subsequently, the model performance is tested against data collected over a wheat canopy. The effect of increased [CO_2] in the atmosphere is discussed in terms of latent heat fluxes and their implications for seasonal water use of this crop plant. In

Chapter 3, the mechanism of hydraulic lift, that may play an important role for the plant water use, is analyzed and discussed in terms of its fundamental principles. This discussion and resulting hypotheses are timely since the phenomenon of hydraulic lift has been reported in several studies but rarely analyzed in terms of its importance in the context of plant or ecosystem water balance. In order to determine the likely relevance of hydraulic lift, in Chapter 4 two types of scenarios are analyzed. An initial case in which the vegetation is allowed to perform hydraulic lift and a second case in which the roots have rectifying properties that prevent hydraulic lift from happening. First the model is parameterized according to the conditions found in Sardinia, Italy where a sclerophyll shrub (*Pistacias lentiscus*) is commonly found, then two sets of simulations with different climatic conditions are produced. The first run was obtained with hourly meteorological data recorded at the site in 1996, while the second set of simulation used the same data but with a reduced amount of rainfall. Because the year 1996 was a relatively rainy one, the reduction by 160 mm of rainfall used for the second simulation was meant to reproduce a more typical climatic scenario.

The synthesis of the study is the focus of Chapter 5, which is a quantitative analysis of the role of reduced transpiration due to increased [CO_2], and the greater water availability obtained via hydraulic lift, which can prevent or delay water stress. Finally, the discussion concentrates on how the inclusion of these processes may contribute to improvements in our ability to predict future changes in plant water relations in water limited environments in the view of climatic changes.

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[1]Chapter 2

Changes in mass and energy transfer between the canopy and the atmosphere: model development and testing with a free air CO_2 enrichment (FACE) experiment.

2.1 Introduction

There is growing realization that terrestrial ecosystems are dynamically linked to global climate. An improved representation of these ecosystems must be included in models used to predict how climate will respond to human perturbation. During the last decade a wide variety of ecosystem models have been used to represent terrestrial processes. Three classes of these models have emerged (Foley, 1995): 1) terrestrial biogeochemical models (TBMs), 2) potential vegetation models (PVMs) and 3) soil-vegetation-atmosphere transfer (SVAT) models. TBM's are designed to simulate net primary productivity (NPP) and usually include important carbon pools such as vegetation biomass, litter and soil organic matter (Parton *et al.*, 1993). PVMs, also known as equilibrium vegetation models, are designed to reproduce geographic distributions of vegetation at the global scale. In some instances the use of these models has been extended to the investigation of global vegetation patterns as affected by different predicted climatic scenarios (Prentice *et al.*, 1992). SVAT models supply the Atmospheric General Circulation models (AGCMs) with surface boundary conditions such as energy flux, water and momentum transfer using geographically referenced vegetation and soil characteristics. Coupled SVAT - AGCMs may be extended to simulate the effects of climate change on terrestrial ecosystem productivity.

Surface hydrology (sensible and latent heat transfer, runoff) has been indicated as a key component of SVATs (Garret, 1993). Therefore the geographic distribution of vegetation is important in the parameterization of SVATs due to its influence upon surface albedo and surface roughness used in the simulation of surface hydrology. Canopy

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[1] The work reported in this chapter has been produced almost entirely under the supervision of Dr. Robert Grant of the Dept. of Renewable Resources, University of Alberta. Subsequentelly this chapter was revised to accommodate the changes made to the computer coding.

stomatal conductance is important in SVATs because it affects energy and mass exchange between terrestrial ecosystems and the atmosphere. Stomatal conductance depends upon several interacting environmental conditions such as physiological conditions of the plant, soil water availability, intensity of short-wave radiation, air humidity, leaf temperature, and [CO_2] (Steward, 1988; Jones and Higgs, 1989). A technique for calculating canopy stomatal conductance proposed by Jarvis (1976) uses an unconstrained value for conductance multiplied by a series of dimensionless factors representing constraints imposed by each environmental condition known to affect conductance. However it is difficult to determine the unconstrained conductance for different plant species and the extent to which this conductance is reduced by different combinations of environmental conditions. Such a non-mechanistic representation of stomatal conductance may cause inaccuracies in the simulation of latent and sensible heat transfer. Although a truly mechanistic model is most likely to be successful in predicting stomatal responses, its implementation is not always feasible because parameters such as maximum stomatal conductance or the sensitivity to leaf vapor pressure deficit need to be readjusted to fit a particular vegetation type. The approach used in this chapter expands upon the analysis of Ball (1988) and the experimental findings of Wong *et al.* (1979), which suggest an implicit dependence of stomatal conductance on photosynthesis, and therefore the role of stomatal conductance in regulating the balance between transpiration and net uptake of CO_2 during photosynthesis (Collatz *et al.*, 1991). Although some of the components of this model, particularly CO_2 fixation, are based on fundamental properties of the plant biochemical processes, this approach remains largely empirical. The first step of this work was to separate the response of stomatal conductance to changes in those environmental variables that have an effect on photosynthesis from those that do not. For example, changes in incoming PAR (photosynthetically active radiation) are likely to cause a proportional change in stomatal conductance so as to maintain a constant proportionality between stomatal conductance and photosynthesis, if all other factors are held constant. On the contrary, changes in leaf water potential cause a direct change in stomatal conductance (Cline and Campbell, 1976). It could be argued that opening and closing of the pore is turgor-dependent (Raschke, 1979), however the ion transport processes and the sensory system that control the closing are not fully understood.

New insights into the biochemical mechanisms governing stomatal conductance were provided by plant physiologists in the 1980s and early 1990s (Farquhar *et al.*, 1980; Ball 1988; Collatz *et al.*, 1991) and are being used in SVATs (Foley *et al.*, 1996; Sellers *et al.*, 1996) in contemporary AGCMs.). Wong *et al.* (1979) concluded that stomatal conductance is determined by the CO_2 fixation rate of the mesophyll. When they applied inhibitor of photosynthetic electron transport or abscisic acid (ABA), changes in the stomatal conductance were proportional to those in CO_2 fixation rate. A mesophyll signal that governs stomatal aperture is plausible, but mechanistic evidence in support of this hypothesis is still missing. It has been argued that a regulatory system of stomatal functioning must activate a compromise between providing CO_2 for assimilation and restricting water loss (Raschke, 1979).

Two processes that are expected to be affected by higher [CO_2] in atmosphere are assimilation and conductance to water vapor. Previous studies report that when [CO_2] was raised from ambient to 530 μmol mol^{-1} wheat photosynthetic rate increased by about 12% (Sicher and Bunce, 1997). Other authors reported an increase of about 50% when [CO_2] was elevated from ambient to about 600 μmol mol^{-1} under light saturated conditions (Miglietta *et al.*, 1996). Although the absolute increase could be affected by plant nutrition status and perhaps by acclimation, Guehl *et al.* (1994) reported that higher [CO_2] produces a higher biomass accumulation. Although reduced stomatal conductance to water vapor leads to a decrease in transpiration (Kimball and Idso, 1983; Senock, 1996), the extent of this decrease is a balance between the higher CO_2 fixation and the reduced stomatal aperture induced by higher [CO_2].

Water stress reduces stomatal conductance by decreasing soil and plant water potentials and by inhibiting mesophyll carbon fixation (Chaves 1991). Foley *et al.* (1996) represented heuristically the effect of water stress on fixation by calculating a stress factor based on plant available water. I recognize that this representation is justified by uncertainties about the extent to which water stress causes stomatal closure or inhibits fixation capacity. However, I propose an alternative approach that is easier to test with field measurements. My approach involves the calculation of leaf water potential which is then used in the stomatal model to reduce conductance and consequently fixation rate. The leaf water potential is calculated by accounting for the balance between plant water content and plant water uptake vs. transpiration. This calculation takes also into account the amount of water stored in the plant tissue. Plant water uptake is a function of root and soil properties that together constitute a series of resistances to water flow from the soil through the plant.

I present here a formulation of canopy stomatal conductance that could be used in SVAT models, which is based on the biochemical mechanisms described above as represented by Ball (1988). This formulation is extended to include the effects of plant water potential on stomatal conductance as proposed above, and it includes explicit calculations of plant CO_2 fixation, respiration and both above- and below-ground productivity as affected by soil and atmospheric conditions. The purpose of this formulation is to provide estimates of latent and sensible heat, as well as of net carbon assimilation rates, from which ecosystem productivity may be calculated. These estimates are compared with diurnal energy fluxes, and with seasonal water use and phytomass of a wheat crop exposed to ambient vs. elevated CO_2 (355 vs. 550 μmol mol^{-1}), and to optimum vs. sub-optimum irrigation as part of a Free Air CO_2 Enrichment (FACE) experiment. Assessing the accuracy of this simulation is crucial in determining our level of confidence in estimates of the vegetation - atmosphere mass and energy exchange provided by land surface models to Global Circulation Models used in climate change or water balance studies.

2.2 Methods

2.2.1 Model development

The approach used in the model development was aimed at easier testing with field data such as energy balance, leaf level photosynthesis, conductance and water potential. Calculation of canopy water potential is used in the stomatal formulation to eventually reduce conductance and CO_2 fixation rate. Leaf water potential is used to represent canopy water status as affected by transpiration and available soil water. The leaf water potential is calculated by accounting for the changes in plant water content that result from the balance between plant water uptake and transpiration. Water capacitance of the plant tissue is also used in the calculation of the changes in plant water content. Plant water uptake is a function of root and soil properties that together constitute a series of resistances to water flow from the soil through the plant. The overall structure of the model is summarized in the form of a relational diagram (Fig. 2.1). The plant component, including the stomatal conductance, photosynthesis and plant growth have been integrated with the formulation of the energy balance described in detail by Verseghy *et al.* (1993). Computation of the plant and soil water balance is obtained by coupling the exchange of mass and energy between the canopy and the atmosphere to the three soil layers (Verseghy, 1991). Further details regarding the formulation of the energy balance equation including the approach used to account for partial canopy cover can be found in Verseghy *et al.*, (1993). The work reported here has the implicit advantage of using calculated values of soil water content and energy balance that otherwise would have to be provided as direct input to the plant model as done in previous studies (Williams *et al.*, 1993).

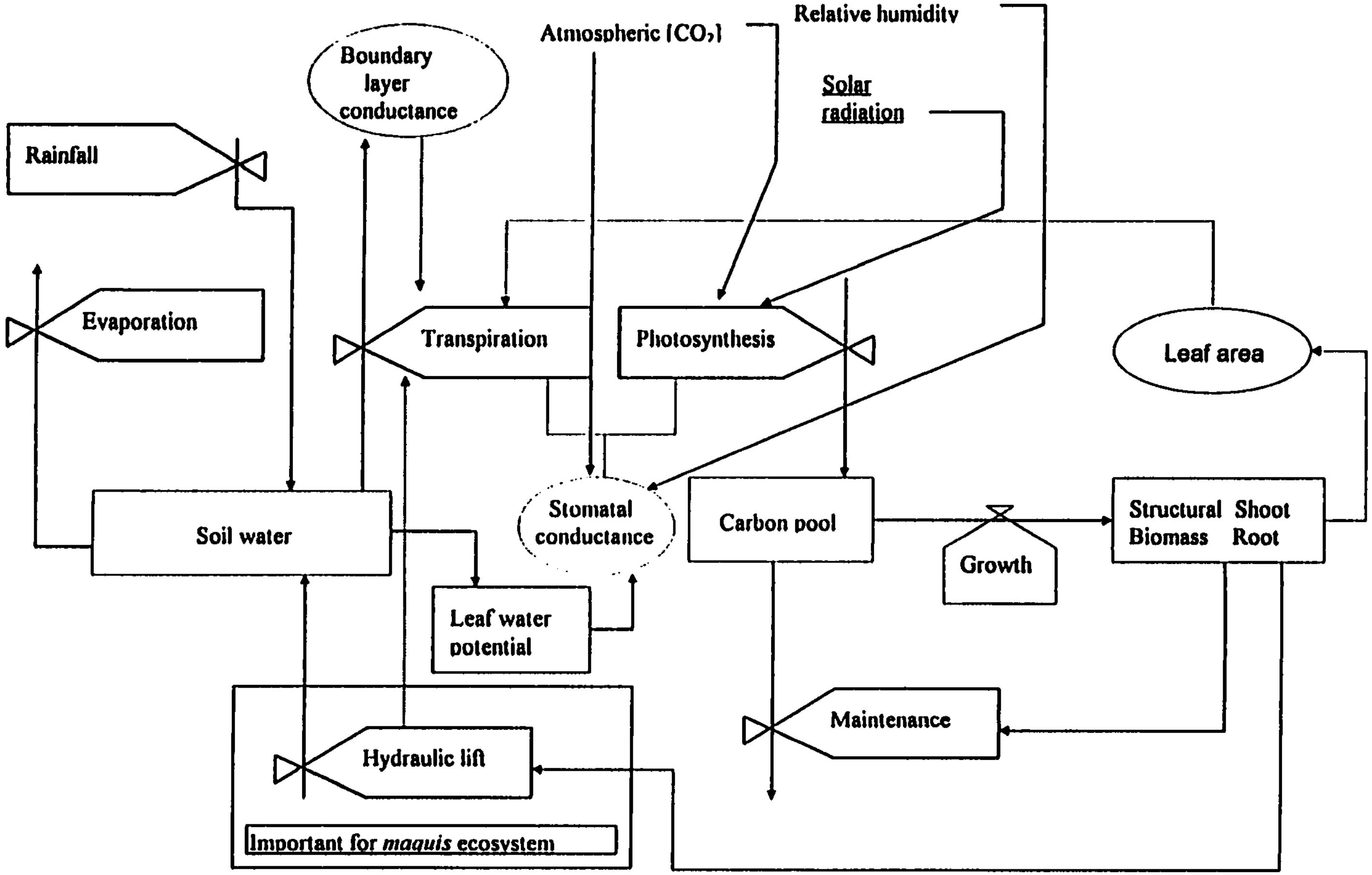

Fig. 1. Relational diagram of the essential components of gas exchange between the canopy and the atmosphere where water shortage is a controlling factor. Rectangles represent state variables, valve symbols rates, circles auxiliary variables and underlined variables external variables. Solid lines represent flows of material, broken lines flow of information.

2.2.2 Plant water relations

The exchange of water vapor between the canopy and the atmosphere makes use of a modified version of stomatal formulation proposed by Ball (1988). This model is used to calculate the value of conductance (g_s in mol m^{-2} s^{-1}) for two classes of leaves, sunlit and shaded respectively.

$$g_s = \left(m \frac{A_n}{C_a} + b \right) \frac{1}{\left(1 + \left(\frac{\Psi_l}{\Psi_c} \right)^n \right)} \qquad [2.1]$$

Conductance is driven by CO$_2$ uptake (A_n in µmol m^{-2} s^{-1}), and reduced by atmospheric [CO$_2$] (C_a in µmol mol^{-1}). The terms m and b in Eq. [2.1] are slope and the intercept parameters obtained independently from linear regression analysis of leaf level measurements by Ball (1988) and Collatz *et al.*, (1991). Plant water status is expressed as the ratio between Ψ_l, leaf water potential (MPa) and Ψ_c the critical water potential at which stomatal conductance becomes half of the maximum value observed (Campbell, 1985). The n value is a slope factor that expresses the increase in resistance as a function of the leaf water potential. Relations of this type have been reported by several authors (e.g., Cline *et al.*, 1976; Glatzel, 1983). This value for n can be as low as 3 or as high as 20 depending upon species (Campbell, 1985). For reason of convenience the conductance is converted into cm s^{-1}, a conductance of 1 cm s^{-1} is approximately 0.4 mol m^{-2} s^{-1} at 25 °C and an atmospheric pressure P=101.3 kPa. Conductance to water vapor expressed in cm s^{-1} is then converted into resistance unit of m s^{-1}.

The value of A_n in Eq. [2.1] is modelled as the minimum of dark (Jc) and light (Je) reaction rates in CO$_2$ fixation (in µmol m^{-2} s^{-1}):

$$A_n \approx \min(Jc, Je) \qquad [2.2]$$

The dark reaction rate is calculated for conditions of saturating irradiance and competitive inhibition by oxygen according to the following formulation (Farquhar *et al.*, 1980) :

$$Jc = \frac{V_{cmax}\left([C_i] - \Gamma^*\right)}{[C_i] + k_c\left(1 + \frac{[O_i]}{k_o}\right)} \qquad [2.3]$$

The maximum dark reaction rate (V_{cmax} in µmol m^{-2} s^{-1}) is assumed to be at ambient temperature and saturating CO_2 in the absence of oxygen. The variables $[C_i]$ and $[O_i]$ represent the liquid concentrations (in µM) of CO_2 and O_2 in the stroma, Γ^* is the compensation point for gross photosynthesis (in µM) at current level of CO_2 and O_2, k_c and k_o are the Michaelis-Menten constants (in µM) for CO_2 and O_2 (Douglas *et al.*, 1984). The value of V_{cmax} is derived from a standard value obtained at 30° C and adjusted for temperature according to Sharpe and DeMichelle (1977) using parameters from Farquhar *et al.*, (1980). Intercellular CO_2 ($[C_i]$in µM) and O_2 ($[O_i]$in µM) concentrations are obtained from the intercellular concentration of CO_2 and O_2 (in µmol mol^{-1}) using a temperature dependent solubility function (Wilhelm *et al.*, 1977) assuming that mesophyll resistance to CO_2 is negligible. Intercellular CO_2 concentrations for C_3 and C_4 plants is set to be a fraction of the atmospheric concentration (0.7 and 0.5 respectively). The compensation point for gross photosynthesis Γ^* in Eq. [2.3] (µM) at current level of CO_2 and O_2 is calculated as:

$$\Gamma^* = \frac{0.5 V_{omax} k_c O_i}{V_{cmax} k_o} \qquad [2.4]$$

where V_{omax} represents the maximum rate of oxygenation under conditions of saturating O_2 and in absence of CO_2 (in µM) and it is assumed to be 0.21 of V_{cmax} (Farquhar *et al.*, 1980). As in the case for maximum capacity of Rubisco, the maximum oxygenation rate

V_{omax} at ambient temperature is derived from a standard value obtained at 30° C and adjusted for temperature according to Sharpe and DeMichelle (1977) using parameters from Farquhar *et al.* (1980).

The light reaction rate of photosynthesis is given by:

$$Je = JQ \qquad [2.5]$$

where Q, is the ratio of CO_2 fixation to electron transport (mol mol^{-1}) which is estimated as:

$$Q = \frac{C_i - \Gamma^*}{e^- C_i + 10.5\Gamma^*} \qquad [2.6]$$

(Farquhar and von Caemmerer, 1982) The term e^- is the electron requirements for CO_2 fixation. This value is set to be equal to 4.5 and to 7.5 for C_3 and C_4 plants respectively. The potential electron transport rate J (µmol m^{-2} s^{-1}) in Eq. [2.5] is obtained as:

$$J = \frac{\alpha I + J_{max} - \left[(\alpha I + J_{max})^2 - 4\theta\alpha I J_{max}\right]^{0.5}}{2\theta} \qquad [2.7]$$

(Evans and Farqhuar, 1991) where $\alpha =$ quantum efficiency (0.5 mol electrons mol $quanta^{-1}$), I is the absorbed photosynthetically active radiation (µmol quanta m^{-2} s^{-1}), and J_{max} is the maximum rate of electron transport (µmol electrons m^{-2} s^{-1}) adjusted for temperature according to Farquhar *et al.* (1980). The curvature factor θ ranges from 0 to 1 and represents the transition of J from the region of maximum quantum yield to the light saturated rate. The region where quantum yield is maximized is found at low irradiance level, where the relation between J and I is most linear.

The value of I is calculated as a spatially-averaged value for each of two leaf classes, sunlit and shaded. The sunlit class intercepts the direct solar beam plus diffuse sky radiation and the shaded class receives only diffuse sky radiation. This approach represents the non-linear response of leaf level physiological processes to different intensities of solar radiation within the canopy (Forseth and Norman, 1993; Norman, 1993). Because the actual fraction of sunlit and shaded leaves changes with time of the day, the extinction coefficient representing random leaf inclination and orientation is corrected for the sine of the solar elevation angle.

The assimilation rate A_n of each leaf class (Eqs. [2.2] - [2.7]) is used to calculate its stomatal conductance unconstrained by water availability (Eq. [2.1] with $\Psi_l = 0$ MPa). This conductance is multiplied by the leaf area of each class, and the products of both classes are added to estimate unconstrained canopy stomatal conductance. Although temperature, humidity and wind speed might differ for different positions inside complex canopies this scaling technique does not specifically account for these variations.

Leaf water potential is calculated by coupling canopy transpiration T to soil water uptake U_z, calculated as the sum of that from each soil layer l, and where z is the number of soil layers:

$$T = \sum_{z=1}^{l} U_z \sum_{z=1}^{l} \frac{(\Psi_l - \Psi_{sz})}{(rr_z + rs_z)} \qquad [2.8]$$

Root resistance to water uptake rr_z is related to the amount of roots present in each layer (Campbell, 1985):

$$rr_z = \frac{\rho r}{L_z \Delta z} \qquad [2.9]$$

where ρr is root radial resistivity (s m^{-1}), L_z is the root length density (m m^{-3}) and Δz is the depth increment (0.10, 0.25, and 3.75 m) of the three soil layers. Radial water flow from the soil to the roots is represented as that through a hollow cylinder (Gardner, 1960;

Cowan 1965). Passioura and Cowan (1968) solved numerically the non linear equation of radial flow to the root and found that a more exact result is obtained under the assumption of "steady rate" rather than "steady state" flow as previously suggested by Gardner (1960). The following equation is used then to approximate radial flow resistance under "steady rate" conditions:

$$rs_z = \ln\left(\frac{b_z}{2.1a}\right) / \left(2\pi K_z L_z \Delta z\right) \qquad [2.10]$$

where a is the radius of the root (m), K_z is the soil hydraulic conductivity (m s^{-1}) and b_z is the path length for water uptake (m) obtained as:

$$b_z = (\pi L_z)^{-0.5} \qquad [2.11]$$

Conductance to water vapor decreases as Ψ_l drops, Eq. [2.1], while water uptake varies positively with a decreasing Ψ_l due to the effect of Ψ_l upon the gradient between Ψ_l and Ψ_{sz} in Eq. [2.8]. The resulting water uptake is inversely related to the sum of the root rr_z and soil rs_z resistance . Outward (transpiration) and inward (uptake) fluxes are mediated in part by the leaf water potential, there is therefore an equilibrium value for Ψ_l under any combination of soil and atmospheric conditions at which transpiration equals uptake. This value is calculated through an iterating procedure, thereby a value for Ψ_l is found at which transpiration from the energy balance is equilibrated with total water uptake from Eqs. [2.8] - [2.11]. After the initial leaf water potential is computed, the difference between the transpiration and the water uptake by the roots and the water stored in the canopy is calculated. When the difference is < 0 the calculated water uptake by the roots is too large, therefore the gradient between plant and soil is too steep, consequently the leaf water potential is lowered. If on the other hand the difference is > 0 the water uptake by roots is too small, therefore the gradient between plant and soil is too low, consequently the leaf water potential is increased. The process continues until the difference is close to 0, then the iteration stops and the leaf water potential calculated is used to represent the plant water status (Grant *et al*, 1999). When the stomatal conductance is reduced because of leaf water potential, the CO_2 fixation is also proportionally reduced while preserving the internal [CO_2]. Therefore the reduction in CO_2 fixation via reduction in stomatal conductance preserves the formulation proposed by Ball (1987), in which the assimilation rate is the result of conductance times the difference between the atmospheric and internal [CO_2].

2.2.3 Plant carbon balance and vegetation dynamics

Products of CO_2 fixation (A_n from Eqs. [2.2] - [2.7]) are accumulated in a storage pool from which C is partitioned among leaves, stems and roots as functions of accumulated degree days (van Keulen and Seligman, 1987), and from which C is respired according to maintenance and growth requirements for energy (Amthor, 1984). The maintenance requirement is calculated by multiplying the phytomass of leaves, stems and roots by organ maintenance coefficients (in $g\ C\ g\ C^{-1}\ h^{-1}$) and by a temperature function with a Q_{10} of 2 (McCree, 1988). The growth requirement is calculated from organ growth yields (McCree, 1988) and is removed from storage C after the maintenance requirement has been removed. Growth in leaf and root phytomass is converted into growth in leaf area and root length according to a function for specific leaf area and specific root length. Leaf areas and root lengths are used to calculate irradiance interception and water uptake as described above. Finally, plant senescence is controlled by the accumulation of heat units.

2.2.4 Field experiment[2]

Spring wheat (*Triticum aestivum* L. cv. Yecora rojo) was planted at a density of 180 plants m^{-2} on 8 December 1993 in a 4 ha. field of Trix clay loam (calcareous) soil (Table 2.1) at the Maricopa Research Center 30 km from Phoenix, AZ. Shortly after planting two 25 m. diameter rings were placed in each of four replicates near the center of the field. Each replicate was divided in two strips one receiving high irrigation and one receiving low irrigation. The rings were constructed to emit CO_2 through holes in a series of vertical pipes 2.5 meters in height connected to the ring every 2.0 meters. Inside the ring there were two plots, one receiving high irrigation and one receiving low irrigation. An average [CO_2] of 550 µmol mol^{-1} was maintained over one of the rings in each replicate by blowing CO_2-enriched air from upwind emitters (Lewin *et al.*, 1994). A [CO_2] close to ambient (355 µmol mol^{-1}) was maintained over the other rings. Irrigation treatments included an optimum treatment in which evapotranspirational demand was fully replaced, and a sub-optimum treatment in which one-half of demand was replaced, were applied on one half of every ring using a subsurface drip system (Table 2.2). The experimental area is located within the boundaries of an irrigation district so that the CO_2-enriched (FACE) and the control treatments were surrounded by more than 1 km of irrigated fields in all directions.

During the entire experiment hourly averaged values were recorded for solar radiation, air temperature, wind speed, humidity, and precipitation. Phytomass was measured weekly from approximately 24 plants collected in each treatment replicate (Pinter *et al.*, 1996). Soil moisture measurements were made twice a week with neutron probes at 0.20 m intervals to a depth of 2.1 meters. Using a portable gas analyzer (Model 6200, Li-cor, Inc., Lincoln, NE, USA), leaf stomatal conductance and photosynthesis measurements were taken from three or four recently expanded sunlit leaves in each replicate.

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[2] Data collected during this field campaign were made available as a part of a collaborative effort between Dr. Robert Grant and the U.S. Water Conservation Lab. The author was also involved in part of the activities that took place at the U.S. Water Conservation Lab. in Phoenix, AZ in the spring of 1997.

The sampling took place between sunrise to sunset at stem extension (March 22nd , DOY 81), anthesis (April 5th , DOY 95) and grain filling (May 3rd, DOY 123).

During the experiment, net radiation was measured with net radiometers (Model Q6, Radiation and Energy Balance Systems, Seattle, WA, USA) mounted 0.4 m above the canopy. Soil heat flux estimates were obtained using four heat flux plates per plot (Model HFT-3, Radiation and Energy Balance Systems, Seattle, WA, USA) placed 0.10 m deep, and thermocouples 0.05 m above the plates to measure the heat stored in that portion of soil. The air temperature was measured with a pair of customized aspirated psychrometers placed at 2 m in each plot. Canopy temperature *Tc* was measured with a set of two stationary infrared thermometers (Model 4000a, 15° field of view, Everest Interscience, Tustin, CA) in each plot (Kimball *et al.* 1995). Prior to installation in the field the infrared thermometers were calibrated over a wide range of temperatures using a black body source (Model 250, Advanced Kinetics, Huntington Beach, CA, USA). Aerodynamic resistance was calculated from wind speed at 2 m measured with a cup anemometer (Model 12102D, R.M. Young Co., Traverse City, MI, USA), and from zero plane displacement, roughness length and a non isothermal stability correction (Mahrt and Ek, 1984). These measurements were used to calculate sensible heat flux, and latent heat flux was estimated as the residual term in the surface energy balance. Limitations in instrumentation allowed these measurements to be taken only on the optimally irrigated plots.

2.2.5 Simulation experiment

In the model the soil hydraulic properties are derived from tabulated values grouped in 11 soil textural classes (Clap and Hornberger, 1978), the model was then initialized with soil texture data recorded at the site (Table 2.1). The model was also initialized with the biological properties of the plant functional type (C_3) (Table 2.3) and with the atmospheric [CO_2] (μmol mol^{-1}). Although a subsurface irrigation system was used in the field, the model does not allow subsurface water additions, so that irrigation was delivered during the simulation in the form of rainfall events (Table 2.2). Transport of sensible heat and water vapor through the boundary was proportional to aerodynamic conductance calculated according to van Bavel and Hillel (1976). To prevent erroneous values in the calculation of the aerodynamic resistance due to extremely low wind speed found at the experiment location, the Richardson number was constrained between -0.10 and 0.05. In order to minimize modelled losses due to evaporation, subsurface irrigation was added as rain occurring at night. Model outputs for energy balance, canopy temperature, leaf conductance and phytomass growth were compared with those measured in the field experiment under ambient vs. elevated CO_2.

2.3 Results

Modelled vs. measured results were compared over two representative weeks, (10 to 16 March, DOY 69 to 75, and 24 to 30 April, DOY 114 to 120) of the FACE experiment (Figs. 2.2 and 2.3). Average values for solar radiation, air temperature and vapor density during the first week were 243 W m^{-2}, 15.7 °C and 6.6 g m^{-3} ; and those during the second week were 297 W m^{-2}, 15.73 °C and 5.7 g m^{-3}.

During the first week of comparison in March, latent heat fluxes were underestimated by 50 to 100 W m^{-2} during 10 and 13 March (DOY 69 and 72) but were otherwise within 50 W m^{-2} (2 x SE of the measured fluxes) under both 355 and 550 μmol mol^{-1} CO_2 with optimum irrigation (Fig. 2.2a and b). During the second week of comparison in April, latent heat fluxes were overestimated by 50 to 100 W m^{-2} during April 24th and 26th (DOY 114 and 116) but were otherwise within 50 W m^{-2} (2 x SE of the measured fluxes) under both 355 and 550 μmol mol^{-1} CO_2 with optimum irrigation (Fig. 2.3a and b).

With optimum irrigation in March, both simulated and measured latent heat fluxes were reduced under 550 vs. 355 μmol mol^{-1} CO_2 by amounts that varied diurnally from zero W m^{-2} during the nights to about 50 W m^{-2} during the afternoons (Fig. 2.4a). With suboptimum irrigation in March, simulated latent heat fluxes were reduced less under 550 vs. 355 μmol mol^{-1} CO_2 than they were under optimum irrigation (Fig. 2.4b). With optimum irrigation in April, both simulated and measured latent heat fluxes were reduced under 550 vs. 355 μmol mol^{-1} CO_2 by amounts that varied diurnally from zero W m^{-2}

during the nights to between 50 and 100 W m^{-2} during the afternoons early in the week. The changes were less than 50 W m^{-2}, however, during the afternoons later in the week as the soil dried following irrigation on DOY 115 (Fig. 2.5a). With suboptimum irrigation in April, simulated latent heat fluxes were not greatly affected by CO_2 (Fig. 2.5b).

Diurnal changes in simulated plant water relations, including leaf water potential, temperature, sunlit leaf conductance and photosynthesis, were compared with measured values during three selected days: March 22nd (DOY 81), April 5th (DOY 95) and May 3rd (DOY 123). On March 22nd the optimum irrigation plots had last been irrigated one day earlier, and the suboptimum irrigation plots six days earlier (Table 2.2), so that simulated canopy water potential remained comparatively high (Fig. 2.6a). Under elevated [CO_2], midday values of simulated and measured leaf water potential increased by 0.1 and 0.24 ± 0.13 MPa with optimum irrigation, and by 0.05 and 0.14 ± 0.25 MPa under suboptimum irrigation. Because both treatments had been irrigated 6 days before, simulated and measured conductance were only slightly lower under suboptimum vs. optimum irrigation (Fig. 2.6b). Comparison of simulated vs. measured values was complicated by large variability in the latter. Midday values of simulated and measured stomatal conductances were reduced under 550 μmol mol^{-1} CO_2 relatively more with optimum vs. suboptimum irrigation (to 0.72 vs. 0.86 of those under 355 μmol mol^{-1} CO_2), as were measured conductances (to 0.57 ± 0.21 vs. 0.68 ± 0.14 of those under 355 μmol mol^{-1} CO_2). Irrigation applied 6 days before, caused both simulated and measured canopy temperatures to be only 1.5 - 2.0 °C higher under suboptimum vs. optimum irrigation (Fig. 2.6c). Reduced conductance under 550 μmol mol^{-1} CO_2 caused simulated midafternoon canopy temperatures to increase by 0.9 °C and 0.5 °C under optimum and suboptimum irrigation respectively. These increases were slightly less than those of 1.5 °C and 1.0 °C measured with the mobile IRT's. The conductance simulated on March 22nd (Fig. 2.6b) allowed high carbon fixation rates even under suboptimum irrigation (Fig. 2.6d). Simulated CO_2 fixation was generally lower than measured one, due to the spatial averaging of irradiance intensity on the sunlit leaf surface in the model. Simulated carbon fixation was increased under 550 μmol mol^{-1} CO_2 relatively more with suboptimum vs.

optimum irrigation (to 1.33 vs. 1.12 of those under 355 μmol mol^{-1} CO$_2$), as were measured rates (to1.26 ± 0.18 vs. 1.20 ± 0.13 of those under 355 μmol mol^{-1} CO$_2$).

On April 5th, the high irrigation plots had last been irrigated one day earlier, and the low irrigation plots eight days earlier (Table 2.2). Simulated and measured values of leaf water potential Ψ_l were lower than those on March 22nd, especially under suboptimum irrigation (Fig. 2.7a vs. 2.6a). Increases in leaf water potential of 0.2 MPa were simulated and measured under 550 vs. 355 μmol mol^{-1} CO$_2$ and optimum irrigation, although the water potential was little affected by CO$_2$ under suboptimum irrigation. Lower Ψ_l simulated on April 5th vs. March 22nd caused lower conductance, especially under suboptimum irrigation (Fig. 2.7b). As on March 22nd, simulated conductance was reduced under 550 μmol mol^{-1} CO$_2$ relatively more with optimum vs. suboptimum irrigation (to 0.74 vs. 1.00 of that under 355 μmol mol^{-1} CO$_2$), as was measured conductance (to 0.65 ± 0.10 vs. 0.73 ± 0.12 of that under 355 μmol mol^{-1} CO$_2$). Both simulated and measured canopy temperatures were 4 to 5 °C higher under suboptimum vs. optimum irrigation (Fig. 2.7c), reflecting large irrigation effects on Ψ_l (Fig. 2.7a) and conductance (Fig. 2.7b). Reduced conductance caused simulated midafternoon canopy temperature to increase under 550 vs. 355 μmol mol^{-1} CO$_2$ by 1.0 °C and 0.3 °C with optimum and suboptimum irrigation respectively. These increases were slightly less than those of about 1.5 °C and 0.5 °C measured with the mobile IRT's. Lower conductance simulated and measured on April 5th vs. March 22nd (Fig. 2.7b vs. Fig. 2.6b) caused lower carbon fixation, especially under suboptimum irrigation (Fig. 2.7d). As on March 22nd, simulated assimilation was increased under 550 μmol mol^{-1} CO$_2$ relatively more with suboptimum vs. optimum irrigation (to 1.55 vs. 1.14 of that under 355 μmol mol^{-1} CO$_2$), as was measured assimilation (to 1.21 ± 0.12 vs. 1.15 ± 0.13 of that under 355 μmol mol^{-1} CO$_2$).

On May 3rd, the optimum irrigation plots had last been irrigated eight days earlier, and the suboptimum irrigation plots fourteen days earlier (excluding the small irrigation on April 30th) (Table 2.2). Simulated and measured values of Ψ_l were lower than those on earlier dates under suboptimum irrigation, reaching minimum values of less than -2.0 MPa

(Fig. 2.8a). Increases in Ψ_l of 0.2 MPa were simulated under 550 vs. 355 µmol mol^{-1} CO_2 and optimum irrigation, although smaller increases were measured. Simulated Ψ_l was little affected by CO_2 under suboptimum irrigation, although measured Ψ_l was increased by about 0.3 MPa. Lower Ψ_l simulated and measured under suboptimum irrigation on May 3rd vs. April 5th caused lower conductance g_s (Fig. 2.8b vs. 2.7b). As on earlier dates, simulated g_s was reduced under 550 µmol mol^{-1} CO_2 relatively more with optimum vs. suboptimum irrigation (to 0.76 vs. 1.00 of that under 355 µmol mol^{-1} CO_2), as was measured g_s (to 0.68 ± 0.16 vs. 0.75 ± 0.13 of that under 355 µmol mol^{-1} CO_2). Simulated and measured canopy temperatures were 6 and 10°C respectively higher under suboptimum vs. optimum irrigation (Fig. 2.8c), reflecting large irrigation effects on Ψ_l (Fig. 2.8a) and g_s (Fig. 2.8b). Reduced conductance caused simulated midafternoon canopy temperature to increase under 550 vs. 355 µmol mol^{-1} CO_2 by 1.0 °C and 0.5 °C with optimum and suboptimum irrigation respectively. These increases were slightly less than those of about 1 °C and 2 °C measured with the mobile IRT's. Low g_s simulated and measured on May 3rd (Fig. 2.8b) caused low assimilation under suboptimum irrigation (Fig. 2.8d). Simulated and measured photosynthesis were increased under 550 vs. 355 µmol mol^{-1} CO_2 by 1.09 and 1.10± 0.18 under optimum irrigation and both simulated and measured assimilation remained close to zero under suboptimum irrigation.

The time-integrated effects of CO_2 and irrigation on mass and energy exchange can be seen in the growth and water use of above-ground phytomass. The seasonal time course of LAI was simulated within the SE of the measured values after mid-February except when leaf senescence under suboptimum irrigation was underestimated during April (Fig. 2.9a). LAI in the model was increased under 550 µmol mol^{-1} CO_2 to 1.10 and 1.16 of its value under 355 µmol mol^{-1} CO_2 with optimum and suboptimum irrigation respectively. LAI in the FACE experiment was not increased under 550 vs. 355 µmol mol^{-1} CO_2 and optimum irrigation, but was increased by 1.23 with suboptimum irrigation before anthesis. The seasonal time course of phytomass growth was simulated within the SE of the measured values except when late-season growth under suboptimum irrigation was underestimated (Fig. 2.9b). Total phytomass at both [CO_2] was overestimated with optimum irrigation and underestimated with suboptimum irrigation (Table 2.4), mostly because senescence during May was not accurately simulated (Fig. 2.9b). Seasonal phytomass simulated and measured under 550 μmol mol^{-1} CO_2 was 1.14 and 1.10 that under 355 μmol mol^{-1} CO_2 with optimum irrigation, and 1.28 and 1.18 that under 355 μmol mol^{-1} CO_2 with suboptimum irrigation. These increases in the model arise directly from those in leaf CO_2 fixation (Figs. 2.6d, 2.7d and 2.8d) scaled to canopy CO_2 fixation as affected by increases in [CO_2].

Seasonal water use was simulated within 1 SE of measured values for all CO_2 x irrigation treatments (Table 2.4). Simulated and measured water use under 550 μmol mol^{-1} CO_2 was about 6 % lower than that under 355 μmol mol^{-1} CO_2 with optimum irrigation, and about 2% lower than that under 355 μmol mol^{-1} CO_2 with suboptimum irrigation. These decreases in the model arise directly from those in canopy latent heat flux (Figs. 2.1 to 2.4) as affected by decreases in stomatal conductance over time.

2.4 Discussion

The soil-plant-atmosphere water transfer scheme proposed above offers several advances in the simulation of land surface interactions:

First, the stomatal resistance model (Eq. [2.1]) avoids assumptions in existing land surface schemes about interactions among environmental conditions (radiation, temperature, CO_2) upon stomatal behavior. These interactions are resolved in the calculation of CO_2 fixation (Eqs. [2.2] to [2.7]) in which processes are already well understood.

Second, the model may be parameterized from independent studies of stomatal response to CO_2 fixation conducted at temporal and spatial scales smaller than those at which the land surface scheme is to predict (e.g. Table 2.3). It should be acknowledged, however, that important plant features such as osmotic adjustment, are not represented in the model. In the case of a wheat canopy the osmotic adjustments that might be associated with water stress have been reported to be about 0.5 MPa (Simmelsgaard, 1976). Although during a water stress event the osmotic adjustment can weaken the relationship between the leaf potential and the stomatal conductance, the value reported by Simmelsgaard (1976) was measured when the stomatal conductance tended to be close to zero. Therefore if the use of this model might be inaccurate under extremely severe water stress it is also unlikely that field farming practices would let a crop with economic value to experience such a level of stress. This in turn supports the use of this model in land and water resource studies, while it does not support its use to investigate the physiological response of plant canopies under extremely water limited conditions. Furthermore the risk for inaccuracy can become quite significant if we attempt to simulate mass and energy fluxes from a plant canopy such as cotton, in which an osmotic adjustment equal to 1.2 MPa was reported, when the stomatal conductance tended to zero (Brown *et al.*, 1976).

The model may be tested with a diverse set of routinely measured data (e.g. leaf conductance, water potential, CO_2 fixation, temperature) at spatial scales smaller than those at which the land surface scheme is to predict (e.g. Figs. 2.6 to 2.8).

Changes in LAI and root length are driven from internal C transfer processes that are sensitive to soil and climate constraints, providing opportunities to simulate more complex atmosphere-ecosystem interactions than is possible with models in which LAI and water uptake are prescribed.

In the proposed transfer scheme, stomatal conductance varies inversely with atmospheric $[CO_2]$ and directly with leaf CO_2 fixation rate. The model thus reproduces the observation of Wong *et al.*, (1979) that stomatal conductance varies with CO_2 fixation rate to maintain a constant CO_2 concentration ratio across the stomata. The response of CO_2 fixation to 550 vs. 355 μmol mol^{-1} CO_2 was consistent with that measured in the FACE experiment at both diurnal (Figs. 2.6d, 2.7d and 2.8d) and seasonal (Fig. 2.9b) time scales. Because the internal $[CO_2]$ is maintained as a constant fraction of the atmospheric $[CO_2]$, carbon fixation increases with $[CO_2]$ (Eq. [2.3]), however this increase in assimilation rate is not sufficient to compensate for the reduction in stomatal conductance caused by higher atmospheric $[CO_2]$ (Eq. 2.1). Therefore the stomatal conductance in the model was reduced under 550 vs. 355 µmol mol^{-1} CO_2 to an extent that was consistent with reductions measured in the FACE experiment (Figs. 2.6b, 2.7b and 2.8b) and elsewhere (e.g. Morison, 1985). Consequent reductions in latent heat flux (Figs. 2.4 and 2.4; Table 2.4) and increases in canopy temperature (Fig. 2.6c, 2.7c and 2.8c) were also measured in the FACE experiment and elsewhere (Idso *et al.*, 1987; Kimball *et al.*, 1992b; Kimball *et al.*, 1995). Reductions in transpiration under 550 vs. 355 µmol mol^{-1} CO_2 caused less negative leaf water potential (Figs. 2.6a, 2.7a and 2.8a) that were also measured in the FACE experiment and elsewhere (Allen *et al.*, 1994; Huber *et al.*, 1984; Sionit *et al.*, 1980).

Suboptimal vs. optimal irrigation caused lower soil water potential and hence lower leaf water potential (Figs. 2.6a, 2.7a and 2.8a), lower stomatal conductance (Figs. 2.6b, 2.7b and 2.8b), lower CO_2 fixation (Figs. 2.6d, 2.7d and 2.8d; Fig. 2.9b; Table 2.4) and higher canopy temperature (Fig. 2.6c, 2.7c and 2.8c). A less negative leaf water potential under 550 vs. 355 µmol mol^{-1} CO_2 caused stomatal resistance to rise less from unconstrained values during convergence to low water potentials, so that stomatal conductance was less affected by CO_2 under suboptimum vs. optimum irrigation (Figs. 2.6b, 2.7b and 2.8b). This reduced effect was apparent in the simulated energy balance (Fig. 2.4b vs. 2.4a and Fig. 2.5b vs. 2.5a) and in both simulated and measured seasonal water use (Table 2.4). The significance of the CO_2 x irrigation interaction upon stomatal conductance was obscured by spatial variability in the measured values. However, both simulated and measured canopy temperatures increased less under 550 vs. 355 µmol mol^{-1} CO_2 with suboptimum than with optimum irrigation (Figs. 2.6c, 2.7c and 2.8c). The simulated CO_2 x irrigation interaction on stomatal conductance provides a mechanistic explanation for the observation of Allen *et al.* (1994) that conductance is little affected by CO_2 in water-stressed plants, and for the observation by Curtis (1996), Huber *et al.* (1984) and Rogers *et al.* (1984) that conductance decreases less with water stress under elevated vs. ambient CO_2.

The smaller effect of CO_2 on stomatal conductance with suboptimum vs. optimum irrigation in the model allowed a larger effect of CO_2 on CO_2 fixation with suboptimum vs. optimum irrigation to be simulated at both the hourly (Figs. 2.6d, 2.7d and 2.8d) and seasonal (Fig. 2.9b; Table 2.4) time scales. This larger effect is consistent with findings from the FACE experiment (Table 2.4; Kimball *et al.*, 1995) and elsewhere (Gifford, 1979; Rogers *et al.*, 1986) that plant growth increases more with CO_2 under water-limited conditions. These findings suggest that the effect of increased CO_2 on canopy mass and energy exchange depends upon soil water availability. Such dependence is an important terrestrial feedback to the atmosphere under gradually increasing atmospheric concentrations of CO_2.

Further work is needed to refine some of the model algorithms. The underestimation of phytomass in the suboptimum irrigation treatment may have been caused by the assumption that the constraint imposed by stomatal resistance on CO_2 fixation is commensurate with what imposed on transpiration whereas it can be slightly less. The underestimation may also have been caused by the requirement in the model that all irrigations be applied at the canopy surface whereas the FACE irrigations were applied below the soil surface, thereby reducing unproductive evaporation. The overestimation of LAI in the suboptimum irrigation treatment will require reconsideration of the algorithm for leaf senescence. There is also a need for further development of the algorithm for root extension because it controls the rate at which soil water reserves are accessed by the plant canopy.

Table 2.1. **Selected soil properties of the Trix clay loam at the FACE site (Kimball *et al.*, 1992).**

Depth (m)	0.01	0.05	0.10	0.20	0.30	0.50	0.70	0.90	1.10	1.30	1.70	2.10
BD (Mg m^{-3})	1.31	1.31	1.31	1.27	1.27	1.27	1.30	1.47	1.57	1.57	1.57	1.57
ΘFC (m^3 m^{-3})	0.30	0.30	0.30	0.30	0.30	0.29	0.29	0.23	0.23	0.23	0.23	0.23
ΘWP(m^3 m^{-3})	0.21	0.21	0.21	0.21	0.21	0.20	0.20	0.16	0.16	0.16	0.16	0.16
Ksat (mm h^{-1})	23.0	23.0	23.0	23.0	23.0	7.6	7.6	16.9	16.9	16.9	16.9	16.9
Sand(kg kg^{-1})	0.35	0.35	0.35	0.35	0.35	0.35	0.35	0.45	0.50	0.55	0.60	0.60
Silt (kg kg^{-1})	0.31	0.31	0.31	0.31	0.31	0.31	0.31	0.25	0.20	0.20	0.17	0.17

Table 2.2. Schedules of each irrigation treatment at the FACE site and used in the simulation.

Date	Irrigation (mm)	
	Optimum	Sub-optimum
21 January	30	
03 February	30	30
23 February	35	
04 March	30	
16 March	36	30
21 March	25	
28 March	30	30
04 April	30	
08 April	50	50
14 April	50	
19 April	50	50
25 April	50	
30 April	7	7
04 May	60	60

Table 2.3. Plant biological parameters used in the simulation. The number in squared brackets indicates the equation in the text in which the parameters are used.

Parameter	Value for C_3 (Broadleaf)
	Photosynthesis Formulation
V_{cmax} [2.3,2.4]	90 μmol m^{-2} s^{-1} at 30 °C
k_c [2.3,2.4]	12.5 μM
k_o [2.4,2.5]	500 μM
e^- [2.6]	4.5 mol e^- mol CO_2^{-1}
α [2.7]	0.5 mol e^- mol $quanta^{-1}$
J_{max} [2.7]	180 μmol electrons m^{-2} s^{-1}
θ [2.7]	0.8
	Stomatal Conductance Formulation
m [2.1]	6.0
b [2.1]	0.020 mol m^{-2} s^{-1}
Ψ_c [2.1]	0.2 MPa
n [2.1]	10

Table 2.4. Evapotranspiration and phytomass measured (M) and simulated (S) under 355 vs. 550 μmol mol^{-1} CO$_2$ and suboptimum vs. optimum irrigation. Measured values of evapotranspiration are calculated as irrigation + rainfall - change in soil water content (0 - 2.1 m) between January 10th and May 28th 1994. Simulated values are total surface water fluxes (soil + canopy) between the same dates. Measured values of phytomass are averages of those from 11, 18 and 25 May, and simulated values are maxima during the growing season. Water use data from Hunsaker *et al.*, (1996).

[CO$_2$]	355		550		550 vs.355	
Irrigation	M	S	M	S	M	S
	Phytomass (g m^{-2})					
Suboptimum	1361 ± 97	1176	1604 ± 151	1505	+18%	+28%
Optimum	1856 ± 145	2279	2044 ± 167	2589	+10%	+14%
	Evapotranspiration (mm)					
Suboptimum	476 ± 27	478	465 ± 15	470	-2.3%	-1.7%
Optimum	751 ± 10	757	710 ± 17	711	-6.6%	-6.6%

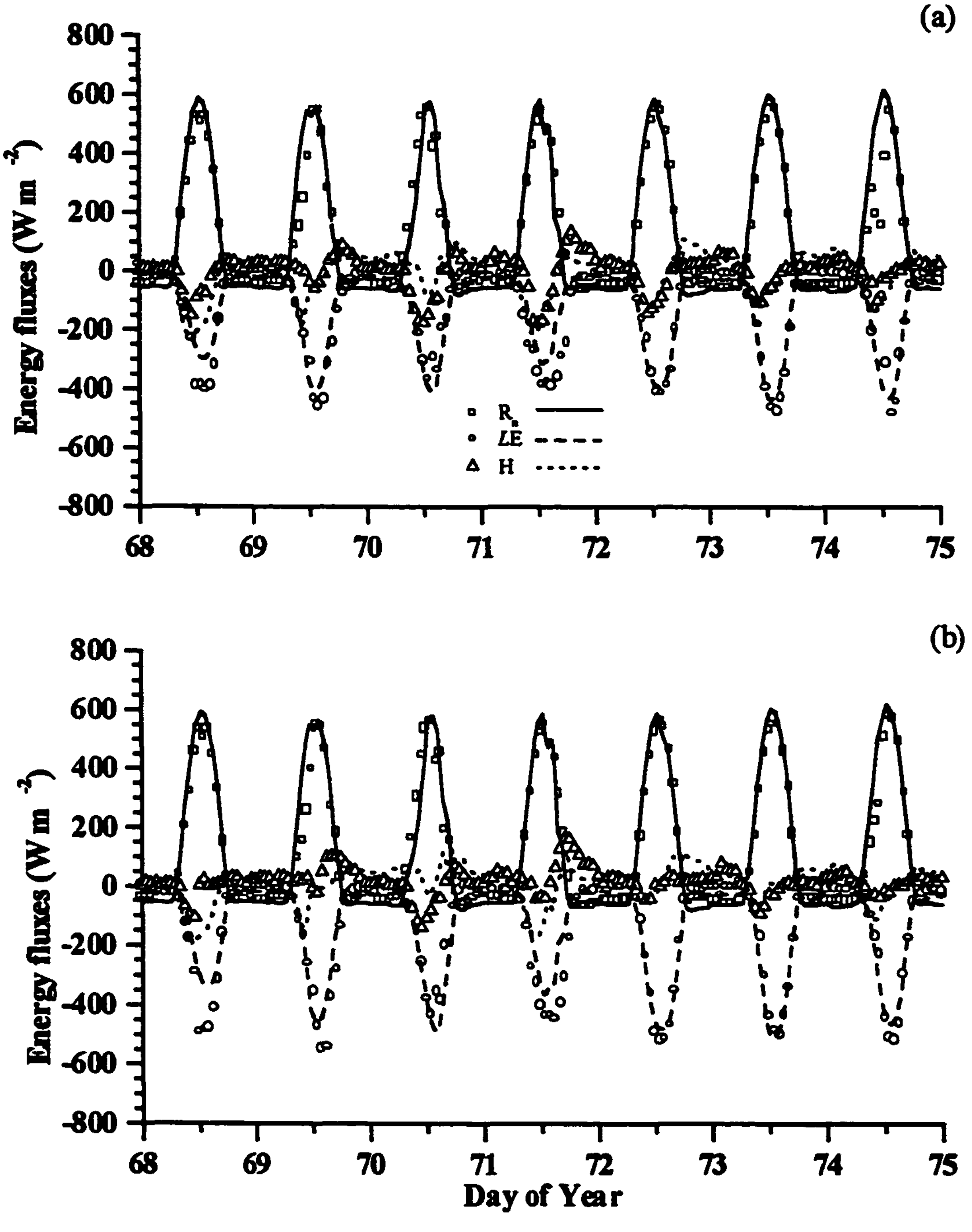

Fig. 2.2 Net radiation (Rn), sensible heat (H) and latent heat (LE) fluxes simulated (lines) and measured (symbols) under (a) 550 and (b) 355 µmol mol^{-1} CO$_2$ and optimum water supply from 10 to 16 March 1994 (DOY 69 to 75).

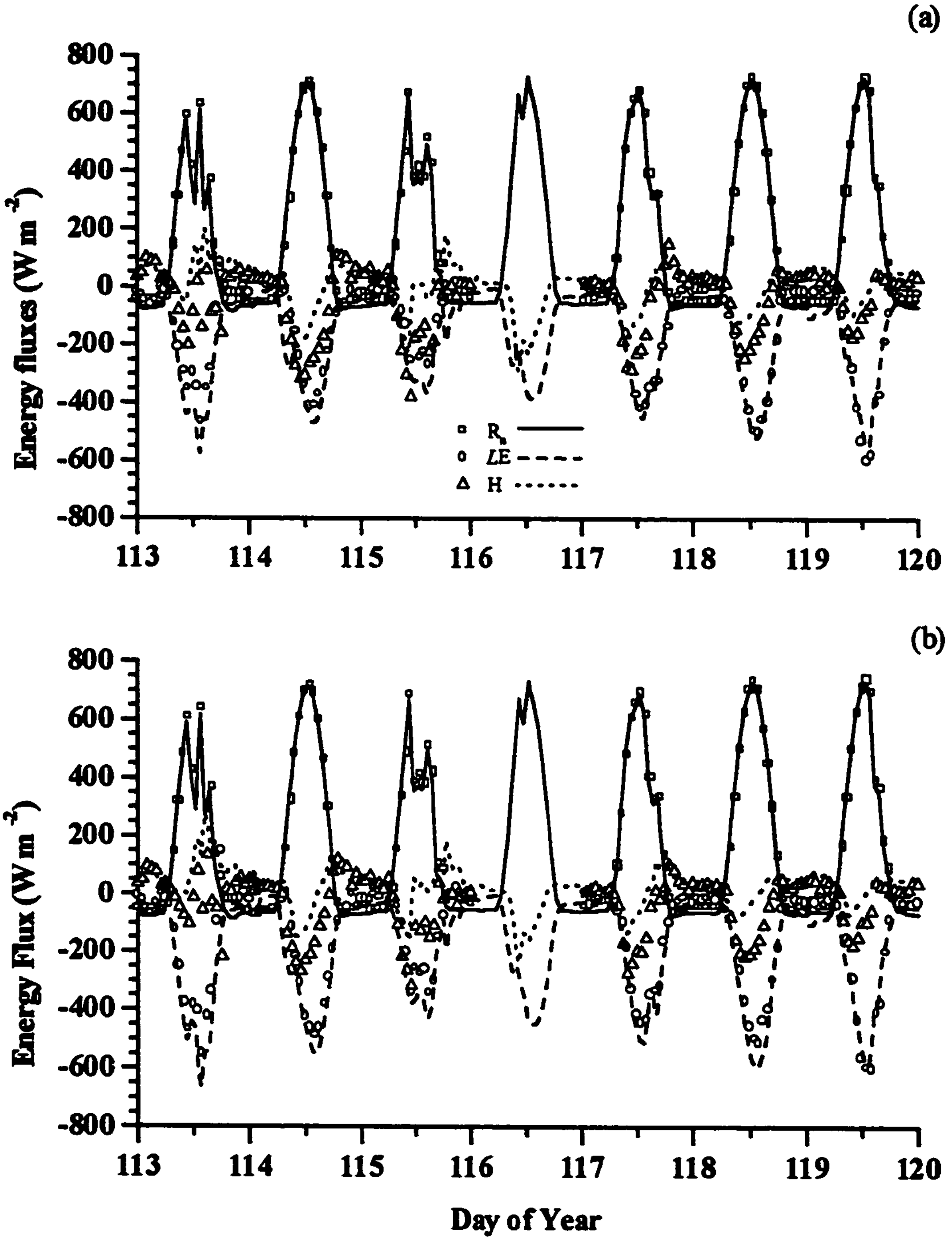

Fig. 2.3 Net radiation (Rn), sensible heat (H) and latent heat (LE) fluxes simulated (lines) and measured (symbols) under (a) 550 and (b) 355 μmol mol^{-1} CO$_2$ and optimum water supply from 24 to 30 April 1994 (DOY 114 to 120).

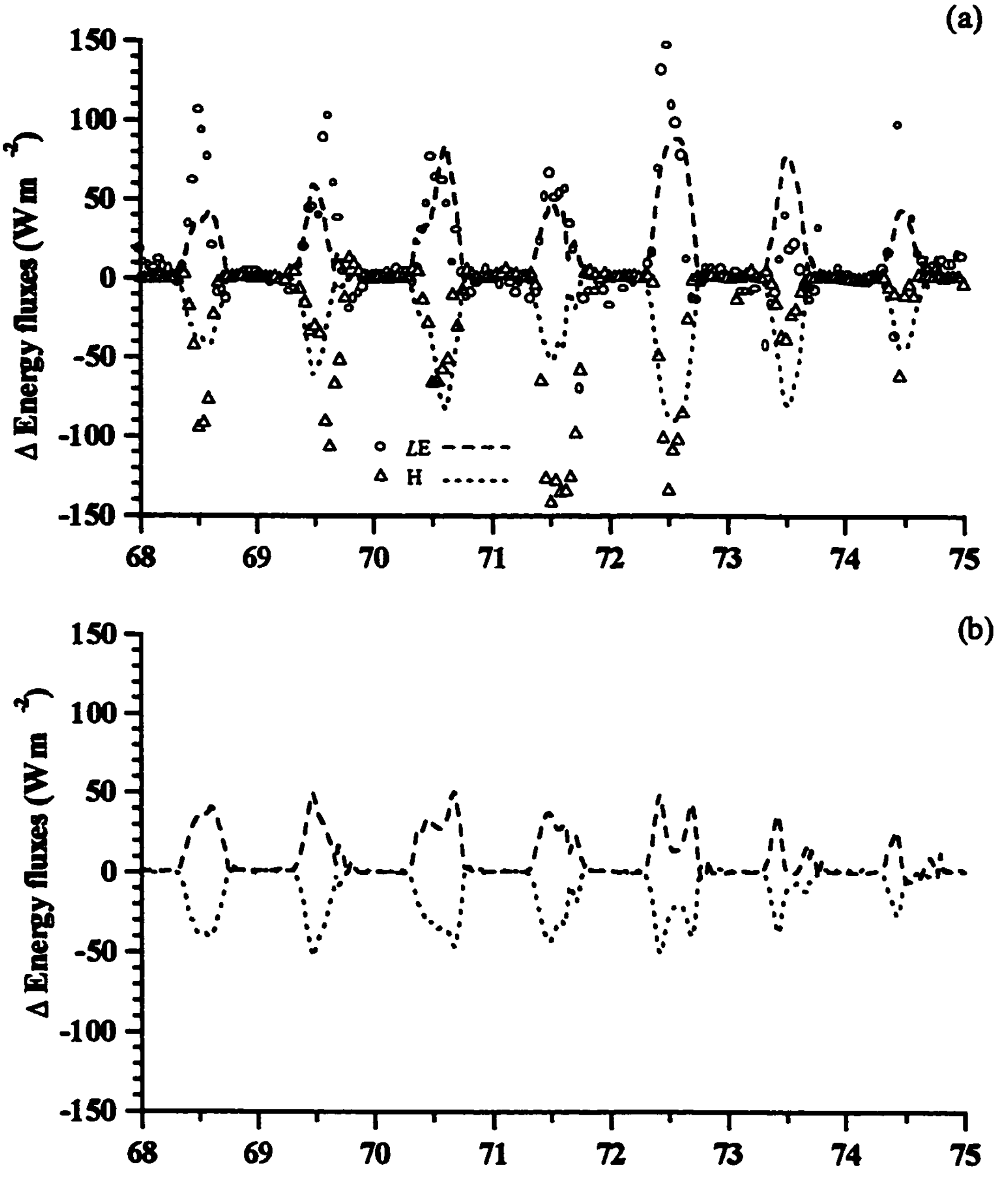

Fig. 2.4 Changes in latent and sensible heat fluxes (LE and H) simulated (lines) and measured (symbols) under (a) optimum, and (b) sub-optimum water supply; 550 vs. 355 μmol mol^{-1} CO_2 from 10 to 16 March 1994 (DOY 69 to 75).

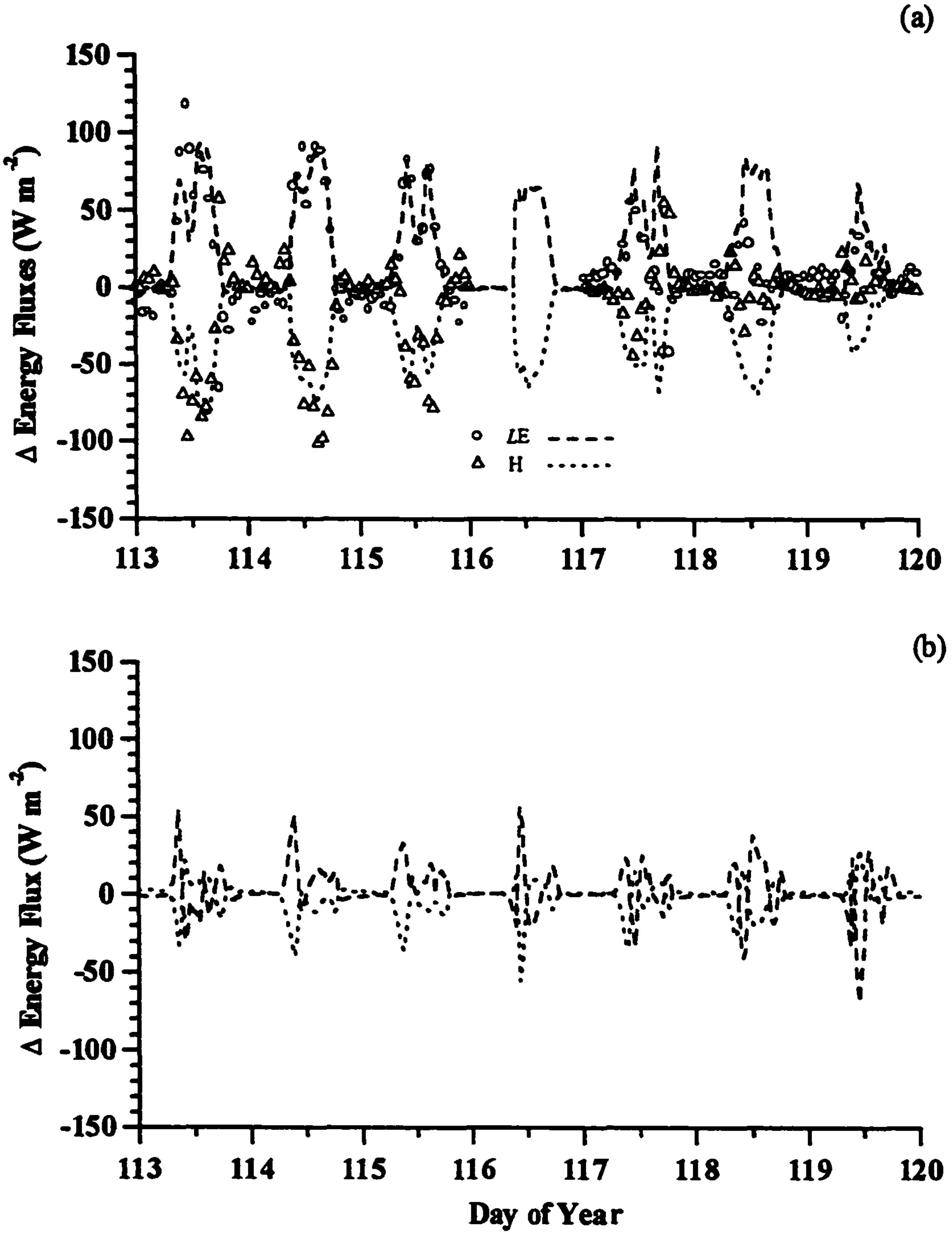

Fig. 2.5 Changes in latent and sensible heat fluxes (LE and H) simulated (lines) and measured (symbols) under (a) optimum, and (b) sub-optimum water supply; 550 vs. 355 µmol mol^{-1} CO_2 supply from 24 to 30 April 1994 (DOY 114 to 120).

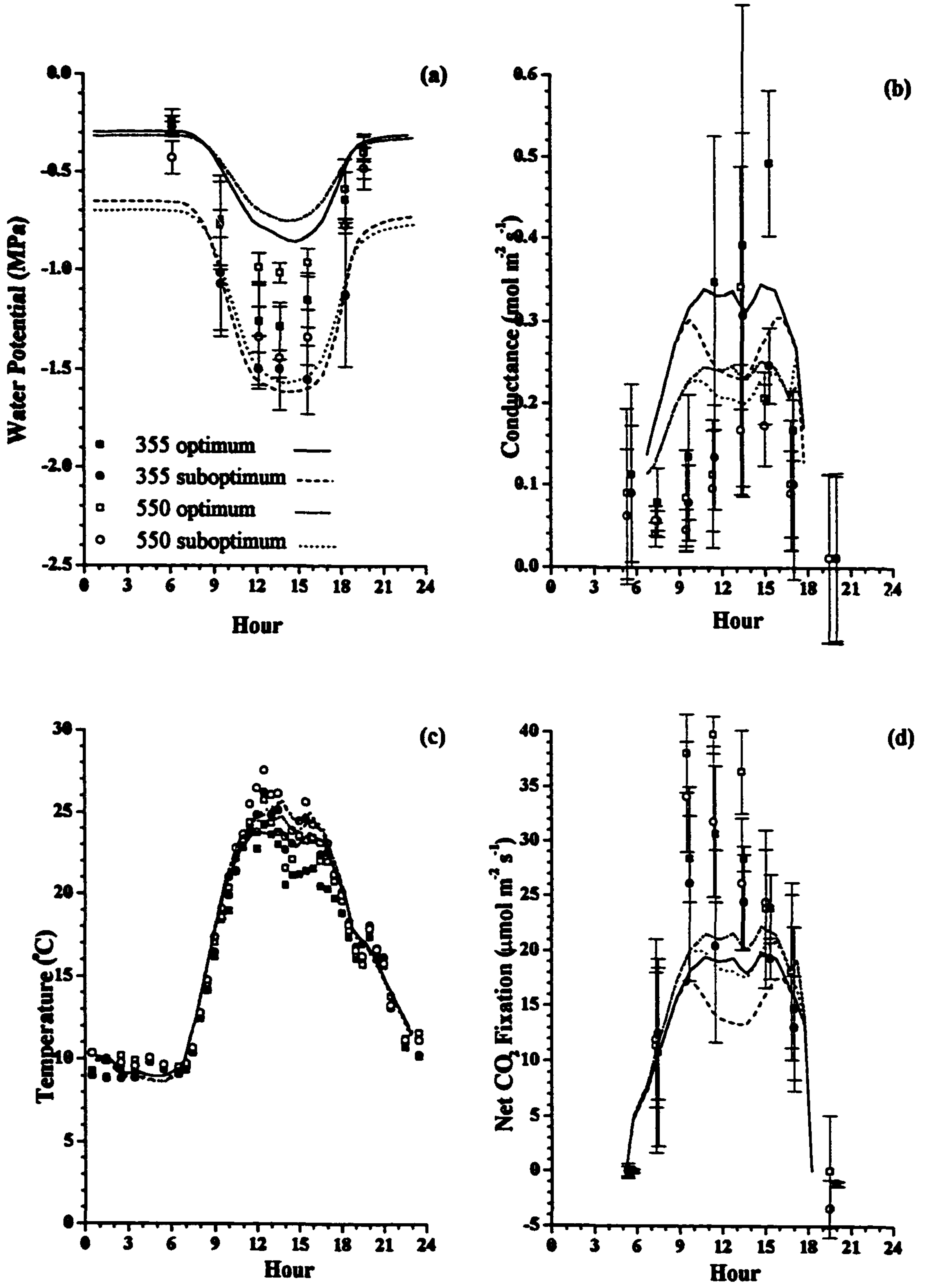

Fig. 2.6 (a) Leaf water potential, (b) leaf stomatal conductance, (c) canopy temperature and (d) leaf net CO_2 fixation simulated (lines) and measured (symbols) under optimum vs. sub-optimum water supply and 550 vs. 355 μmol mol^{-1} CO_2 on March 22nd 1994 (DOY 81).

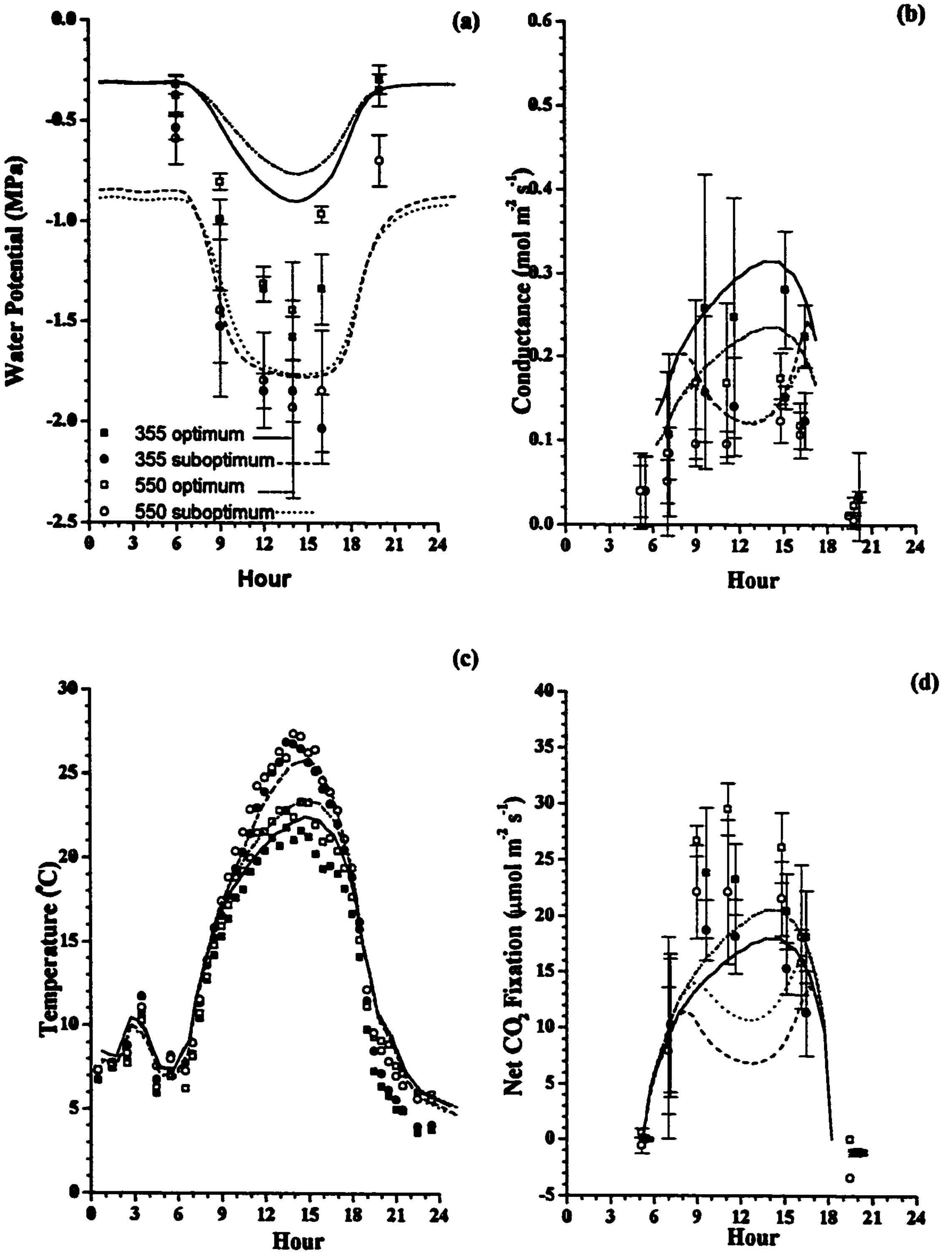

Fig. 2.7 (a) Leaf water potential, (b) leaf stomatal conductance, (c) canopy temperature and (d) leaf net CO_2 fixation simulated (lines) and measured (symbols) under optimum vs. sub-optimum water supply and 550 vs. 355 µmol mol^{-1} CO_2 on April 5th 1994 (DOY 95).

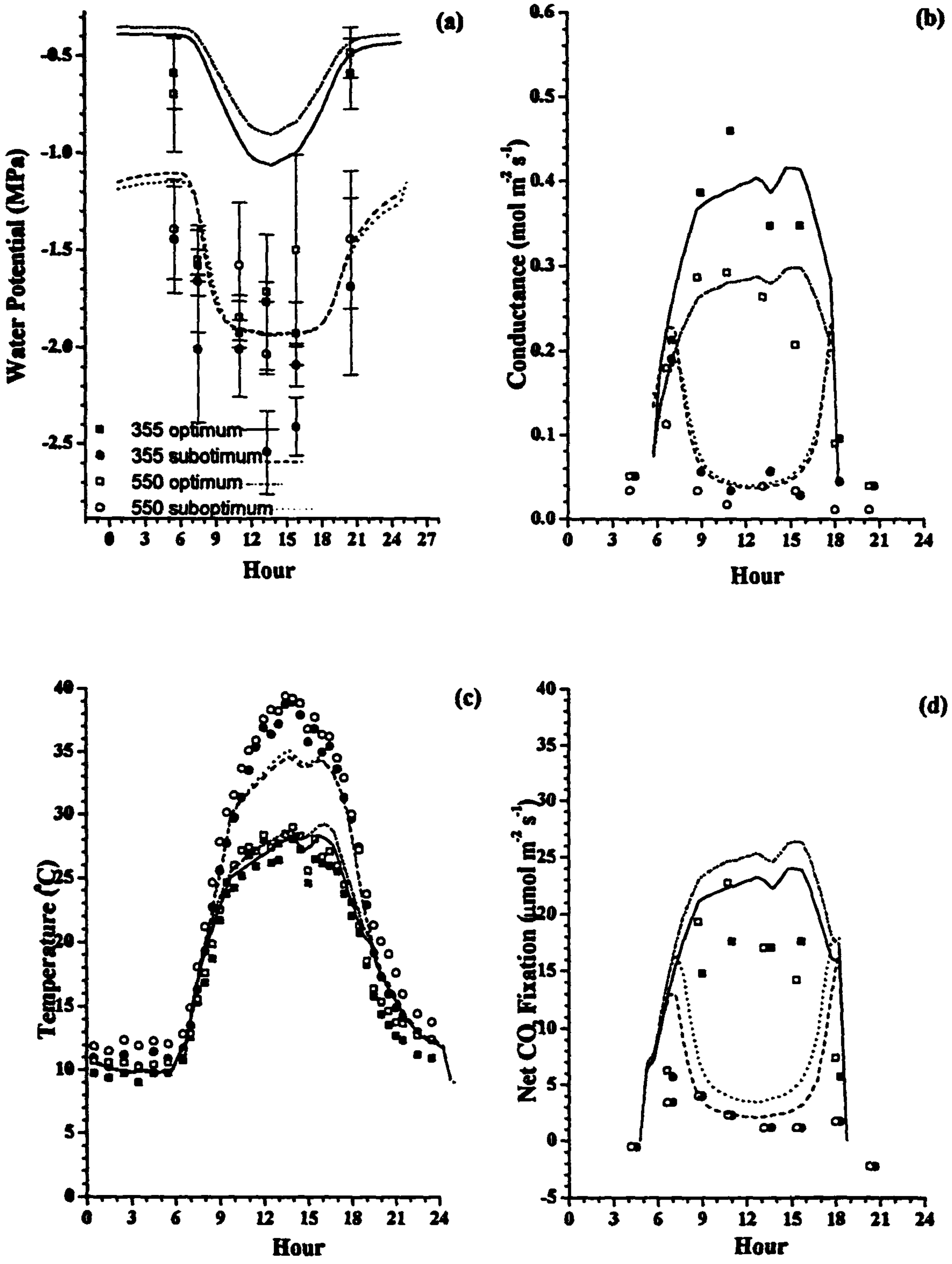

Fig. 2.8 (a) Leaf water potential, (b) leaf stomatal conductance, (c) canopy temperature and (d) leaf net CO_2 fixation simulated (lines) and measured (symbols) under optimum vs. sub-optimum water supply and 550 vs. 355 μmol mol^{-1} CO_2 on May 3^{rd} 1994 (DOY 123).

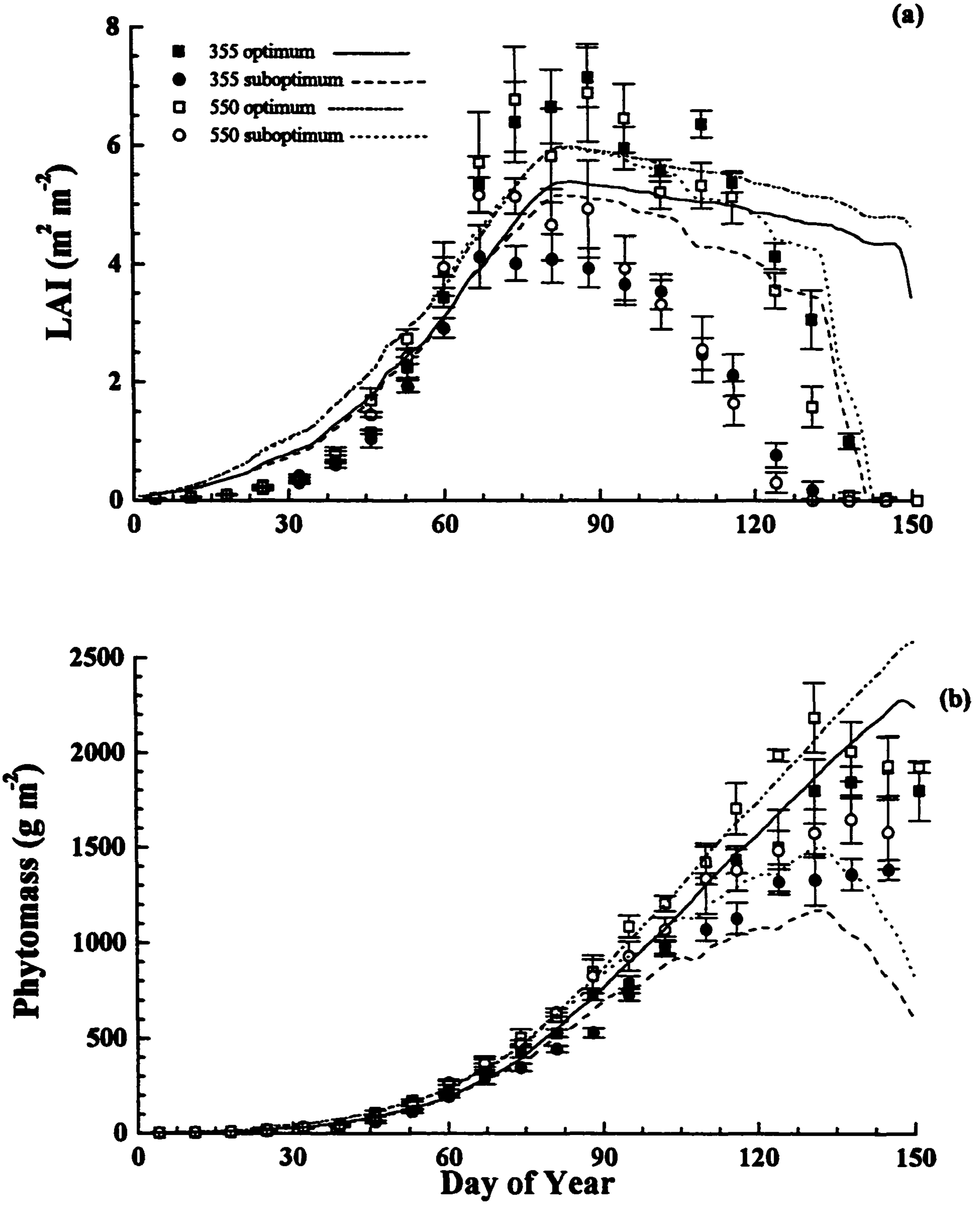

Fig. 2.9 (a) Leaf are index (LAI) and (b) above-ground phytomass simulated (lines) and measured (symbols) under optimum vs. sub-optimum water supply and 550 vs. 355 μmol mol^{-1} CO$_2$.

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Chapter 3 Fundamental aspects of soil water re-location via hydraulic lift: development of hypotheses.

3.1 Introduction

Movement of water in the soil-plant system is driven by water potential gradients. As transpiration starts, loss of water from the leaves lowers the leaf water potential. As a result, water is drawn to the leaves from the xylem vessels, resulting in lower water potential in the xylem. Water moves from roots to the shoots through the xylem system following the water potential gradient. The process continues until the lower water potential of the plant roots draws water in from the surrounding soils. There is a continuous path of water movement from soil to root surface, from the root surface into the xylem system, then to the stems, and finally leaves (Nobel, 1991; Kramer and Boyer, 1995). The water potential gradient in this continuous flow path remains as transpiration ceases. As a result, continued water movement to the leaves in the absence of transpiration, results in accumulation of water, or hydration, in the leaves. This raises the water potential of the leaves, reduces the water potential gradient and the rate of water movement to the leaves until a close to equilibrium condition is established in the soil-plant system.

The rate at which water moves in the soil-plant system is dependent upon the water potential gradient and the hydraulic resistance along the flow path. The resistance in the soil varies inversely with soil hydraulic conductivity and root density. For the major components of the flow path in the plants, i.e. radial flow across the root surface, and longitudinal flow in the xylem through roots and stems, the resistance for the radial movement across the root surface into the xylem tissue is considered dominant (Nobel, 1991; Kramer and Boyer, 1995). During active transpiration, the water potential difference across any segment of the flow path is proportional to the total water potential difference between leaves and soil, and to the portion of the total resistance accounted for by that particular segment. Within the plant system, there is therefore a large water potential difference between the root surface and xylem in plant roots. The water potential difference between xylem vessels in roots, stems and leaves is relatively small because of the low resistance of the xylem system. However, xylem resistance of large woody boles might limit water transport and therefore affect the magnitude of water potential within the plant.

For transpiring plants growing in soils of uniform water potential, the lowest water potential is in the leaves and the highest in the soil. There is little difference in xylem water potential between roots located in different parts of the soil profile, as a result of the relatively low resistance of the xylem system. As transpiration ceases, the water potential of the whole soil-plant system equilibrates as plants re-hydrate.

However, for plants grown in soils where soil water content, and water potential, varies with soil depth, the situation is more complex.

First, consider a soil with high water content in the lower part of the root zone while water content near the surface is slightly lower. In this situation, during active transpiration, the lowest water potential in the soil-plant system is in the leaves. The xylem water potential in the roots located in the upper portion of the soil profile is slightly lower than xylem water potential in the roots located in the lower part of the profile. Both are lower than the water potential of the surrounding soils. Water is taken up from all parts of the soil profile. The pattern of water uptake is a function of the root density distribution in the soil. As transpiration ceases and the plant re-hydrate, a new equilibrium with the bulk soil can not be established because of the water potential differences in different parts of the soil profile. As plants re-hydrate, the xylem water potential will first reach the water potential of the drier, upper soil layer. However, because of the more moist lower soil layer water will continue to be taken up by roots located there. As a result, the xylem water potential of the plants will become higher than the water potential of the upper soil layer. A reverse gradient develops from xylem to soil in the drier upper soil layer.

The second case to be considered is a moist lower soil layer coupled with a much drier upper soil layer. In this case, during the period of active transpiration, plant water requirement is entirely satisfied by roots in the moist, lower soil layer and leaf water potential may be higher than that of the dry, upper soil layer. The lowest water potential is in the dry upper soil. The reverse water potential gradient from root xylem to the soil exists in the upper soil layer even during the period of active transpiration.

Some interesting phenomena may be theoretically possible if the properties of the plant roots and xylem systems are such that significant reverse water movement in the flow path is possible. For the first scenario, during periods of low transpiration, water could be released from roots into the drier upper soil layer while being taken up by roots in the more moist, lower soil layer, and subsequently taken up by the plants during the period of active transpiration. The relocation of soil water through the plant system from moist and usually deeper soil layers to drier, and closer to the surface soil layers has been termed hydraulic lift (Richards and Caldwell, 1987).

For the second scenario, however, there could be continued relocation of water from the moist lower soil layer to the drier upper soil layer both during the period of active transpiration and when the transpiration has ceased. The relocated water can not be taken up immediately and thus may be lost to the plants performing hydraulic lift.

The concept of hydraulic lift has been proposed in the literature (e.g., Richards and Caldwell, 1987) with some observational evidences supporting its validity. However, several critical questions remain. Do properties of plant root system allow hydraulic lift to occur? If so, to what extent and under what circumstances does hydraulic lift occur? What benefit do plants derive from allowing hydraulic lift? In the second scenario, such relocation is clearly to the disadvantage of the plants. Could the plants allow hydraulic lift for the first scenario while preventing it for the second? How much water can be relocated by hydraulic lift? What factors control the occurrence of hydraulic lift? By what means could plants exert control upon hydraulic lift? What are the ecological advantages of hydraulic lift to the plants?

In the following discussion, I will explore possible answers to these questions based on considerations of fundamental physical principles governing water movement in the soil-plant system.

3.2 Water movement process

Before addressing specifically the issue of hydraulic lift, a brief discussion of the basic principles that govern the movement of water from soil into the plant roots, and finally into the atmosphere, is needed. This analysis focuses mainly on the mechanisms that drive the flow and the resistances that limit it.

3.2.1 Water movement in the soil

The water movement process in soils is generally described by Darcy's law:

$$q = -K\frac{\Delta(\Psi + Z)}{\Delta L} \qquad [3.1]$$

where q is water flux (m s^{-1}), Ψ is the matric potential (m), K is the proportionality factor designated as hydraulic conductivity (m s^{-1}), Z gravitational potential (m), and L is the distance between the two points (m). Soil hydraulic conductivity K varies with soil texture, structure, and with soil water content. In saturated soils, hydraulic conductivity is about 10^{-4} - 10^{-5} m s^{-1} in a sandy soil and 10^{-6} – 10^{-9} m s^{-1} in a clay soils (Hillel, 1982). As soils become unsaturated, hydraulic conductivity decreases. At field capacity, soil hydraulic conductivity may be more than three orders of magnitude lower than the values at saturation (Miroslav and Nielsen, 1994).

An alternative expression of Darcy's law allows water flux in unsaturated soils to be treated in terms of soil water diffusivity:

$$q = -D\Delta\theta \qquad [3.2]$$

where soil hydraulic diffusivity D = (K$d\Psi/d\theta$), $\Delta\theta$ is the water content gradient (Hillel, 1982). As soil water content decreases, K decreases sharply, however, $d\Psi/d\theta$ increases at the same time. As a result, soil water diffusivity is less sensitive to changes in soil water content than hydraulic conductivity K. For example, in a sandy loam soil, hydraulic conductivity K decreased by approximately 2 orders of magnitude as soil water potential decreased from –0.025 MPa to –0.3 MPa. While, soil hydraulic diffusivity decreased by only 15% (Gardner, 1956). It is common for D to decrease by 2 to 3 orders of magnitude as soil water content decreases from saturation to permanent wilting point (Miroslav and Nielsen, 1994).

Because of the dependence of soil hydraulic properties on soil water content, the solutions of the equation of water movement in soils, except for some simple cases, generally require the use of numerical computer simulations. However, some insight into water movement in the soil, could be gained by simple analytical arguments. Consider the movement of water from a moist subsoil to the drier upper soil layers. Solution of the diffusion equation (i.e., Eq.3.2) with a constant diffusivity indicates that when the influence of gravity is small the horizontal distance X, over which the water moves equals:

$$X=(2Dt)^{1/2} \qquad [3.3]$$

For example, in a clay soil with a water potential of -1.0 MPa and a corresponding water diffusivity D of 10^{-8} m^2 s^{-1} (McCoy *et al*, 1984), the water would move only 4 cm when time t, equals 24 hours. When the movement takes place over a one month period, the distance traveled by water would be only 22 cm. These calculations overestimate the actual upward movement of water from lower moist soil layers however, mainly because gravity works against such a movement and because water diffusivity D drops as water moves from wet to dry soil. Conversely, these calculations underestimate the overall downward infiltration, since gravity works to enhance downward movement.

What could be concluded from this simple analysis is that the long distance upward movement of water in unsaturated soils is generally a slow process and in many cases insignificant. As a result, plant roots must develop where soil water is available.

An alternative way to illustrate this point is to consider 2 points in the soil profile, one located in the upper dry layer at wilting point and the other located in the lower moist layer at field capacity. Consider the case where the distance between the 2 layers equals 1 meter. Effective mean hydraulic conductivity K_{EFF} of the soil separating the 2 points is between the maximum at field capacity K_{FC} and the minimum at wilting point K_{WP}. For a medium textured soil with saturated hydraulic conductivity K_{SAT}, of 10^{-6} m s^{-1}, K_{FC} is expected to be 2-4 orders of magnitude lower, and K_{WP} may be several orders of magnitude lower still than K_{FC}, therefore for this examples we can assume K_{EFF} to be 10^{-12} m s^{-1}. Hydraulic gradient of about 150 m m^{-1} develops between the 2 points, one at wilting point (i.e. water potential close to -1.5 MPa) and the other one located 1 meter apart but at field capacity (i.e. water potential close to -0.03 MPa). If we now apply Darcy's law and multiply the hydraulic gradient by K_{EFF} we get a water flux of about 1.3×10^{-4} m day^{-1} or 1.3×10^{-1} mm day^{-1}. This water flux from the wet to the dry soil can be considered to be negligible in comparison to daily ET requirements.

3.2.2 Water flow through the plant

In the previous section we briefly discussed the water movement in the soil. It is now germane to highlight the dynamics of water flow within the plant before addressing the specific issue of what limits the water flow along the soil-atmosphere pathway. Water lost via transpiration causes a drop of the water potential in the cell wall located at the interface between liquid water and air. The plant conducting system ensures water flow from those areas located either in the plant or in the soil that have higher water potential. Decreasing water potential of the plant transpiration pathway creates the force for water movement from adjacent tissues such as leaf mesophyll, xylem vessels in the stems, xylem vessels in the roots and root cortex. Water is then in continuous motion in cells, between cells, in tissues and between tissues. Distances traveled by water can vary from a few nano-meters when passing across a cell membrane to more than several meters when moving along the roots and stems. Once water has crossed the cortical cells of the roots, it moves radially into the xylem, then moves longitudinally along the xylem vessels to the stem xylem before being distributed into branches and leaves. Finally the water stream reaches the evaporation site located in the mesophyll by previously crossing from the xylem into the leaf veinlets.

In the context of plant water relations it is worth noting that a form of active transport is conceivable but rather difficult to demonstrate in plant cells (House, 1974). It seems that primary active transport could take place in two different ways: a) true active movement of water molecules through the transport tract; and b) water flow driven by osmotic potential gradient that results from metabolically controlled concentration gradients of solutes (Kolek and Kozinka, 1992). For the latter, the active component of the phenomenon is only the active accumulation of solutes. However, by far the dominant mechanism of water movement in plants is the passive flow driven by water potential gradients (Nobel 1991, Kramer and Boyer 1995). Plant transpiration T, occurs through a network of flow resistances located in the soil, the roots, the stems, the leaves and boundary layer. Water flux is proportional to the gradient between the water potential in the leaf canopy ψ_l and the water potential in the soil ψ_s. In Fig. 3.1, water flux from the soil to the atmosphere is represented as a series of hydraulic resistances located in two soil layers R_{s1} and R_{s2}, roots R_{r1} and R_{r2}, stem R_{st}, leaf canopy R_l and boundary layer R_{bl}. The water potential at different positions in the pathway constitutes the driving force in the roots ψ_r, stem ψ_{st}, leaf canopy ψ_l and air ψ_a.

The decrease in water potential along the flow pathways is proportional to the resistance and flow rate. For any given flow rate, higher resistance requires higher water potential gradient. For constant resistance, higher flow rate would demand higher potential gradient.

3.2.3 Source of major resistance

In regards to the plants the resistance to the flow located at the root surface must be of a large magnitude. This is confirmed by the fact that when roots are removed, and the transpiring leaves or branches are put in the water, the rate of absorption increases. Also it is not unusual to observe on a hot and sunny day, transpiring plants with a water potential anywhere around –1.5 MPa in different leaves at different locations within the canopy (Hellkvist *et al.*, 1974). During vigorous transpiration the water potential in the xylem of the plant is about -1.0 MPa lower than the soil water potential (van Bavel and Baker, 1985).

Newman (1974), after analyzing resistance of plants at various levels of leaf water potential and transpiration rates, concluded that root resistance as a percentage of the total ranged between 50-70 % for maize and about 70 % for sunflower.

It is conceivable that the soil resistance can represent the main limiting factor of plant water uptake, especially in dry soils. However, the exact soil water content range in which soil resistance becomes dominant over the root resistance is a function of the hydraulic properties of the soil and the magnitude of resistance of the plant root system. In transpiring plants the root segment draws water from a surrounding cylindrical volume of soil. The soil immediately next to the roots is found to have lower water potential than the overall bulk soil. Nobel (1991) indicated that the soil adjacent to the root could have a water potential of –1.0 MPa as opposed to –0.6 MPa of the soil located only 10 mm away from the root. According to Gardner and Ehlig (1962), the total resistance in the soil-plant system begins to increase significantly at soil water potentials below -0.06 MPa, indicating that soil resistance is becoming a significant part of the total resistance in the soil-plant system. The authors concluded that soil resistance could limit water uptake only when the soil approaches a water potential lower than -0.1 or -0.2 MPa. However, because the impedance to water movement is inversely proportional to the hydraulic conductivity and root density, it seems that the root density developed by the pepper plants (*Capsicum frutctescens* L.) grown in the greenhouse might have been lower than actual values found under field conditions. Also Newman (1969) questioned the validity of Gardner's results because the root density used during his calculations is much lower than the ones found under natural field conditions. He concluded that soil resistance in the proximity of the roots becomes limiting only at soil water contents close to the permanent wilting point. It is possible, however, that a decrease in water uptake by plants at relatively high soil water potentials is attributable to the loss of soil-root contact as the soil dries. This theory is based on two possible processes that might take place in a drying soil: a) the soil shrinks as it dries; and b) roots also shrink if dehydrated. Both processes lead to loss of root-soil contact. In conclusion, although soil resistance can be important under certain circumstances, the root resistance seems to be generally higher and dominant. The above conclusions are based on the fact that plants found in the field have a high root density, about 2 – 4 cm cm^{-3} (Glinski and Lipiec, 1990), this in turn allows the plant to intensively explore the soil volume for water. A well developed rooting system is probably sufficient to offset the slow water movement due to low water potential gradient and hydraulic conductivity ranging from 10^{-6} to 10^{-5} m day^{-1}. This narrow range of unsaturated hydraulic conductivity is found to be constant for a wide range of soils that experience a total potential between -0.02 and -0.2 MPa (Gardner and Ehlig, 1962).

3.2.4 Other sources of resistance

The process of longitudinal water flow is responsible for supplying the upper portion of the canopy with water for transpiration. Longitudinal water transport starts at the root level by flowing inside dead and empty conducting elements, i.e. the xylem vessels, that together form an open tubing. Although a resistance to longitudinal axial flow exists, it is considered to be relatively low as compared to the resistance to radial flow (Frensch and Steudle, 1989; Glinski and Lipiec, 1990). The latter statement seems to be valid when dealing with small plants, nevertheless, several authors reported many instances in which the boles of large woody plants are the site for the main water flow resistance (e.g., Tyree *et al.*, 1975; Tyree 1988). Long-distance water transport takes place via vessels and tracheids of the xylem and through lateral pits that interconnect the conducting elements (Esau, 1965). Vessels are made up of a series of vessel members stacked on top of each other and interconnected by perforation plates at the end walls. Their length ranges from less than 1 mm to several meters depending on the species (Zimmermann and Jeje, 1981). Because gymnosperms lack vessels they entirely rely upon tracheids. Tracheids are individual elongated conducting cells ranging from 2 mm to 6 mm in length. According to the Poiseuille's law the resistance to water movement in a capillary is inversely related to the square of radius. The overall resistance of the xylem system is also inversely related to the total cross sectional area of the xylem system, in addition to the size of the individual xylem vessels. In plants, the diameter of the xylem vessels largely determines the hydraulic efficiency of the conducting unit. High hydraulic efficiency is associated with wide vessels. However, the safety of the transport process decreases with increasing vessel diameter. Water flow in the plant is made possible by the integrity of the water columns in the vessels, that if not maintained can create additional resistance to upward flow. It seems, however, that plants retain the ability to circumvent the problems associated with a slow down of the upward flow imposed by air-blocked vessels. Bordered pits could facilitate water to move to the next vessel and by-pass the obstructing air bubble. Nevertheless the role of bordered pits has important implications in the context of hydraulic lift and radial flow of water. The issue of radial movement of water and the resistance that might limit it is discussed more extensively in section 3.5 of this chapter.

Microscopic observations performed on plant xylem network of both dicotyledons (Zimmermann and Brown, 1971), and monocotyledons (Zimmermann *et al.*,1982) reveals that different vessels are connected through pit areas. When concerned with the resistance to flow it is helpful to quantify how large these interconnecting areas are and in this respect we should use the approach and data of Zimmermann (1983). We start then with a metaxylem vessel of 60 x 10^{-3} mm in diameter, the transverse area of the vessel lumen is 2.8 x 10^{-3} mm^2. A scalariform pit has a width of about 35 x 10^{-3} mm, therefore if the overlap between two vessels is about 20 mm long, we have 0.7 mm^2 of surface area potentially available for the water to flow through. However about 60% of the pit area is occupied by secondary wall leaving about 40% of the total, i.e. 0.28 mm^2, available for water transfer (see Fig. 2.8 in Zimmermann, 1983). Although we do not know directly what this will cause in terms of resistance to the flow, it can be argued that an inter-vessel area, that is 100 times larger than the cross sectional area of the vessel itself, would generate a low resistance to the flow. Although what has been just illustrated is particularly valid for palms we can say that in general angiosperms have relatively lower resistance to lateral transport than gymnosperms. Dealing with gymnosperm and the fact that vessels are missing, poses the basis for a different type of analysis. Conducting elements such as tracheids are much shorter than vessels, conifers have only tracheids which lack perforated plates at their ends, forcing the upward water flow through a larger number of pits than in the case of angiosperms. In angiosperms the single conducting elements overlap with each other at their ends and because overlap takes place along the side of the elements this may cause a slight shift on the side of the upward flow.

Anatomical differences between angiosperms and gymnosperms have an effect upon the overall resistance. In the stems for example, and in particular the size and shape of the pits might play a key role for lateral water transport and how this connects to hydraulic lift (see the xylem bundle resistance R_{xb} in Fig. 3.1c). Microscopic analysis reveals that bordered pit-pairs found in conifer tracheids are particularly elaborate in their structural details (Esau, 1965). The pit membrane has thickening of primary nature, called the torus. The torus is surrounded by a thin portion of the membrane that constitutes the margin and named margo. The pit membrane is flexible and under certain conditions the torus is laterally positioned, which means lying against one or the other pit aperture of the pit-pair. This particular circumstance is also regarded as aspiration of the pit-pair. Pressure relations within the tracheids influence the movements of the pit membranes together with the movement of the torus. Therefore aspiration of pits that occurs in connection with the formation of heartwood is ascribed to the drying out of the central core of the wood and appearance of air in the non-conducting tracheids (Esau, 1965). When the torus is in the median position the water passage through the pit-pair is presumably happening via the pores of the margo. If the torus is instead in lateral position the water movement through the pit-pair is most likely to be restricted. The displacement of the pit membrane seems to occur when a tracheid filled with water lies against one filled with air. Finally because the torus is a characteristic formation of bordered pits found in gymnosperms, but rarely found in angiosperms, I presume that the resistance to lateral flow is a more pronounced phenomena in gymnosperm species. Since the hydraulic lift process includes some sort of lateral water transfer during outflow in the dry soil, as illustrated in Fig. 3.1c; I conclude that the higher resistance due to the wood anatomy of gymnosperms might prevent this phenomena from occurring in this particular plant group.

3.3 Root and water distribution in soil profile

In our example I have previously discussed that long-distance movement of water in a profile of unsaturated soils is relatively minor. As a result, roots must grow where there is available soil water. Spatial distributions of water and roots in the soil profile thus play an important role in the ability of plants to fully utilize available water resources.

Although it could be argued that the optimal condition would be the one in which the distribution of roots in the soil profile coincides with that of the available water, there are often times in a season when this condition can not be maintained. Soil water content, especially near the soil surface, can experience large and frequent changes during a season. The frequency and magnitude of these changes are functions of precipitation, infiltration and redistribution processes, as well as evaporation and root water uptake (Parsinejad, 1998). The distribution of plant roots, however, is not likely to respond to such dramatic and frequent changes in a season because of the high metabolic costs involved in growing new roots. As a result, distribution of plant roots and available soil moisture in the soil profile often do not match. A question arises naturally, that is, what mechanism would allow plants to best utilize limited water resources under these circumstances? One of the suggested mechanisms is hydraulic lift (Richards and Caldwell, 1987).

3.3.1 Infiltration and redistribution from precipitation

If roots develop where the soil is moist, it is of paramount importance to understand the distribution of water in the soil profile, particularly under natural conditions where the plant community has had the opportunity to adapt to the soil and climatic conditions.

In temperate regions, major precipitation events occur at typical intervals of 1 to 2 weeks (Harte, 1988; Parsinejad, 1998). In many regions, most of the precipitation during the growing season is used by plants. A typical growing season precipitation of approximately 300 mm would thus translate into an average of approximately 2 to 3 mm per day. Thus, a precipitation interval of 1 to 2 weeks would lead to a typical recharge of 20 to 30 mm per precipitation event. Depending on the extent of soil water depletion before precipitation as well as the porosity and water holding capacity of the soil (Hillel, 1982), this amount of water could recharge the surface 10 to 30 cm of soil to field capacity.

The process of soil water movement does not stop when rain stops. The redistribution process will see water moving to lower depths, before depletion by evaporation and plant uptake. The complexity of the water movement process in unsaturated soils does not allow simple formulae to predict the maximum depth to which water could move during a dry period of 1 to 2 weeks. However, because of the sharp drop in hydraulic conductivity with lower soil water content (Hillel, 1982; Miroslav, and Nielsen, 1994), substantial water movement is not expected, in general, after the surface layer has reached field capacity. Accounting for variations among different soils and precipitation events, as well the redistribution process during dry periods, the major recharge-depletion cycle is not expected to reach depths much more than approximately 40 cm. Numerous experimental observations and computer simulations have confirmed this result (Jury, 1992 *et al.*; Miroslav and Nielsen, 1994; Parsinejad, 1998).

In addition to the recharge-depletion cycles that arise from individual precipitation events, in many places there is also an annual soil water cycle. In this cycle soil water in the lower portion of the profile is gradually depleted during the growing season, as a result of the net precipitation deficit during the season. This water is recharged during the other part of the year, i.e. winter snow fall and the following snow melt in Canada. This annual cycle is especially profound in areas that experience wet and dry seasons, such as in the Mediterranean (Carboni *et al.*, 1980). Because of the longer time period, this annual soil water cycle affects a greater depth of the soil profile, often >1 m, and as much as 2 m (Ren, 1997).

3.3.2 Root distribution

In order to utilize soil moisture efficiently, plant roots must grow where soil water is available. As a result of the characteristic of soil water distribution, most of the plant roots are distributed in the upper portion of the soil profile and exploit the precipitation during the growing season. However, in areas where there is a moisture deficit in the growing season, deeper roots are also needed to exploit seasonal recharge of soil moisture in the lower part of the soil profile (Robertson *et al.*, 1980). A complete quantitative analysis of the relationship between root distribution and soil water distribution as a result of plant, soil and climate interactions, despite its obvious importance, has not been reported.

High root density in the upper soil horizon is required to exploit the precipitation during a single growing season. However, during periods when the upper portion of the soil profile is dry, and at the same time there is available soil moisture in the lower part of the soil profile, transpiration demands are satisfied primarily by deep roots (Hellmers, *et al.*, 1955). Maintenance of high root density in the dry upper soil layers during this period thus constitutes a net metabolic cost with little gain in water uptake. However, if water could be temporarily relocated, during times of low transpiration demand, from moist lower soil layers into the dry upper soil layers through the root system, roots in the upper soil layer would be able to play at least a partial role in absorption of water. This is in addition to their role in absorbing water when it is available in the upper part of the soil profile.

If we now look at the issue of roots in terms of metabolic cost for the plant, we can start by stating that a large amount of photosynthate goes into root growth. Namely three different pathways are distinguishable: production of new tissue, respiration that is the result of supplying energy for the metabolic processes related to growth, and maintenance respiration of existing tissue (Amthor, 1989). Caldwell (1976) indicated that 50% of the annual net primary phytomass production of a deciduous forest and fescue meadow goes into roots, and this already large fraction goes up to 75% for short grass prairie and shrub steppe communities. Such a large amount of carbon is needed since the turnover rate of roots seems to exceed the one commonly found for leaves (Woods, 1980 in Kramer and Boyer, 1995). Despite the efforts to find a plausible explanation for what appears an extremely costly operation for plants we still do not know why so much carbon is allocated for the production of more roots than seems necessary (Kramer and Boyer, 1995). However, it may be postulated that although very costly, large rooting systems bring the benefits of exploiting the soil water storage capacity in the rooting zone, and under the natural variability of rainfall patterns that occur from year to year and within the same year. In conclusion, what may seem to be an advantageous strategy, i.e. shedding the roots in the presence of dry soil, might actually be more costly in the long run if roots have to be re-grown as soon as the rainfall comes.

3.4 Hydraulic lift

When a lower part of the root system is exposed to moist soil and the upper portion is exposed to drier soil, the condition for water to be temporarily re-located may exist. Richards and Caldwell (1987) coined the term “hydraulic lift” to describe this water movement from relatively moist to dry soil layers using the plant root system as a conduit. The occurrence of hydraulic lift requires that at night the water potential of the topsoil is below that of the donor roots, and that the water potential of the root drops below that of the topsoil during day. Eventually the water will be stored at night in the topsoil, and taken up during daytime when transpiration resumes.

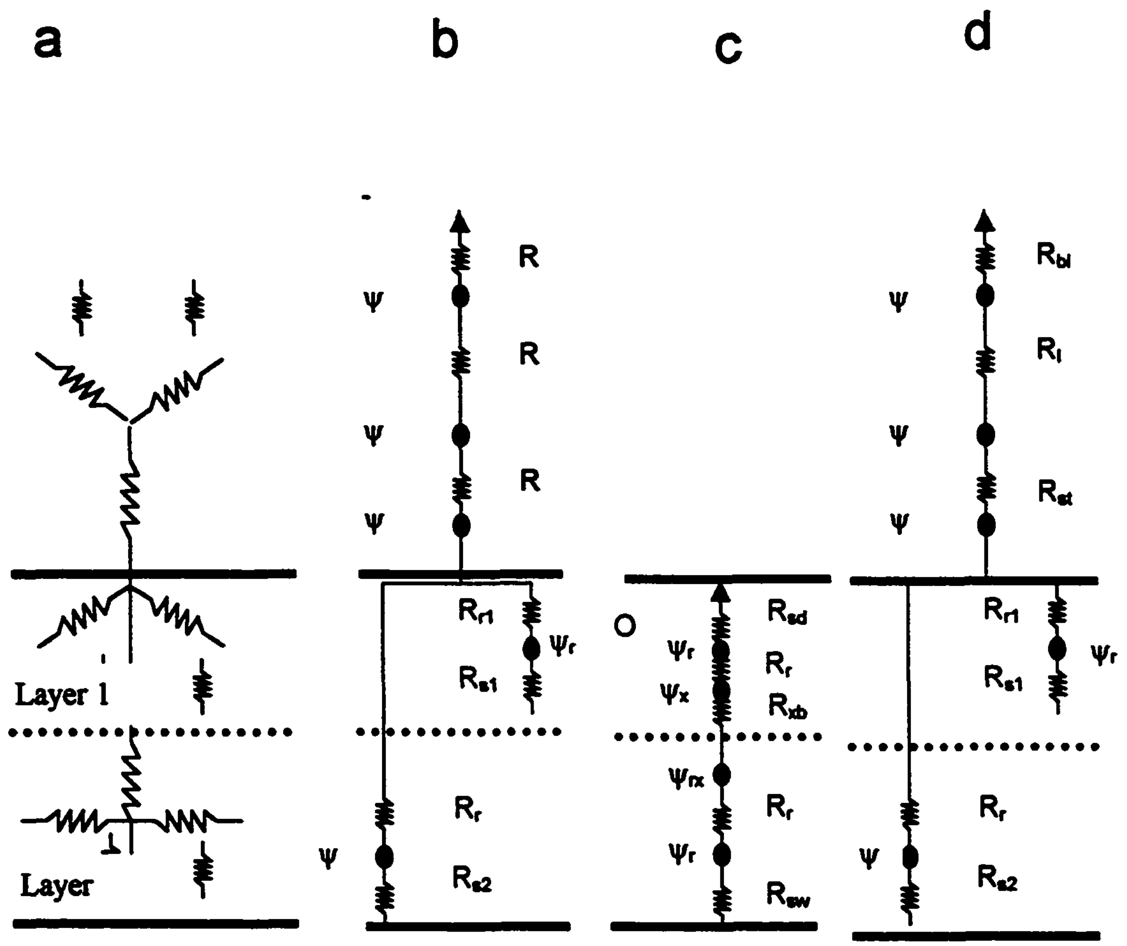

Fig. 3.1. (a) Representation of plant transpiration (T) through a network of flow resistances located in the soil, the roots, the stems, the leaves and boundary layer. The plant has roots which are in contact with two different soil layers. (b) Simplified catenary model of water flux from the soil to the atmosphere represented as a series of hydraulic resistances in the two soil layers (R_{s1} and R_{s2}), roots (R_{r1} and R_{r2}), stem (R_{st}), leaves (R_l) and boundary layer (R_{bl}). Water potential at different positions in the pathway constitutes the driving force in the roots (ψ_r), stem (ψ_{st}), leaf canopy (ψ_l) and air (ψ_a). (c) Simplified catenary model of the hydraulic lift process in which roots are exposed to dry soil (layer 1) and to moist soil (layer 2). The outward water flux (O) in soil layer 1 is inversely proportional to the resistance in the soil (R_{swet} and R_{sdry}), roots (R_{r1} and R_{r2}), xylem bundles (R_{xb}), and proportional to the water potential in the roots (ψ_r) and within the xylem bundles (ψ_{xb}). (d) Simplified daytime water flow after a nighttime water re-location that took place via hydraulic lift. The shallow soil

3.4.1 Development of water potential gradients

Consider the case where a water potential gradient exists in the soil profile, in which a drier, low water potential shallow soil layer is over a moist, higher water potential deep soil layer. During the day when active transpiration takes place, water is primarily absorbed by the roots in the deeper, more moist portion of the soil. A water potential gradient exists, between the moist lower soil layer, the deeper roots, and the transpiring leaves. If the water potential in the drier, upper soil layer is not exceedingly low, the lowest water potential in the whole soil-plant system will be at the leaves. Water potential of the plant roots in the upper soil layer is lower than that of the surrounding soil. Absorption of water occurs in all roots.

During the low transpiration period, such as during night and under shading, water absorbed by deeper roots will supply the re-hydration process of the plant. This is likely to raise the water potential of the plants to values higher than that of the drier, upper portions of the soil profile. There is thus a reversal of water potential gradient at the root-soil interface. The lowest water potential in the soil-plant system will be at the drier upper soil layer. As a result, a water potential gradient from moist, deeper layers of the soil through plant roots to drier, upper portion of the soil profile develops.

The situation becomes quite different where a much drier upper soil layer, at water potentials near or lower than the permanent wilting point, overlays a moist and deeper soil layer. In this case the lowest water potential, regardless of the transpiration demand, is in the drier upper soil layers. During the periods of high transpiration demand, a water potential gradient exists from moist lower soil layers, through roots, to leaves. At the same time, a water potential gradient also exists from the moist lower soil layer, through roots to the drier upper soil layer. During periods of low transpiration, as plants re-hydrate, the gradient from moist lower soil layer to leaves diminishes but the gradient between the moist lower soil layer and much drier upper soil layer persists. This creates the condition for water re-location during daytime.

Finally consider the case in which the soil is uniformly wet. During periods of transpiration a water potential gradient exists from the soil, through roots to leaves. As the season progresses and unless rainfall or irrigation replaces the transpired water, the soil will dry and soil water potential will drop. Because the soil is drying uniformly no gradient between soil layers develops, causing the roots to be in contact with soil which has the same water potential throughout. Therefore the gradient will still be from soil layers through roots to leaves. As the soil water continues to be depleted, the soil water potential will keep dropping, this causes the leaves to develop a more negative water potential in order to keep the water flowing to the site of transpiration. As the transpiration drops during nighttime the water potential of the plant re-equilibrates with the one of the soil. This scenario does not allow the water to be relocated via hydraulic lift.

3.4.2 Process of water relocation

Water movement in the soil-plant system is a function of the water potential gradient and resistance (Fig.3.1). Water will not move, regardless of the potential gradient, if the resistance is infinite. It is generally accepted that water uptake by plant roots is dominantly passive, driven by water potential gradients. Uptake of water by plant roots occurs in response to an hydraulic gradient that exists between the fluid in the xylem and the liquid in the soil. However, one could ask what if the water potential gradient between roots and the surrounding soil is reversed? Could there be flow of water from roots to soil when the soil water potential is lower than that in the plant roots? If we accept the concept of passive water movement, the only possibility to prevent such a reverse in water movement is by significantly increasing the resistance in the flow path. Thus, the question is naturally whether hydraulic resistance for outflow is of the same magnitude as that for uptake.

Some insights into this question are provided by the split-root experiments of van Bavel and Baker (1985), in which two separated compartments of 0.094 m^3 in volume, were filled with rooting medium. A bermudagrass sod was allowed to grow in one compartment and the roots grew to pass the barrier that separated the two soil compartments. By maintaining a significant potential difference between the two soil compartments, ranging from -0.7 to -1.2 MPa, an overnight flux of 0.2 to 0.6 Kg of water occurred from the more moist compartment to the drier compartment. These results lead van Bavel and Baker (1985) to conclude that water could flow from roots to soil when the soil water potential is lower than that in the plant. Using a similar experimental set up Baker and van Bavel (1986) calculated that the hydraulic resistance to outflow from the roots was of similar magnitude as the one independently estimated for water uptake. The resistance to water efflux from the roots into the dry soil was reported to be 1.2 x 10^7 MPa s^{-1} as compared to 0.83 10^7 MPa s^{-1} for water uptake. The rate of water transfer from the wet to the dry compartment was formulated to be proportional to the gradient in water potential of the two soils and inversely proportional to the sum of the resistance to uptake (wet compartment) and to the resistance of efflux (dry compartment). The authors calculated the resistance to water efflux by rearranging this formula and using the recorded mean value of water transferred in the dry compartment and then solved for the resistance to water efflux. It should be noted that the resistance to uptake and the resistance to efflux are also inclusive of the soil resistance to water movement. However the soil resistance was estimated to be minimal in both dry and wet compartments. We can ascribe the low soil resistance to: a) fritted clay used as rooting medium in this experiment is able to retain nearly 30 % of the water contained at saturation even at a potential of –1.0 MPa; b) *Gramineae* species such as Bermugrass develop rooting densities that are at least one order of magnitude higher than the dicotyledons found in the field. In conclusion we can probably speculate that the slightly higher efflux resistance as compared to the uptake resistance, is due to some resistance encountered by the water while crossing the vascular bundles. And although the inter-bundle resistance might exist, it is probably not large enough to prevent water efflux from the roots of herbaceous plants into soil.

When part of the root system is exposed to a moderately dry soil, whole other parts are in a moist soil, the following analysis could be made.

In the context of water movement from soil to plant roots, the cylindrical coordinate system is most suited. In this case we ignore the effect of gravity, Darcy's law in conjunction with considerations of mass conservation leads to:

$$\frac{d\theta}{dt} = r^{-1}\left(\frac{d}{dr}\left(D\frac{d\theta}{dr}\right)\right) \qquad [3.4]$$

where D is soil water diffusivity, θ is the water content, and r is radial distance from the center of the root.

As plant roots take up water, the water content around the root decreases. For the simple case where we approximate the system with a constant average diffusivity, the mathematical solution for water content distribution around a fine root, represented as a line source releasing a constant flux into the surrounding soil, is given by:

$$\Delta\theta = -\left(\frac{q_r}{4\pi D}\right)\mathrm{Ei}\left(\frac{-r^2}{4Dt}\right) \qquad [3.5]$$

where $\Delta\theta$ is change in water content, q_r is water flux per unit root length, D is soil water diffusivity, r is radial distance from the center of the root, and Ei is the exponential integral function. A graph of the solution is shown in Fig.3.2 where $\Delta\theta/(q_r/4\pi D)$ is plotted against $r/(4Dt)^{1/2}$.

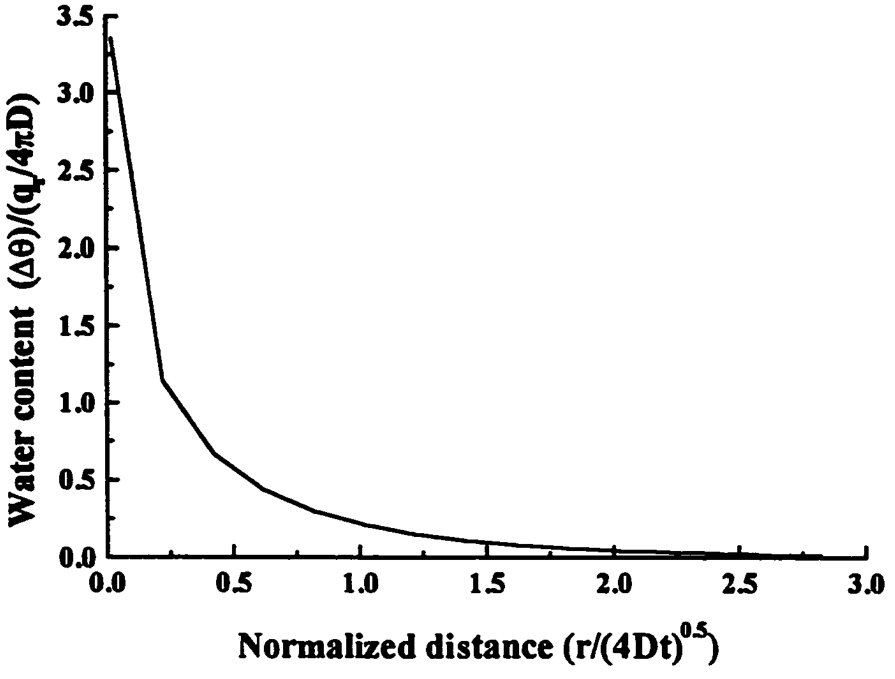

Fig. 3.2 Water content distribution around a root with constant soil diffusivity.

The mean distance to which water movement occurs is calculated as:

$$\bar{r} = \left(\frac{\pi}{9Dt}\right)^{1/2} \qquad [3.6]$$

When average soil water diffusivity is 10^{-8} m^2 s^{-1}, the average distance over a 12 hour period is calculated to be 1.2 cm. In soils, water diffusivity generally decreases with decreasing soil water content. When roots are absorbing water, the lower diffusivity is near the root, while away from the root the diffusivity gets higher. The mean distance of influence by the roots thus is larger than what is estimated by these equations. If the direction of flow is reversed, these equations overestimate the mean distance of influence by the roots. However, these calculations do give an order of magnitude estimate on the extent of spatial influence of water absorption/release process by plant roots.

In an ideal case, water uptake by plant roots undergoes cyclic changes in a 24 hour period. The most efficient density of the roots is such that there is little overlap of the sphere of influence of the roots. Thus, the mean distance between neighboring roots should be approximately twice the sphere of influence of the individual roots. According to this calculation, for a mean separation of around 2.4 cm, this should give a root density of around 435 m m^{-3}, a value well within the range frequently observed. With their lower unsaturated soil water diffusivity, sandy soils would thus require higher root density than finer textured soils for most efficient exploitation of soil water. In a drier climate, because of the low soil water diffusivity associated with low soil water content, it will require higher root density to fully exploit soil water. However, at the same time, higher root density would also result in higher maintenance costs. For optimal growth, the root density could increase as long as the increase in water uptake offsets the cost for maintaining a higher root mass.

If, according to the hypothesis of hydraulic lift, roots in drier soil layers allow reverse water flow into the surrounding soil during periods of low water requirement, two questions need to be answered. The first one is how much of the water that is released during periods of low water requirement can be taken up during the subsequent period of high water requirement? If the fraction of subsequent uptake is low, there seems little advantage to the plant. Secondly, what is the response time of experimental measurement techniques, such as soil psychrometers, to the onset of reverse water flow from the plant roots to the soil? The latter is of particular importance for the design of actual field experiments, and for the interpretation of the measurements.

Semi-quantitative answers for these questions could be derived from our analysis. If the root density is such that the average distance between neighboring roots does not exceed twice the distance of the average distance of water movement from roots during the period of water release, most of the water released could be taken up during the subsequent period of high water demand. For example, in a 24 hour transpiration cycle, the root density would need to be around 400-1000 m m^{-3}. The exact value would be a function of soil type and soil water content as these parameters affect soil water diffusivity. If the upper soil layer is not exceedingly dry, there seems to be substantial benefit for hydraulic lift. In an exceedingly dry soil layer, however, full utilization of water released into the soil during periods of low transpiration demand would require high root density. It is conceivable that at some point the increase in maintenance cost would outpace the benefit of additional water uptake.

The time constant in equation 3.5 is $r^2/4D$. Using the representative values derived from the previous discussions and for our example, $D=10^{-8}\,m^2\,s^{-1}$, and $r=1.2$ cm, the time constant is calculated to be 1 hour. Taking into account the variations in soil water diffusivity and average distance between roots, it thus seems reasonable to expect the response time to be in the range of less than an hour to a few hours. Thus, if an actively transpiring plant is shaded to reduce the transpiration demand, water potential of the plant roots will increase to equilibrate with that of the soil. Roots in a moist lower soil layer will equilibrate with the surrounding soils to raise the water potential of the xylem system in the roots. This could lead to a reversal of the soil-root water potential gradient in the drier, upper soil layer. The overall response time is the summation of the equilibration time of the root system and the diffusion time of water from the roots. The lower limit of this response time, not including the root equilibration time, is thus seen as from less than 1 hour to a few hours. This would, theoretically, suggest that water could move away and towards the roots before night and daytime transpiration are respectively over. This in turn would allow plants to derive some benefits from a 24 hour transpiration cycle.

The opposite case to the one just illustrated above, would be characterized by a soil with a constantly higher water potential than that of the roots, and by roots which exploit water from a soil profile of a fairly uniform water content. Under these circumstances reversal gradient does not take place so that any water re-location is impaired.

The next question is how often; and under which circumstances a reverse gradient may, or may not develop. In order to address this question, two hypothetical scenarios will be discussed: an agricultural crop and a natural vegetation stand. Usually an agricultural crop in the field has most of the roots concentrated near the surface, and usually it is well supplied with either precipitation or irrigation water. This in turn would probably result in a fairly uniform soil moisture distribution through the soil profile and with a water potential higher than the one of the roots. These two effects combined might then be associated with a rare occurrence of the reverse gradient, mainly because the soil where roots are is most likely to be moist throughout the crop season. On the contrary, a natural vegetation stand found in areas that are of a marginal interest for agriculture would probably experience a more irregular recharge of the topsoil, that in turn creates heterogeneous water content with depth. If the natural stand has then a root apparatus that extends downward, conditions for a reverse gradient might develop. It could be then concluded that at the ecosystem level, chances for a reverse gradient to occur and to develop into an advantageous phenomenon, are probably higher in natural vegetation stands than in an agricultural annual crops.

Although the conditions for the reverse gradient might exist, when the roots are able to exert control upon the outflow they might prevent water being released in the soil. Despite the structural evidence that supports a reverse flow in roots, there are data sets that suggest the opposite. The whole argument about the ability of plants to have control upon the direction of the flow, starts with many literature citations that refer to plant roots having rectifier properties. However, Caldwell *et al.* (1998) analyzed the available data and concluded that the degree and time scale of rectification vary. It seems that when we refer to rectifying properties of the roots it should be meant as if one portion of whole root system absorbs water relatively easily and the rest of the root system prevents the water from leaking out. This is totally different than assuming that the same segment of root can uptake water much easily than it can actually lose it in the presence of an outward gradient. Furthermore, if we have few deeper roots and many shallow roots, the sum of the conductances in the shallow layer may still be significant even if the roots have some rectifying properties.

Finally although it would be desirable to predict how often and for how long a given ecosystem would experience hydraulic lift, it is very difficult unless data such as climatic and edaphic conditions are considered. Some computer models are meant to reproduce the interaction of climatic and edaphic conditions with the plant physiological processes. When a computer model successfully reproduces plant transpiration and carbon fixation together with its partitioning, its use might be extended to estimate magnitude and temporal evolution of hydraulic lift (Manunta *et al.*, 1998).

3.4.3 Contribution of hydraulic lift to daily ET

The potential for reverse flow has been analyzed in a quantitative fashion only during the last decade. Considerable amount of water presumably lifted at night was related to the fluctuations of the soil water potential where the roots of several taxa were located. The importance of hydraulic lift in the context of water used by vegetation has been pointed out by Caldwell *et al.* 1998. Wan *et al.* (1993) found that hydraulic lift of a suffrutescent shrub *G. sarothrae*, accounted for about 14% of its daily ET. During a modelling exercise Manunta *et al.* (1998) estimated that about 10-15 % of the water dissipated during evapotranspiration by *Pistacia lentiscus* could be water relocated via hydraulic lift. Richards and Caldwell (1987) reported that as high as 30% of *A. tridentata* ET is accounted for by hydraulic lift. The latter figure seems to represent an extreme daily value rather then the seasonal average. If this would be the case the discrepancy between the simulated (Manunta *et al.*, 1998) and the values reported by Richards and Caldwell (1987) might be caused by different climatic and soil moisture conditions. In some cases, the use of psychrometers and their sensitivity to soil temperature gradients could generate errors due to the conversion of the soil water potential readings into soil water content. Overall the theoretical values of 10-15 % of the total ET seems to be the more a conceivable one.

3.5 Root/soil properties and hydraulic lift

In the next few sections specific attention will be given to the radial and axial flow and the plant structures or conditions that constitutes the resistances to these two types of flow. Structural root properties, that are eventually responsible for outward flow of water are also discussed.

3.5.1 Radial movement of water in the roots

The largest resistance to water flow in plants is exerted by the array of cortical, endodermal and stelar cells, and the magnitude of this resistance is five orders of magnitude higher than the resistance found in the conducting elements of the xylem (Kolek and Kozinka, 1992). Water can flow across the tissue following three different pathways:

1) Crossing the cell wall, plasmalemma, cytoplasm and tonoplast at the boundary of each cell. By doing so water enters the cortex, and via the endodermis passes directly into the vessel or alternatively enters the conducting vessel via the pericycle and stelar parenchyma.
2) The second pathway for water flow is via the symplast, in this case water enters through the plasmodesmata and it leaves the symplast through the plasmalemma and cell wall of endodermal or stelar parenchyma cell adjacent to the vessel. As opposed to the vacuolar pathway, the symplastic water movement operates by crossing only two cell membranes while entering and leaving the symplast.
3) The last type of water flow occurs via the apoplast. Initially the inward water flow is interrupted by the Casparian strip, but further radial water movement can take place by entering the endodermal cells via the cell wall and plasmalemma. At this stage water continues flowing via either the plasmalemma and inner cell wall, or via plasmodesmata or via the apoplasmic pathway into the central cylinder. Regardless of the pathway, symplasmic or apoplasmic, the water has to cross the plasmalemma only twice.

3.5.2 Radial movement of water within and out of the xylem

Intervessel pits are usually found where vessels that are running parallel to each other have some areas of overlap. These contact regions are the sites where the water moves from one vessel to the one next to it, while flowing upward to the site of transpiration. Mechanical strength is ensured by the characteristic bordered structure of the pits, in particular the secondary wall provides support through the arcuate structure that allows exposures of membrane area for water movement. Because the pressure drop across them is rather moderate, intervessel pit membranes usually are not under much stress. However, the pressure drop across them can get fairly high as soon as the vessels experience air clogging. In this case the vapor blocked lumen is most likely to have a pressure close to atmospheric (+ 1 atm), at the same time vessels located nearby may have a negative pressure close to -10 or even -20 atm. The rather high pressure drop across the pit membrane can cause a large stress upon the pit membrane itself. But because bordered pits are structured to resists mechanical stress, water can move radially to the next vessel and continue to flow upward (Zimmermann, 1983).

Although there is no direct evidence on how bordered pits could facilitate water efflux from the roots it is conceivable that in the presence of a strong gradient water can move laterally. What has been indicated as possible mechanism for radial water movement in the xylem can help in explaining the following example:

1) One portion of the root apparatus is exposed to a soil water potential of -0.5 MPa, and the rest to a soil water potential of -1.0 MPa. If water cannot move radially from one root branch to the other, the root water potential would be probably lower for those sections of the roots in contact with the drier soil. However, the root water potential has been found to be about the same regardless of the outside soil water potential (Slavikova, 1967). This fact could be a supporting evidence of radial water movement among the different root branches.
2) If we now extend our analysis to the above ground part of the plant, we can start saying that a set of leaves in a plant is supplied with a flux of water coming from a

set of vascular bundles that originates in the roots. From the scenario described in point one, at least one set of vascular bundles would be exposed to a soil with a soil water potential of -0.5 MPa and another one to -1.0 MPa. If water could not move radially inside the plant we should then observe a set of leaves with a water potential at least 2 times more negative than the other one. However, such a strong difference in leaf water potential is not usually found.

In regards to the ability of water to flow radially within the conducting tissue, field experiments have provided interesting results. Greenidge (1955) found that lateral transfer in 12 woody species ultimately led to the development of a complete ring of stained wood. His experimental design consisted of fitting the living tree with cone frustums at the bottom of the trunk and the stem incised to allow a fluid to be injected. Above the point of injection the trunk was partially sawn to investigate how the interruption of the conducting elements would affect the pattern of the upward flow. Sawing at several positions above the point of cutting where the interruption of the flow was induced, revealed that while still flowing upward the water was also flowing radially above the partial saw cut. It is possible that suction forces generated by transpiration drove the radial flow. Ability of water to cross-transfer in living trees was also observed by Furr and Taylor (1933).

3.5.3 Radial movement of water from the roots

What seems to be more important in the context of hydraulic lift is the fact that much of the uptake and efflux of water may occur from young roots. If water exudation is identified only in the younger portions of the roots, this would indicate that water fluxes depend on certain structural characteristics of these roots. A possible explanation may be found in the Casparian strip and in the suberin lamellae of the hypodermis that are not fully formed yet. Another easy pathway with a relative low resistance to water flow is formed by the apoplastic gaps found in roots. Their importance is crucial since not only they allow water to pass into the transpiration stream, but they also permit water to leak out in the process of hydraulic lift or during exudation induced by internal root pressure. The presence of these apoplastic gaps allows the direction of the flow to be determined solely by the gradient in water potential (Caldwell *et al.*, 1998).

An additional form of relatively easy pathway for the water to flow is made up by the selective water channels called aquaporins (Steudle and Henzler, 1995) and their inability to rectify the flow. It seems that these structures constitute a symplastic preferential pathway for the water to flow out of the roots, even when the apoplastic pathways are obstructed by well developed exodermis and endodermis.

However, it could be argued that when the soil gets too dry (e.g., -1.5 MPa and lower) the roots undergo structural changes that might prevent water to be lost to the soil. Nobel and Huang (1992) observed that desert plants exposed to drought exhibit a loss in radial conductivity due to development of intercellular lacunae in the root cortex, and to the shedding of lateral roots.

3.6 Observable consequences of hydraulic lift

Within the context of hydraulic lift special attention should be given to the techniques used to measure this phenomenon, particularly when the objective is to prove that hydraulic lift takes place under field conditions. Some of the problems are related to the relative small and hardly measurable change in soil water content associated with hydraulic lift. And also to the temperature sensitivity of instruments such as psychrometers which may cause erroneous readings and fluctuations.

3.6.1 Changes in soil water content

In order to measure changes in water content associated with the phenomenon of hydraulic lift, Topp and colleagues (1996) placed time domain reflectometry (TDR) probes in the proximity of maize roots. Their results indicated an increase in water content at night, and these measurements were interpreted as supporting evidence of hydraulic lift. Although an increase in water content is an indication of water efflux from the roots, in this case the use of TDR probes might have caused some problems. Increase of the dielectric output is an indication of increase in water content in the medium. However, if the TDR probes are place too close to the roots there is no guarantee that the increase in water potential is actually happening in the soil and not simply in the plant tissue. This poses the problem of how close the instrument should be with respect to the roots that supposedly will experience the water efflux. When TDR probes are used for measuring water efflux from the roots it becomes important to consider the result of a theoretical analysis and the resolution characteristics of the instrument. This would lead toward a more reassuring interpretation of the instrument readings. For example TDR probes are able to detect a change in soil water content of about 1 %, and in section 3.4 we estimated that the hydraulic lifted water could be about 10-15 % of the daily ET. This could probably correspond to only about 1% of the soil water content in the first 10 cm of soil. Therefore if a diurnal fluctuation of about 1% is detected, chances are that this could be the amount of water re-located at night and used by evapotranspiration during daytime. Although TDR seems to be a proper tool for the detection of the hydraulic lift, I conclude that some problems might arise with the interpretation of the measurements. This is mainly because the instrument might be detecting a small change in water content that is near the limit edge of its resolution.

3.6.2 Changes in soil water potential

One of the strongest evidence of hydraulic lift taking place in the field has been obtained in the form of diurnal fluctuations in the water potential. Investigations of hydraulic lift and determination of the source of water used by different species have made use of different field techniques such as soil psychrometers (Richards and Caldwell, 1987). The use of psychrometers to determine soil water potential requires measurement protocols that account for the thermal gradients that might exists in the pyschrometers. Due to the magnitude of the log of the ratio between the actual and saturated vapor pressure, a temperature difference of 1 °C is equivalent to an 8 MPa difference in water potential. This can cause substantial errors in psychrometric measurements if the air immediately surrounding the thermocouple is at a different temperature than the air next to the sample. Because temperature gradients occur naturally in soil and usually change in magnitude and direction, it is therefore expected that such gradients may profoundly influence the psychrometer measurements. Laboratory testing of different soil psychrometers indicated that an induced temperature gradient equal to 1 °C cm^{-1} in the surrounding medium resulted in errors ranging from 1 to 6.2 MPa depending on sensor design (Wiebe *et al.*, 1977). In the case of hydraulic lift measurements in the field, special attention should be paid to the possibility that a placement of psychrometers close to the surface might depict diurnal fluctuations due to the soil temperature cycle rather than a real change in soil water potential.

3.7 Ecological benefits and significance

3.7.1 Ion transport

There is growing evidence that deep rooted shrubs and trees found in arid, semi-arid and even mesic environments exhibit hydraulic lift. This water transport process supports the plant diurnal demand for water, while improving the soil water status underneath the canopy (Richards and Caldwell, 1987). A comparison between open grassland and woody canopies reveals a better soil development for the latter. Greater water storage and higher soil nutrient concentration are usually attributes of a well developed soil (Joffre and Ramball, 1988). Richards and Caldwell (1987) have pointed out the implications of hydraulic lift for nutrient uptake. For instance, although nutrients are usually more abundant in the upper soil portion of the profile they are not always available to plants. Low soil water content constrains their mobility, thus plant growth could be restrained by both water and nutrient availability. In particular the nitrogen cycle is affected by soil water content. For example, despite nitrogen fixation being facilitated by some degree of soil dryness that allows O_2 and N_2 to move to the nitrogen fixing bacteria, a severe dehydration causes fixation to decrease. Non-legume plants acquire their nitrogen supply in the form of NO_3^- before then being reduced to NO_2^- and finally to NH_3^-. Nitrate reduction decreases with low water content in the soil, because NO_3^- is transported more slowly to the root surface by the transpiration stream.

Other salts of various inorganic ions are also essential for the plant metabolism and need to be concentrated near the roots from the surrounding solution. In soil, ions move through a combination of bulk flow and diffusion. Bulk flow takes place in water traveling in the transpiration stream, while diffusion occurs as gradients in ion concentrations that develop as ions are depleted next to the root surface. Ion uptake has been treated by Siddiqi and Glass (1982) by taking into consideration tissue and substrate concentration. Their formulation is an extension of the Michaelis-Menten equation for which influx rate is affected by several factors, including tissue and substrate concentrations. This model proved successful in simulating both K^+ (Läuchhli, 1984) and phosphate influx in barley roots (Lefebvre and Glass, 1982).

From what has been illustrated so far, it can be concluded that the phenomenon of hydraulic lift may be beneficial for ion accumulation in the proximity of the root surface. In addition, having water that is released in a ion rich soil and subsequently re-absorbed, could represent a considerable advantage over having water exclusively taken up from soil poor in ion content. However, it should be pointed out that plant ion uptake is also regulated by internal process in the root itself, ion compartmentation and nutrient status of the plant.

Water leaking out from roots is believed to generate rhizosheat formations, these soil micro coherent structures are formed under the influence of roots. They remain attached to the root and because these entities have higher water content than the surrounding they may facilitate nutrient uptake in dry soil (Watt *et al.*, 1994).

3.7.2 More water available for the plants

Water relocation through hydraulic lift has important implications in terms of water use by the plant community. For example, water released in the root mat region increases the amount of water resources made available to the plant community. Thus hydraulic lifted water combined with the water extracted from other portions of the profile can potentially extend the productive period of the plant. This fact is even more important in plant communities found in Mediterranean regions, where the ability of vegetation to fix carbon decreases as the drought season develops. During the summer drought, the highest photosynthetic rate occurs during the period of low incident photon flux density and relatively low temperature found in the early part of the day (Tenhunen *et al.*, 1985). As the day progresses the carbon fixation is probably limited by the stomatal closure induced by water stress. Having additional water available in the morning as a result of nocturnal lift could delay stomatal closure and in turn promote carbon fixation for longer time.

There may be cases in which water re-located in the upper drier soil is used by species other than the one performing hydraulic lift. Such a scenario of parasitism may originate from the fact that natural vegetation stands often consist of a mixture of species that have their roots located in different portions of the soil profile. It is not unusual to find heterogeneous root distribution with respect to soil depth; thus having species that grow roots in different part of the soil profile cause them to be dependent upon different sources of water. However, hydraulic lift can change the scenario described above by allowing shallow rooted plants to partially rely upon sources of water that would otherwise be inaccessible. An example could be the shallow rooted grasses for which the water available is that one closest to the surface as opposed to deeply rooted oaks for which the source of water is located at several meters depth. Suppose that water gets re-located through hydraulic lift by the oak, the water now becomes also available to the shallow rooted grass. This situation of parasitism may have some potential negative implications for the oak species that is losing some of the water absorbed by its roots. Regardless of the fact that water parasitism due to hydraulic lift can cause a waste of resources for the plant that is actually performing the work, water parasitism does have some important implications in terms of ecosystem dynamics. It is conceivable that the total amount of fixed carbon per unit ground is higher than it would be with plants unable to perform hydraulic lift.

Finally, another scenario could also arise, for example when the trees performing the lift are much taller than the understory vegetation they intercept solar radiation sooner in the day. This in turn drives evapotranspiration of the tree canopy so that the water is re-absorbed before the understory can actually make use of the hydraulically lifted water.

3.7.3 Implications at the ecosystem level

Water moved and stored by hydraulic lift is believed to aid several species in meeting their transpirational demand. An analysis of mean annual ET reveals that the tree-grass component of the dehesa ecosystem accumulated about 30 % more ET than the grass component (Belsky *et al.*, 1989; Koechlin *et al.*, 1986). A dependence of evapotranspiration upon annual rainfall was found for the grass component of the ecosystem but not for the tree-grass portion of the vegetation stand. These results have been presented as supporting evidence of the phenomenon of hydraulic lift. In addition, because hydraulic lift has a strong influence upon the water status of the soil underneath a woody canopy, a series of indirect effects could be attributed to this peculiar mechanism of water transport: 1) better soil development; 2) greater water storage capacity; 3) greater soil nutrients concentration; 4) higher floristic diversity. Thus, the extra amount of water re-located via hydraulic lift may increase biomass in the understory. Eventually, the physical and chemical properties of this soil may benefit from the biomass, that upon senescence, contributes to the soil carbon and nutrient pools.

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Chapter 4 Implications of hydraulic lift: a quantitative perspective

4.1 Introduction

Increasing evidence of soil water relocation through plant root system, defined as hydraulic lift by Richards and Caldwell (1987), suggests that hydrological and physiological models of plant water uptake should incorporate this mechanism. Several experimental studies have been reported with the objective of furthering the knowledge regarding the significance and extent of the hydraulic lift phenomenon (Burgess *et al.*, 1998; Caldwell and Richards, 1989). Data are now available to confirm that at least 27 plant species have root systems that can facilitate transfer of water from moist deep soil layers to dry surface soil (Caldwell *et al.*, 1998). Despite the growing number of reports on the occurrence of hydraulic lift, its ecological implication is still a matter of investigation. The hydraulic lift process could represent: a) a gain of water resources that would support evapotranspiration (ET); b) a survival strategy that extends the life span of root systems; c) a parasitism of water resources by shallow rooted species. For example a woody plant that sustains hydraulic lift when evapotranspiration exceeds rainfall could delay the development of water stress by complementing the available soil moisture while meeting the demand for evapotranspiration. A relatively small amount of water relocated to the surface soil could be significant for the survival of the fine roots, and for the continued uptake of nutrients.

Water relocated by hydraulic lift also represents a gain in water resources for coexisting species with shallow roots (Emerman and Dawson, 1996). Although part of the water located closer to the surface can also be lost by soil evaporation, such a loss could be partially prevented by reducing root conductance when exposed to dry soil. Nobel and Sanderson (1984) concluded that a partial loss in permeability experienced by roots when exposed to dry soil is presumably due to suberization.

At the landscape level, the process of hydraulic lift can carry significant consequences for the vegetation dynamics and hydrological regimes. Plants with deep root systems that can access the water table or water stored in deep soil layers could relocate this water into upper soil by hydraulic lift. This should influence the distribution of these species which may use this water.

Models of water movement through shrubs, trees and plant stands need to incorporate hydraulic lift into the calculation of both hydraulic resistance as well as into their ET estimates (Dawson, 1993). To date there is no documented effort on the incorporation of hydraulic lift into water uptake models and analysis of the resulting canopy resistance and ET fluxes. It is timely then to include hydraulic lift into soil-plant-atmosphere water transfer scheme and analyze its effect in terms of what was discussed above. Through modelling I will attempt to demonstrate the implications of water re-location and more specifically how a vegetation canopy might benefit from it. The objectives of this work are: 1) implementation of the hydraulic lift mechanism into my model; and 2) to elucidate on the ecological implication of having or lacking hydraulic lift.

4.2 Methods

4.2.1 Model specifications

Details in regards to the model development are given in Chapter 2 of this thesis. The plant component of the model, including stomatal conductance, photosynthesis and plant growth, have been integrated with the formulation of the energy balance described in detail by Verseghy *et al.* (1993). Computation of the plant and soil water balance is obtained by coupling the exchange of mass and energy between the canopy and the atmosphere to the three soil layers (Verseghy, 1991). Calculation of canopy water potential is used in the stomatal formulation to eventually reduce conductance. Leaf water potential is used to represent the canopy water status as affected by transpiration and available soil water. The leaf water potential is calculated by accounting for the balance between plant water content plus plant water uptake vs. transpiration. Plant water uptake is a function of root and soil properties that together constitute a series of resistances to water flow from the soil through the plant.

The exchange of water vapor between the canopy and the atmosphere makes use of a modified version of stomatal formulation proposed by Ball (1988). This formulation is used to calculate the value of conductance for two classes of leaves, sunlit and shaded respectively. Conductance is driven by photosynthesis, and reduced by atmospheric [CO_2], photosynthesis is modelled as the minimum of dark and light reaction rates in CO_2 fixation.

Canopy conductance is reduced according to the plant water status, whenever the plant experiences water stress. Plant water status is represented as the ratio between Ψ_l, leaf water potential (MPa) and Ψ_c the critical water potential at which stomatal conductance becomes half of the maximum value observed (Campbell, 1985). This ratio is then multiplied by the n parameter, which is the slope factor describing the increase in resistance as a function of the leaf water potential. Relations of this type have been reported by several authors (e.g., Cline *et al.*, 1976; Glatzel, 1983). This parameter can be as low as 3 or as high as 20 depending upon species (Campbell, 1985). Leaf water potential is calculated by coupling canopy transpiration to soil water uptake, calculated as the sum of that from each soil layer.

Conductance to water vapor decreases as Ψ_l drops, while water uptake varies positively with a decreasing Ψ_l due to the effect of Ψ_l upon the gradient between leaf and soil water potential. The resulting water uptake is inversely related to the sum of the root and soil resistance. Outward (transpiration) and inward (uptake) fluxes are mediated in part by the leaf water potential, there is therefore an equilibrium value for Ψ_l under any combination of soil and atmospheric conditions at which transpiration equals uptake. This value is calculated through an iterating procedure, thereby a value for Ψ_l is found at which transpiration from the energy balance is equilibrated with total water uptake. After the initial leaf water potential is computed, the difference between the transpiration and the water uptake by the roots and the water stored in the canopy is calculated. When the difference is < 0 the calculated water uptake by the roots is too large, the gradient between plant and soil is too steep, consequently the leaf water potential is lowered. If on the other hand the difference is > 0 the water uptake by roots is too small, the gradient between plant and soil is too low, consequently the leaf water potential is increased. The process continues until the difference is close to 0, then the iteration stops and the leaf water potential calculated is used to represent the plant water status. When the stomatal conductance is reduced because of leaf water potential, the CO_2 fixation is also proportionally reduced while preserving the internal [CO_2]. Therefore the reduction in CO_2 fixation via reduction in stomatal conductance preserves the formulation proposed by Ball (1987), in which the assimilation rate is the result of conductance times the difference between the atmospheric and internal [CO_2].

Previous findings reported that the root hydraulic resistance during outflow is about 40% greater than the hydraulic resistance during uptake (Baker and van Bavel, 1986). Therefore, whenever the soil water potential decreases to a value lower than the leaf water potential, the model assigns a radial resistivity to water outflow 40% greater than the radial resistivity for water uptake. Furthermore, the scenario with no hydraulic lift is obtained by forcing the roots to exert infinite hydraulic resistance whenever the soil water potential Ψ_s drops below the one of the canopy.

4.2.2 Characteristics of the site

In many arid and semi-arid regions, dry soils are often above moist soils or aquifers. For example, in the northwestern part of Sardinia about 23 % of the total rainfall infiltrates the Mesozoic marine deposits (Carboni *et al.*, 1980). This relatively high infiltration rate constitutes an essential supply mechanism for the underground water reservoir. A large water resource is therefore available below ground (Carboni *et al.*, 1980), this water may be utilized by deep rooted plants. In the Mediterranean area, especially in coastal areas and regions with hilly topography, the "maquis" ecosystem is widely distributed (Schonfelder and Schonfelder, 1996). This ecosystem consists of a dense vegetation stand of evergreen scrubs and small trees. In general the maquis is the results of intense exploitation for timber of *Quercus ilex* forest (Schonfelder and Schonfelder, 1996).

The site of the investigation is located in the north west part of Sardinia, Italy, 20 kilometers ca. from the city of Alghero, the dominant woody species at the site is *Pistacia lentiscus*. These plants present two of the main attributes that might support hydraulic lift: a) they are phreatophitic, therefore able to tap into the water table or water stored in rock interstice; and b) in the summer their roots traverse very dry soil.

Hilly topography at the site is characterized by Chromic Luvisols (Tavernier and Louis, 1985) with a relative stony and shallow profile along the slopes and a rather deeper one at the bottom of the valley. Soil sampling in the proximity of three mature *Pistacia lentiscus* shrubs revealed a distinct hard-pan layer at a depth of about 40 cm. Visual examination of road cut banks show that large roots (about 2-3 cm in diameter) did penetrate the hard-pan layer. Similar circumstances were observed by Dawson (1993) beneath sugar maple trees (*Acer saccharum*) for which hydraulic lift was successfully measured using stable isotope analysis.

4.2.3 Simulation experiment

In the model the soil hydraulic properties are derived from tabulated values grouped in 11 soil textural classes (Clap and Hornberger, 1978), the model was then initialized with soil texture data from the site. The model was also initialized with the biological properties of the plant functional type (C_3) as in Chapter 2 (Table 2.3), with the only exception being the n parameter set equal to 4 for the *Pistacia lentiscus*. At the beginning of the simulation the model was initialized with a leaf area index of 2.7, this value is the average I have recorded at the site. Leaf area index was estimated in 12 different points in the canopy using a digital plant canopy imager (Model CI-100, CID, Inc. Vancouver, WA, USA).

In order to investigate the importance of hydraulic lift two study case scenarios were simulated, one having roots capable of losing water in the presence of an outward gradient, and a second having roots with rectifying properties (i.e. preventing the outward water flow despite a lower water potential in the soil). These two study case scenarios were simulated using two rainfall regimes. The two rainfall regimes (Fig. 4.1b) are here referred as wet (811 mm per year) and dry (650 mm per year). Meteorological variables used to drive the model, were recorded at a nearby location by the Sardinian Agrometeorological Service (SAR) in 1996.

Model outputs for canopy conductance, transpiration, soil evaporation, leaf and soil water potential were used to compare how the presence or absence of hydraulic lift affects soil moisture distribution beneath a canopy growing in a water limited environment, and therefore the overall plant water status.

4.3 Results

The driest period of the year 1996, when the conditions were favorable for hydraulic lift (i.e. June 8th to August 27th, DOY 160 to DOY 240), was selected for the analysis. When the canopy of *Pistacia lentiscus* was allowed to perform hydraulic lift the two soil layers closer to the surface (i.e., 0.0-0.10 m, and 0.10-0.35 m) showed a similar response in terms of their water potential (Fig. 4.2a and b). Simulated soil water potentials with wet boundary conditions caused the mean value for the two layers to drop from –0.2 MPa to –1.0 MPa by the end of the drought period. A similar trend was obtained when the model was run under the dry climatic conditions and the soil water potential dropped from –0.6 to –1.3 MPa. Assigning rectifying properties to the roots imposed the lack of hydraulic lift and caused a remarkably different soil water potential distribution in soil. In Fig. 4.3a the soil water potential of the top soil layer (0.0-010 m) shows that after approximately 15 days from the beginning of the drought, a sharp drop in water potential stars to develop. In the case of drier case scenario the sharp drop in water potential becomes visible soon after the beginning of the dry period. By the end of the month of August the water potential of the top soil layer has dropped to about -20 MPa under wet and to about -28 MPa under dry conditions. The middle layer (0.1-0.35 m) did not change much under both climatic conditions. Water potential of the lower layer (0.35-4.1 m) reflected the conditions caused by the presence or absence of the water relocation via hydraulic lift (Fig. 4.3b). At the beginning of the period under consideration the water potential of the four study case scenarios [i.e, (hydraulic lift and no hydraulic lift) x 2 climatic conditions], ranged around –0.025 MPa, after 35 days the drop in water potential became more pronounced. Water uptake used for transpiration was the primary cause of drying in the third layer. However the phenomenon was even greater when the water was relocated via hydraulic lift into the two upper layers. Lowest value of all (i.e. -0.65 MPa), was reached by the soil beneath the canopy that performed hydraulic lift under dry climatic conditions. Differences in water potential of the two upper layers caused by the presence or lack of hydraulic lift were reflected in the leaf water potential of the two canopies (Fig. 4.4a and b; 4.5a and b). In comparing Fig. 4.4a and b with Fig. 4.5a and b it is apparent that the daily swing in leaf water potential is greater for the canopy unable to relocate water. This trend was also found in the simulations obtained using the dry climatic conditions. Usually the leaf water potential of the canopy performing hydraulic lift fluctuated within +/- 0.15 MPa, while the leaf water potential of the canopy unable to perform hydraulic lift within +/- 0.6 MPa. Evapotranspiration was also affected by hydraulic lift, starting around June 28th (DOY 180) the evapotranspiration of the canopy performing hydraulic lift exceeded the one of the canopy not performing hydraulic lift, by about 1 mm day^{-1} under wet climatic conditions. When the simulations were carried out using the dry climatic conditions the difference in terms of ET started to show as soon the dry period started (i.e. DOY 180). On some ET of the canopy performing hydraulic lift exceeded by about 1.5 mm the one of the canopy without hydraulic lift.

Toward the end of August and under both climatic scenarios, differences in ET associated with hydraulic lift were no longer discernible (Fig. 4.6a and b). A separation between evaporation and transpiration showed that the difference between the two canopy types is mainly in terms of soil evaporation. Water relocated via hydraulic lift is partially lost from the soil via evaporation. Under wet climatic conditions the soil evaporation of the canopy with hydraulic lift exceeded the one of the canopy unable to relocate the water by about 0.5 mm day^{-1} (Fig. 4.7a). In the drier case the soil evaporation beneath a canopy with hydraulic lift features exceeded the one without it by about 0.6 mm day^{-1}, with extreme values of 1.2 mm day^{-1}.

Cumulated evapotranspiration for the period under consideration and for the canopy performing hydraulic lift under wet conditions reached the highest value with more than 4.8×10^5 g m^{-2}. While the lowest simulated ET (i.e., about 4.0×10^5 g m^{-2}) was simulated for canopy exposed to dry climatic conditions and unable to perform hydraulic lift (Fig. 4.8a). The other two cases of study, canopy without hydraulic lift under wet conditions and canopy performing hydraulic lift under dry conditions, dissipated about 4.5×10^5 and 4.4×10^5 g m^{-2} of water respectively.

Cumulated fixed carbon was highest for the canopy with hydraulic lift and under wet conditions, by the end of 27th of August the value of 1802 g m^{-2} was reached (Fig. 4.8b). Under the same climatic conditions but without the water being relocated in the upper layers, the cumulated carbon approached 1755 g m^{-2}. When the canopy was allowed to perform hydraulic lift but under drier conditions, the fixed cumulated carbon dropped to 1629 g m^{-2}. Lowest of all, 1601 g m^{-2}, was the value obtained under dry climatic conditions and without the water being relocated closer to the surface.

Because of the role of the stomata in controlling transpiration and affecting carbon fixation, and because the plant water status is linked to the stomatal conductance formulation, I tested how the presence or absence of hydraulic lift could affect different canopies with different behaviors. Cline and Campbell (1976) reported that different woody species show different stomatal conductance responses to leaf water potential. In this model canopy conductance is reduced according to the plant water status, whenever the plant experiences water stress. Plant water status is represented as the ratio between the leaf water potential Ψ_l, and the critical water potential Ψ_c, at which stomatal conductance becomes half of the maximum value observed (Campbell, 1985). This ratio is then multiplied by the n parameter, which is the slope factor describing the increase in resistance as a function of the leaf water potential. The range of the slope parameter n was indicated to be between 3 and 20 (Campbell, 1985). In table 4.1 the cumulated ET and carbon are reported for several types of stomatal responses obtained with the use of different parameter values. The higher the value of the parameter *n*, the higher was the amount of cumulated ET and carbon. The canopy that relocated water as compared to the canopy lacking hydraulic lift accumulated a greater amount of carbon and ET. This trend was retained for all the simulated stomatal response to leaf water potential, and in particular the relocated water sustained an increase in carbon fixation that ranged from about 2.7 to 5.7 % for the wet and from 1.7 to 2.7 % for dry conditions respectively. Similarly the extra water in the soil closer to the surface sustained an increase in seasonal ET that ranged from about 6.5 to 10 % for the wet and from 9.7 to 10.7 % for dry conditions respectively.

Diurnal courses of leaf water potential and canopy conductance have been selected and plotted to integrate the analysis of the 80 day time series. Two 48 hours cycles were selected, one in the middle of the period under consideration and one at the end. Starting on July 17th (DOY 199), Fig. 4.9a and b, show the simulated leaf water potentials of the two canopy types exposed to wet conditions. At night when the transpiration is at its minimum the canopy re-hydrates, the canopy without hydraulic lift approaches a nocturnal value of leaf water potential of –0.4MPa as compared to –0.8 MPa of the canopy performing hydraulic lift (Fig. 4.9a). During the day the most negative value (-1.3 MPa) is the one reached by the canopy with roots acting as rectifier, while the canopy carrying on with hydraulic lift never drops below –1.2 MPa. During the early daylight hours of July 17th the higher leaf water potential of canopy unable to perform hydraulic lift causes the canopy conductance to peak around 0.010 m s^{-1}. This value is about 0.002 m s^{-1} higher than the other canopy type. As the day progresses, the trend reverses and the canopy without hydraulic lift drops about 0.002 m s^{-1} below the one of the canopy with hydraulic lift for the rest of the day. On the following day a similar trend is observed and the previous morning afternoon pattern reflects again the course of the leaf water potential. This allows the canopy without hydraulic lift properties to generate a greater canopy conductance but only before noon.

A similar analysis was performed at later time in the season (Fig. 4.10a and b), and simulation results confirmed the trend observed at the beginning of the period under consideration. In this case the canopy conductance of the canopy unable to perform hydraulic lift becomes lower than the one able to perform hydraulic lift a little later in day. Overall the canopy with hydraulic conductance exceeds the conductance of the other canopy by 0.001 m s^{-1} only from noon till dusk; while the canopy without hydraulic lift exceeds the other canopy conductance by the same amount, but only during the hours before noon (Fig. 4.10a and b). When the model was run under dry climatic conditions the leaf water potential and canopy conductance of the first 48 hours cycle show a similar response to the one obtained under wet conditions (Fig. 4.11a). For the 48 hours cycle starting on August 25th (DOY 238) the dry climatic conditions caused the leaf water potential in the afternoon hours to be of similar magnitude for both canopies (Fig. 4.12a). Conductance values for both canopies were also similar from noon to dusk. However, leaf water potential of the canopy unable to perform hydraulic lift was about 0.3 MPa higher, and caused its canopy conductance to exceed the one of the canopy without hydraulic lift by about 0.002 m s^{-1} in the early morning. This tendency was even stronger on August 27th (DOY 240) when this value was about 0.003 m s^{-1} (Fig. 4.12b).

In the model, water relocated via hydraulic lift in the upper layers caused a pronounced daily swing in soil water potential. Relocated water under wet climatic conditions caused the soil water potential of the 0.0-0.10 meter layer to go from the minimum value of –1.2 MPa at 15:00 hours to –0.86 MPa shortly before dawn (Fig. 4.13a). The second layer from the top (0.10-0.35 m) had higher water potential values, and the extreme values for both daytime and nighttime occur about one hour later than in the layer closest to the surface. In terms of absolute values the minimum value of – 1.1 MPa is also approached shortly before dawn, whereas by the end of the day a value close to –0.8 MPa is reached. For the same 48-hour cycle but obtained under dry climatic forcing the evolution over time of soil water potential resembles the results obtained under wet conditions (Fig. 4.13b). Different rainfall regime causes the maximum soil water potential value to be close to –0.94 MPa for the 0.0-0.10 m, and -

0.99 MPa for the 0.10-0.35 m soil layers. A 48-hour time series at the end of the period under consideration shows that the main difference under both climatic conditions is due to the soil water depleted by ET together with the absence of precipitation (Fig. 4.14a and b). Lower water content is reflected in the general lower maximum and minimum soil water potential as compared to the cycle that starts on July 17th (DOY 199).

4.4 Discussion

Simulated results showed the diurnal changes in plant-soil water balance associated with hydraulic lift, and in particular how the water relocated via hydraulic lift contributes to canopy transpiration fluxes. These results were obtained by linking the leaf water potential to stomatal conductance, so that the importance of hydraulic lift could be evaluated at the canopy level. Simulations of water use and fixed carbon allowed an assessment of the possible effects of hydraulic lift on total carbon assimilated during the growing season.

In the upper layers the water relocated via hydraulic lift resulted in a pronounced diurnal variation of soil water potential. Under the wet climatic conditions the soil water potential of the 0.0-0.10 meter layer fluctuated from −1.2 MPa at 15:00 hours to −0.86 MPa shortly before dawn (Fig. 4.13a). Similar diurnal fluctuations in soil water potential have been reported elsewhere (Dawson, 1997). Previous studies indicate that water relocated at nighttime via hydraulic lift was transpired by the same species during the following day (Caldwell and Richards, 1989). For example when hydraulic lift was circumvented by artificially inducing nighttime transpiration under artificial light, the transpiration rate during the following day dropped substantially (Caldwell and Richards, 1989). This effect was found to be largely reversible, providing circumstantial evidence in support of the hypothesis that hydraulically lifted water is a substantial portion of daily ET. Other field observations and experiments produced estimates in which the relocated water could account for as low as 15 % of the whole plant transpiration (Wan *et al.*, 1993) to as much as about 30% (Richards and Caldwell, 1987 in Caldwell *et al.*, 1998). In this modelling exercise I explored the same hypothesis for the *Pistacia lentiscus* canopy. The amount of hydraulically lifted water was about 1 mm day^{-1} for most of the period under consideration (Fig. 4.1a), this amount is about 15 % of the daily ET. Although these results are in accordance with those measured by other authors in the field, it is worth noting that when water was relocated closer to the surface the soil evaporation increased from about 0.2 to 0.6 mm day^{-1} (Fig. 4.7a), and from about 0.2 to 0.8 mm day^{-1} (Fig. 4.7b). Increase in seasonal ET due to relocated water via hydraulic lift, was however lower than some of the daily values discussed previously. This increase in seasonal ET ranged from about 6.5 to 9.6 % for the wet and dry conditions respectively. However the gain in fixed carbon was less pronounced and by the end of the period under consideration ranged between 1.7 and 2.7%.

While other authors (Caldwell *et al.*, 1998; Wan *et al.*, 1993; Dawson, 1996) suggest that hydraulic lift provides an additional source of water, model simulations indicate that although this hypothesis is valid in its principles, the gain in additional ET did not result into a significant carbon gain for the same species responsible for the lift. This type of analysis was extended to explore how different stomatal responses to leaf water potential, would affect seasonal ET and seasonal fixed carbon. Results indicated that the relocated water sustained a higher carbon fixation that ranged from about 2.7 to 5.7 % for the wet and from 1.7 to 2.7 % for dry conditions respectively. Similarly the extra water in the soil closer to the surface sustained a higher seasonal ET that ranged from about 6.5 to 10 % for the wet and from 9.7 to 10.7 % for dry conditions respectively (Table 4.1).

The analysis of seasonal ET reveals that although the relocated water could make up about 15 % of the daily ET, not all the water is evaporated from the soil or transpired by the plant. Over time then, an accumulation of soil moisture in the upper layers develops, leading to a moister soil beneath the canopy performing hydraulic lift. Hence this study reveals that although hydraulic lift contributes to ET, it maintains the soil moist and perhaps creates favorable conditions for plant physiological functions.

Among a number of important physiological functions that water relocated by hydraulic lift may facilitate we can include root longevity. Burgess *et al.* (1998) suggest that reverse water flow maintained the fine roots in a functional state throughout the dry season, allowing rapid water uptake from the newly wetted soil. On the recovery of uptake by roots after watering the dry soil carries a great agricultural and ecological importance. It could be argued that in the case of light-medium rain (less than 10 mm) infiltration into a medium textured soil would probably do not exceeds 50 mm, therefore the proximity to the surface would make this water prompt to be evaporated (Passioura, 1988). Unless of course roots are able to take up the water before a potential evaporation rate of 5 mm day^{-1} would dissipate the water into the atmosphere. During an experiment targeted to release resources, reduce stem competition and improve productivity of a holm oak (*Quercus ilex* L.) forest in Spain, López *et al.*, (1998) found that growth of fine roots was more closely associated with soil water content. Several authors (Dowdy *et al.*, 1995; Kätterer *et al.*, 1995) indicated that water availability is probably the main factor responsible for changes in species root growth strategy. Simulated conditions under lack of hydraulic lift caused the soil water potential to drop to extremely negative value, i.e. about –20 MPa and –30 MPa for wet and dry conditions. This in turn could create difficult conditions for roots to grow or survive. Deans (1979) reported that mortality of fine roots in a Sitka spruce (*Picea sitchensis*) plantation occurred whenever incident precipitation failed to maintain soil water potential near zero.

Roots increase hydraulic conductance of the soil-root system, therefore in areas where drought is frequent and rainfall events small (e.g., less than 15 mm), relocated water via hydraulic lift maintains the root system functional, so that when the rainfall occurs the water could be readily taken up before it evaporates.

I argue that the absence of hydraulic lift can represent a danger for the roots to loose their ability to uptake water. Nobel and Sarderson (1984) found that the roots of desert succulent plant lost much of their permeability when exposed to dry conditions over a period of days. Within few hours from rewatering the lost permeability was partially recovered, however a substantial recovery in permeability was associated with the growth of new roots, for which a period of at least two days was needed. In summary if the roots of these desert succulents can be regarded on one hand as water use efficient due to their rectifying properties, it is argued that the recovery of permeability reached only after two days can cause a great amount of light rain events to be lost by evaporation.

It is however surprising that despite the large amount of work carried out in the area of plant water relations very little is known in regards to the amount and rate at which water is lost from the roots (Boyer, 1985; Passioura, 1988). This, besides the widely reported exudation of carbohydrates and water by plant (Fiscus, 1986, Kramer and Boyer, 1995), and the fact that water potential of plant tissue can be higher than the one of the soil (Nobel and Sanderson, 1984). However a very rapid increase in radial resistance has been demonstrated for two desert plants when the roots were exposed to air at 20 C with a vapor pressure deficit of 1.2 kPa, or water potential of –93.6 MPa. Therefore although rapid increase in radial resistance is conceivable, it takes large changes in soil water potential before radial resistance can rise high enough to prevent water loss (Richards and Caldwell, 1987). Simulated conditions for a Mediterranean type of ecosystem support the hypothesis that even when the water is prevented from being relocated closer to the surface, the soil water potential can rarely approach the values needed to induce a rapid increase in radial resistance. Evidence supporting rapid increase in radial resistance associated to changes in soil water potential is believed to be valid for extremely dry conditions such as those found in deserts.

While the number of species reported to be able to perform hydraulic lift is growing the need for the including this mechanism into water balance calculation is very much unfulfilled. Emerman and Dawson (1996) concluded that the volume of hydraulically lifted water is sufficiently great, and therefore ecosystems model used for water balance calculation should include the hydraulic lift mechanism if ought to be used where hydraulic lift occurs. With this work I included the hydraulic lift into a plant water uptake scheme and use it to make some considerations in regards to phreatophitic plant canopy growing in water limited environments. It is suggested that until substancial evidence of a fundamental plant mechanism that prevents roots from leaking water is found, soil-plant-atmosphere models that are meant to be used under water limited conditions should incorporate the hydraulic lift phenomenon. Even more desirable if the plant canopy: a) grows over soils that have an hard-pan layer that prevents capillary rise; b) has large diameter roots that pierce through the hard-pan; c) has roots growing in soils that at some point in the season could drop to a water potential lower than the one of the plant tissue.

4.5 Conclusion

With this series of simulations I have demonstrated that when a plant canopy in the Mediterranean type of ecosystem is hypothesized to have roots acting as a rectifier-like, the soil layer near the surface becomes extremely dry. This fact is not usually observed under *Pistacia lentiscus* where soil is usually dry only at the beginning of the fall when the ground water level is at its seasonal minimum. It is conceivable that phreatophitic plants share a common survival strategy. For example a phreatophytic plant such as *Prosopis tamaguro* (Mooney *et al.*, 1980) demonstrated unique water relations and surviving drought by: a) tapping into the relatively shallow water and b) subsequently reabsorbing the water that was leaked out due to the low water potential of the surface soil. Another indication of water relocated closer to the surface is the fact that in the Mediterranean areas the microclimate beneath or in the immediate proximity of woody canopies, it is remarkably different from the surrounding. This supports the theory of a canopy-induced microenvironment and improved soil water balance results in a better soil development, greater soil nutrient concentrations and higher floristic diversity (Joffre and Rambal 1988; Belsky *et al.*, 1989). Although evidence is only be circumstantial, hydraulic lift can be the triggering factor of series of ecological benefits that can be tangible on the short or long term. An example of short-term benefit could be maintaining roots alive and able to uptake water of small rainfall events before it evaporates, while supporting a better soil formation is the hypothesized long-term benefit.

Table 4.1. Cumulated fixed carbon and cumulated ET from DOY 160 to DOY 240. The results were obtained assigning different values to the parameter (n), which represents the type of stomatal response to leaf water potential (Campbell, G.S., 1985). The simulations obtained with the (n) parameter equals 4, refer to the *Pistacia lentiscus* stand.

Canopy	HL	NO-HL	HL	NO-HL	HL vs. NO-HL	
Climate	WET	WET	DRY	DRY	WET	DRY
	(n) parameter equals 4					
C (g m^{-2})	1802	1755	1629	1601	+2.7%	+1.7%
ET (g m^{-2})	480530	450905	444079	404848	+6.6%	+9.7%
	(n) parameter equals 10					
C (g m^{-2})	1941	1852	1757	1710	+4.8%	+2.7%
ET (g m^{-2})	511000	469000	468000	423000	+9.0%	+10.6%
	(n) parameter equals 20					
C (g m^{-2})	1992	1883	1789	1749	+5.8%	+2.3%
ET (g m^{-2})	522000	474000	473000	427000	+10.1%	+10.8%

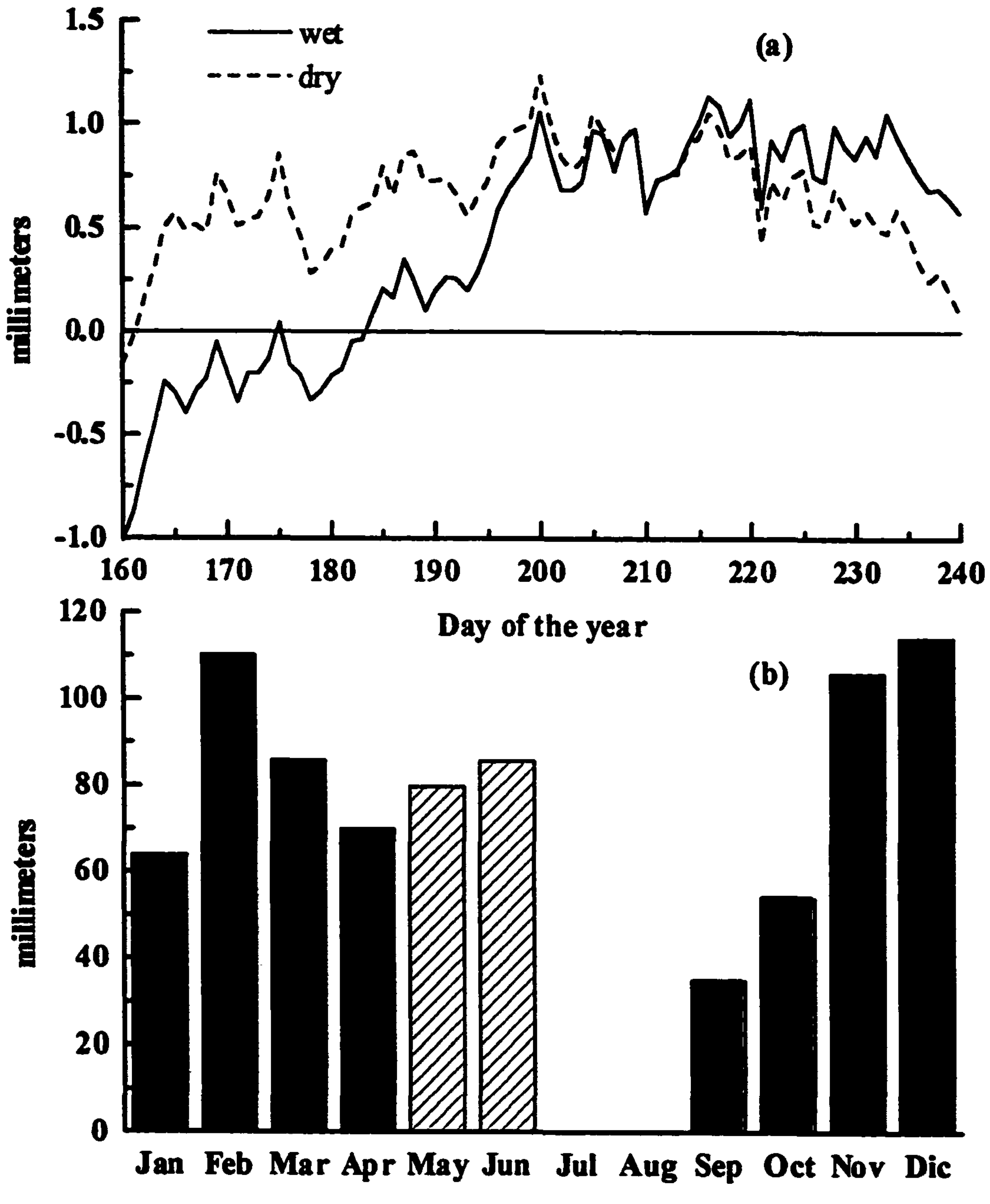

Fig. 4.1 (a) Water relocated via hydraulic lift from 8 June to 27 August 1996 (DOY 160 to 240); (b) monthly rainfall in 1996 solid bars plus hatched pattern, and relatively drier season solid bars only.

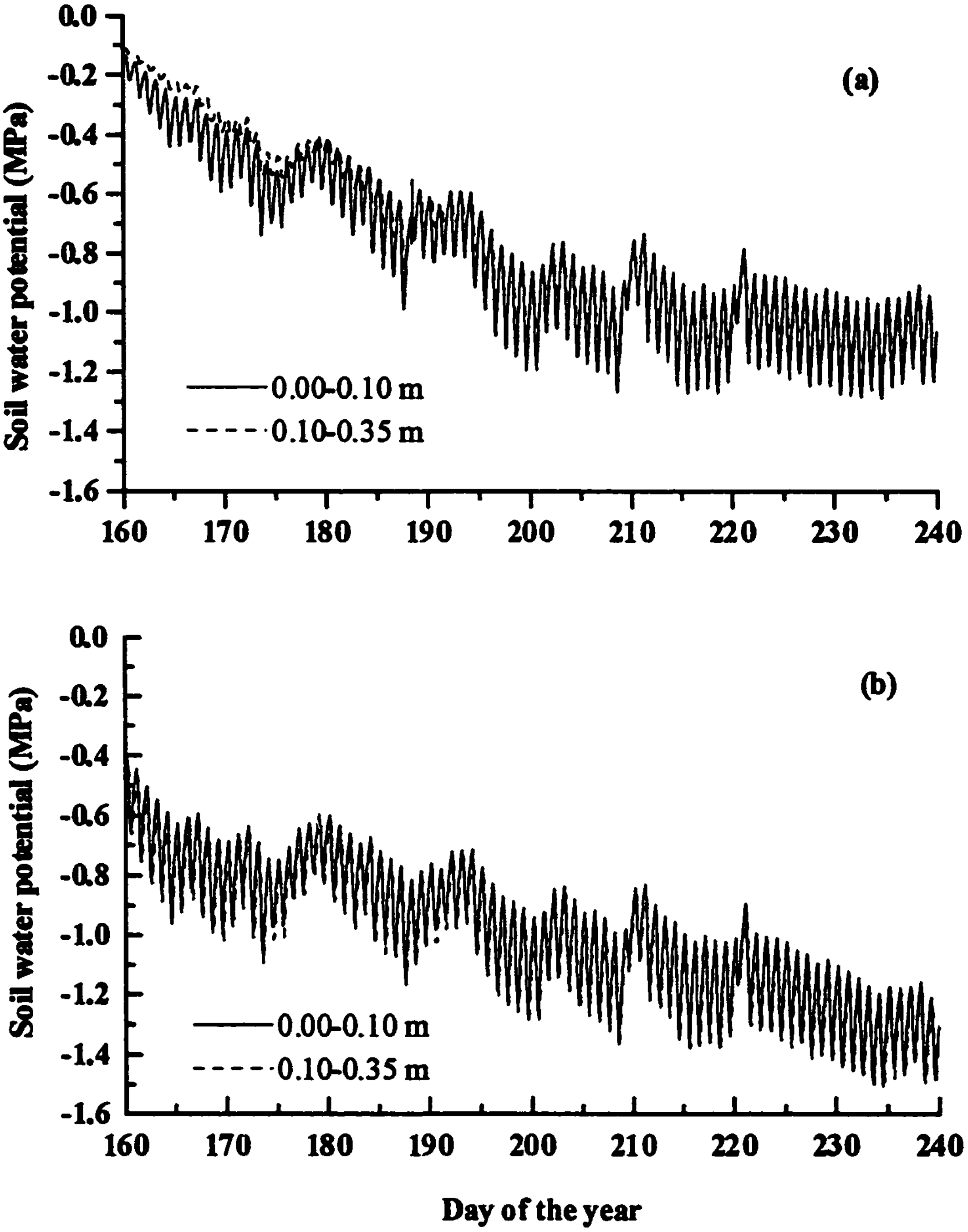

Fig. 4.2 Soil water potential under wet (a) and dry (b) conditions beneath a canopy able to perform hydraulic lift. The simulations span from 8 June to 27 August 1996 (DOY 160 to 240).

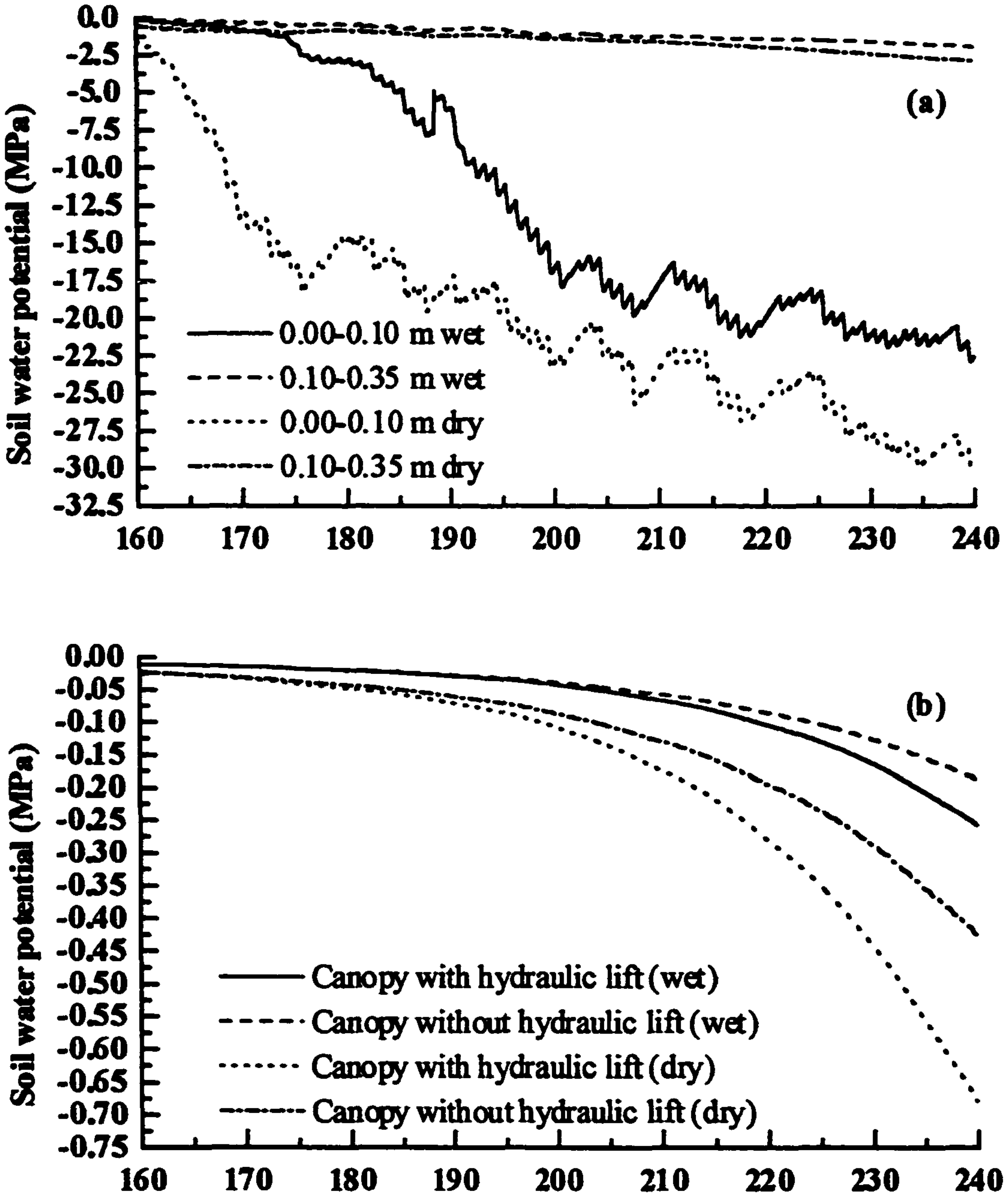

Fig. 4.3 (a) Soil water potential under wet and dry conditions beneath a canopy unable to perform hydraulic lift; (b) soil water potential of the 0.35-4.10 m layer for climatic conditions as illustrated in graph (a) for a canopy able and unable to perform hydraulic lift. The simulations span from 8 June to 27 August 1996 (DOY 160 to 240).

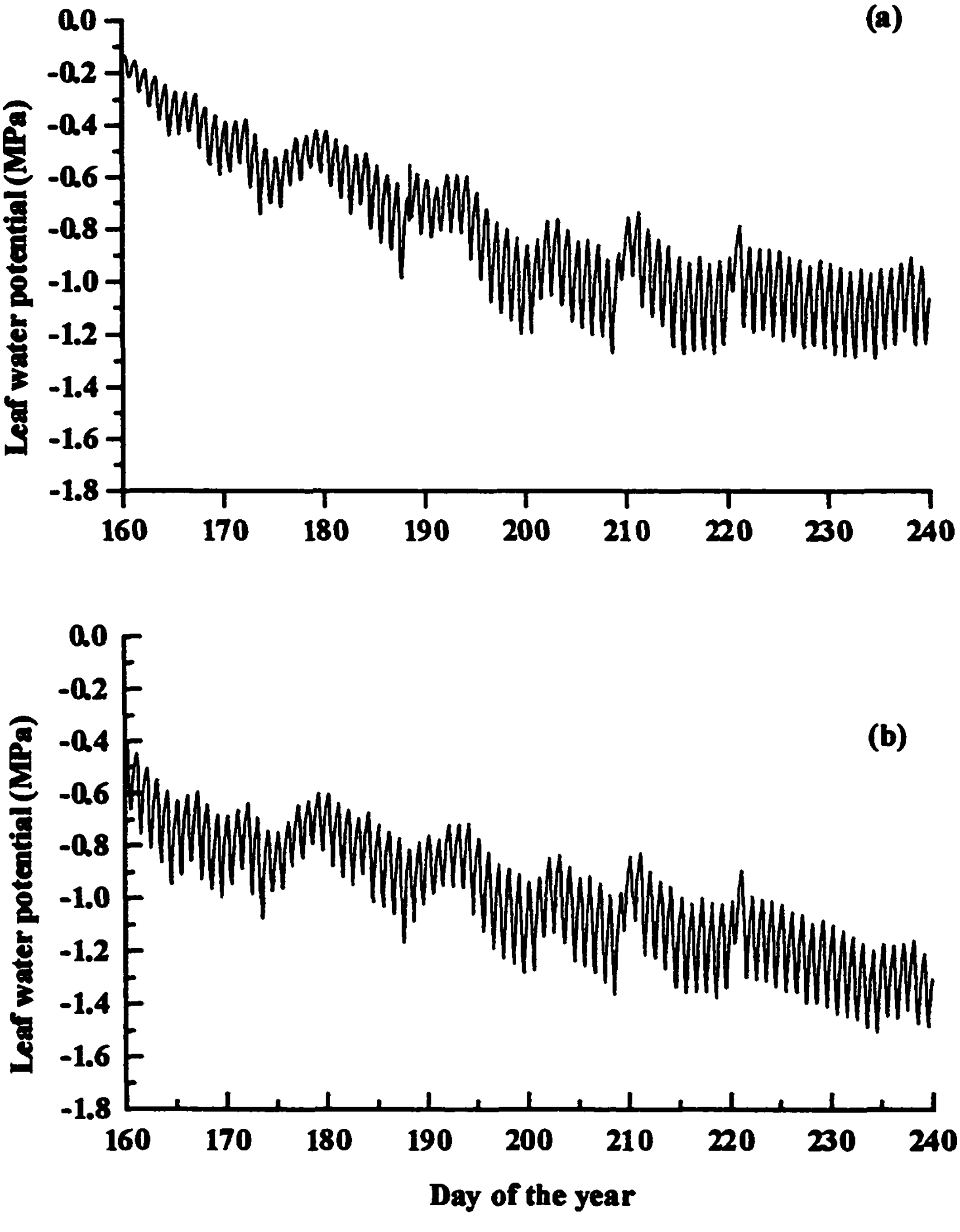

Fig. 4.4 Leaf water potential of a canopy able to perform hydraulic lift, under (a) wet conditions and (b) dry conditions, from 8 June to 27 August 1996 (DOY 160 to 240).

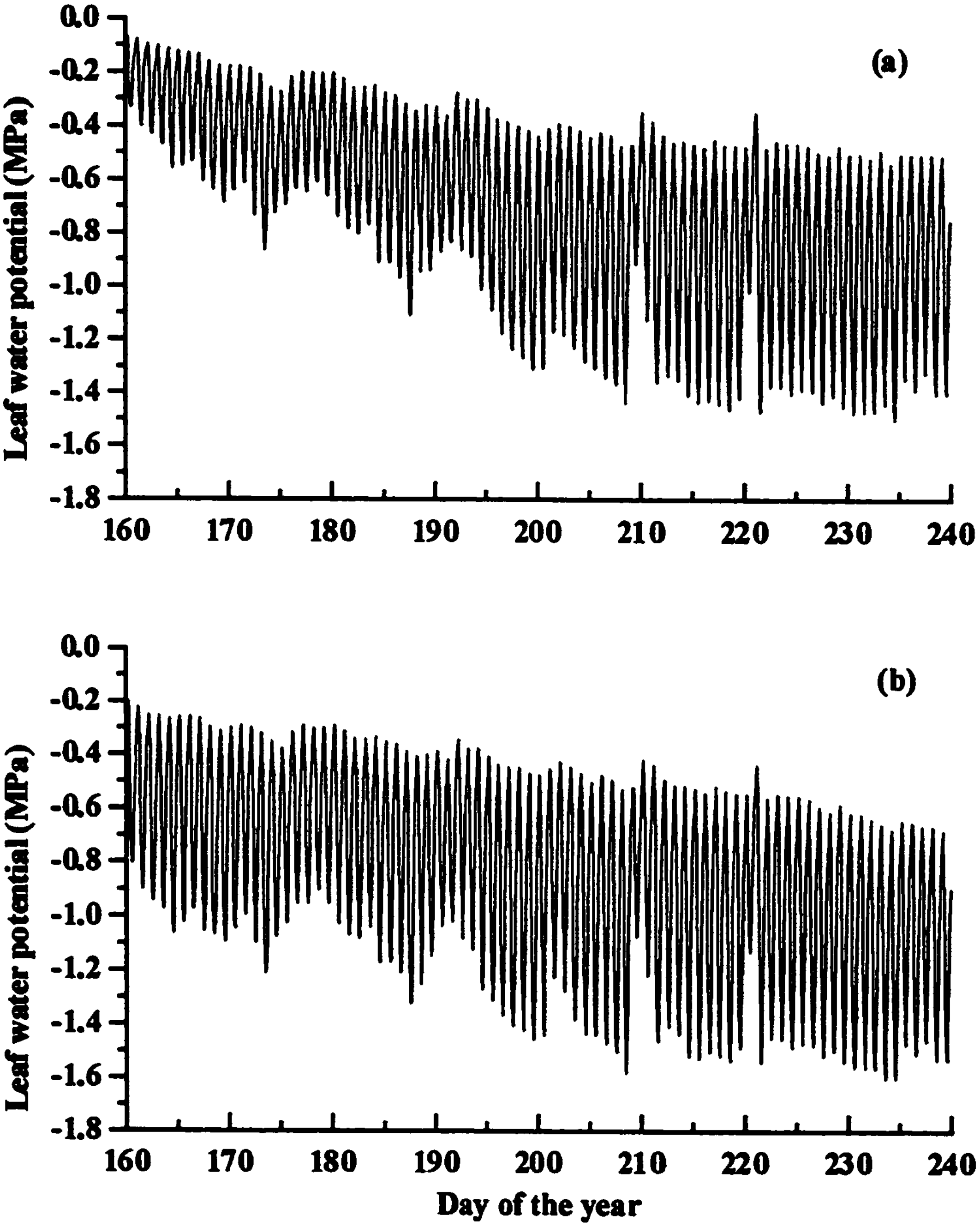

Fig. 4.5 Leaf water potential of a canopy unable to perform hydraulic lift, under (a) wet conditions and (b) dry conditions from 8 June to 27 August 1996 (DOY 160 to 240).

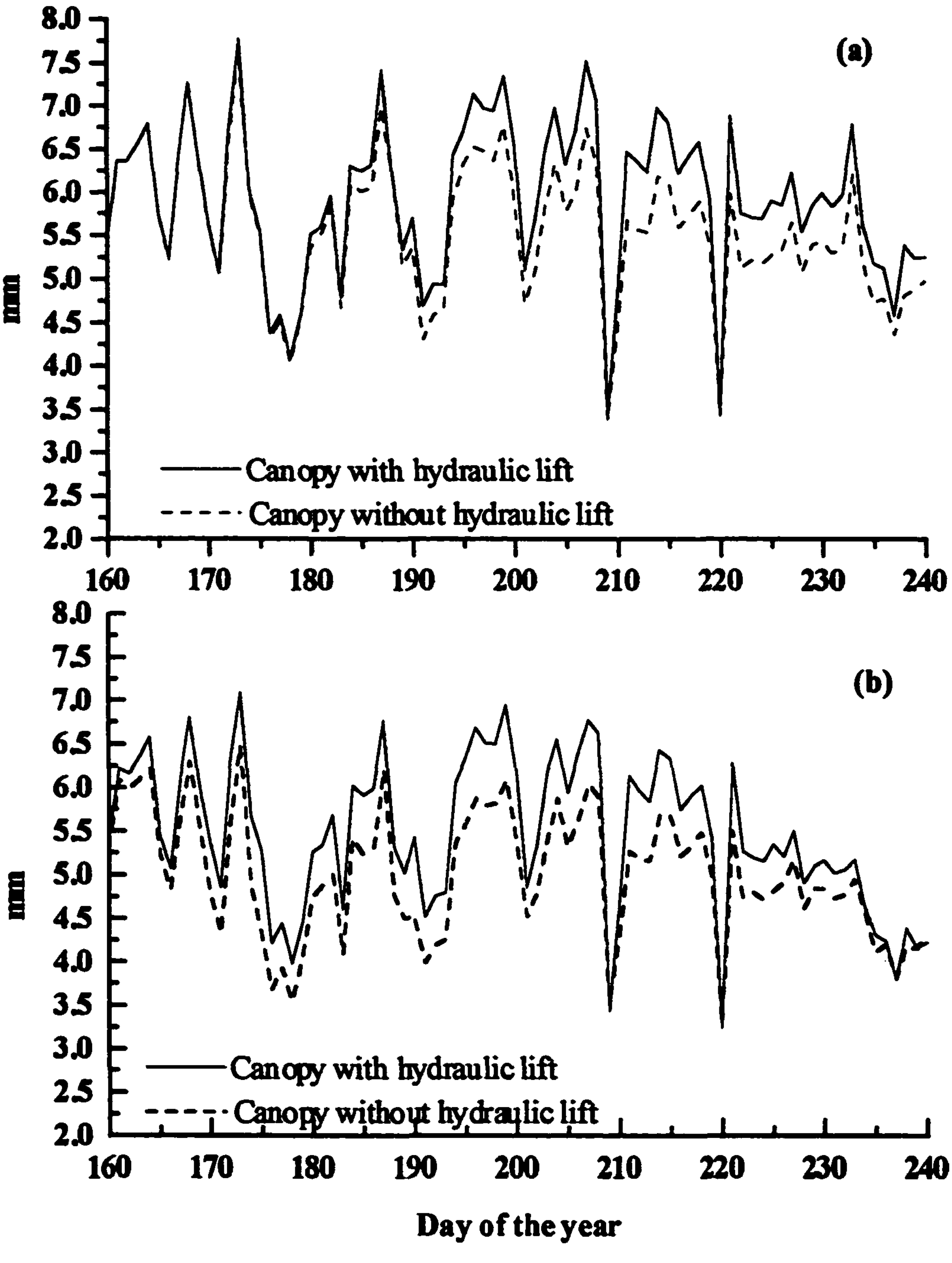

Fig. 4.6 Evapotranspiration under (a) wet conditions and (b) dry conditions from 8 June to 27 August 1996(DOY 160 to 240).

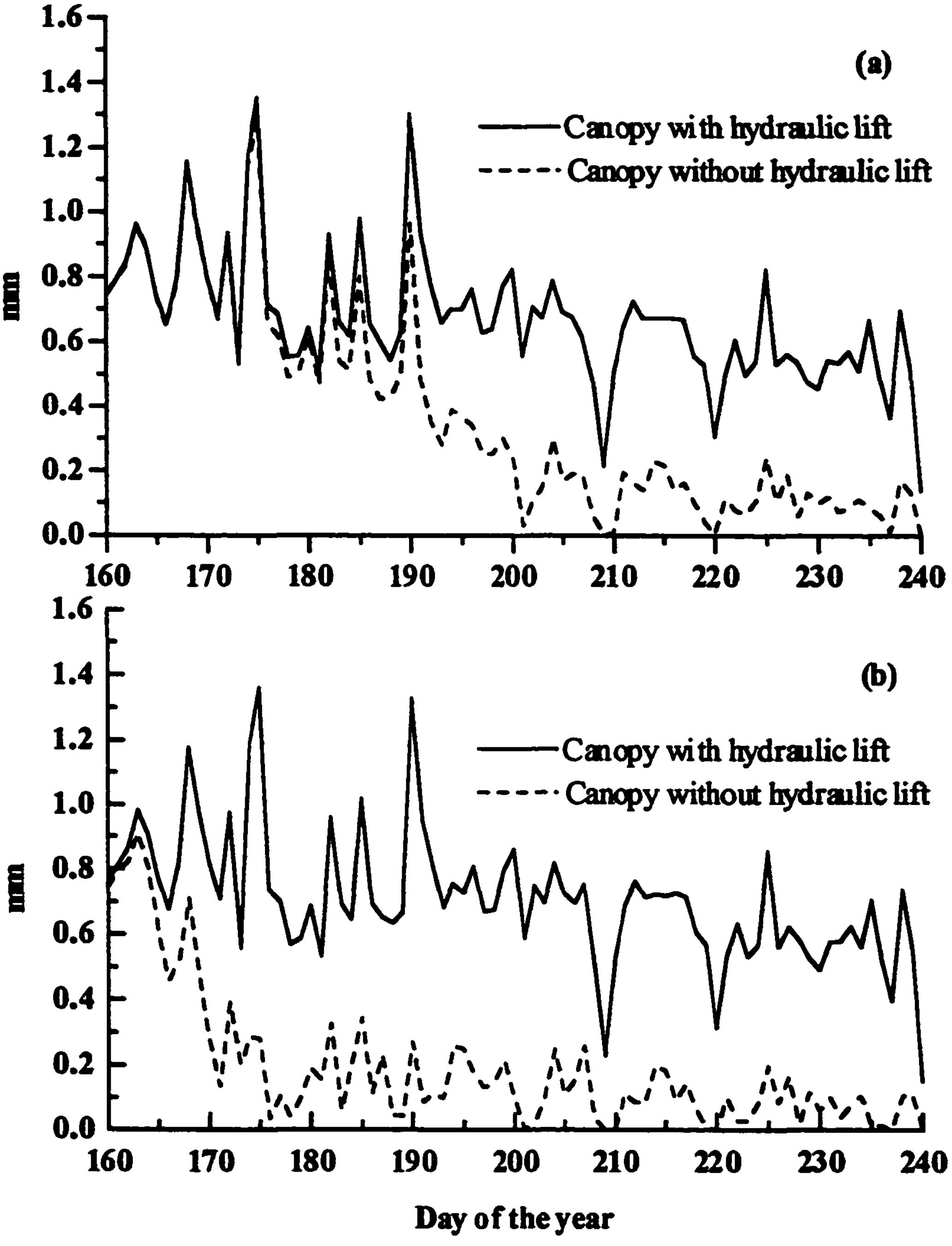

Fig. 4.7 Evaporation under (a) wet conditions and (b) dry conditions from 8 June to 27 August 1996 (DOY 160 to 240).

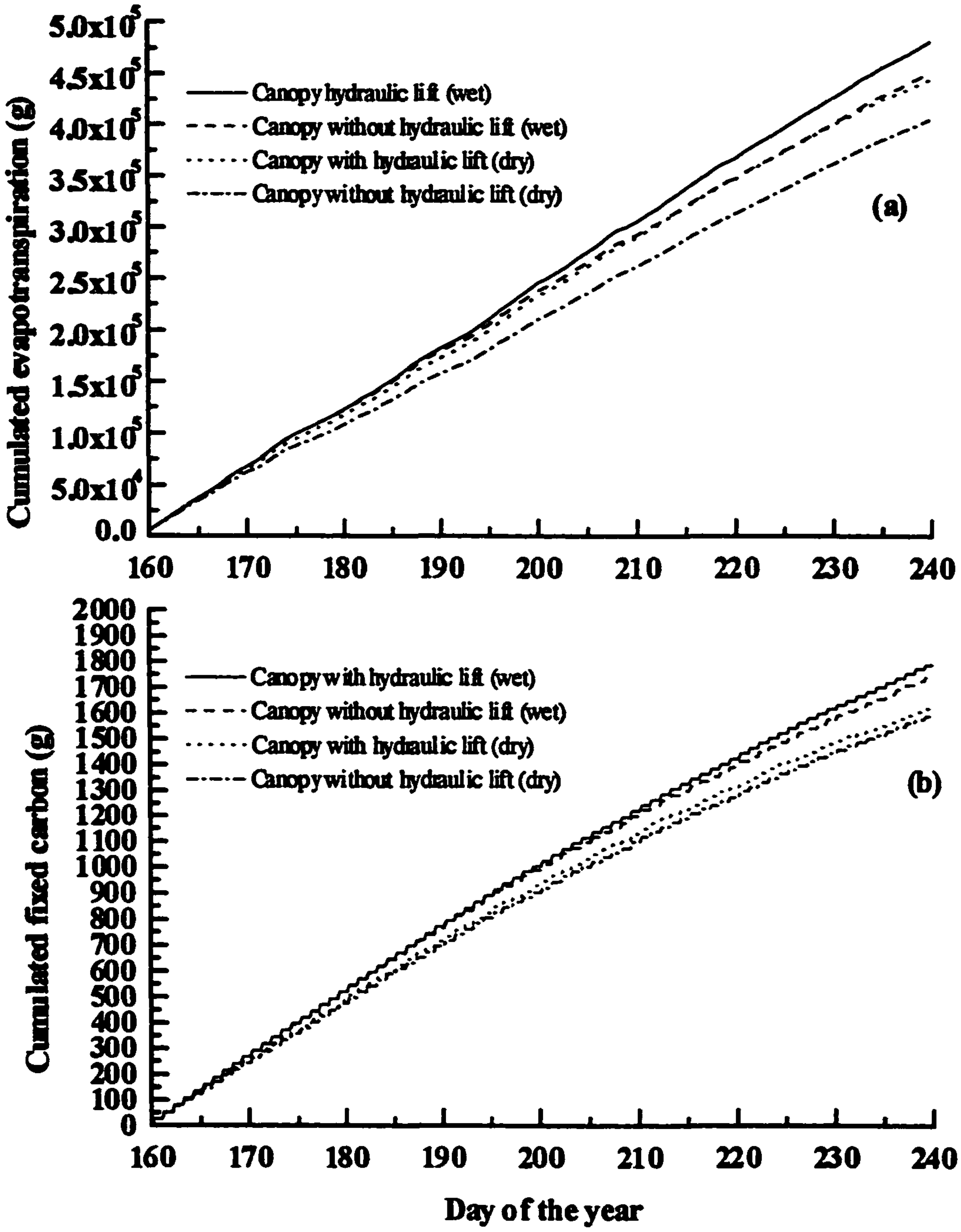

Fig. 4.8 (a) Cumulated fixed carbon for the two types of canopy, able and unable to perform hydraulic lift and under two climatic conditions, wet and dry. The simulations span from 8 June to 27 August 1996(DOY 160 to 240).

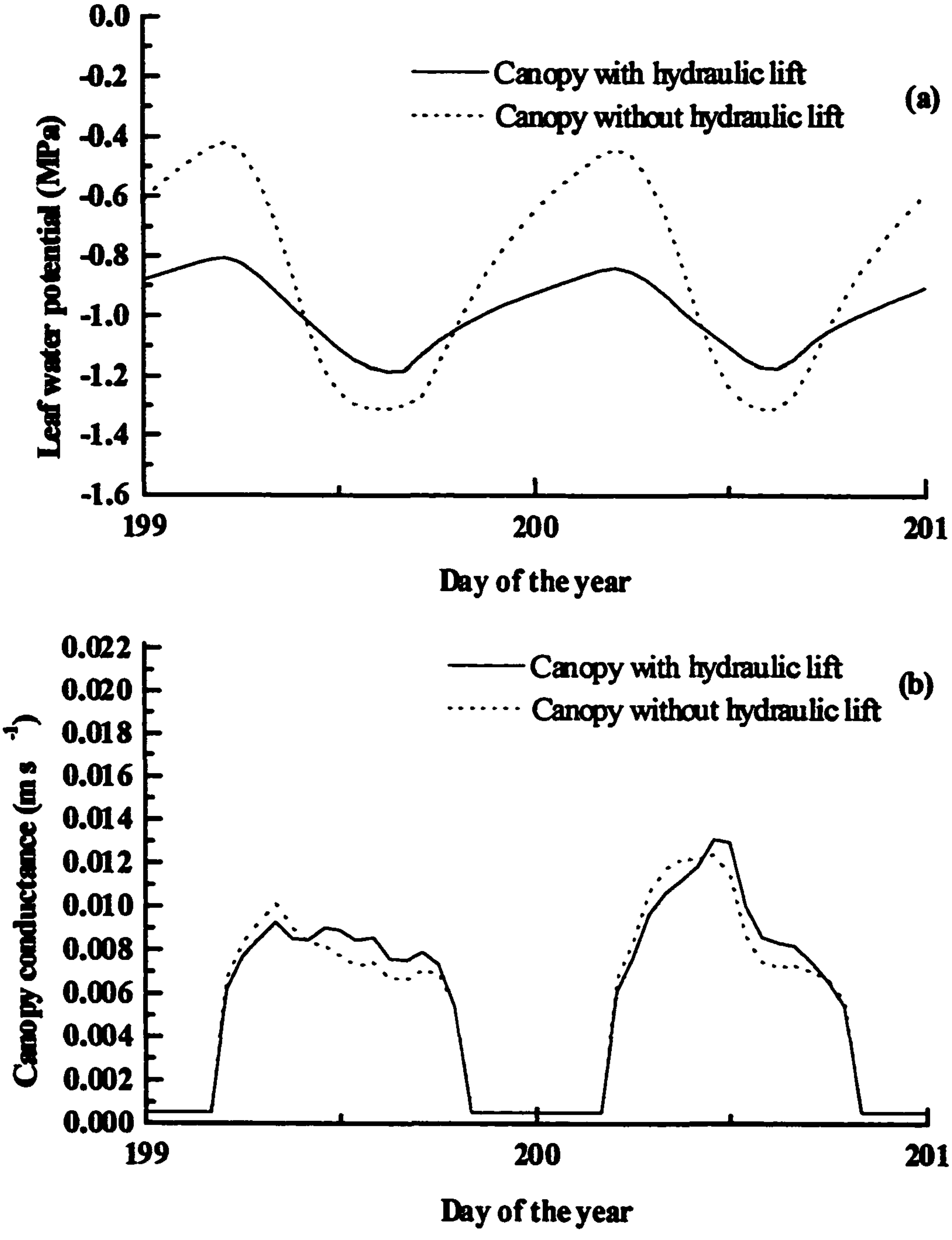

Fig. 4.9 (a) Leaf water potential and (b) conductance of a canopy unable and able to perform hydraulic lift, under wet conditions from 17 to 19 July 1996 (DOY 199 to 201).

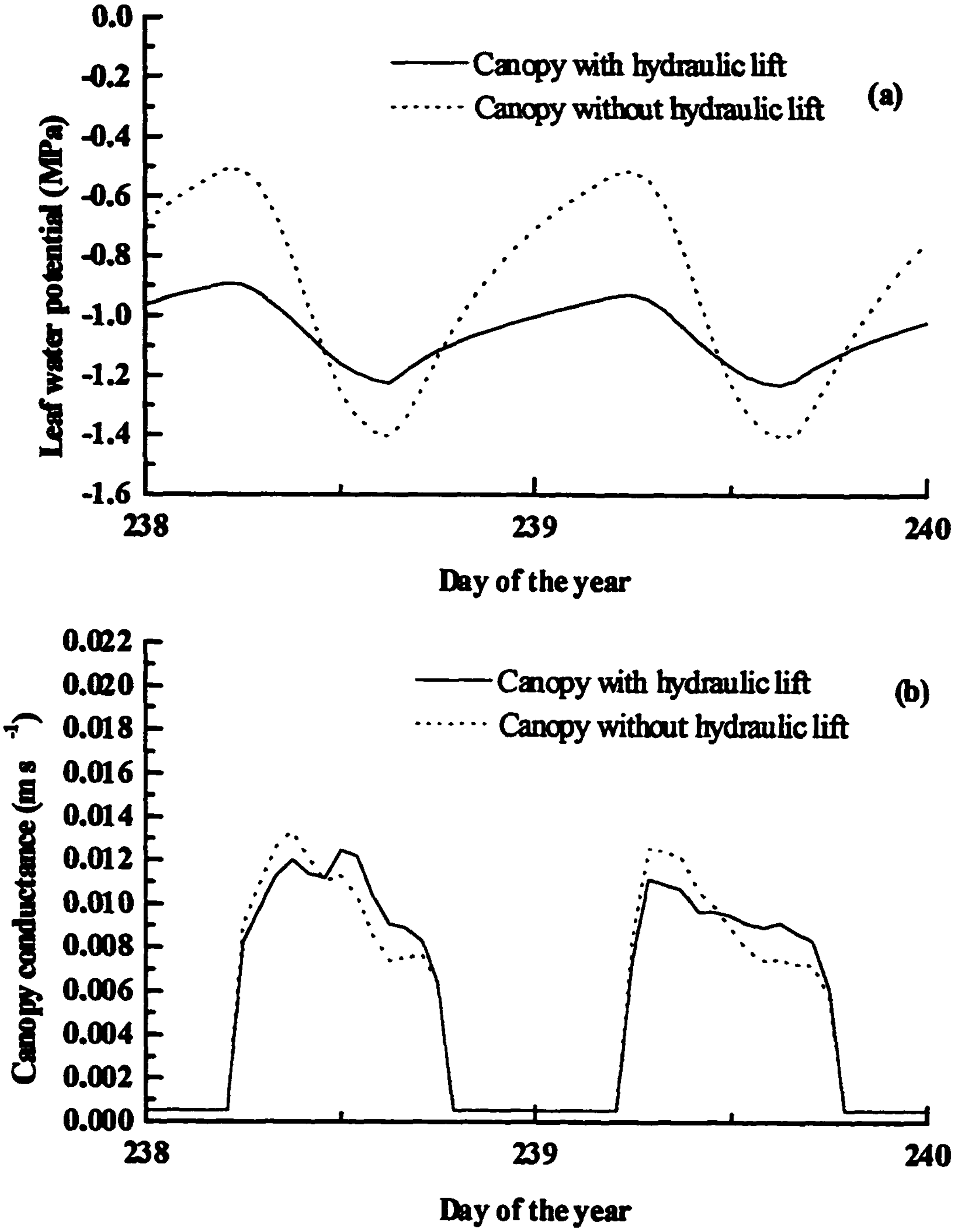

Fig. 4.10 (a) Leaf water potential and (b) conductance of a canopy unable and able to perform hydraulic lift, under wet conditions from 25 to 27 August 1996 (DOY 238 to 240).

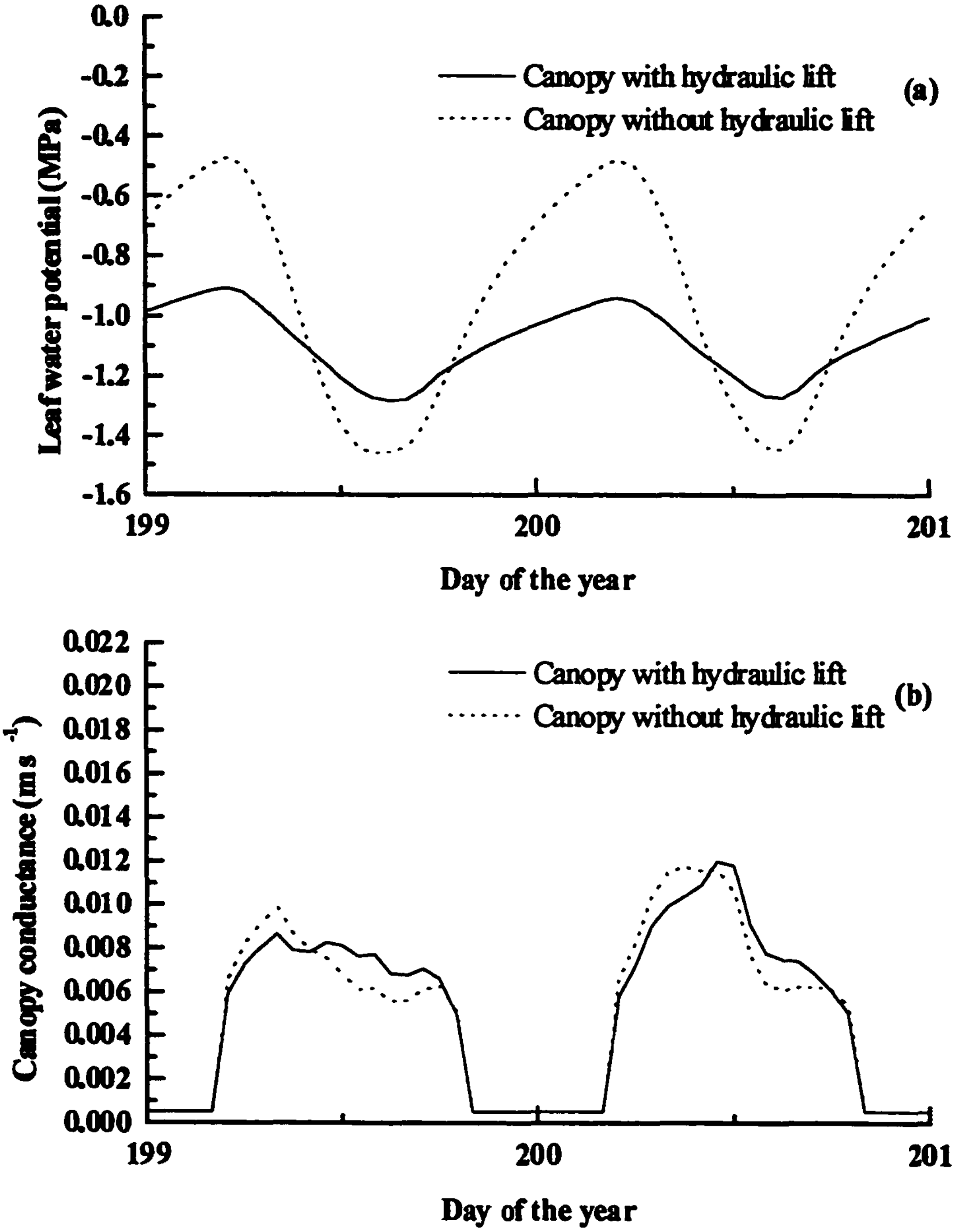

Fig. 4.11 (a) Leaf water potential and (b) conductance of a canopy unable and able to perform hydraulic lift, under dry conditions from 17 to 19 July 1996 (DOY 199 to 201).

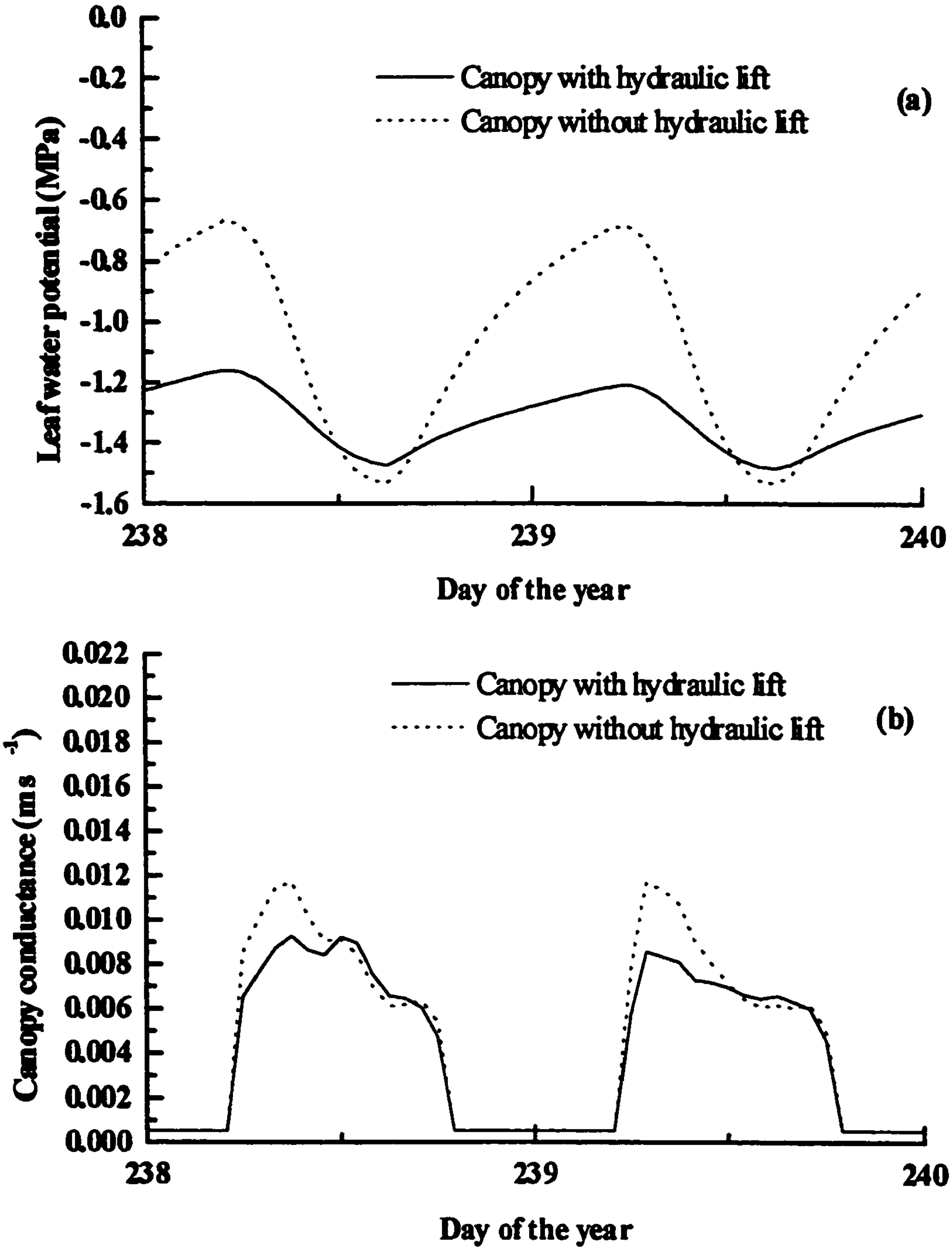

Fig. 4.12 (a) Leaf water potential and (b) conductance of a canopy unable and able to perform hydraulic lift, under dry conditions from 25 to 27 August 1996 (DOY 238 to 240).

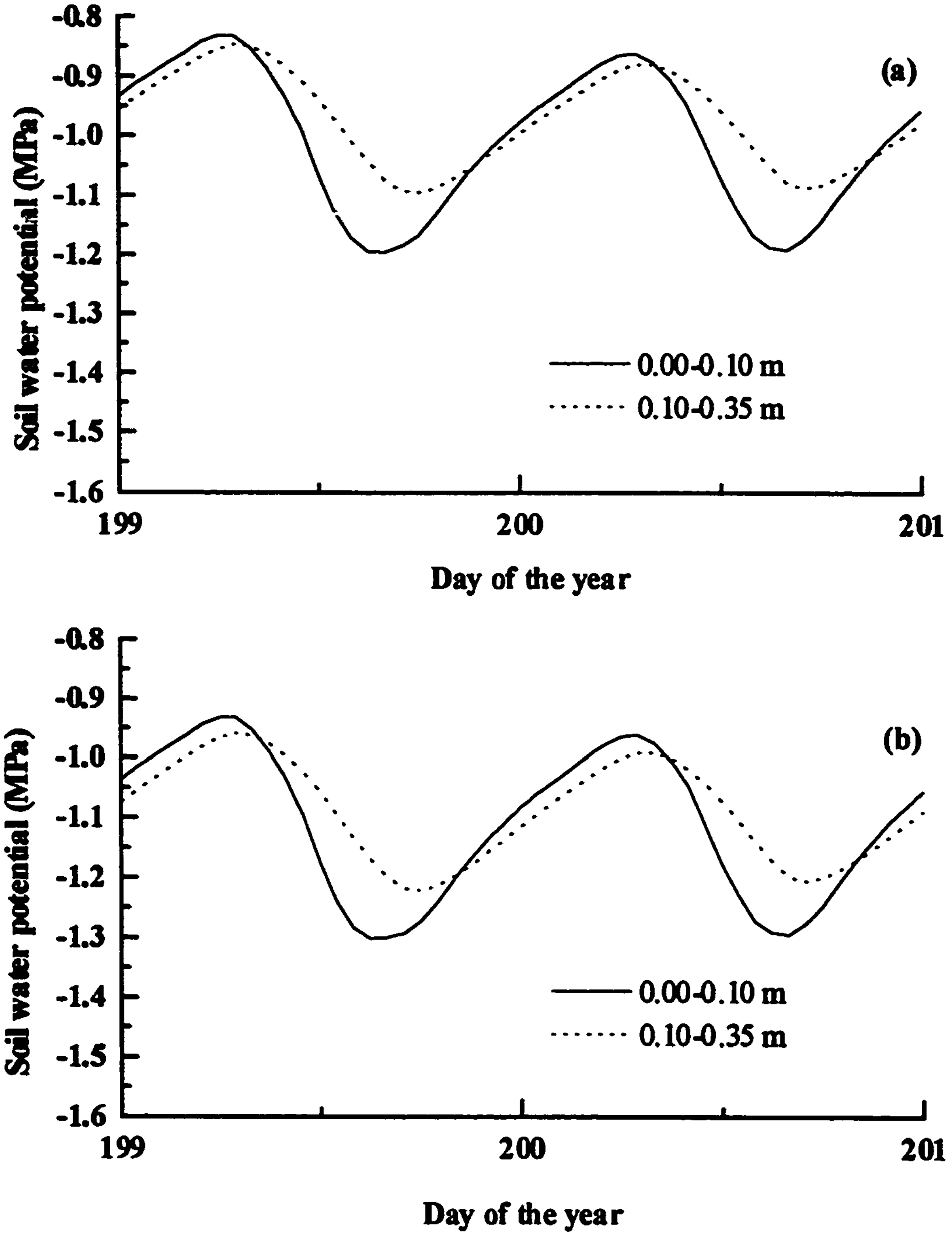

Fig. 4.13 Soil water potential beneath a canopy able to perform hydraulic lift under (a) wet and (b) dry conditions, from 17 to 19 July 1996 (DOY 199 to 201).

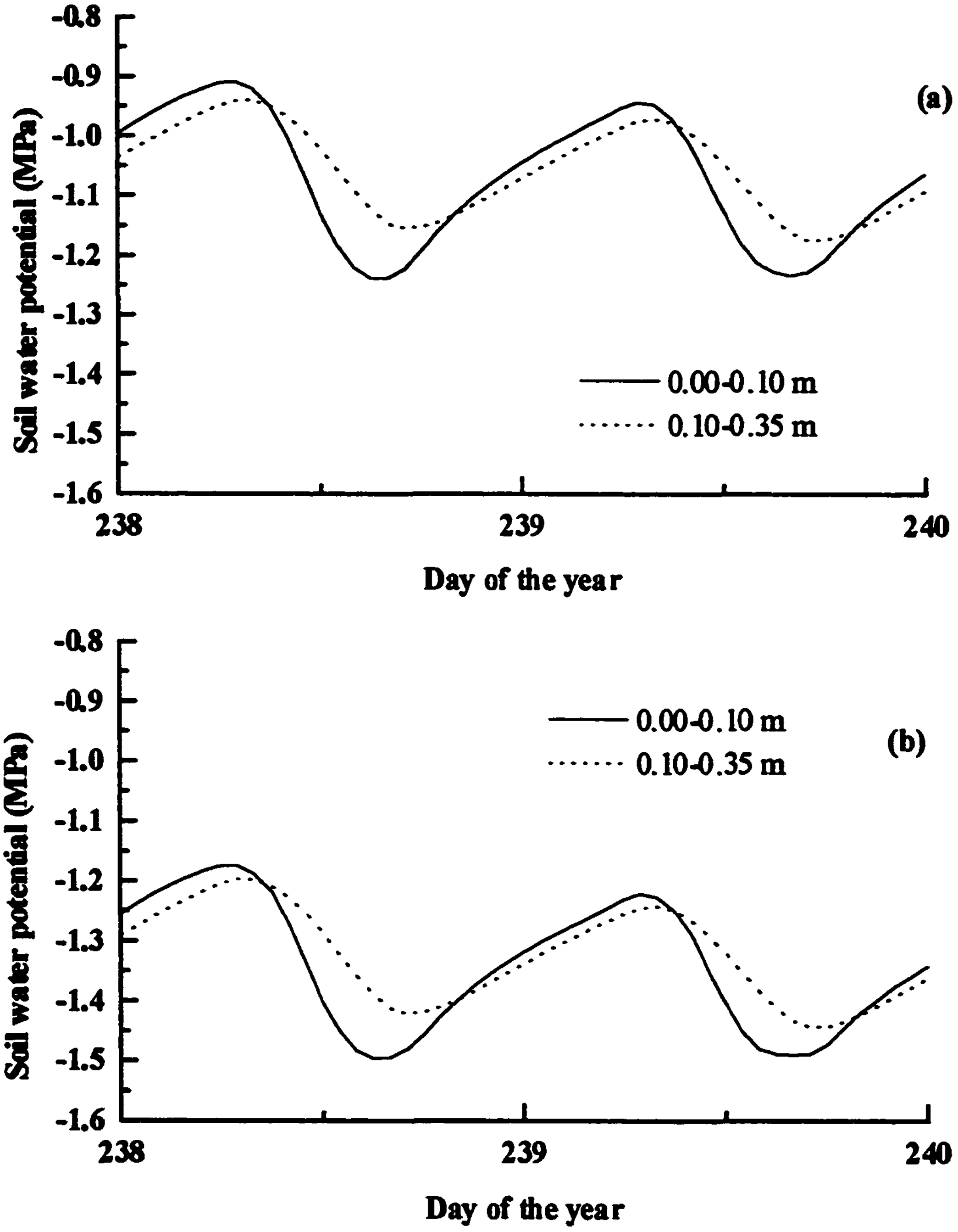

Fig. 4.14 Soil water potential beneath a canopy able to perform hydraulic lift under (a) wet and (b) dry conditions, from 25 to 27 August 1996 (DOY 238 to 240).

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Chapter 5 Synthesis

In thesis I have investigated the water movement from the soil in the atmosphere via the plant canopy. Wheat (*Triticum aestivum* cv. Yecora Rojo) and a Mediterranean evergreen shrub (*Pistacia Lentiscus*) were selected because found in areas where predicted climate changes are most likely to cause changes in rainfall pattern, and therefore to affect the availability of soil water. The methodology used in this thesis includes the development of a plant model that is linked with energy balance calculation which have been borrowed from a larger Land Atmosphere Surface Scheme model, i.e. CLASS (Verseghy 1991; Verseghy *et al.*, 1993). Components of the plant model include a modified version of an existing stomatal conductance formulation (Ball 1988). Stomatal conductance for C_3 plants increases with photosynthesis and decreases as [CO_2] rises (Ball 1988). As the leaf water potential decreases also does stomatal the stomatal conductance. In the model this happens when leaf water potential becomes closer to a critical value at which conductance will be half of its maximum value under no water limitation. Linking the plant water status to the stomatal conductance was achieved by first developing the formulation for water uptake by the plants in response to the gradient between soil-plant-atmosphere. Water uptake is modelled as being proportional to the gradient that develops between plant and the soil and proportional to the root density. Water flow from the soil into the roots is limited by the hydraulic resistance of the soil which increases as soil water content decreases. Radial resistance represents the permeability of the root tissue to water absorption, and it constitutes the final barrier to water flux before entering the xylem system. Because hydrated plants tissue contains water potentially available for transpiration, the model accounts for the water capacitance of the biomass. Leaf water potential is used to represent the plant water status, this value is calculated via an iterating solution as illustrated in Chapter 2 and in Grant *et al.* (1999).

In this thesis it was also stated that increasing [CO_2] in the atmosphere and the mechanism of hydraulic lift are two key elements limiting canopy water stress in water limited environments. The first one by limiting transpiration of C_3 plant canopies and the second one by re-allocating water resources where they could be used to meet transpiration demand. These two issues of plant water relations become of paramount importance in the context of predicted climatic change, as computer simulations forecast a regional decrease in rainfall precipitation under a doubling of the [CO_2] (Cubash *et al.*, 1996).

The further development and validation of realistic land surface parameterizations for use in computer models (Foley *et al.*, 1996; Sellers *et al.*, 1996) are of paramount importance in climate change studies. There is a growing interest in the use of physiologically-based vegetation submodels for land surface parameterizations because of the effects that increasing CO_2 levels in the atmosphere have upon canopy conductance and hence on mass and energy exchange. The main objective of Chapter 2 was to develop a model to give a quantitative understanding on how increased CO_2 in the atmosphere affects the water and energy balance of a crop canopy. It was also hypothesized that CO_2 effects on mass and energy exchange can be simulated if stomatal conductance is presumed to decrease with increasing atmospheric [CO_2], decreasing leaf water potential and to increase with increasing leaf carboxylation rate. Chapter 2 describes a water transfer scheme in which the canopy conductance is linked to the carbon fixation and plant growth. This model is tested with diurnal energy fluxes measured in a Free Air CO_2 Enrichment (FACE) experiment for a wheat canopy grown under ambient (355 μmol mol^{-1}) vs. elevated CO_2 (550 μmol mol^{-1}) and under optimum vs. suboptimum water supply. Simulated and measured conductances were reduced by about 30% under elevated vs. ambient CO_2 under optimum water supply. These lower conductances caused reductions in latent heat fluxes and increases in canopy temperatures. These reductions varied diurnally from ca. zero W m^{-2} and zero °C at night to ca. 100 W m^{-2} vs. 50 W m^{-2} and 1 °C vs. 0.5 °C at midday with optimum vs. suboptimum irrigation. Reductions in latent heat fluxes under elevated [CO_2] caused reductions in both simulated and measured seasonal water use of about 6% with optimum and about 2% with suboptimum irrigation. Conductances, heat fluxes, canopy temperatures and seasonal water use were less affected by elevated vs. ambient [CO_2] under suboptimum vs. optimum water supply (2% vs. 6%). Conversely [CO_2] fixation and crop growth were increased more by elevated [CO_2] under suboptimum water supply (18 %) than under optimum water supply (10%).

The discussion of the fundamental aspects of hydraulic lift in Chapter 3 provided the opportunity for a quantitative analysis of this phenomenon in a water-limited environment and for a canopy in which hydraulic lift is hypothesized but was never successfully measured. Other studies indicated that the water relocated via hydraulic lift is a substantial portion of daily ET (Caldwell and Richards, 1989). Other field observations and experiments indicated that relocation of water by hydraulic lift may account for as little as 15 % (Wan *et al.*, 1993) or as much as 30% (Richards and Caldwell, 1987 in Caldwell *et al.*, 1998) of plant transpiration. However if the water relocated via hydraulic lift represents 10 or only 15 % of the daily ET, this would correspond to only about 1% of the soil water content in the first 10 cm of soil. Such a small diurnal variation may fall below the limits of instrument resolution, of soil moisture measurements with automated Time Domain Reflectometry (TDR). It should be noted that estimates given by previous studies have been derived from the conversion of water potential measurements obtained with psychrometers. For example, measurements of diurnal variation in soil water potential Ψ_s were combined with an empirically determined relationship between Ψ_s and soil water content (Emerman and Dawson, 1996), to show that hydraulic lift temporarily recharged the upper soil layer with nearly 25% of the total daily use of the tree. Because some of this water could be lost through evaporation or made available to other plants (Dawson 1993 and 1996), the model exercise of Chapter 4 was useful in clarifying the possible fate of relocated water in the ecosystem. Model simulations indicate that the gain in additional ET did not result in a significant carbon gain for the same species responsible for hydraulic lift. When the *Pistacia lentiscus* was allowed to perform hydraulic lift, cumulated ET was between 6 and 10 percent more, depending on the rainfall regime, than for the case in which the water was prevented from being relocated (Table 4.1).

Although hydraulic lift is expected to have only a small direct effect on transpiration and carbon uptake, it may exert a profound influence on moisture gradient within the soil. Furthermore, results obtained in Chapter 4 indicate that the *Pistacia lentiscus* stand would not gain much more carbon (less than 3%) when water is made available via hydraulic lift. However, the stronger effect ascribable to the lack of hydraulic lift is the dropping of Ψ_s potential to an extremely negative value, i.e. about -20MPa and –30MPa for the wet and dry conditions. This in turn could create difficult conditions for roots to grow or survive as reported by Deans (1979). In his study mortality of fine roots in a Sitka spruce (*Picea sitchensis*) plantation occurred whenever incident precipitation failed to maintain soil water potential near zero.

Thus hydraulic lift seems more likely to be important in terms of short and long terms ecological benefits. Although the evidence could only be circumstantial, hydraulic lift can be the triggering factor maintaining roots alive and functional, while supporting soil formation in the long-term.

One of the objectives of this thesis was to develop model predictions of canopy responses to both increased [CO_2] combined with different water regimes, and to water relocation via hydraulic lift. These modelling approaches could be used to investigate stand level responses to global change, and for applications in ecosystem models (e.g. Parton *et al.*, 1988; Rastetter *et al.*, 1991). Observed and simulated reductions of about 30% in wheat canopy conductances under elevated [CO_2] resulted in reductions in both simulated and measured seasonal water use of about 6% and 2% with optimum and suboptimum irrigation. After confirming simulations against observations we can use this formulation to develop more aggregated representation of canopy processes. In this respect the inclusion of hydraulic lift becomes justifiable when an attempt is made to simulate response of canopies that: a) grow over soils that have an hard-pan layer that prevents capillary rise; b) have large diameter roots that pierce through the hard-pan; c) have a clear tendency to cope with water stress better than other species found in the area; d) have roots growing in soils that at some point in the season could drop to a water potential lower than that of the plant tissue.

It is worth noting that the model performed well in terms of simulated CO_2 and water regimes interactions over the whole season and in terms of total water use. Daily flux of mass and energy were also simulated but with less accuracy. However, further work is needed to refine some of the model algorithms. The underestimation of phytomass in the suboptimum irrigation treatment may have been caused by the assumption that the constraint imposed by stomatal resistance on CO_2 fixation is commensurate with the one imposed on transpiration whereas it may be slightly less. Model outputs captured the general diurnal trend in latent and sensible heat, showing that the role of the stomatal conductance in controlling the latent heat fluxes seems to reflect the general condition found in the field. Stomatal opening controls the transpiration fluxes having an effect on canopy temperature and therefore on the sensible heat fluxes. It should be however pointed out that the simulated effect of $[CO_2]$ on the latent and sensible heat fluxes obtained for the period that spans from March 10th to March 16th was not captured in full. Reduction in latent heat and increase in sensible heat were generally underestimated during this period (Fig. 2.4a). This may indicate that either the formulation of the stomatal conductance was not able to fully represent the physiological response of the wheat canopy to carbon dioxide enrichment, or else that some components of the boundary layer conductance formulation to latent and sensible heat are in need of improvement. It is however encouraging that seasonal water use for the canopy (Table 2.4) was well simulated. Finally the model as a whole seems to perform best over integrated amount of time, i.e. seasonal estimates of canopy water use.

Simulation of the hydraulic lift process allowed to demonstrate the possible consequences of the absence of hydraulic in a Mediterranean area where the evergreen shrub *Pistacia lentiscus*, is commonly found. Simulations show that an evenly distributed soil moisture profile is due to the water re-located via hydraulic lift. Absence of hydraulic lift produced the opposite scenario, i.e. an extremely dry top soil layer which started to developed as the dry season progressed. Although the results of the simulation should be interpreted with caution the observations at the site of investigation tend to agree with scenario characterized by an evenly distributed soil moisture. Computer simulation allowed to analyze two contrasting scenarios (i.e., hydraulic lift and no hydraulic lift) that would be difficult to set up under field study conditions. An attempt to measure hydraulic lift directly was also made in the summer of 1996. At that time six automated Time Domain Reflectometry (TDR) probes were installed in the first 0.3 meter of the soil profile beneath the *Pistacia lentiscus* stand. An increase in soil water content was occasionally measured during nighttime, these changes were however of a small magnitude (ca. 1%). Although the fact that soil water content increased at nighttime could be a supporting evidence of the hydraulic lift process, the very small change in water content that was detected could also be also due to electrical noise in the measurement apparatus. Finally the model simulation is providing us with indications that the phenomenon of hydraulic lift at the site of investigation could more important for the seasonal hydrological cycle rather then for the daily evapotranspiration rates. In particular a moist soil at the top could support long-term soil formation. Although previous work tend to indicate hydraulic lift as an important survival strategy for the plant, these findings tend to show that the *Pistacia lentiscus* stand could avoid summer water stress even without hydraulic lift. This fact is mainly due to the fact that a large root apparatus is able to exploit water located deep in the soil profile. Finally, the hypothesis that hydraulic lift could create favorable conditions for fine to survive throughout the dry season remains purely speculative at this stage.

5.1 Future directions

Having demonstrated the relative limited importance of hydraulic lift in terms of canopy gain in carbon, we can say that hydraulic lift can be a key element for the water balance of the ecosystem as a whole but not for the single plant species. It would be especially important to include hydraulic lift in those models that deal with plant competition for water resources, and more in general with plant communities.

Reduction of transpiration due to increased [CO_2] has been demonstrated to be more of an issue when a C_3 plant canopy is fully supplied with water. However the coupling of stomatal conductance with plant-water status becomes more important when the water stress develops and the leaf water potential becomes the factor limiting stomatal conductance.

Water relocated via hydraulic could create the conditions for the fine roots to survive during droughts. Testing of this hypothesis however requires some laboratory experiments to measure at which water potential the *Pistacia lentiscus* roots would start to dye. These observations could be used in turn to formulate the algorithm for root mortality in the model.

5.2 Advancement of knowledge

With this thesis I have shown that modelling canopy responses to environmental factors that are either part of the present (e.g., hydraulic lift) or future (e.g., increased [CO_2]), cannot be properly represented unless the water transfer scheme is dynamically linked from the soil up to the stomatal conductance. In particular the changes to the existing stomatal conductance formulation (Ball 1988), allowed the stomatal conductance to respond to changes in plant water status. In this new formulation the stomatal conductance decreases as the leaf water potential does. This happens when the leaf water potential becomes closer to a critical value at which conductance will be half of its maximum value under no water limitation.

Secondly, simulations of the water fluxes from the soil into the atmosphere indicate that when water is re-located via hydraulic lift it produces an evenly distribution of moisture in the soil profile. This allowed the *Pistacia lentiscus* to gain about an extra 3% in fixed carbon. The model simulations together with observations during the summer of 1996 support the hypothesis that hydraulic lift cannot exclusively accounted as a survival strategy of this evergreen shrub. Other forms of adaptation, such as deep roots and stomatal control could be more important than the actual hydraulic lift. It is however concluded that a moist top-soil could support at least in part, a long term soil development. Furthermore, a moist soil environment could create favorable conditions for the fine roots to survive.

Finally in my simulations the relocated water by *Pistacia lentiscus* via hydraulic lift, represents less than 10% of the daily ET, this would correspond to only about 1% of the soil water content in the first 10 cm of soil. Interpretation of these findings offers the opportunity to analyze some of the aspects that may be the cause for unsuccessful measurements of the hydraulic lift phenomenon. In particular, the small diurnal variation may fall below the limits of instrument resolution, of soil moisture measurements with automated Time Domain Reflectometry (TDR). Because a small change in water content can cause a large change in soil water potential the use of psychrometers could be considered as a valid alternative to the automated Time Domain Reflectometry (TDR). Although this approach has been chosen by others (e.g., Emerman and Dawson, 1996), it should be noted that the hot summer conditions found in Sardinia may cause problems for the interpretation of the readings. In particular, the soil temperature at the site of investigation can fluctuate considerably from day to night. Because psychrometers are sensitive to gradient in soil temperature the readings can be erroneously interpreted as a response to change in soil water potential due to change in water content while instead responding to soil temperature gradients.

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