Plant water relations along a rainfall gradient, between the Succulent Karoo and Mesic Mountain Fynbos, in the Cedarberg Mountains near Clanwilliam, South Africa.

A Thesis presented for the degree of
Master of Science
at the University of Cape Town

by

Jeffrey Miller

Department of Botany
University of Cape Town
July 1985

This is to declare that this dissertation has not been previously submitted for a degree at any other University.

Summary:

The similarities in the structure of the sclerophyllous evergreen shrublands of the five disjunct mediterranean-type ecosystems is thought to be the result of convergent evolution. In the Mediterranean, California, and Chile the length of the summer drought and the cold winter temperatures are hypothesized to be the primary selective pressures. In Australia and South Africa low soil nutrients are thought to be important, as they are in defining the structurally similar heathlands found with a range of climatic types.

The fynbos vegetation in an area with a mediterranean-type climate was sampled for a period with low xylem pressure potentials and restricted leaf conductances to water loss during the summer drought, and the patterns of plant response to desiccation. The presence of patterns of plant water relations in the fynbos similar to those found in other mediterranean-type ecosystems could demonstrate the importance of water as a selective pressure in the fynbos.

The seasonal course of the pre-dawn and midday xylem pressure potentials were measured on representative species at five sites with rainfalls between 225 and 675 mm/year in the Cedarberg Mountains in the western Cape Province, South Africa. At 3 of the sites the diurnal courses of leaf conductances and xylem pressure potentials were measured during the season.

The length of the period of water stress increased, and the minimum values in the middle of the summer decreased, from the wettest site to the middle site. Following the

switch in vegetation type from an evergreen sclerophyllous community to drought-deciduous and succulent communities there was a constant period of water stress and seasonal minimum xylem pressure potentials.

The species measured showed various responses to the drought. At the xeric end of the transect the species were either succulent and maintained high xylem pressure potentials, or were drought-deciduous or semi-deciduous, or were able to maintain leaf conductances at low xylem pressure potentials, probably through the adjustment of the osmotic potentials. At the mesic end of the transect the fynbos overstory species had low leaf conductances, and high xylem pressure potentials throughout the year. The stomata of the fynbos overstory species were sensitive to water stress. The fynbos understory species continued leaf conductances and exhibited low xylem pressure potentials.

The length of the summer drought, and the switch from the evergreen sclerophyllous fynbos to the drought-deciduous and succulent communities, followed the patterns found in the mediterranean-type ecosystems of Chile and California. However, the fynbos species did not exhibit patterns of water relations that were clearly adaptive to arid conditions. At the mesic end of the transect the canopy development seemed to be limited by some other factor than water. There probably was an insufficient increase in leaf area to cause equal periods of water stress throughout the transect, which was the pattern in California. These two observations, coupled with the broader distribution of the fynbos, which follows the distribution of the Table Mountain

Sandstone derived soils rather than the mediterranean-type climate, would seem to imply that fynbos is possibly functionally more similar to a heathland than the other mediterranean-type ecosystems.

Acknowledgements:

This research was conducted while I was employed by the Directorate of Forestry of the Department of Environment Affairs. Additional funding for the research was supplied by the Fynbos Biome Project of the Foundation for Research Development. Dr. Steve Roberts designed and built the null balance porometer I used, and the Systems Ecology Research Group, San Diego State University, California provided most of the equipment used in the research.

I would like to thank William Maliepaard, Cedric Ables, Leonard Bickerstaff, Hans Peters, George Davis, Hugh Bently, and Elisabeth Klaussner for the long hours they spent in the field helping me gather the data, and Dirk Versfeld and Mike Cotton (of MC Systems, Cape Town) who helped me keep my equipment running. I would also like to thank Dave le Maitre and Dr. Karl Schütte for their advice throughout the project.

I am especially indebted to Leonard Bickerstaff who allowed me to use his computer when mine "died", and all the people who helped me recover my thesis from the old machine, and to the Versfeld family who provided a home away from the sea whenever we asked.

And finally I would like to thank my father, mother and wife.

Table of Contents

2. Sampling techniques

3. Site description

4. Seasonal patterns of pre-dawn and midday xylem pressure potentials along a rainfall gradient between Succulent Karoo and Mesic Mountain Fynbos

List of Figures

List of Tables

1. INTRODUCTION

In five areas of the world; in parts of the area around the Mediterranean Sea, the southwest tip of Africa, the southwestern and southern areas of Australia, southern California in the United States, and in central Chile, there is a climatic pattern marked by hot dry summers and cool wet winters. In these five areas there occurs a structurally similar vegetation type that is dominated by evergreen sclerophyllous shrubs. The vegetation found in these disjunct ecosystems is floristically dissimilar, with each area, except for California and the Mediterranean, falling into a separate floristic realm (Walter 1973).

Based on this co-occurrence of climate and vegetation form with differing floristic backgrounds it has been hypothesized that there have been similar selective pressures operating in these ecosystems. The present structural similarities of these ecosystems therefore also reflect the functional similarities of the ecosystems, and there should now be similar patterns of resource utilization and optimization (Miller 1981). This pattern of convergent evolution results from environmental pressures which primarily select the vegetative organs of nourishment and development, upon the success of which the continuation of the individual depends, rather than the organs of reproduction, upon which the continuation of the species depends (Cody and Mooney 1978). In two of these mediterranean-type ecosystems, in Chile and in California, the present patterns of resource use, and resource use efficiency, were found to be more similar between similarly sited communities in Chile and California that had dissimilar species, than between dissimilarly sited communities with similar species in California (Miller 1981).

The amount and seasonality of the rainfall, and the winter temperatures low enough to inhibit growth, that characterize the mediterranean-type climate are thought to be important selective pressures shaping the vegetation (Mitrakos 1980). Another important selective pressure in mediterranean-type ecosystems is the low levels of nutrients, especially nitrogen and phosphorus, found in the soils (Kruger _et al._ 1983). These ecosystems are also subject to repeated disturbance, with fire being the most common form of disturbance in California, South Africa, and Australia, and grazing being the most common disturbance in Chile and the Mediterranean.

The relative importance of these three selective pressures, the moisture and temperature regime, the level of the soil nutrients, and disturbance, in defining the evergreen sclerophyllous shrublands of mediterranean-type ecosystems is difficult to determine. In each of the five mediterranean-type ecosystems there are not independent gradients of all three selective pressures. Walter (1973) also emphasizes that, except in environmental extremes where the distribution of a species may be limited by its absolute physiological tolerances, the limits of the distribution of a species are reached when the environment reduces its ability to compete, and it is replaced by another species. The distribution of a species, or a community, therefore can not be explained by its physiological tolerances without simultaneously studying the behavior of its replacement along an environmental gradient. In some of the mediterranean-type ecosystems suitable replacement species may not exist, and this will also have important impacts on the distribution of the evergreen sclerophyllous shrubs.

In southern California and central Chile the distribution of the evergreen sclerophyllous shrubland is bounded by communities of summer drought-deciduous and succulent species on one side, and winter deciduous and evergreen forests on the other (Di Castri 1981). From the drought-deciduous community, through the evergreen sclerophyllous shrubland, to the forest community the primary environmental gradient is increasing rainfall. Miller (1979) hypothesized that, based on a carbon cost-benefit analysis, it is the length of the summer drought which determines the boundary between the drought-deciduous species and the evergreen sclerophyllous species, and the length of the winter cold period which defines the distribution of the winter deciduous species.

In seasonally arid areas plants either have to limit their water loss, or be able to endure periods of high water stress. The sclerophyllous leaf form is thought to be an adaptive feature for both reasons (Shields 1950). The thick cuticle of sclerophyllous leaves prevents water loss except through the stomata, and the rigid cell walls may be important in turgor maintenance during periods of water stress. Sclerophyllous leaves are not without drawbacks. Because of their high density, sclerophyllous leaves require more carbon to create than the low density leaves of drought-deciduous species. Drought-deciduous species have been found to have higher photosynthetic rates, respiration rates, and rates of water loss than sclerophylls (Miller and Mooney 1976), but shed their leaves at lower levels of water stress than cause the sclerophylls to close their stomata. Because of their lower photosynthetic rates, and in some cases higher costs of construction (Merino 1982), a sclerophyllous leaf can not show a positive carbon balance in a single season and must survive for more than one spring growth period.

Following the hypotheses of Miller (1979) an evergreen sclerophyll attempting to live in the drier range of the drought-deciduous species would not be able to keep its stomata open for a period of time during the course of the year that was long enough to meet the respiratory costs of its leaves and recover the initial costs of their growth. The higher rates of water loss of the neighboring drought-deciduous species would also help increase the length of the drought. The drought-deciduous species, with their higher photosynthetic rates and lower leaf costs, function much like annuals and, instead of having to satisfy the respiratory costs during summer when there is no photosynthesis, discard their leaves each year.

A drought-deciduous species attempting to grow in the natural range of the evergreen sclerophylls would shed its leaves before the sclerophylls had to close their stomata, because of their differing tolerances to water stress. This would put the drought deciduous species at a competitive disadvantage, especially since these species are usually less tolerant of shading than sclerophylls.

With increasing levels of rainfall in California and Chile the biomass increases, and with high levels of rainfall a forest can be supported. The winter deciduous tree species, with their higher photosynthetic and growth rates, will be benefited by the cold period, but will probably be subject to successional replacement by evergreen species, which, although slower growing, have better shade tolerance.

The evergreen sclerophyllous shrubs of Chile and California would seem to be sclerophyllous in order to tolerate water stress, and evergreen in order to recover the carbon costs of being sclerophyllous. They are shrubs because the water supply does not allow high leaf area indices, and the limited growth period does not allow sufficient carbon accumulation to build and maintain large quantities of extra wood.

In Chile and California the distribution of the sclerophyllous vegetation is restricted to areas with predominantly winter rainfall between about 350 and 650 mm/year. In Australia a similar rainfall limit of about 600 to 700 mm/year brings a switch from shrublands to woodlands

(Milewski 1979). However, the details of the transition are sensitive to the substrate quality (Beard 1983). Where rainfalls exceed 600 mm/year in areas of Israel edaphic factors also play an important role in determining the nature of the plant communities (Rabinovitch-Vin 1983). In South Africa the distribution of the evergreen sclerophyllous vegetation extends beyond the limits of the mediterranean-type climate.

The fynbos of South Africa extends from the Cedarberg Mountains in the western Cape Province, which receive little summer rain and have a mediterranean-type climate, through areas with predominantly winter rainfalls up to 3000 mm/year, to the Oteniqua mountains of the southern Cape, which have little seasonality in the distribution of rainfall and receive up to 2000 mm/year. Throughout the complete range of the fynbos the transition from Table Mountain Sandstone to some other soil type brings a change in vegetation type. Moll and Jarman (1984) have hypothesized that the fynbos may be functionally more similar to the sclerophyllous heathlands of the world than to the sclerophyllous mediterranean-type ecosystems, following the emphasis Specht and Moll (1983) have placed on soil nutrients as determinants of the vegetation type.

Low levels of available nutrients in soils can result from poor parent material with low mineralization rates, high rates of leaching, low pH, or slow rates of decomposition (Jacobson *et al.* 1981). When ecosystems with low levels of available nutrients in the soil are subjected to frequent disturbances, such as fire, which remove the above-ground biotic components of the ecosystem, the soil nutrient supply can be quickly depleted. Low rates of nutrient release from the soil can inhibit plant growth because of the inability to form proteins and other compounds, and may inhibit photosynthesis (Beadle 1966).

With decreasing nutrient availability the life spans of leaves should increase because, even if re-translocation is efficient, the plant will loose nutrients with leaf drop (Chabot and Hicks 1982). If the decomposition rate is slow, and fires periodically destroy the litter, then the plant may have to depend on the mineralization of the parent material for the nutrients required for the growth of new tissue, rather than on the recycling processes of the ecosystem. If the rate of leaching in the ecosystem is high, then there will be a high rate of nutrient loss from the litter, and a gradual degradation of the ecosystem. When nutrients are limiting, the shedding of leaves may also increase the competitive fitness of a neighbor. Evergreen communities which have leaf fall all through the year may also have tighter nutrient cycling (Monk 1966). In areas where growth is inhibited in the winter because of low temperatures, evergreens can continue photosynthesis and nutrient uptake for re-translocation and incorporation into growth in the spring (Mooney and Rundel 1979).

Although evergreenness may be adaptive for survival in areas with low nutrients, it does not imply sclerophylly, or xerophylly (Seddon 1974). The sclerophyllic structure of some of the plants found in heathlands can be lessened, and the plant become more mesophytic, with the addition of nutrients, especially the addition of phosphorus (Beadle 1966). The lignification, and build up of carbon compounds in the leaves may represent nothing more than the inability of the plant to form nitrogen or phosphorus bearing compounds and continue growth. Following fertilization of heath in Australia, Specht and Jones (1971) found that there was a flush of mesophytic growth, and then death during the next drought. Because the longer life span of evergreen leaves increases the probability of herbivory, evergreen plants may adopt a sclerophyllous leaf structure, since the high lignin contents in sclerophyllous leaves may decrease herbivory (Mooney and Gulmon 1982).

It would seem that the evergreen sclerophyllous shrubs of a heathland may be evergreen in order to minimize nutrient loss, and sclerophyllous because of the production of carbon compounds without sufficient nutrients to channel them into growth rather than lignification. The species may also be sclerophyllous in order to minimize herbivory.

Unless a plant characteristic is lethal, there is no selective pressure to remove it until it is tested in a competitive interaction with another species without the characteristic. Xeromorphic leaf structure has been described as a secondary phenomenon resulting from any deficiency that inhibits leaf development (Levitt 1980). Xeromorphy is not necessarily always related to the aridity of the environment, but drought resistant plants frequently owe part or all of their resistance to xerophylly. Small (1973) has hypothesized that the xerophyllic structure of plants growing in arid environments, and the xeromorphic structure of plants growing in nutritionally deficient environments may preadapt the species for the other environment. Xerophyllic structure, which creates a high resistance to carbon uptake at the stomata, may not be a hindrance in nutrient deficient areas where plants may also have low photosynthetic rates, because of the low rates of carbon dioxide fixation at the cellular level. The xeromorphic structure resulting from nutrient deficiency does not necessarily imply the necessary stomatal control to limit water loss. Xeromorphic species may survive in arid areas with low levels of nutrients because there is not sufficient transpiring biomass to create a period of water stress. These species, however, could not survive in an equally arid area that had higher nutrient soils.

If the fynbos is functionally equivalent to the evergreen sclerophyllous heathlands, rather than the evergreen sclerophyllous shrublands of the mediterranean-type ecosystems, then the plants should not necessarily be adapted to endure a period of water stress, nor, given that the biomass is nutrient limited rather than water limited, should there be the characteristic period of water stress found in mediterranean-type ecosystems. If the fynbos is functionally equivalent to the mediterranean-type ecosystems then the high rainfalls may be obviated by the poor water holding capacity of the soils, and only the amount of rain in the spring may be available for plant growth. Or, in some areas xerophyllic species may have colonized low nutrient mesic environments, and vice versa, and the fynbos may be functionally similar to a mediterranean-type ecosystem toward the western part of its range, and a heathland in the eastern part of its range (Miller et al. 1983).

Very little plant water relations, or other ecophysiological, research has been conducted in the fynbos. Earlier surveys of plant water relations in the fynbos (Miller et al. 1984), and studies of the seasonal and diurnal progressions leaf conductances and xylem pressure potentials (Miller et al. 1983; Miller et al. in prep.), as well as studies at specific sites (Moll and Sommerville 1985; Kruger pers. comm.), have generally not found the long periods of water stress during the summer months that characterize other mediterranean-type ecosystems. The sites in the survey of Miller et al. (1984), which included those studied by Moll and Sommerville and Kruger, had annual precipitations ranging from 550 to 1600 mm/year. Since there was not a significant period of plant water stress at these sites, which received more rainfall than the 600 to 900 mm/year upper limit used to define the mediterranean-type climate (Aschmann 1973), it would not seem that low soil water holding capacities were causing these areas to be functionally similar to a mediterranean-type ecosystem. The lack of a period of water stress at the fynbos sites that have been studied to date would seem to indicate that the fynbos is not water limited, and the biomass may instead by limited by the nutrient availability as hypothesized in the evergreen sclerophyllous heathlands.

1.1 Overview of the research

The water relations of fynbos species, and of the species that replace fynbos in drier communities have not been studied. The purpose of this study was to investigate the plant water relations of fynbos species in an area that had a mediterranean-type climate. If fynbos can be described as being functionally similar to the other mediterranean-type ecosystems then there should be a similar pattern of water stress, and similar switches in community type at similar levels of rainfall. If fynbos plants are xerophyllic, rather than merely xeromorphic, they should show patterns of water use that can be described as positive adaptations to survival under drought.

The spatial and temporal patterns of water stress at the arid edge of the distribution of the fynbos, and in the communities that replace fynbos, were sampled at five sites, all on Table Mountain Sandstone derived soils, along a rainfall gradient between 200 and 700 mm/year. Water stress was measured by the pre-dawn and midday xylem pressure potentials of selected dominant or characteristic species. At the most xeric site, which was in the Succulent Karoo veld type, and at the middle and most mesic sites, which were both in the Fynbos veld type, the diurnal patterns of leaf conductance and xylem pressure potentials were measured during the season in order to determine the plants response to water stress.

2. SAMPLING TECHNIQUES

2.1 Pressure chamber techniques of plant water potential measurement

In order to understand the response of a plant to decreasing levels of available moisture, such as the spatial pattern from the Algeria Forestry Station to Clanwilliam or the temporal pattern from winter to summer, there needs to be some measurement of the internal water status of the plant. This is especially important since there is not always a direct correlation between the internal status of a plant and the external environment, and the interest of this study was to investigate the mechanisms that controlled species and community distributions.

Rainfall is usually measured as a depth, with the common measurement unit of millimeters easily multiplied by any surface area to give a volume. Measuring the amount of water in a plant, and therefore keeping the units the same as those of the measurement of the external environment, is usually done through various weighing methods. Water deficits can be quantified by relating the amount of water actually in the plant to the maximum amount of water that the plant tissue could hold. Larcher (1980) defines the relative water content (RWC) as;

$$RWC = ([\text{Act water cont}]/[\text{Sat water cont}]) * 100$$

and the water deficit (water saturation deficit; WSD) as;

$$WSD = (([\text{Sat water cont}]-[\text{Act water cont}])/[\text{Sat water cont}]) * 100.$$

In practice relative water content can be calculated as;

$$RWC = ((\text{Fresh weight}-\text{Dry weight})/(\text{Turgid weight}-\text{Dry weight})) * 100$$

and water saturation deficit as;

$$WSD = 100 - RWC$$

(Turner and Burch 1983). The fresh weight is the weight of the tissue immediately after it has been sampled. The turgid weight is the weight of material after it has been floated on distilled water and allowed to come to an equilibrium, and the dry weight is the weight after the material has been dried to a constant weight.

These measurements of quantities of water are easy to determine, but have disadvantages. They cannot always explain the movement of the water through the hydrological cycle, which a measurement in thermodynamic terms could. Water moves from the soil to the plant, and through the plant to the atmosphere, along a decreasing energy gradient. At any stage the energy content of the water can be calculated from the temperature, pressure, volume, and solute concentration of the water (Slayter 1967). The energy content of water increases with increasing temperature or pressure. An increase in the solute concentration in the water decreases the energy content, and when the water is in the gas phase an increase in the volume will decrease the energy content of the water vapor. The chemical potential per unit volume of water, or water potential, has units dimensionally equivalent to pressure, and is usually measured relative to the energy content of pure water at a standard temperature and pressure.

When a solution is confined within a semipermeable membrane and allowed to equilibrate with pure water, the movement of water down the energy gradient into the solution will cause a hydrostatic build up of pressure within the membrane. When the positive pressure within the membrane and the negative osmotic potential balance and equal the energy content of the pure water there will be no further water movement.

The water potential in a plant cell, which is usually less than that of pure water, and therefore negative, can be broken into four components; osmotic potential, pressure potential, matric potential, and gravitational potential. Osmotic potential is usually described by a negative number because the presence of solutes decreases the energy content relative to pure water. Pressure potential, or turgor potential, is the outward hydrostatic pressure on the cell walls, and it is usually described by a positive number because pressures above the standard reference increase the energy content of the water. Matric potential results from the adsorption of water on the surfaces of cellular structures and hygroscopic cellular constituents, and is described by a negative number since the bound water has a lower potential to do work than free water. Gravitational potential results from the altitudinal displacement of water from a reference height, and will vary about 0.01 MPa/m.

The changes in plant water potential due to gravity are usually ignored, especially in shrubs, and the matric potential is usually thought to be constant and unable to vary. The pressure potentials in plants are highly variable, and these changes are the primary response of a plant to water stress. Positive pressure potentials are necessary to maintain stomatal opening, and therefore for photosynthesis, and for cell expansion, and therefore growth. In order to maintain a positive pressure potential within a cell a plant may actively increase the osmotic concentration in the cell, above the rate of the passive concentration which occurs as the volume decreases (Turner and Jones 1980). The drop in the energy content of the water in the cell, because of the increase in the solute concentration, will then pull water into the cell from surrounding cells and raise the pressure potential.

The ability to adjust the osmotic potential depends on the rate of the development of the water stress, low temperature (due to build up of photosynthates with no growth), and is genetically determined. Osmotic adjustment is a temporary phenomenon and the osmotic potential usually returns to near the original value when the period of stress is over. Low osmotic potentials are thought to inhibit photosynthesis (Hsiao 1973), although carbon uptake has been reported in Larrea tridentata at very low water potentials (Odening *et al.* 1974).

Plant water potential and component potentials can be measured by several methods. A quick method that can be used in the field is the pressure chamber. Pressure chamber techniques can measure the xylem pressure potential, and the cell pressure and osmotic potentials.

Following Tyree and Hammel (1972), a leafy shoot in a pressure chamber can be described as a set of leaf cells and conducting xylem, each with a osmotic concentration C, and a pressure potential P. The water potential of a leaf cell in the pressure chamber is;

$$\psi_{leaf} = P_{leaf} + P_{bomb} - O_{Leaf}$$

where the osmotic potential of the leaf, O_{Leaf}, equals RTC_{Leaf} when R is the universal gas constant, and T is the temperature (°K).

In a cut xylem cell exposed to the air outside the pressure chamber the water potential is;

$$\psi_{xylem} = -f(\text{meniscus}) - O_{xylem}$$

where f(meniscus) is a function of the surface tension of the meniscus and decreases as the radius of curvature of the meniscus increases, and is zero when the water in the xylem cell is not pulled inwards. Between the leaf cells and the xylem there is the possibility of a potential gradient so the following is true;

$$\psi_{leaf} = \psi_{xylem} + \Delta\psi$$

or;

$$P_{leaf} + P_{bomb} - 0_{leaf} = -f(\text{meniscus}) - 0_{xylem} + \Delta\psi$$

Boyer (1967) states that the leaf water potential and the xylem water potential seem to come to equilibrium quite quickly and that $\Delta\psi$ can be set to zero. Boyer (1967) also reports that xylem osmotic potentials are usually quite low (>-0.1 MPa), and the term is often set to zero (Tyree and Hammel 1972). The value measured by the pressure chamber is therefore;

$$P_{bomb} = -P_{leaf} + 0_{leaf} - f(\text{meniscus})$$

As the pressure in the chamber is increased to offset the leaf turgor potential, the water potential increases (note the osmotic potential in the above equation has a positive sign) and the surface tension of the meniscus decreases until the water in the xylem comes to the surface of the xylem. At this point the surface tension of the meniscus is zero. If the pressure in the chamber is increased the meniscus could bow outwards and take on small positive values until there was exudation. At the balance pressure the opposite of the pressure chamber value is;

$$-[P_{bomb}] = P_{leaf} - 0_{leaf}$$

which is the leaf water potential.

The chamber actually only measures the xylem pressure potential since in an intact plant;

$$\psi_{leaf} = \psi_{xylem} + \Delta\psi$$

which expands to;

$$P_{leaf} - O_{leaf} = P_{xylem} - O_{xylem} + \Delta\psi.$$

The rigid structure of the intact xylem cell maintains its volume and allows a reduction in the pressure potential. When the xylem cell is cut to place the sample in the pressure chamber, the xylem pressure potential equilibrates with the atmosphere, pulling the meniscus of the water into the cell, and is replaced by f(meniscus);

$$P(\text{intact cell}) * V(\text{intact cell water}) = k = P(\text{cut cell}) * V(\text{cut cell water}) - f(\text{meniscus}).$$

Since the cell is open to the atmosphere the pressure in the cut cell is the same as the atmosphere. When the pressure on the cells inside the chamber is increased, water will be forced back through the cell membranes into the xylem cell. As the volume of the water in the cut xylem cell just fills the cell, i.e. returns to the volume before cutting, f(meniscus) is equal to zero. At this stage, because k is constant, and the volume of water in the cut cell is equal to the volume of water in the intact cell, the pressure inside the chamber reflects the pressure in the intact xylem cell.

If the pressure is increased in steps above the balance pressure, and the exudate is collected and quantified a "pressure-volume" curve can be constructed. From a pressure-volume curve the osmotic and turgor potential components can be determined for the range of cell water contents, as can the original volume of osmotic water in the cell (Cheung _et al._ 1975). Roberts (1982) has shown that in chaparral a modification of the pressure-volume technique may be necessary since osmotic adjustment seems to occur during the period of rehydration causing an underestimation of the osmotic potential.

Although measurements of osmotic potential, by the pressure-volume method, would have been useful, the amount of time required for a single measurement precluded such measurements in this study. At each step above the balance point an equilibrium period of about 15 minutes is required, so a single curve takes several hours. With a single pressure bomb only one sample can be made each day, since sampling throughout the day would include the diurnal changes in osmotic potential. Sampling over several days then begins to include the seasonal changes in osmotic potential and would have invalidated any attempt at replication.

2.2 The null balance porometer technique of leaf conductance measurement

The chemical reactions of photosynthesis that occur inside the leaf require an aqueous environment. An inescapable side effect of the plants need to trap gaseous carbon dioxide is the loss of some of this aqueous medium. Since the water molecule is smaller than the carbon dioxide molecule, any permeable membrane that will allow the passive diffusion of carbon dioxide will also allow the loss of water. In an arid environment a plant must find a way to limit water loss, and prevent "dying from thirst", while still maintaining carbon uptake, to prevent "starvation".

In still air the rate of the molecular diffusion of water vapor is 1.67 times that of carbon dioxide (Cowan 1978). If the air in the sub-stomatal cavity of a leaf is considered to be saturated with water vapor, because of the free exchange with the cells, and to contain no carbon dioxide, because of the efficient cellular uptake, then the concentration gradients for water and carbon dioxide can be calculated (Monteith 1973). At 25 °C, with a relative humidity of 50%, and an external carbon dioxide concentration of 300 ppm, the water vapor pressure gradient is 15.8 mbar, and the carbon dioxide gradient is 0.56 mbar. Because of the lower gradient, and the slower rate of diffusion, the movement of carbon dioxide is only 1/50 that of water vapor. When the internal physiological steps of fixation are also included the actual water use efficiency, the amount of carbon gained per unit of water lost, is rarely 1/5 of the physical potential, and has values such as 1 mole of carbon dioxide per 350 moles of water lost (Nobel 1980).

The process of water loss is dependent on the environment, especially the air temperature and the relative humidity, and is beyond the control of the plant unless it can control the diffusive resistance to water loss. Transpiration rate measurements are therefore not as informative as measuring rates of leaf conductance to water loss. It is through modifications of leaf conductance that the plant can avoid periods of high rates of water loss during the middle of the day, or conserve water on a seasonal basis. With a measurement of the leaf conductance, the transpiration rate can be calculated, and then be used to determine the effectiveness of the plants stomatal response.

The movement of water from inside the leaf to the surrounding air causes a localized increase in the relative humidity. Porometry uses this increase in external water vapor concentration as the basis for measuring transpiration and leaf conductance. Dynamic diffusion porometers measure the length of time required for the humidity in a chamber surrounding a leaf to rise from one previously determined point to another (Bell and Squire 1981). Steady state diffusion porometers introduce a known humidity gas into the chamber, and then measure the increased relative humidity in the out-flowing gas leaving the chamber (Parkinson and Legg 1972). Transpiration is a function of the increase in relative humidity and the flow rate.

Null balance porometers operate similarly to steady state diffusion porometers except that the relative humidity inside the chamber is kept constant by varying the flow rate of dry air (Beardsell _et_ _al._ 1972).

Transpiration, leaf resistance, and leaf conductance are related to the vapor pressure gradient between the sub-stomatal cavity and the outside air by the equations;

$$E = \Delta C / r$$

and;

$$g = 1/r$$

where the leaf resistance, r (measured in s/m), is the total leaf resistance which includes the stomatal resistance, the boundary layer resistance, and the cuticular resistance. Transpiration, E, has units of $g/m^2/s$, the absolute humidity gradient from inside the leaf to the outside air, ΔC, has units g/m^3, and leaf conductance, g, is the inverse of leaf resistance and has units of m/s. In this study the leaf conductances are reported in mm/s and transpiration in $mg/m^2/s$ because of the magnitude of the fluxes.

It is usually assumed that the air spaces inside the leaf are saturated, which allows the water vapor concentration to be calculated as the saturated vapor concentration at the temperature of the leaf. Transpiration can therefore be written as;

$$E = ([C_{sat}(T_{leaf})] - [C_{amb}])/r$$

where $[C_{sat}(T_{leaf})]$ is the saturated vapor concentration at T_{leaf}, the temperature of the leaf, and $[C_{amb}]$ is the vapor concentration of the ambient air.

When a leaf is in a null balance porometer chamber, water vapor is being transpired into the chamber at the same rate as the metered incoming flow of dry air, creating a constant humidity in the gas leaving the chamber. This can be expressed as;

$$[C_{out}] = (E * \text{Leaf area})/\text{flow}$$

where $[C_{out}]$ is the water vapor concentration in the air flowing out of the chamber, E is transpiration, and flow is the flow rate of dry air entering the chamber. With rearrangement, and maintaining the water vapor concentration in the out flowing air at the ambient concentration $[C_{amb}]$, transpiration is;

$$E = (\text{flow} * [C_{amb}])/\text{Leaf area}.$$

Combining the two expressions for transpiration gives;

$$([C_{sat}(T_{leaf})] - [C_{amb}])/r = (\text{flow} * [C_{amb}])/\text{Leaf area}$$

which rearranges to;

$$(([C_{sat}(T_{leaf})] - [C_{amb}]) * \text{Leaf area})/(\text{flow} * [C_{amb}]) = r$$

or;

$$(([C_{sat}(T_{leaf})] - [C_{amb}])/[C_{amb}]) * (\text{Leaf area}/\text{flow}) = r.$$

which when expressed as;

$$([C_{sat}(T_{leaf})]/[C_{amb}] - 1) * (\text{Leaf area}/\text{flow}) = r$$

and then substituting the ratio of relative humidities for the ratio of concentrations gives;

$$(100/RH_{amb} - 1) * (\text{Leaf area}/\text{flow}) = r$$

which consists of parameters that are easily measured by sensors inside the null balance porometer chamber.

If the water potential of the leaf is very low then the internal water vapor concentrations will be less than saturation. When the water potentials are below -5 MPa this should be accounted for (Slayter 1967). The reduction in internal relative humidity with decreasing water potential can be calculated from;

$$RH_{int} = 100 * e^{((P * M)/(R * T))}$$

where the water potential, P, is in MPa, M is the partial molal volume of water (18.048 cm^3/mole), R is the universal gas constant (8.3143 J/mole/°K), T is the temperature (°K), and e is the base for the natural logarithm. This then leads to the final expression for leaf resistance as;

$$r = (RH_{int}/RH_{amb} - 1) * (\text{Leaf area/flow}).$$

where leaf resistance has units of s/cm when leaf area is in cm^2 and flow is in cm^3/s. This resistance is the sum of the stomatal and cuticular resistances, since the air inside the porometer chamber is stirred and it is assumed that the boundary layer has been disturbed so its resistance is negligible.

In order to arrive at a transpiration rate the actual vapor concentrations inside the leaf and of the ambient air must be calculated. Vapor concentrations can be found from vapor pressures by the equation;

$$X = (217 * e_{amb})/T$$

where the vapor concentration, X, is in µg/cm^3, the ambient vapor pressure, e_{amb}, is in mbar, and the temperature is in degrees Kelvin (Monteith 1973). Relative humidity is related to the vapor pressure of the air by;

$$RH = (e_{amb}/e_{sat}) * 100$$

and the saturated vapor pressure can be found from the air temperature in degrees Celsius from;

$$e_{sat} = 0.6108 * e^{(17.2674 * T/(T+237.28))}$$

where e_{sat} has units of kPa (Milthorpe and Moorby 1979), and e is the base for the natural logarithm. The internal leaf vapor pressure can be calculated from;

$$e_{int} = (RH_{int} * e_{sat})/100$$

and the ambient vapor pressure from;

$$e_{amb} = (RH_{amb} * e_{sat})/100.$$

The vapor concentration gradient corresponding to the vapor pressure gradient from inside the leaf to the outside air is then;

$$X = (217 * (e_{int} - e_{amb}))/T$$

and transpiration can be calculated from;

$$E = X/r.$$

It is important to note that since this resistance does not include the boundary layer resistance the calculated transpiration rates are probably higher than those actually occurring, and should be considered as a "potential" transpiration rate.

2.3 Microclimate

In order to record the climatic conditions during the sampling season a data logger (CR21 Micrologger, Campbell

Scientific Inc.) recorded hourly averages of solar radiation (300-3000nm; W/m^2) (Kipp and Zonen CM6), wind speed (m/s) (Met One 014A), wind direction (degrees from north) (Met One 024A), relative humidity (%) (Vaisala HMP14U), rainfall (mm) (Remco TBR8), and air and soil surface temperatures (°C) (Campbell CSI 101 and 102 thermistors), along with daily absolute maximum and minimum temperatures at site 5. At the Algeria Forestry Station the daily rainfall was recorded with a standard rain gauge. At sites 2, 3, and 4 standard rain gauges were measured on each of the sampling trips. In order to minimize the evaporation from these rain gauges, 5 to 10 ml of liquid paraffin was added. At the Clanwilliam dam the daily maximum and minimum air temperatures and the rainfall were collected by the Department of Water Affairs.

On the days when the diurnal conductance measurements were made at sites 1 and 3 an automatic weather station (Campbell Scientific Inc., CR21 Micrologger) recorded 30 minute averages of solar radiation (300-3000 nm)(W/m^2) (Kipp and Zonen CM6), wind speed (m/s) (Weather Measure W203D3), relative humidity (%) (Vaisala HMP14U), air temperature (°C) (Campbell CSI 101 thermistor), and ground temperature (°C) (Campbell CSI 102 thermistor). The station was set up at the same place at the two sites throughout the season. At site 5 the microclimate was recorded by the nearby automatic weather station which recorded hourly averages of the same parameters. Because the humidity sensors connected to the two automatic weather stations could not tolerate 100% condensing humidity and frequently broke, Assmann ventilated psychrometer readings were made at hourly intervals while the leaf conductances were being measured on some of the later trips.

3. SITE DESCRIPTION

3.1 Site Selection

Although there are many established research sites in the fynbos biome, few are in areas with a mediterranean-type climate as defined by Aschmann (1973). The sites in the southern Cape receive too high of a percentage of the rainfall during the summer months. Most of the sites in the western Cape, where there is the correct seasonal distribution of rainfall, receive too much rainfall, or are restricted in area so that a gradient in rainfall can not be sampled. None of the research sites have a complete and long term climatological record, and are dependent on the records from the nearest town. Because these towns are usually in the valleys, whereas the fynbos is in the mountains, their climatological records are difficult to extrapolate from. Over much of the range of the fynbos, the drop from the mountains into the valleys also includes a switch from the low nutrient and coarse soils derived from Table Mountain Sandstone to soils derived from shales and other sources.

In an area on the western slopes of the Cedarberg Mountains both the environmental and edaphic conditions were appropriate for a study of a rainfall gradient without the complication of a change in soil type. The area was included in a survey of soils by Campbell (unpublished), and the mesic end of the transect has been the site of studies on the seasonal effect of proscribed burning (le Maitre 1984), and earlier ecophysiological work (Miller et al. 1983; Miller et al. 1984; Miller et al. in prep.). Site descriptions also occur in these papers.

3.2 Site Characteristics

Five sites were chosen between the town of Clanwilliam (Long. 18° 53´07"E, Lat. 32° 10´37"S, Elev. 180m) in the western Cape Province, South Africa and the Algeria Forestry Station (Long. 19° 03´40"E, Lat. 32° 22´30"S, Elev. 520m) which lies 31.7 km to the southeast up the valley of the Rondegat river (Figure 3.1). The sites are referred to by number, with site 1 being near Clanwilliam, and site 5 at the Algeria Forestry Station. The five sites along the transect were located so that site 3 was near the edge of the distribution of the fynbos species, and sites 2 and 4 were physically about half the distance from site 3 to the ends of the transect at sites 1 and 5. All of the sites had similar slopes (approximately 10%) and aspects (west facing), except site 5 which was on the southwest side of the valley, rather than the northeast side as were the other sites (Table 3.1). All of the sites were on soils derived from Table Mountain Sandstones. Sites 1 and 2 were on the Nardouw Formation, and sites 3, 4, and 5 were on the

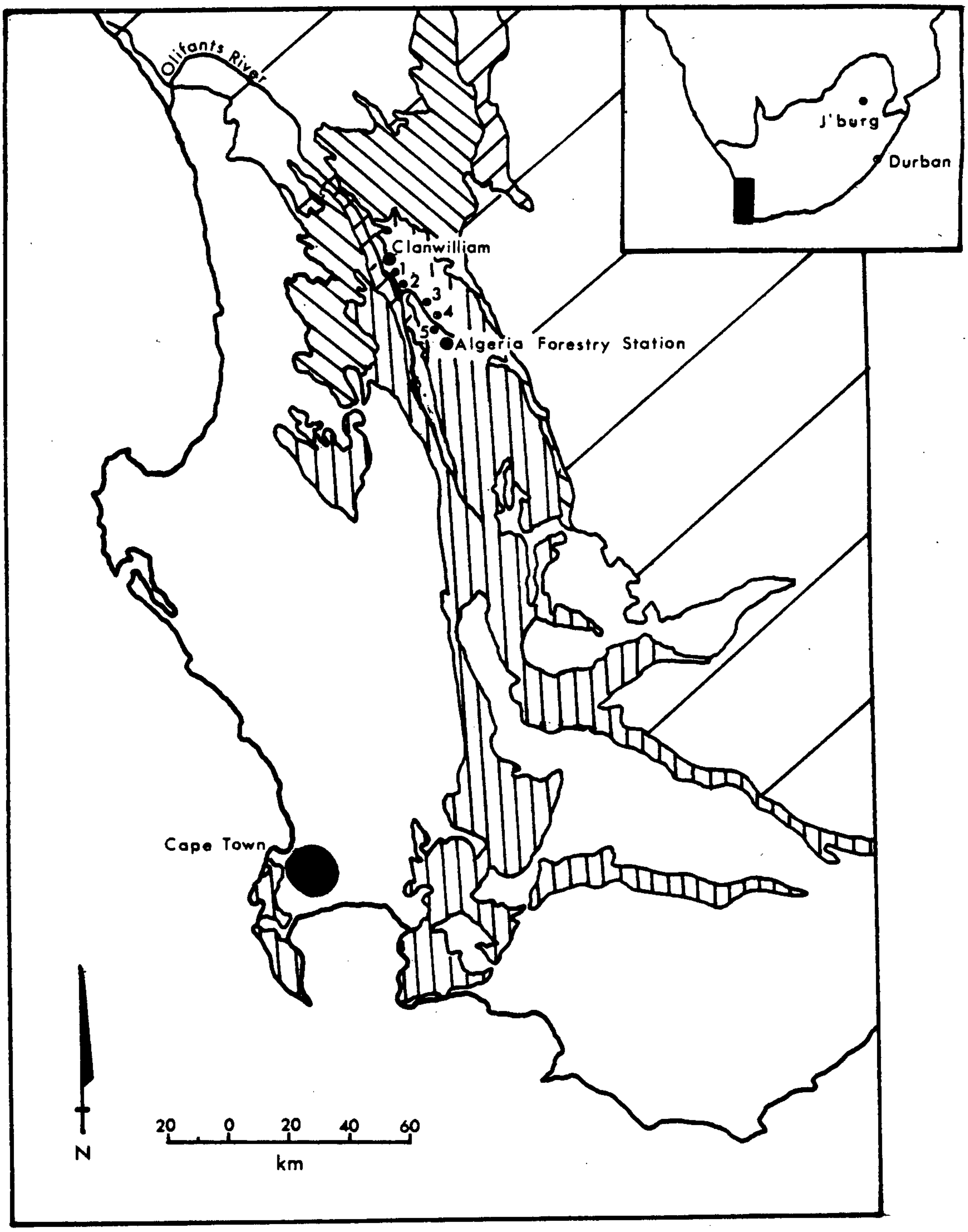


Figure 3.1 The distribution of some of the major veld types in the western Cape, South Africa (after Moll and Bossi 1983). Mesic Mountain Fynbos is denoted by vertical lines, Dry Mountain Fynbos by left slanting lines, a mosaic of Dry Mountain Fynbos and Karroid Shrublands by right slanting lines, and undifferentiated Karroid Shrublands by the wide right slanting lines. The locations of the five research sites along the Rondegat river, which feeds into the Clanwilliam Dam on the Olifants river, are given by the numbers.

Table 3.1 The location and physical characteristics of the 5 research sites along the transect between the town of Clanwilliam and the Algeria Forestry Station.

Site	1	2	3	4	5
Distance from Clanwilliam (km)	3.4	12.5	20.9	26.2	32.3
Aspect	n/a	275	270	280	15
Slope	0	8	15	15	25
Elevation (m)	180	250	270	420	520
Soil type *	ClQ2	ClQ2	ClQ1	ClQ1	ClQ1

* Codes from : Geological Survey, 1973. 3218 Clanwilliam 1:250000 Geological Map Series, Geological Survey, Pretoria.

ClQ2 = Quartzitic sandstone with thin shale and conglomerate lens.
= Nardouw Formation, Table Mountain Sandstone
ClQ1 = Quartzitic sandstone with minor shale and conglomerate lens.
= Peninsular Formation, Table Mountain Sandstone

Peninsular Formation (Geological Survey 1973).

In a soil survey conducted in 1984, Bruce Campbell (unpublished data) found that the Table Mountain Sandstone soils in the area had cation exchange capacities of between 9.2 and 20.2 me/100g, and pH values between 3.8 and 4.4. The Bray #2 phosphorus ranged between 9 and 20 ppm, the percent nitrogen between 0.03% and 0.09%, and the percent carbon between 0.85% and 1.58%. Dave le Maitre (unpublished) has analysed the soils at the site 5 of this study and found similar values, with nitrogen between 300 and 600 mg/kg soil, and Bray #2 phosphorus about 5 ppm.

3.3 Climate

At Clanwilliam the mean annual rainfall for the 41 year period between 1941 and 1982 was 223 mm/year (SD=71 mm/year) (South African Weather Bureau unpublished data). At the Algeria Forestry Station the mean annual rainfall for the 75 year period between 1909 and 1983 was 673 mm/year (SD=187 mm/year) (Department of Forestry unpublished data). At both sites the rainfall was highly seasonally distributed with approximately 50% occurring during the winter (June to August), 18% in spring (September to November), 6% in summer (December to February), and 26% in autumn (March to May). The mean air temperature at Clanwilliam was 19.7 °C (Fuggle 1981).

During the 13 month sampling period from 1 July 1982 to 31 July 1983 the amount and seasonal distribution of rainfall at both Clanwilliam and the Algeria Forestry

Station was similar to the long term means (Figure 3.2). Because August and September 1982 were drier than normal the cumulative total rainfall was lower than average at both Clanwilliam and Algeria until May 1983 which was significantly wetter than normal at Algeria ($P<.05$). The total rainfall for the 13 month period was 261 mm at Clanwilliam, and 967 mm at Algeria. Neither total is significantly different from the 13 month long term means of 255 mm (SE 11mm) at Clanwilliam, and 779 mm (SE 23 mm) at Algeria.

The rain gauge at site 3 was measured for the 12 month period 15 July 1982 to 15 July 1983. The rain gauges at sites 2 and 4 were only measured between 16 October 1982 and 15 July 1983 (Table 3.2). When the rainfall was being collected at all 5 sites, site 1 received 170.2 mm, site 2 received 122 mm, site 3 received 291 mm, site 4 received 365.1 mm, and site 5 received 680.8 mm. The decrease in rainfall between sites 1 and 2, and the noticeable increase between sites 4 and 5 may be because of the different sampling techniques. The monthly rain gauges at sites 2, 3, and 4 may have lost water do to evaporation. Since Clanwilliam had 64 days with rain while Algeria had only 49 rain days the gradient in rainfall was a function of intensity rather than number of events.

Air temperatures at Clanwilliam and the automatic weather station at site 5 were similar (Figure 3.3). The yearly mean at Clanwilliam was 20.8 °C, and the mean at site 5 for the period 1 October 82 to 31 July 1983, excluding 13 November 1982 to 14 December 1982, 22 December 1982 to 12

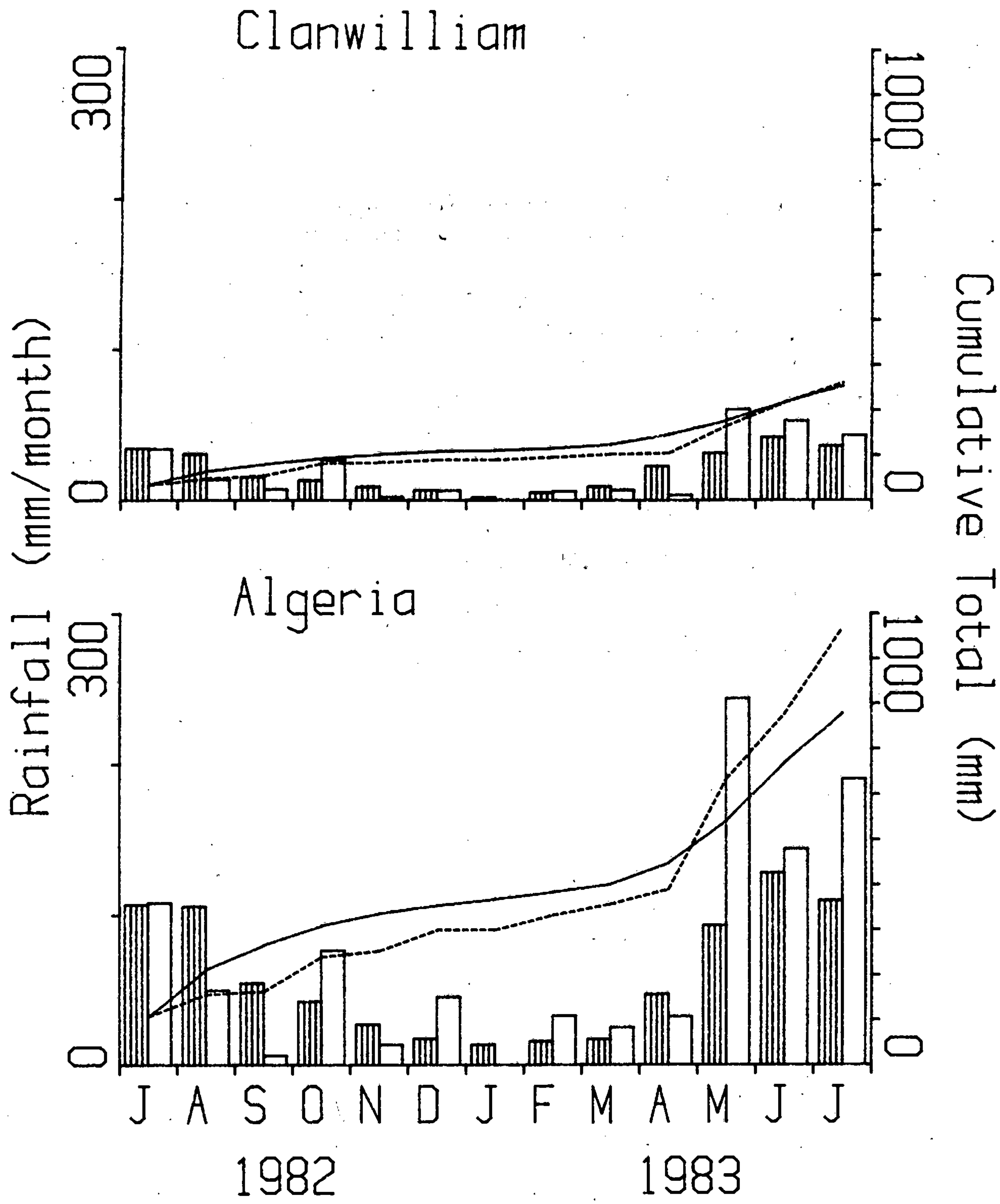


Figure 3.2 The monthly rainfall and cumulative total rainfall at Clanwilliam and the Algeria Forestry Station. The monthly means are the striped bars, and the 1982/83 rainfalls are the clear bars. The average accumulative total is the solid line, and the 1982/83 accumulative total is the dashed line. At Clanwilliam the average for the 13 month period was 255 mm (SE 11 mm) and in 1982/83 was 261 mm. At Algeria the average was 779 mm (SE 23 mm) and in 1982/83 was 967 mm.

Table 3.2 The comparable rainfall totals (mm) at the 5 sites along the transect.

Time period	Rainfall at site: 1	2	3	4	5
1 Jul 1982 - 15 Jul 1982	3.2				16.9
15 Jul 1982 - 16 Oct 1982	77.7		120.9		224.1
16 Oct 1982 - 15 Jul 1983	170.2	122.0	291.0	365.1	680.8
15 Jul 1983 - 31 Jul 1983	9.5				45.5

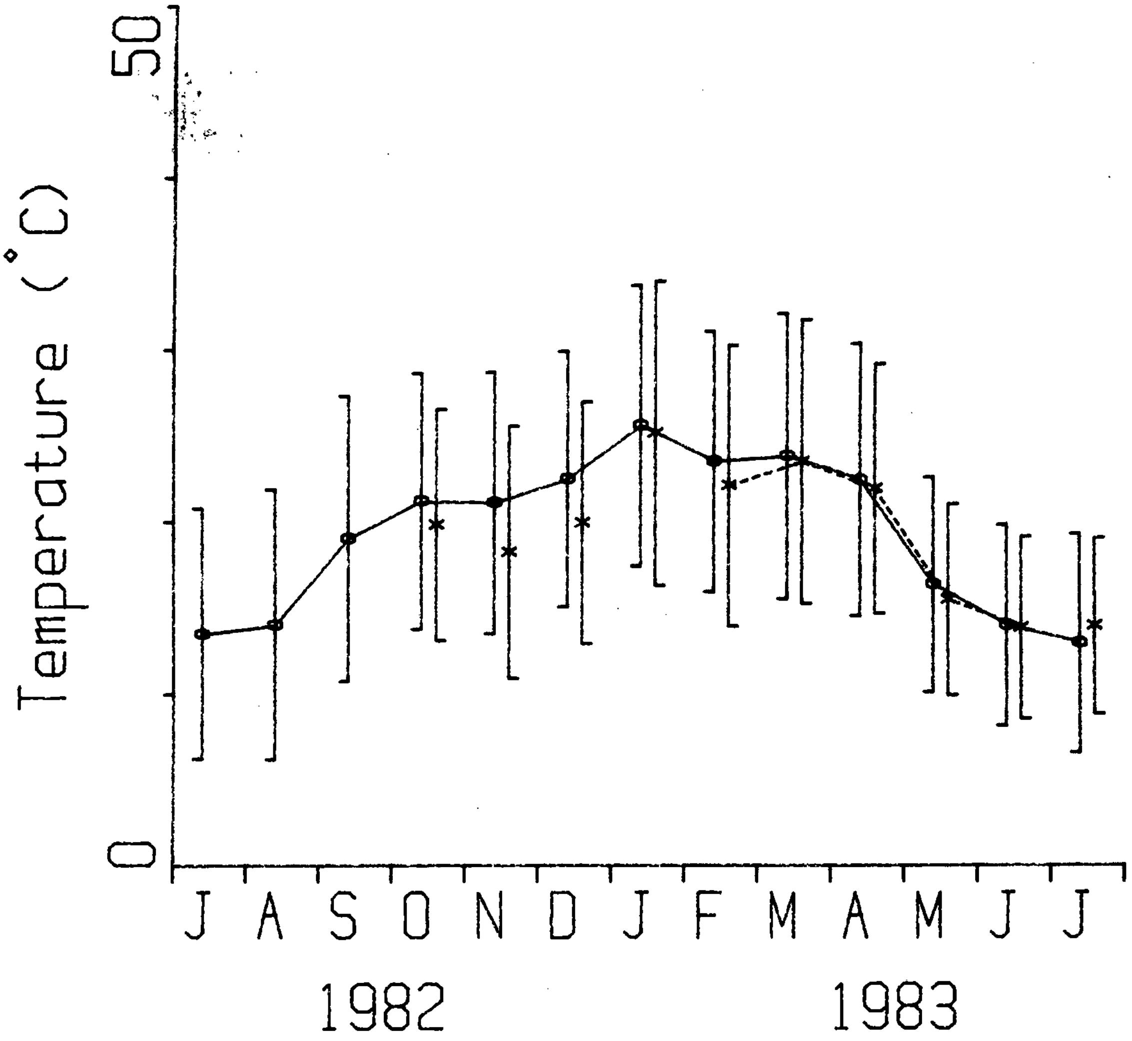


Figure 3.3 The monthly mean, mean maximum, and mean minimum temperature at Clanwilliam (o) and the Algeria Forestry Station (x). Clanwilliam is the solid line, and Algeria the dashed line. Unconected months at Algeria represent incomplete data sets. The yearly mean at Clanwilliam was 20.8 °C, and at Algeria was 19.4 °C.

January 1983, and 2 July 1983 to 10 July 1983 when the automatic weather station was not running, was 19.4 °C. The lowest temperature recorded at both Clanwilliam and site 5 was 2.4 °C. The highest temperatures at Clanwilliam and site 5 were 41.2 °C and 41.1 °C respectively.

The sampling trips in October 1982, December 1982, and May 1983 were immediately preceded by rain events (Figures 3.4 and 3.5). The rain in October stopped 3 days before sampling, and during the 4 day event site 1 received 25.3 mm and site 5 received 76.6 mm. The rainfall in December was only 2.9 mm at site 1 and 12.5 mm at site 5, but occurred on the day before sampling. During the 10 days before the sampling trip in May 1983 site 1 received 41 mm, and site 5 received 202.6 mm. The storms in May dropped the air temperatures, and marked the end of the summer.

3.4 Vegetation

Site 1, near Clanwilliam, is in an area Acocks (1975) mapped as Succulent Karoo (Veld type 31). The vegetation is dominated by Mesembryanthemaceae with _Rhus incisa_, _Galenia africana_, _Nylandtia spinosa_, and _Eriocephalus africanus_ being prominent shrubs. Site 2 is in an area Acocks mapped as Karroid Broken Veld (Veld type 26). Here the vegetation consisted of most of the same shrubs as at site 1, but lacked the Mesembryanthemaceae ground cover. The distribution of _Rhus incisa_ and _Galenia africana_ ended here, while that of _Rhus dissecta_ began. This site was subject to periods of grazing by sheep and defoliation by locusts.

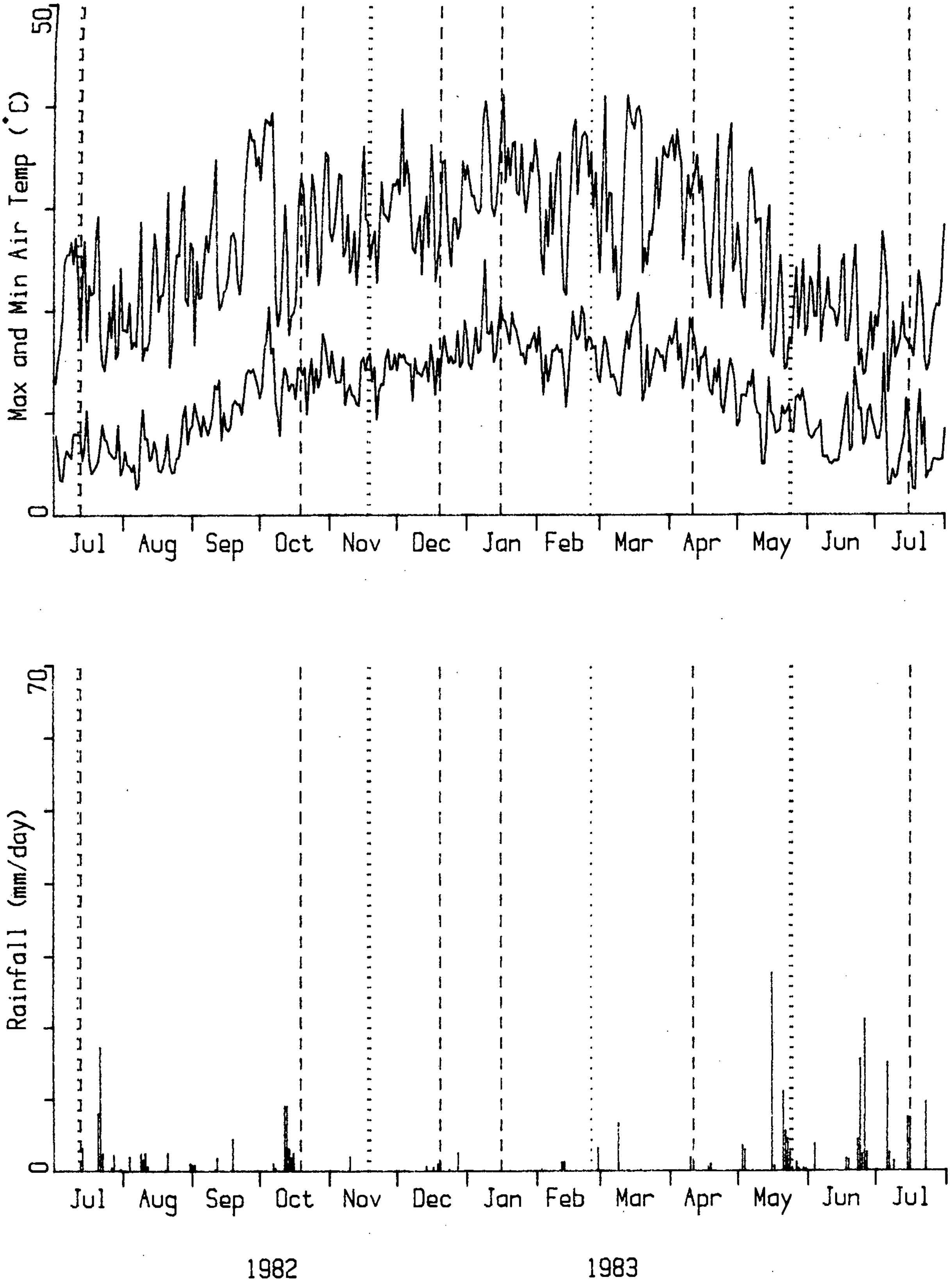


Figure 3.4 The daily maximum and minimum air temperatures, and rainfall recorded at Clanwilliam dam in 1982/83. Dotted lines show days when pre-dawn and midday xylem pressure potentials were measured, and dashed line when diurnal measurements were made.

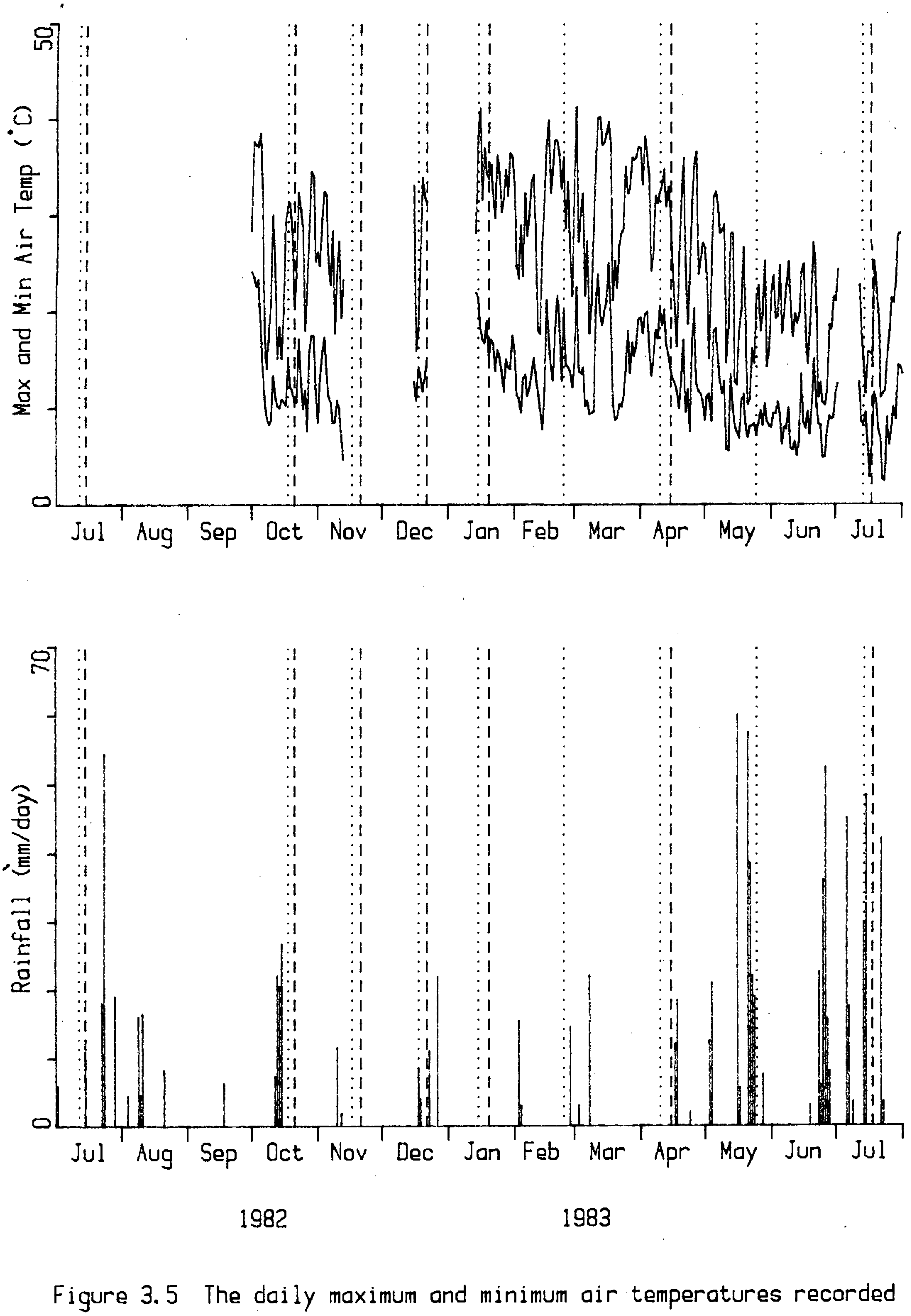


Figure 3.5 The daily maximum and minimum air temperatures recorded at the Algeria automatic weather station, and rainfall recorded at the Algeria Forestry Station. in 1982/83. The dotted lines show the days when the pre-dawn and midday xylem pressure potentials were measured, and the dashed lines show when the diurnal measurements were made.

Sites 3, 4, and 5 are mapped as Fynbos (Veld Type 69) by Acocks. At site 3 *Protea glabra* was present, but did not continue along the transect to any other site. Site 3 was the edge of the distribution of *Elytropappus gnaphaloides* and *Protea laurifolia*. Site 4 and site 5 had similar vegetation with *Protea laurifolia*, *Paranomus bracteolaris*, and *Leucadendron pubescens* dominating the overstory.

In the recent revision of Acocks veld types within the fynbos biome, sites 1 and 2 are mapped as ecotonal areas with a mosaic of Dry Mountain Fynbos and Karroid Shrublands, while sites 3, 4, and 5 are mapped as Mesic Mountain Fynbos (Moll and Bossi 1983). At a more detailed resolution site 3 might be described as Dry Mountain Fynbos (Moll *et al.* 1984) because of the open canopy, and dominance of non-proteoid mid-height shrubs.

At each of the sites 5 to 7 dominant or characteristic species were selected (Table 3.3). At site 1 the species were *Ruschia sp.* (*radicans* L. Bolus ?) (Mesembryanthemaceae), *Rhus incisa* L.f. (Anacardiaceae), *Galenia africana* L. (Aizoaceae), *Nylandtia spinosa* (L.) Dumort. (Polygalaceae), and *Eriocephalus africanus* L. (Asteraceae). Nomenclature follows Bond and Goldblatt (1984).

Ruschia sp. was the most common prostrate, mat forming succulent on the site. It had a woody stem which made it possible to be sampled in the pressure chamber, and succulent light-green leaves up to 80 mm long and 5 mm in diameter. The plants sampled reached 0.3 m in height and were about 1 m in diameter. *Rhus incisa* was a deciduous

Table 3.3 The distribution of the 13 species sampled over the 5 sites along the transect, and the number of individuals sampled per species.

	Number of individuals sampled at site:				
Species	1	2	3	4	5
Karroid species					
Ruschia sp.	5				
Rhus incisa	5	5			
Galenia africana	5	5			
Transitional species					
Nylandtia spinosa	5	5	5	5	
Eriocephalus africanus	5	5	5		1
Rhus dissecta		5	5	5	5
Fynbos understory species					
Elytropappus gnaphaloides			5	5	
Stoebe capitata					5
Agathosma giftbergensis				5	5
Fynbos overstory species					
Protea laurifolia			5	5	5
Protea glabra			3		
Paranomus bracteolaris				5	5
Leucadendron pubescens				5	5

shrub with grey-green leaves. The bushes were usually rather spherical in shape and densely branched, with the individuals sampled being about 1.5 m tall and 2.5 m in diameter. *Galenia africana* was a semi-deciduous soft-leaved shrub with yellow-green leaves. The bushes were usually densely branched, and the individuals sampled were between 0.75 and 1 m in height and diameter. *Nylandtia spinosa* was a spiny, stem-photosynthetic shrub which has small (5 mm in length) leaves seasonally. It was very densely branched, and the individuals sampled varied between 0.75 and 1 m in height, and between 1 and 2 m in diameter. *Eriocephalus africanus* was a semi-deciduous shrub with small (<5 mm long, 1 mm diameter), slightly succulent leaves. Unlike the other deciduous and semi-deciduous species, which shed the older leaves first, *Eriocephalus africanus* shed leaves inwards from the tips of the branches. The individuals sampled were about 1 m in height and diameter.

At site 2 the species sampled were *Rhus incisa*, *Galenia africana*, *Nylandtia spinosa*, *Eriocephalus africanus*, and *Rhus dissecta* Thunb. (Anacardiaceae). At site 2 the *Rhus incisa* were much taller than at site 1, being about 2.8 m tall and 4 m in diameter. The *Nylandtia spinosa* were slightly smaller, and showed signs of having been grazed. The *Eriocephalus africanus* and the *Galenia africana* were about the same size as at site 1. *Rhus dissecta* was much sparser than *Rhus incisa* and only had a few branches from the soil surface. *Rhus dissecta* had shiny, dark-green leaves. The individuals sampled were about 1 m tall and 1 m in diameter.

At site 3 the species sampled were *Nylandtia spinosa*, *Eriocephalus africanus*, *Rhus dissecta*, *Elytropappus gnaphaloides* (L.) Levyns (Asteraceae), *Protea laurifolia* Thunb. (Proteaceae), and *Protea glabra* Thunb. (Proteaceae). *Elytropappus gnaphaloides* was a low shrub with extremely small (<2 mm long, <1 mm wide), rolled grey leaves. The individuals sampled were about 0.3 m tall and about 0.7 m in diameter. Of the two *Protea* species sampled, *Protea glabra* was a smaller bush, and had smaller leaves. From the differences in the sizes of the individuals two of the *Protea glabra* were probably younger than the third, and the *Protea laurifolia* that were sampled. The smaller of the *Protea glabra* were 1.4 and 2.7 m tall and 1 and 2 m in diameter, while the third was 3.8 m tall and 5.6 m in diameter. The *Protea laurifolia* were 3 to 5 m tall and about 4 m in diameter. The leaves of *Protea glabra* were smooth, yellow-green and about 60 mm long and 15 mm wide. The leaves of *Protea laurifolia* were slightly pubescent (especially when young), grey-green and about 120 mm long and 20 mm wide. The leaves of both species, especially those of *Protea laurifolia*, twist so that they are orientated vertically.

The species sampled at site 4 were *Nylandtia spinosa*, *Rhus dissecta*, *Elytropappus gnaphaloides*, *Protea laurifolia*, *Paranomus bracteolaris* Salisb. ex J. Knight (Proteaceae), *Leucadendron pubescens* R.Br. (Proteaceae), and *Agathosma giftbergensis* E. Phillips (Rutaceae). The *Nylandtia spinosa* at site 4 were smaller and more open than at the other sites, and their canopies were often intermingled with those of other species. The *Paranomus bracteolaris* and *Leucadendron pubescens* that were sampled were about 1.75 m tall and 1.75 m in diameter. *Paranomus bracteolaris* has finely divided, almost needle-like leaves about 50 mm long. *Leucadendron pubescens* is dioecious, and only the females were sampled. The males were more finely branched, and had more, but smaller leaves. The female *Leucadendron pubescens* had leaves about 30 mm long and 7 mm wide. *Agathosma giftbergensis* was a low shrub with narrow bright-green ericoid leaves. The individuals sampled were about 0.5 m tall and in diameter.

The species sampled at site 5 were *Eriocephalus africanus*, *Rhus dissecta*, *Agathosma giftbergensis*, *Stoebe capitata* Bergius (Asteraceae), *Protea laurifolia*, *Paranomus bracteolaris*, and *Leucadendron pubescens*. The single *Eriocephalus africanus* at site 5 was an open long-stemmed bush which had larger leaves, but fewer in number, than at the other sites. *Stoebe capitata* was originally thought to be *Elytropappus gnaphaloides* and is vegetatively identical. It is a low grey bush with extremely small rolled leaves reaching about 0.5 m in height and diameter.

The thirteen species sampled could be divided into 4 groups according to a combination of distribution and growth form. *Ruschia sp.*, *Rhus incisa*, and *Galenia africana* were only found at the xeric end of the transect and had "karroid" affinities. *Nylandtia spinosa*, *Eriocephalus africanus*, and *Rhus dissecta* were "transitional" species found in the middle and reaching both ends of the transect. *Rhus dissecta* was not found at the driest site, and

Nylandtia spinosa and *Eriocephalus africanus* were rare at sites 4 and 5 but could be seen near by where there was not the proteoid overstory. The fynbos species, which were limited to the mesic end of the transect, could be divided into "understory" and "overstory" species. The understory species were; *Elytropappus gnaphaloides*, *Stoebe capitata*, and *Agathosma giftbergensis*, and overstory species were; *Protea laurifolia*, *Protea glabra*, *Paranomus bracteolaris*, and *Leucadendron pubescens*.

At sites 1 and 2 the individual plants were widely spaced and there was usually bare soil between them. At site 3 the individuals were still spaced, but in many cases the canopies touched. At site 4 there was a closed canopy, but there was not an overstory and an understory. At site 5 there was a closed proteoid overstory canopy, and most of the understory species were partly covered. At sites 1 and 2 the individuals of each species were well mixed, whereas at site 5 there were areas of solid *Paranomus bracteolaris*, *Leucadendron pubescens* or *Protea laurifolia* with little underneath them.

4. SEASONAL PATTERNS OF PRE-DAWN AND MIDDAY XYLEM PRESSURE POTENTIALS ALONG A RAINFALL GRADIENT BETWEEN SUCCULENT KAROO AND MESIC MOUNTAIN FYNBOS

4.1 Introduction

The study of the responses of individual species to temporal and spatial gradients of an environmental stress, and the integration of this information at the community level, provides a method for understanding the importance of that stress in determining the type and distribution of the vegetation (Mooney 1980). Such studies should be conducted in the field since many species show considerable plasticity in controlled environments. Ecophysiological studies of species distributions should also include species from the communities bordering the community of interest, since the ranges of most species are determined by the environmental impact on competitive fitness, rather than on absolute physical tolerances (Walter 1973).

In this study "drought" is used to describe a period with little rainfall, and is therefore a meteorological event. During a drought period the xylem pressure potential of a plant may decrease, and the term "stress" is loosely used to describe this event. Different species have different responses to decreasing xylem pressure potentials, and the responses of other physiological processes, such as leaf conductance, are necessary in order to determine how the species is affected by water stress.

The plants in areas with a seasonal cycle of water stress must either have life spans which are short enough to avoid the period of stress, or have mechanisms which allow them to either remain hydrostable during the year, or which allow them to be hydrolabile. Growth forms which follow the first pattern, drought escape, are the annuals, which complete at least their reproductive cycle before the period of water stress, the drought-deciduous species, which are functionally similar to the annuals, and possibly the plants with Crassulacean acid metabolism. In mediterranean-type climates, increased tolerances to low temperature in an annual would be an adaptation toward drought escape since the plant could complete its life cycle before the summer drought (Kramer 1980).

Plants that do not escape the drought must be drought tolerant. These plants must either have a pattern of dehydration postponement, through reduced transpiration or increased absorption, or a pattern of dehydration tolerance. Transpiration can be reduced by the presence of a thick cuticle and responsive stomata. Reduced transpirative cooling can cause tissue damage due to overheating and energy absorption must also be reduced by leaf rolling, orientation, or changes in color or pubescence. Water supply can be increased through changes in rooting strategy, or seasonal water storage in the tissue as that found in succulents. Dehydration tolerance, and the maintenance of turgor and stomatal action at low water potentials, usually requires osmotic adjustment.

The stomata of most species are usually closed at night, which reduces the rate of water loss. Even the CAM plants with open stomata usually experience low vapor pressure gradients during the night, and can sometimes even gain water because leaf temperatures are lower than air temperatures (von Willert pers. comm.). Root uptake of water continues during the night, although it is possibly slowed because of the low temperatures, and the water potentials of a plant just before dawn are as high as the equilibrium processes with the soil allow on a diurnal time scale. The pre-dawn water potentials therefore serve as a good index of the seasonal patterns of water stress.

Most plants show the greatest stress during the middle of the day, when the rates of water loss are the highest. The seasonal course of the pre-dawn and the midday xylem pressure potentials can provide information on the "strategy" a plant is following in order survive periods of water stress. Plants can either maintain seasonally stable pre-dawn xylem pressure potentials or exhibit seasonal variations. At the same time the plant can either maintain stable diurnal xylem pressure potentials or exhibit diurnal fluctuations. Any combination of the pre-dawn and midday patterns may occur. Plants which have both seasonally stable and diurnally stable xylem pressure potentials probably have deep or efficient root systems, and low leaf conductances. Plants which are seasonally stable, but are diurnally unstable probably have good root systems which allow recovery during the night, but have high rates of water loss during the day. Plants that are seasonally unstable, but show little change in xylem pressure potential during the day are probably shallow rooted, which causes the seasonal changes in response to the seasonal drying of the soil surface, but have low rates of water loss during the day. Plants that have both large seasonal variations, as well as large diurnal variations probably have shallow roots, and high conductances, and will have to either be annuals, or deciduous, or able to withstand extremely low water potentials.

Along a spatial gradient in water stress there should be a general shift from species with no ability to tolerate water stress, through those which postpone desiccation, to those which tolerate desiccation, and finally to those which escape drought. The seasonal pattern of the pre-dawn plant water potentials, when the plants have had as long as possible to re-hydrate, provides a parameter which can separate those species which tolerate drought, from those which are escaping drought and those postponing drought. The diurnal range of water potentials can be used to separate those species which have low rates of water loss, and are postponing the effects of the drought, from those which will be escaping the drought, and therefore do not need to regulate their rates of water loss.

The three types of plant response to drought; drought escape, dehydration postponement, and dehydration tolerance may exhibit one of the three possible patterns of water relations that a plant may follow during a drying period.

The first of these three patterns would exhibit a limited amount of water loss each day, as the drought progressed, and would maintain high water potentials. With decreasing pre-dawn xylem pressure potentials· the magnitude of the midday depression in the xylem pressure potential, the difference between the midday and the pre-dawn xylem pressure potentials, would decrease, since there is minimum xylem pressure potential at which the leaves can still maintain turgor and therefore water loss (Figure 4.14, top; page 87). Species attempting to postpone dehydration will have this pattern as long as the leaves are sufficiently cutinized to limit water loss other than through the stomata. The xylem pressure potential at which these species loose turgor will reflect their distributions, since species which close their stomata at high xylem pressure potentials will be restricted to mesic areas where the length of the drought is short enough to insure sufficient photosynthesis for survival.

A second pattern, which would allow survival in arid areas, would be one which included physiological changes in the xylem pressure potential corresponding to the turgor loss point, i.e. a pattern of water potentials which included osmotic adjustment. This would result in a semi-constant midday depression in xylem pressure potential as the pre-dawn xylem pressure potentials decreased (Figure 4.14, middle; page 87). As the water potentials of a species following this pattern decreased, the osmotic potentials would be adjusted to maintain a relatively fixed pressure potential. The diurnal fluctuations of xylem pressure potential may then represent the magnitude of the pressure potential. These plants will probably have some minimum xylem pressure potential, corresponding to the limit of the ability to make osmotic adjustments, below which there will be a gradual decline in midday depression. However, plants exhibiting this second pattern should show diurnal fluctuations in xylem pressure potentials at pre-dawn values lower than plants following the first pattern. Because the plants following the second pattern undergo physiological changes during the season there may be a different diurnal pattern of xylem pressure potentials following re-wetting at the end of the summer, than occurred before the drought. Plants that are able to tolerate drought will follow this second pattern of xylem pressure potentials.

The third pattern the midday depression in xylem pressure potential could exhibit with decreasing pre-dawn xylem pressure potentials would be increasing midday depressions (Figure 4.14, bottom; page 87). This would result from the plant having increasing difficulty in extracting water from the soil, and also having increasing rates of water loss due to the higher evaporative demands as the vapor pressure deficits increased going into the summer. Plants following this pattern of water potentials will be limited to areas with short drought periods, otherwise the increasing water loss will probably cause death. A modification of this pattern, which would allow existence in arid areas, would be to reduce the amount of leaf area, if the rate of water loss per leaf area could not be decreased (i.e. an annual or deciduous growth form).

Each of the three patterns, maintaining high water potentials by limiting water loss, allowing variable water potentials through physiological modification, or shedding leaves has relative advantages and can be called a response to drought. The first pattern, decreasing midday depression with decreasing pre-dawn xylem pressure potential, shows passive stomatal response to increasing plant water stress, and if coupled with the sclerophyllous leaf form, would be advantageous as long as the drought was not too long. The thick cuticle of sclerophyllous leaves would restrict water loss, except through the stomata, allowing the reactions of the stomata to insure the limiting of water stress. During the period when the midday depressions are zero the stomata are presumably closed, resulting in no carbon gain. Neighboring plants which do not loose turgor, and continue to photosynthesize and grow into the drought, could overtop a plant showing high sensitivity to water stress. Species following this conservative pattern should be overstory plants or slow growing plants, with a low light requirement for photosynthesis (since even overstory plants have to grow up out of the canopy following a fire). The low metabolic rates of these plants will limit respiration while the stomata are closed, but will also limit the maximum rate of photosynthesis. During the time when there is no transpiration the plant will also have to adopt other methods of cooling the leaves in order to prevent tissue damage.

The second pattern, constant midday depression with decreasing pre-dawn xylem pressure potential, shows physiological modification in response to drought, and probably also active stomatal response. During the development of the summer drought there are increasing evaporative demands, and decreasing soil water potentials, and a plant would have to exhibit some stomatal control in order to not show increasing diurnal fluctuations. The changes in osmotic potential which allow the maintenance of turgor lead to the development of low total water potentials, and the continued extraction of water from the soil. The rigid cell walls found in sclerophyllous leaves are thought to be important in withstanding these low water potentials. This pattern of xylem pressure potentials may represent more of an adaptation to survival in arid conditions than the first pattern, since it involves seasonal modifications in physiology and allows greater gain through maintaining carbon uptake. This pattern would be advantageous in very dry areas, and for understory species which have to compete for water with the more deeply rooted overstory species.

The third pattern of pre-dawn and midday xylem pressure potentials, increasing midday depression in xylem pressure potential with decreasing pre-dawn xylem pressure potential, shows no positive adaptation for survival in drought conditions unless it is found in an annual which can complete its life cycle before it dies, or in a seasonally deciduous plant. If a species that was not adapted to arid regions was moved into such an area, it would probably show increasing amounts of water loss, and diurnal variations in xylem pressure potential, until the turgor loss point. If the species did not have well cutinized leaves it could then continue to show low levels of water loss. Without some method to reduce energy absorption the loss of transpiration would probably cause the leaves to overheat and the tissue to die. In an annual or a seasonally deciduous species this third pattern is advantageous. Since there is no stomatal response to limit water loss the plant can continue maximum carbon uptake until the point where it dies or sheds it leaves. Species following this pattern would probably have high metabolic rates, and should have high maximum rates of photosynthesis, and the concomitant high light saturation values, and therefore would probably not do well as understory species.

4.2 Methods

Pre-dawn and midday xylem pressure potentials were measured at 4 to 6 week intervals between July 1982 and July 1983 with a pressure chamber (PMS Instrument Co. model 1000) using nitrogen gas (Scholander _et al._ 1965; Waring and Cleary 1967; Ritchie and Hinckley 1975). The instrument had a maximum pressure limit of 7 MPa. When presenting the data, values lower than -7 MPa were treated as being -7 MPa. Except for _Protea laurifolia_ and _Protea glabra_, where individual leaves were sampled, the tips of branches were sampled because the leaves where too small to extend through the rubber stopper of the pressure chamber. All of the five sites were sampled within a 2 to 3 day period. One sample was made from five different individuals, except in the cases of *Protea glabra* where there were only three individuals and therefore three samples, and *Eriocephalus africanus* at site 5 where there was only one sample from one individual. The same plants were sampled throughout the year except were death made replacement necessary, and a nearby individual was then used for the rest of the season. A *Leucadendron pubescens* at site 4 was replaced in December, a *Rhus dissecta* at site 3 was replaced in January, and a *Agathosma giftbergensis* at site 5 was replaced in July 1983.

In the three cases where a species was not sampled at one of the sites in July 1982, the values were extrapolated from the closest site during the same month when calculating some of the statistics. For each species a two-way analysis of variance was calculated for the pre-dawn, midday, and midday depression in xylem pressure potential using site and sampling date as the criteria (Sokal and Rohlf 1969). If the species was only present at one site then a one-way analysis of variance was calculated. When a two-way analysis of variance was calculated, Tukey's test for nonadditivity of the interaction was also calculated. In all cases there was no evidence of nonadditivity at a significance level of 0.05. A Student-Newman-Keuls test was used to determine the species and the site groupings. Third order regression lines were calculated for the relationship between the midday depressions in xylem pressure potential and the pre-dawn values for each species using the POLYFIT program (Spain 1984). Additional information on the statistical procedures is given in the appendix.

4.3 Results

The species within the four groups; the karroid species, the transitional species, the fynbos understory species, and the fynbos overstory species had similar seasonal patterns of xylem pressure potentials. Of the four groups, the transitional species had the lowest xylem pressure potentials and the fynbos overstory species the highest xylem pressure potentials, while the karroid species and the fynbos understory species had similar intermediate values (Table 4.1). All of the species at all five sites had similar pre-dawn xylem pressure potentials, between -0.5 and -1.0 MPa, at the beginning of the sampling period in July 1982 and at the end in July 1983. In April 1983, on the last sampling trip before the onset of the winter rains, the transitional species *Nylandtia spinosa* and *Eriocephalus africanus* had pre-dawn xylem pressure potentials between -6.5 and -7.0 MPa, while the fynbos overstory species *Protea laurifolia*, *Protea glabra*, *Paranomus bracteolaris*, and *Leucadendron pubescens* had pre-dawn values between -1.0 and -2.0 MPa. At this time the karroid and fynbos understory species had pre-dawn xylem pressure potentials ranging from -3.0 MPa to -6.5 MPa. The pre-dawn xylem pressure potentials at all five sites began to decline in October, and they all recovered sharply in May. Species that were found at several sites along the transect usually had lower xylem pressure potentilas at the dryer sites, but when a site average was calculated the lowest xylem pressure potentials occurred in the middle of the transect.

Table 4.1 The seasonal range of the xylem pressure potentials (MPa) of the 13 species sampled along the transect. The highest mean pre-dawn value and the lowest mean midday values of the season are given.

Species	Range of the xylem pressure potentials (MPa) at site:				
	1	2	3	4	5
Karroid species					
Ruschia sp.	-0.44 -3.50				
Rhus incisa	-0.30 -5.46	-0.68 -5.32			
Galenia africana	-0.68 -5.64	-1.18 -5.18			
Transitional species					
Nylandtia spinosa	-0.39 -6.30	-0.68 -6.68	-0.85 -6.52	-0.41 -5.88	
Eriocephalus africanus	-0.41 -7.00	-0.84 -6.66	-0.77 -7.00		-0.60 -4.20
Rhus dissecta		-0.65 -5.54	-0.53 -5.50	-0.42 -4.48	-0.43 -3.57
Fynbos understory species					
Elytropappus gnaphaloides			-0.49 -5.64	-0.39 -4.36	
Stoebe capitata					-0.56 -3.92
Agathosma giftbergensis				-0.41 -6.84	-0.69 -6.16
Fynbos overstory species					
Protea laurifolia			-0.31 -2.31	-0.32 -1.87	-0.29 -1.87
Protea glabra			-0.15 -2.05		
Paranomus bracteolaris				-0.36 -1.96	-0.26 -1.94
Leucadendron pubescens				-0.33 -1.72	-0.31 -1.88

4.3.1 The karroid species

Of the three karroid species the succulent Ruschia sp. showed the least water stress, when the term "stress" is used to describe the magnitude of the depression of the xylem pressure potentials rather than the plants response to low xylem pressure potentials. The pre-dawn xylem pressure potentials decreased from -1.06±0.25 MPa (mean and standard error) in July 1982 to -3.26±0.34 MPa in February 1983 and then recovered to -0.44±0.12 MPa in July 1983 (Figure 4.1). The midday xylem pressure potentials decreased from -1.76±0.04 MPa to -3.50±0.20 MPa. Between February and April, in the middle of the summer, there was a slight increase in the pre-dawn xylem pressure potentials. In April there was only a 0.04 MPa difference between the pre-dawn and the midday xylem pressure potentials. A lack of water loss during the day in the late summer may have allowed for more complete rehydration at night, and explain the increase in the pre-dawn values. The pre-dawn values measured in October, which varied between -0.15 and -0.2 MPa, may not be valid as it was found that attempting to measure the succulent leaf tissue rather than the woody stem tissue gave erroneously high values (i.e one was crushing the tissue with the rubber stopper, rather than expressing the water in the xylem). On the January trip the first Ruschia sp. measured had a value of -0.6 MPa, while the others had values between -2.4 and -2.9 MPa. A one-way analysis of variance showed the seasonal differences of both the pre-dawn and the midday xylem pressure potentials were significant at the 0.01 level (Table 4.2; page 80).

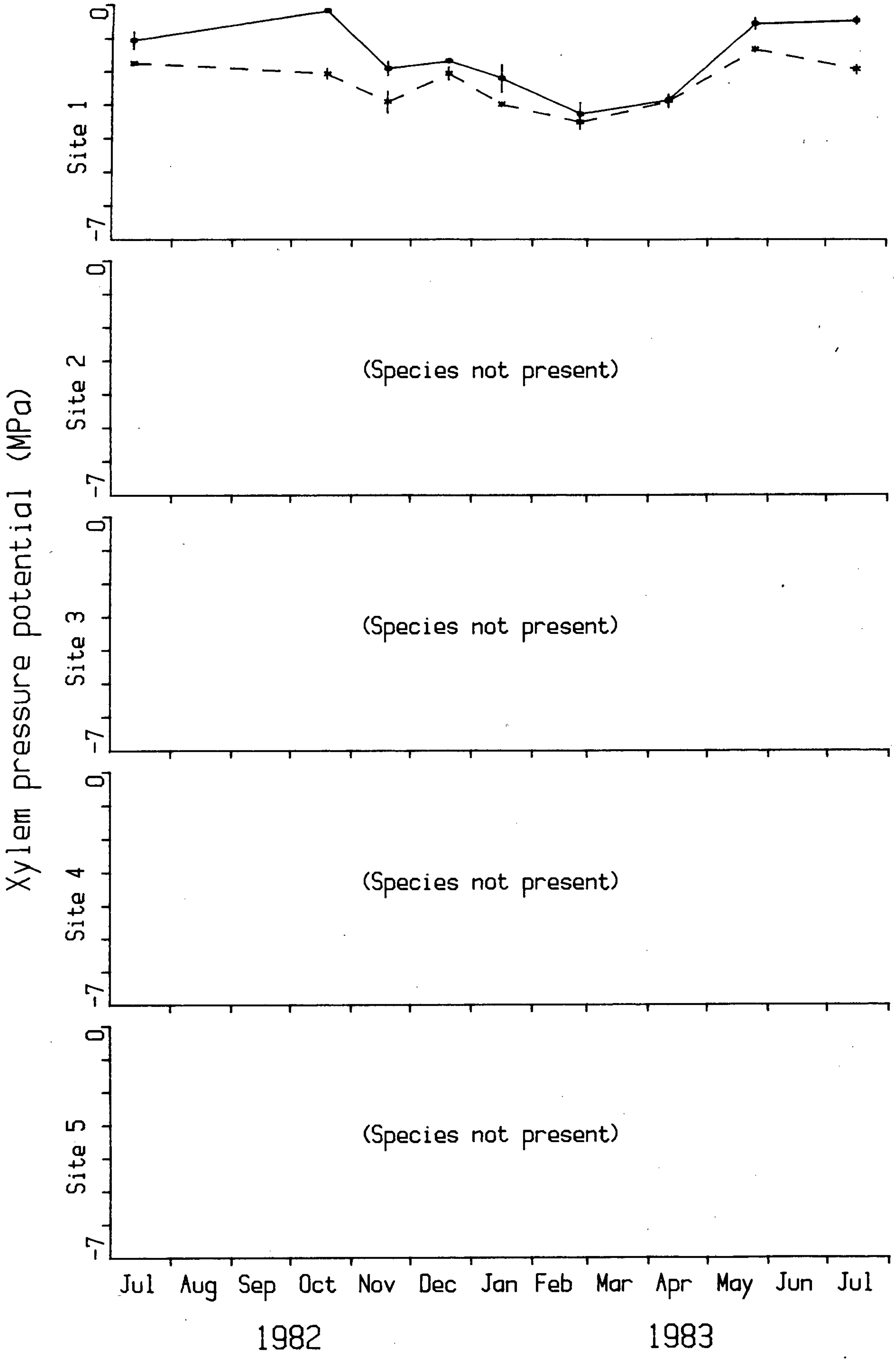


Figure 4.1 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of <u>Ruschia sp.</u> (Mean and SE, n=5)

Rhus incisa had higher pre-dawn xylem pressure potentials than the last karroid species, Galenia africana, at the beginning and the end of the season (Figures 4.2 and 4.3). In July 1982 Rhus incisa was -0.80±0.05 MPa at site 1 and -0.76±0.09 MPa at site 2, while Galenia africana was -1.23±0.08 MPa at site 2. Galenia africana was not sampled at site 1 in July 1982. In July 1983 Rhus incisa was -0.30±0.02 MPa at site 1 and -0.68±0.07 MPa at site 2 and Galenia africana was -0.68±0.03 MPa and -1.18±0.09 MPa at sites 1 and 2 respectively. In the middle of the summer Rhus incisa had lower pre-dawn xylem pressure potentials than Galenia africana, reaching -5.22±0.46 MPa at site 1, and -5.22±0.52 MPa at site 2, while Galenia africana was -5.00±0.33 MPa at site 1 and -4.22±0.29 MPa at site 2. The Rhus incisa at site 2 reached this minimum value a month before those at site 1, and in both cases the pre-dawn xylem pressure potentials rose in the late summer after reaching the minimum. A two-way analysis of variance showed that for Rhus incisa the only significant differences (0.01 level) were between sampling dates, while both sites and sampling dates were significantly different for Galenia africana (Table 4.2; page 80). There was also a significant interaction between site and date for Galenia africana, probably as a result of the elevated values in December.

The midday xylem pressure potentials of Rhus incisa started and ended the season at -2.16±0.27 MPa and -2.17±0.33 MPa at site 1 and -2.10±0.16 MPa and -1.43±0.13 MPa at site 2. The lowest midday values were -5.46±0.17 MPa at site 1 and -5.32±0.32 MPa at site 2.

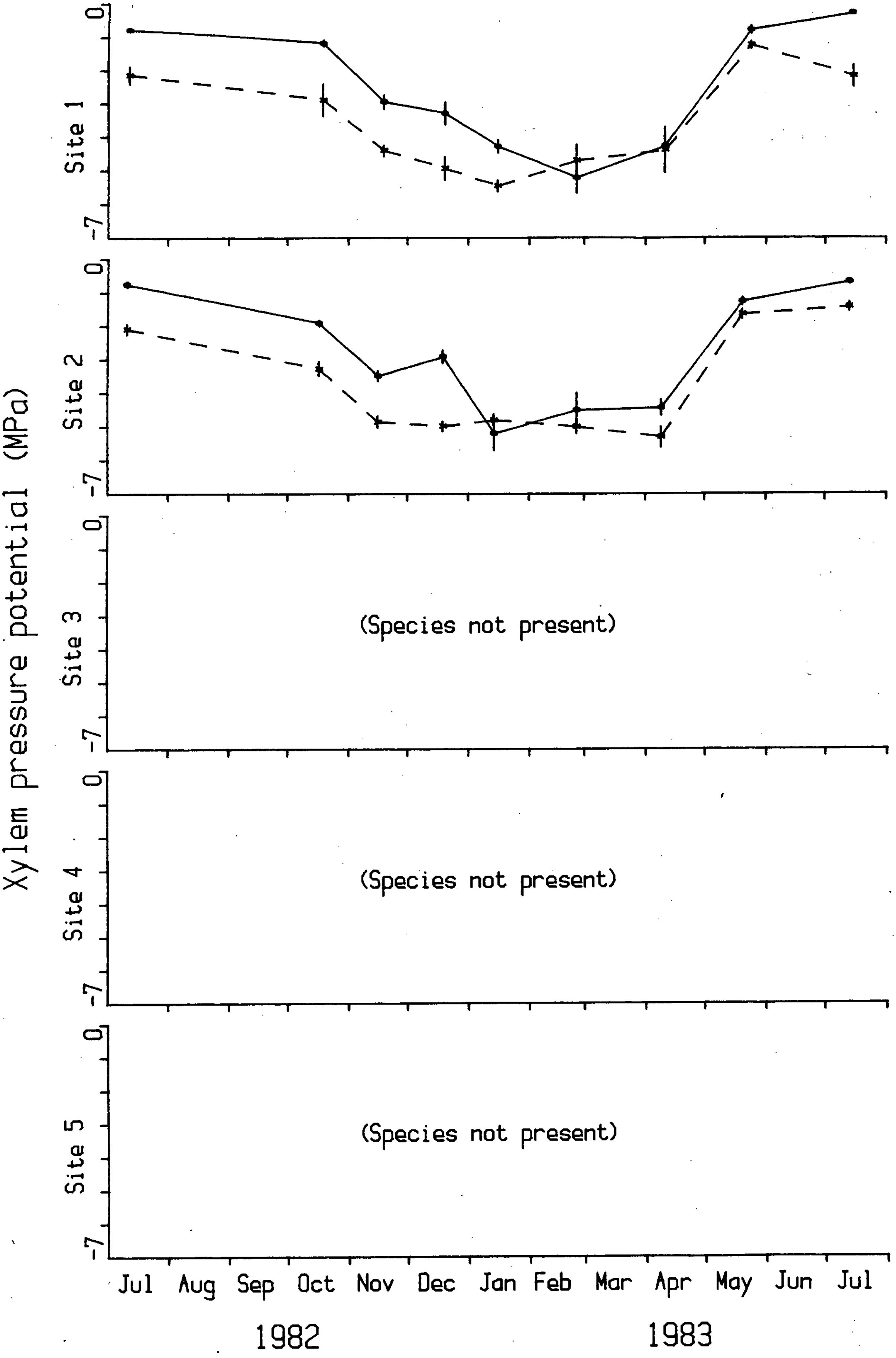


Figure 4.2 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of Rhus incisa. (Mean and SE, n=5)

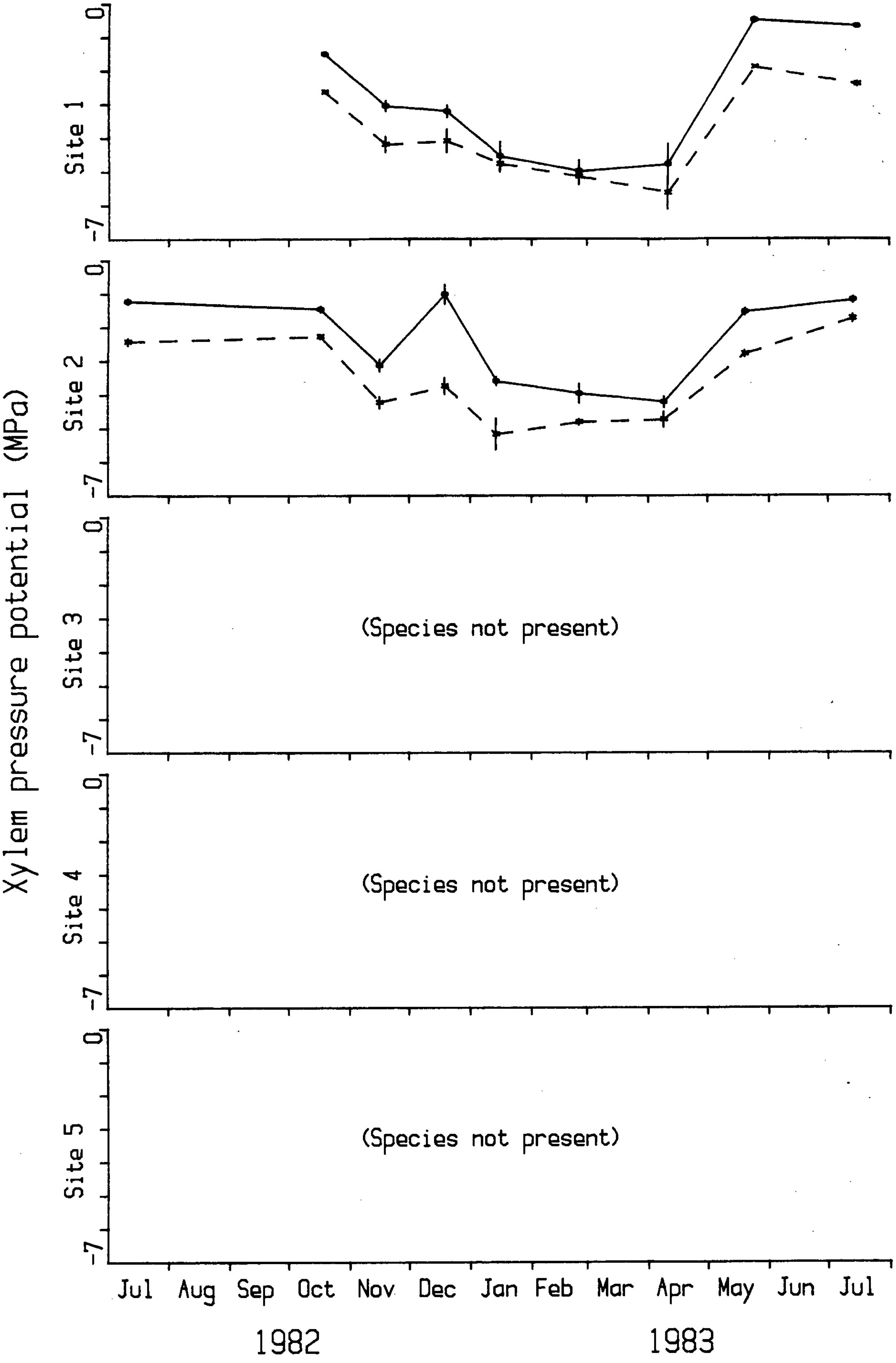


Figure 4.3 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of <u>Galenia africana</u>. (Mean and SE, n=5)

After reaching a threshold of -5 MPa the midday xylem pressure potentials did not continue to drop, while the pre-dawn values dropped to match the midday values. As with the pre-dawn values there were significant differences between sampling dates but not between the two sites.

The midday xylem pressure potentials of Galenia africana were similar to those of Rhus incisa, starting the season at -2.43±0.11 MPa at site 2, and ending at -2.41±0.07 MPa at site 1 and -1.73±0.12 MPa at site 2. In the middle of the season the midday xylem pressure potentials reached -5.64±0.48 MPa and -5.18±0.47 MPa at sites 1 and 2. There were no significant differences between the sites, but there were significant differences between the sampling dates, and there was a significant interaction (Table 4.2; page 80).

4.3.2 The transitional species

In two of the transitional species, Nylandtia spinosa and Rhus dissecta, the lowest pre-dawn xylem pressure potentials were found at site 3, while the pre-dawn values of Eriocephalus africanus at site 3 were almost as low at site 1 (Figures 4.4, 4.5, and 4.6). Nylandtia spinosa and Eriocephalus africanus both had pre-dawn xylem pressure potentials near -1 MPa in July 1982 at all the sites where they were sampled. In July 1982 the Rhus dissecta sampled were slightly above -0.5 MPa at sites 2, 3, 4, and 5. In July 1983 all three species had pre-dawn xylem pressure potentials of about -0.5 MPa throughout their distributions, with the Nylandtia spinosa and Eriocephalus africanus at

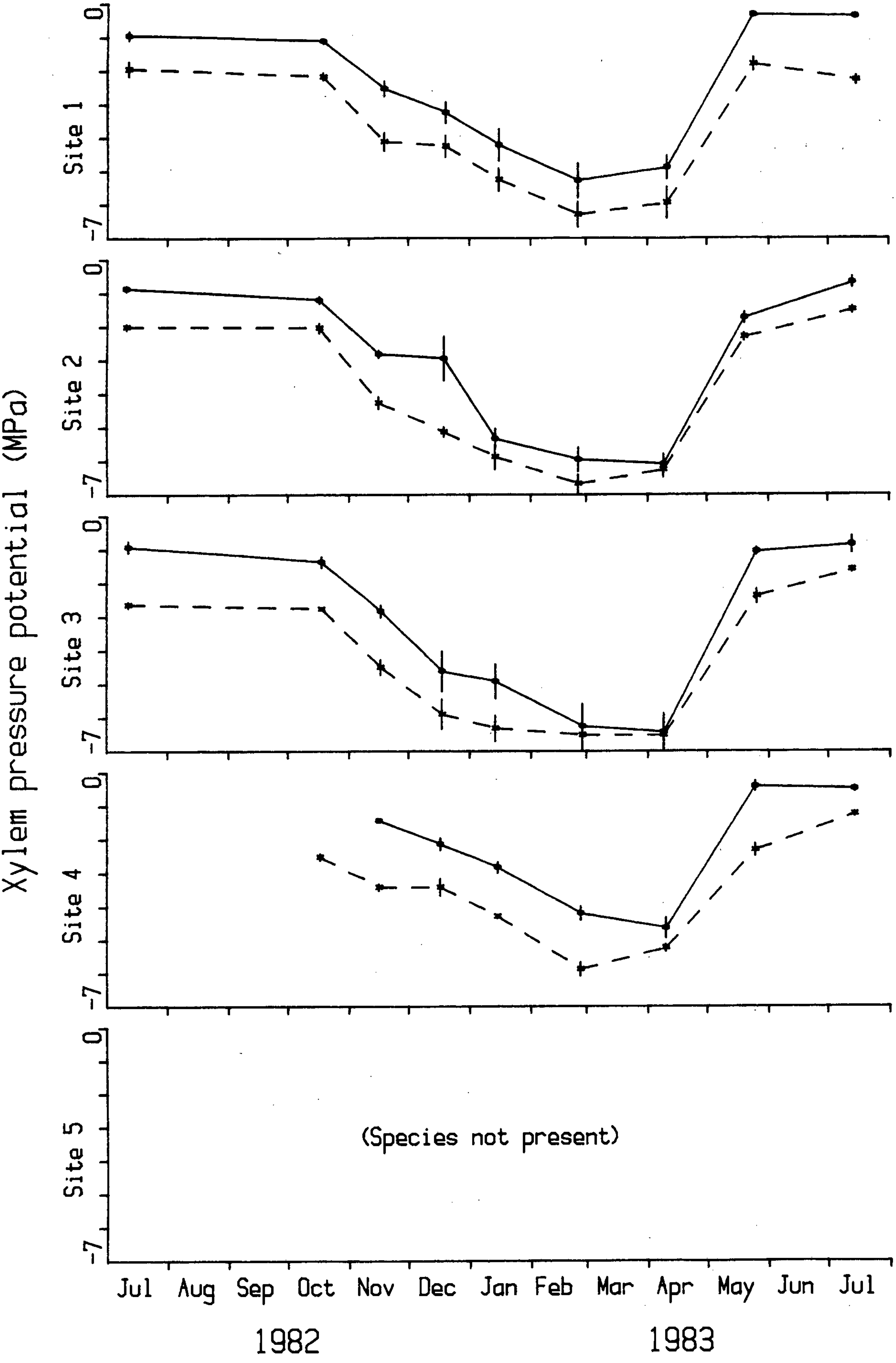


Figure 4.4 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of <u>Nylandtia spinosa</u>. (Mean and SE, n=5)

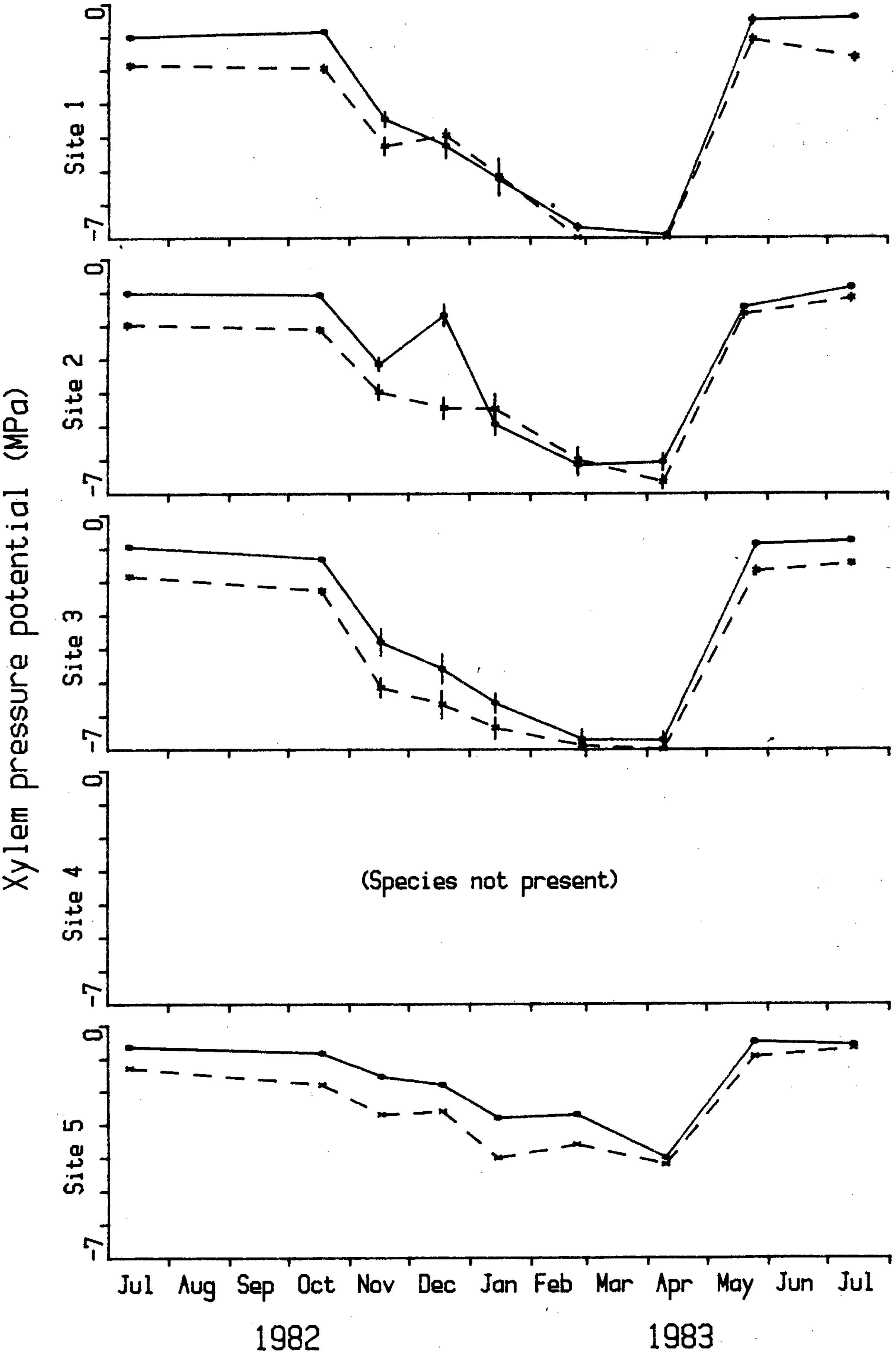


Figure 4.5 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of *Eriocephalus africanus*. (Mean and SE, n=5 except site 5, where n=1)

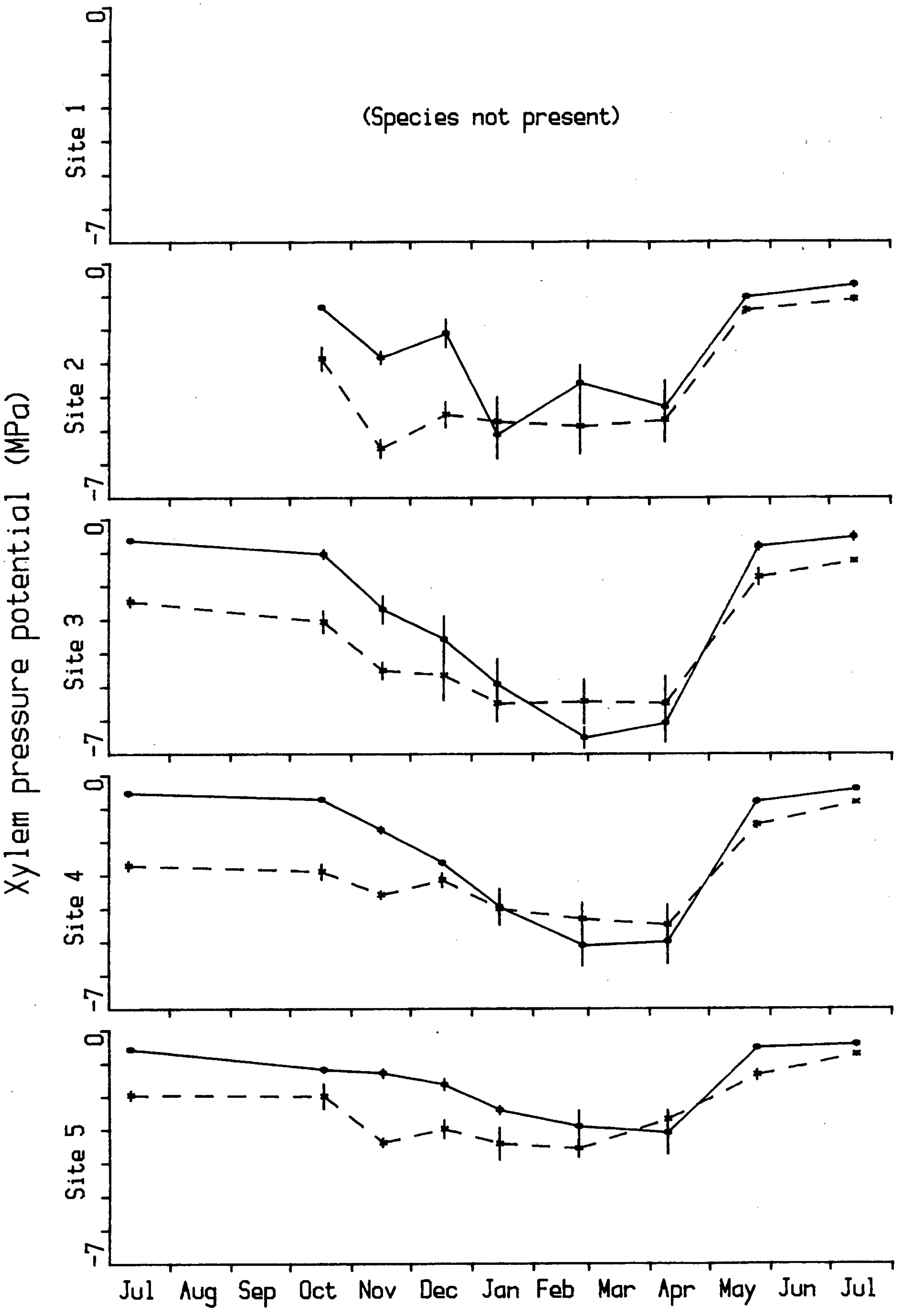


Figure 4.6 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of Rhus dissecta. (Mean and SE, n=5)

site 1 showing the least stress. At the height of the drought the pre-dawn xylem pressure potentials of Nylandtia spinosa at site 3 were -6.44±0.56 MPa and were 0.34 MPa lower than the mean at site 2, 1.56 MPa lower than at site 1, and 1.8 MPa lower than at site 4. Eriocephalus africanus showed smaller inter-site differences, although site 2, with a pre-dawn mean of -6.06±0.025 MPa, was higher than site 1 which was -6.92±0.08 MPa and site 3 which was -6.72±0.23 MPa. The single Eriocephalus africanus measured at site 5, which was -4.0 MPa pre-dawn at its lowest point, was almost 3 MPa higher than the individuals at the other sites. The pre-dawn xylem pressure potentials of Rhus dissecta reached -6.52±0.31 MPa at site 3, which was 1.4 MPa lower than the lowest monthly mean recorded at at site 2, 1.42 MPa lower than that at site 4, and 3.42 MPa lower than that at site 5. In all three species there were significant differences between the pre-dawn xylem pressure potentials at the sites, and between the sampling dates (Table 4.2; page 80). Because the lowest values were found in the middle of the transect there were also significant interactions between sampling date and site for all three species.

The midday xylem pressure potentials of Nylandtia spinosa where consistently lowest at site 3. In July 1982 they ranged from -1.95±0.22 MPa at site 1 through -2.01±0.09 MPa at site 2 to -2.64±0.10 MPa at site 3. The lowest midday values at all 4 sites occurred in February, and the last measurements of the summer drought period in April were slightly higher. In February the midday xylem pressure potentials were near -6.5 MPa at sites 1, 2, and 3 and -5.88±0.20 MPa at site 4. The midday xylem pressure potentials at site 3 were close to -6 MPa about two months before site 1, and about 1 month before site 2.

The midday xylem pressure potentials of *Eriocephalus africanus* dropped from -1.86±0.09 MPa at site 1, -1.97±0.11 MPa at site 2, and -1.84±0.06 MPa at site 3 in July 1982, to -7 MPa at sites 1 and 3 and -6.66±0.20 MPa at site 2 in April 1983. In July 1983 the midday xylem pressure potentials of *Eriocephalus africanus* were -1.60±0.13 MPa at site 1, -1.17±0.12 MPa at site 2, and -1.46±0.07 MPa at site 3. At site 5 the single *Eriocephalus africanus* measured had midday values of -1.3 MPa early in the season, and dropped to -4.2 MPa before recovering to -0.7 MPa.

In July 1982 *Rhus dissecta* had midday xylem pressure potentials between -2.71±0.14 MPa, which occurred at site 4, and -1.95±0.13 MPa, which occurred at site 5. The lowest values during the summer were at site 3; -5.50±0.81 MPa. At this time the mean at site 2 was 0.62 MPa higher, the mean at site 4 was 1.02 MPa higher, and the mean at site 5 was 1.93 MPa higher. In the middle of the summer, when *Rhus dissecta* was without leaves, the mean midday xylem pressure potentials were about 0.5 MPa higher than the pre-dawn values. This inverted pattern was also found, although to a lesser degree, in the other completely deciduous species sampled, *Rhus incisa*, and in the semi-deciduous *Eriocephalus africanus*. The variations in the midday xylem pressure potentials between sites and sampling dates were significant in all three species, and in Nylandtia spinosa and Eriocephalus africanus there were also significant interactions between site and sampling date (Table 4.2; page 80).

In December 1982 the sampling at site 2 was conducted immediately after a small rain event and the pre-dawn values for all of the species were elevated. The karroid species Galenia africana and the transitional species Eriocephalus africanus showed the greatest elevations in pre-dawn xylem pressure potential following the rain, possibly because they were able to absorb some of the water directly into their leaves. The leaves of Galenia africana were not very sclerophyllic, and the leaves of Eriocephalus africanus were rather mesophyllic. The two Rhus species exhibited a smaller increase in the pre-dawn xylem pressure potential following the rain, and Nylandtia spinosa showed the least response. Of the five species sampled at site 2, only Galenia africana showed an increase in midday xylem pressure potential in response to the rain. For most of the species the rain did not bring more than a mornings release from the drought.

This increase in the pre-dawn xylem pressure potentials as a result of the rain explains some of the statistically significant interactions between site and date found in these species. The large midday depressions in xylem pressure potential found at high pre-dawn xylem pressure potentials in Galenia africana at site 2 are also an artifact of this rain event (Figure 4.15c; page 88).

4.3.3 The fynbos understory species

Elytropappus gnaphaloides and *Agathosma giftbergensis*, the two fynbos understory species that were sampled at more than one site, had large differences between the sites, with the plants at the drier sites having lower xylem pressure potentials (Figures 4.7, and 4.9). At the start of the season *Elytropappus gnaphaloides* had pre-dawn xylem pressure potentials of -0.71±0.06 MPa at site 3 and -0.39±0.07 MPa at site 4. At the end of the season sites 3 and 4 had pre-dawn values of -0.49±0.04 MPa and -0.47±0.05 MPa respectively. At the end of the summer, in April, *Elytropappus gnaphaloides* had pre-dawn xylem pressure potentials of -5.40±0.75 MPa at site 3, and -3.48±0.47 MPa at site 4. The midday xylem pressure potentials dropped from a mean of -1.86 MPa for both site 3 and site 4, to -5.64±0.61 MPa at site 3 and -4.36±0.55 MPa at site 4. The midday values at site 3 seemed to reach a threshold of about -5 MPa, until the declining pre-dawn values also dropped to that level. *Stoebe capitata*, which was physiognomically quite similar to *Elytropappus gnaphaloides* and was sampled in its place at site 5, had pre-dawn values of -0.73±0.05 MPa in July 1982, -2.31±0.18 MPa at its lowest in April 1983, and values of -0.56±0.15 MPa in July 1983 (Figure 4.8). The midday xylem pressure potential values of *Stoebe capitata* were -1.56±0.09 MPa in July 1982, -3.92±0.07 MPa in February (increasing to -3.42±0.16 MPa in April), and -0.92±0.01 MPa in July 1983. *Agathosma giftbergensis* had higher pre-dawn xylem pressure potentials at site 4 than 5 in both July 1982 and July 1983. In July 1982 they were -0.41±0.03 MPa at

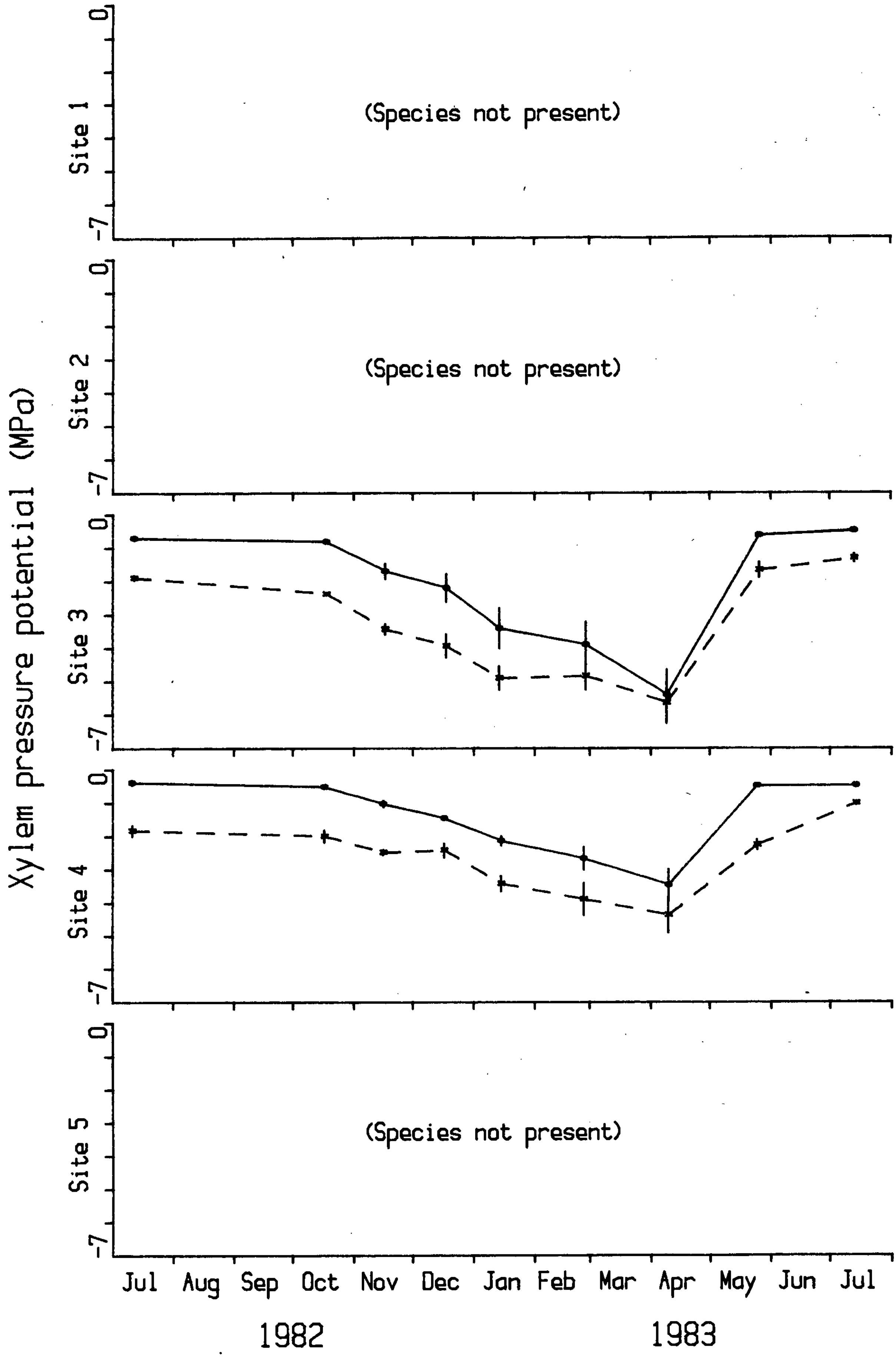


Figure 4.7 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of Elytropappus gnaphaloides. (Mean and SE, n=5)

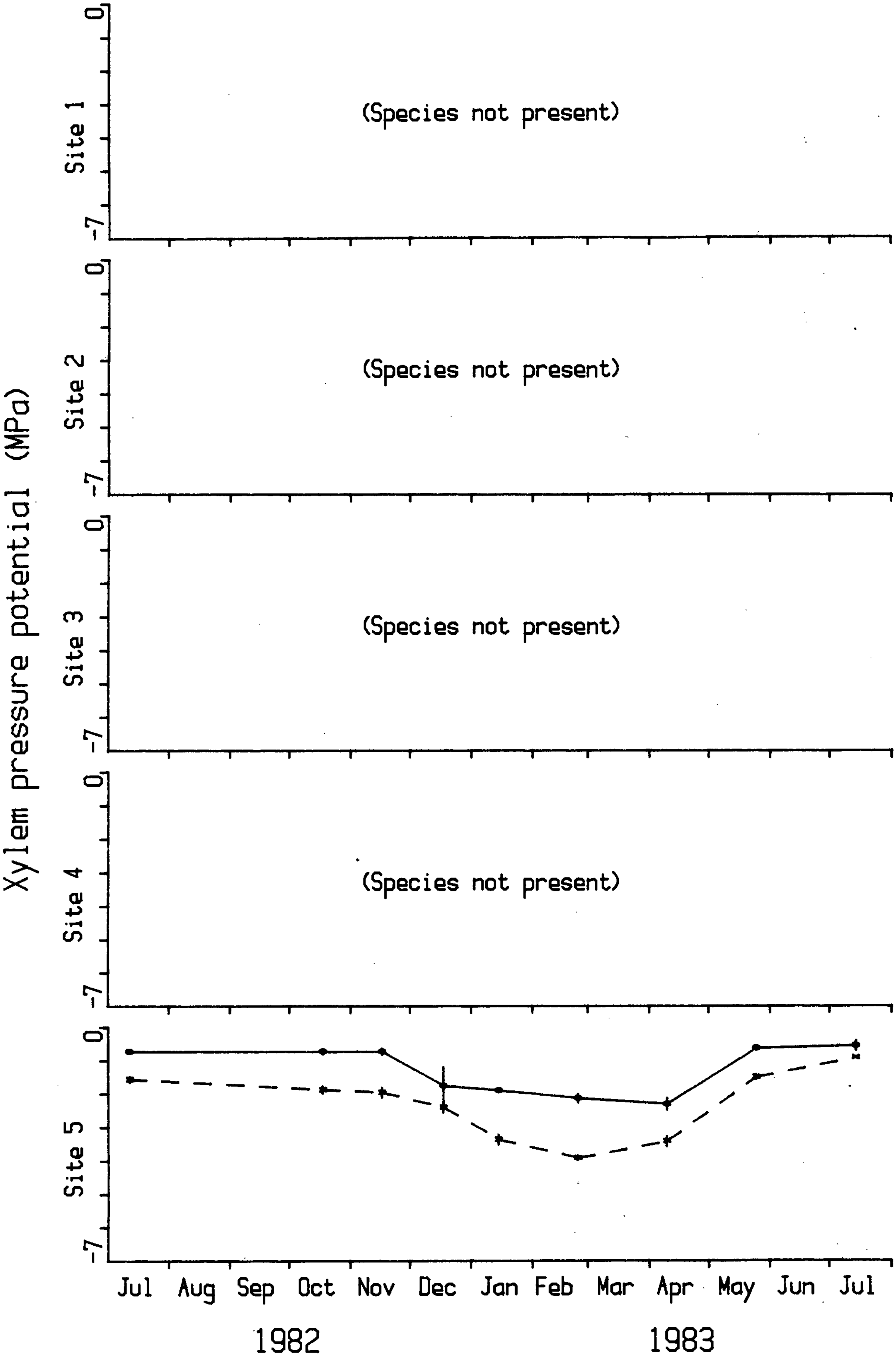


Figure 4.8 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of <u>Stoebe capitata</u>. (Mean and SE, n=5)

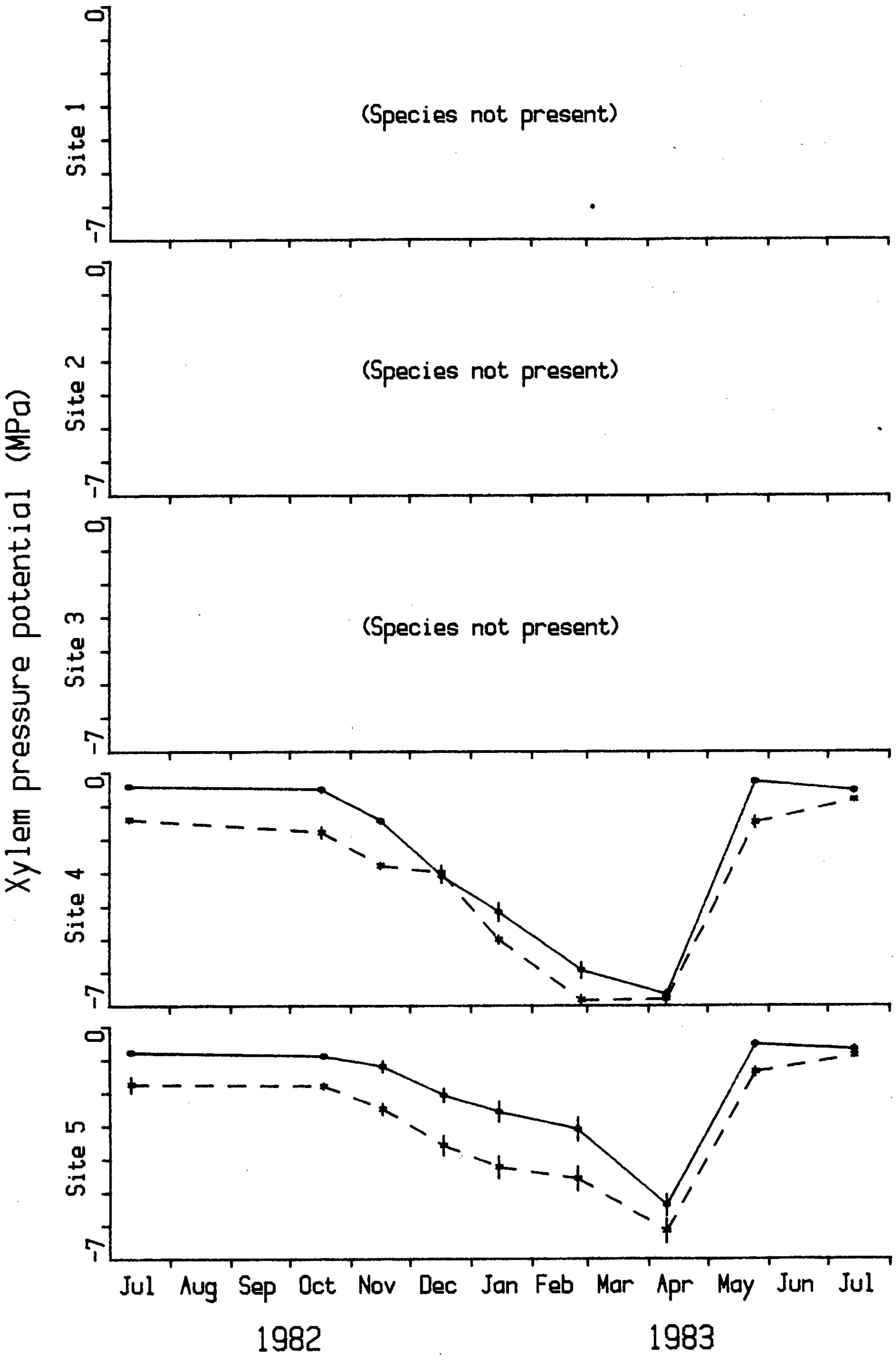


Figure 4.9 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of *Agathosma giftbergensis*. (Mean and SE, n=5)

site 4 versus -0.78±0.04 MPa at site 5, and in July 1983 they were -0.53±0.07 MPa at site 4 versus -0.69±0.11 MPa at site 5. During the summer months the pre-dawn xylem pressure potentials at site 4 averaged 1.4 MPa lower than those at site 5. In April the pre-dawn xylem pressure potentials were -6.66±0.12 MPa at site 4, and -5.38±0.32 MPa at site 5.

The seasonal variations in the pre-dawn xylem pressure potentials of all three species were significant at the 0.01 level (Table 4.2; page 80). Elytropappus gnaphaloides and Agathosma giftbergensis had significant differences between sites, and in the case of Agathosma giftbergensis there was a significant interaction between sampling date and site. The midday xylem pressure potentials of all three species showed significant differences between sampling dates, and where possible between sites, and had significant interactions between site and sampling date.

4.3.4 The fynbos overstory species

The four fynbos overstory species sampled, Protea laurifolia, Protea glabra, Paranomus bracteolaris, and Leucadendron pubescens all maintained high xylem pressure potentials throughout the year (Figures 4.10, 4.11, 4.12, and 4.13). The pre-dawn values of Protea laurifolia dropped from about -0.4 MPa at sites 3, 4 and 5, to -2.09±0.19 MPa at site 3, -1.37±0.17 MPa at site 4, and -1.47±0.12 MPa at site 5 at the end of the summer. In July 1983 the pre-dawn xylem pressure potentials were -0.31±0.02 MPa at site 3, -0.32±0.03 MPa at site 4, and -0.29±0.03 at site 5. The

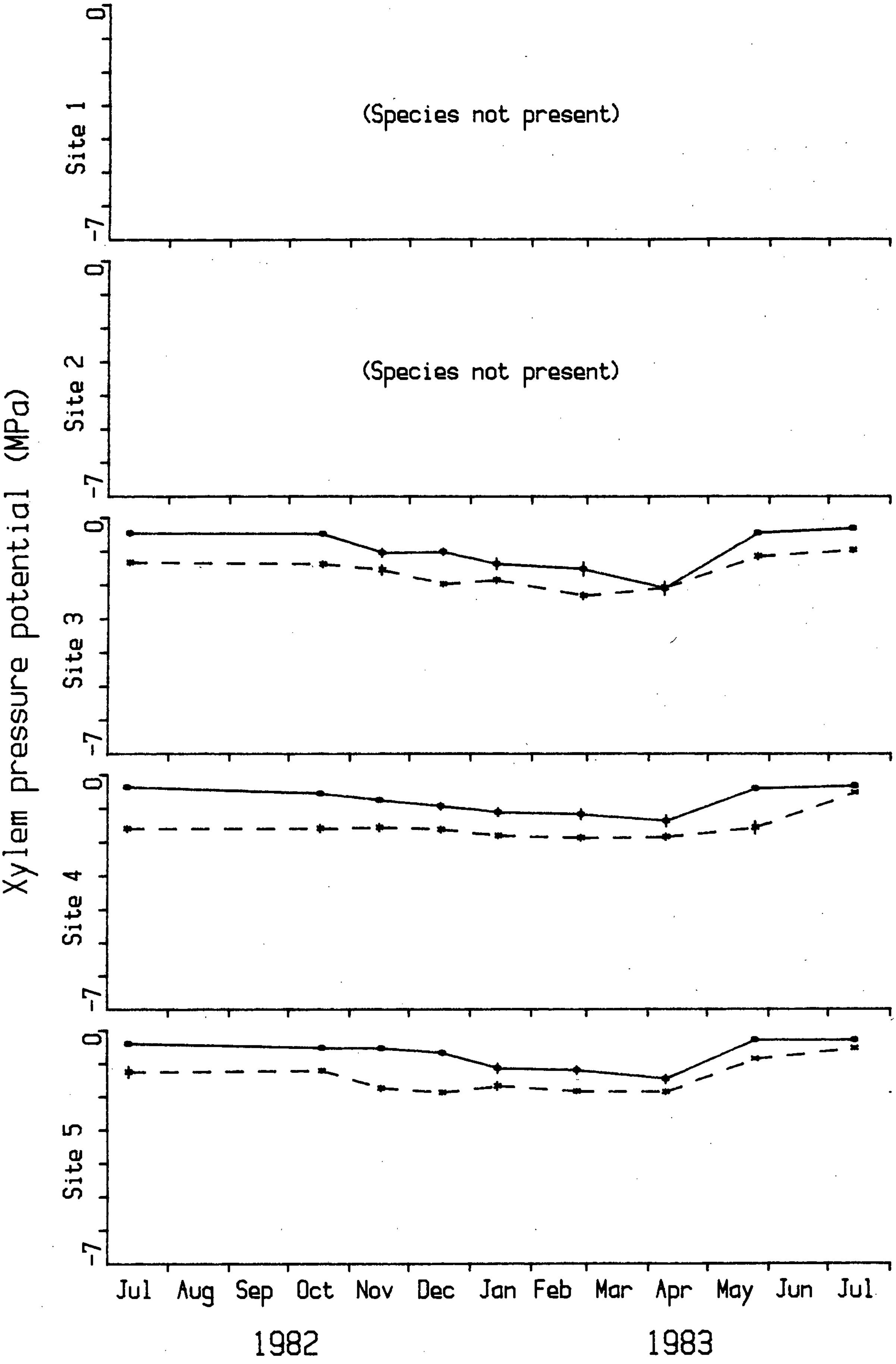


Figure 4.10 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of <u>Protea laurifolia</u>. (Mean and SE, n=5)

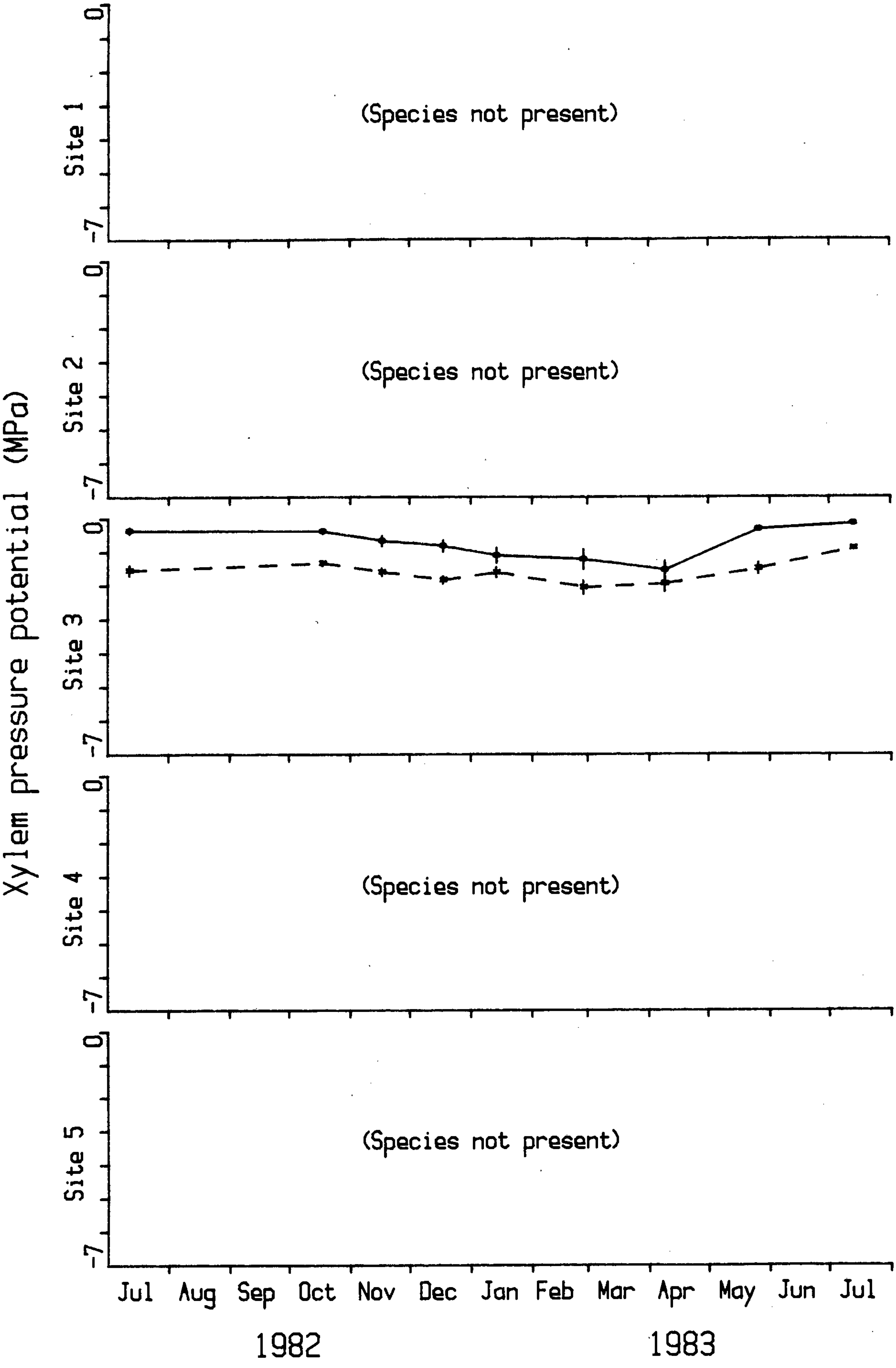


Figure 4.11 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of <u>Protea glabra</u>. (Mean and SE, n=3)

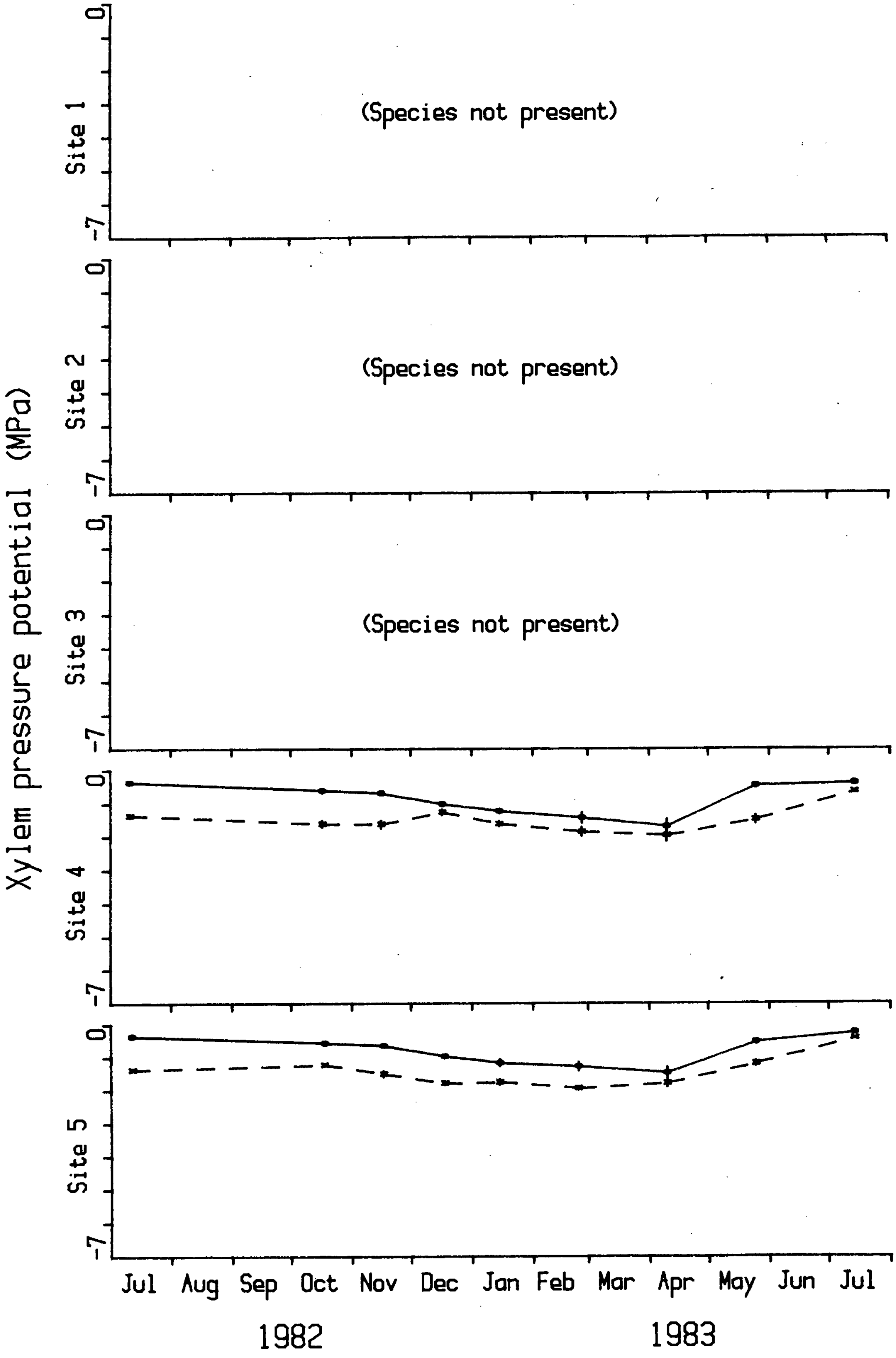


Figure 4.12 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of <u>Paranomus bracteolaris</u>. (Mean and SE, n=5)

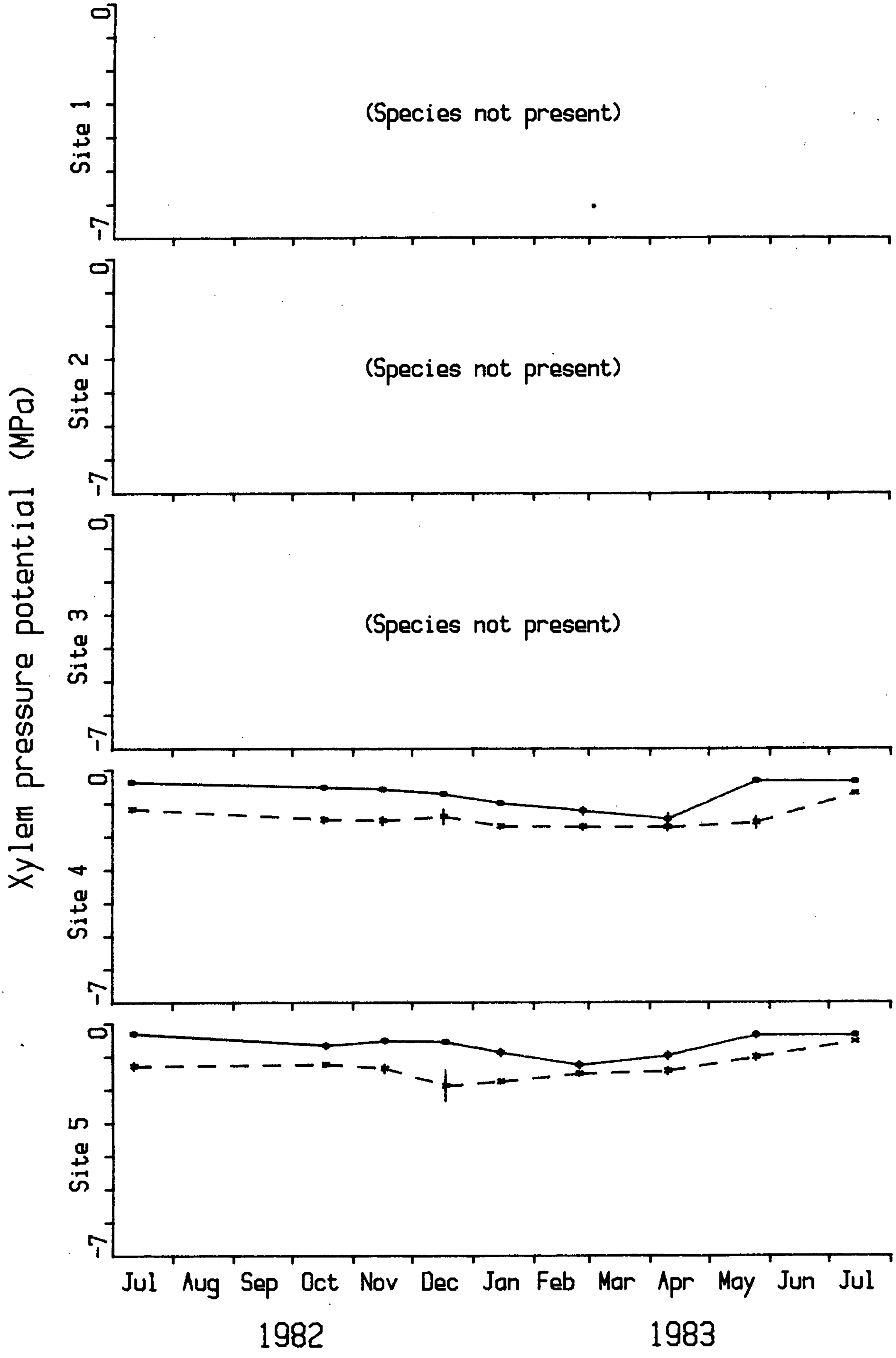


Figure 4.13 The seasonal course of the pre-dawn (solid line) and the midday (dashed line) xylem pressure potentials of Leucadendron pubescens. (Mean and SE, n=5)

midday xylem pressure potentials in July 1982 were -1.33±0.07 MPa at site 3, -1.60±0.09 MPa at site 4, and -1.25±0.16 MPa at site 5. The lowest midday xylem pressure potentials occurred in February and were -2.31±0.10 MPa at site 3, -1.87±0.08 MPa at site 5, and -1.84±0.06 MPa at site 5. In April site 3 had slightly higher midday xylem pressure potentials, -2.07±0.13 MPa, while the values at sites 4 and 5 remained nearly the same. In July 1983 *Protea laurifolia* had midday xylem pressure potentials of -0.96±0.06 MPa at site 3, -0.52±0.03 MPa at site 4, and -0.54±0.04 MPa at site 5.

The pre-dawn xylem pressure potentials of *Protea glabra* at site 3 dropped from -0.37±0.09 MPa to -1.53±0.26 MPa. Throughout the season the pre-dawn xylem pressure potentials averaged 0.24 MPa higher than those of *Protea laurifolia*. The midday xylem pressure potential values of *Protea glabra* were quite similar to those of *Protea laurifolia* in the beginning of the season and dropped from -1.55±0.15 MPa in July 1982 to -2.05±0.20 MPa in April, which was about 0.3 MPa higher than *Protea laurifolia*.

Both *Paranomus bracteolaris* and *Leucadendron pubescens* started and ended the season at sites 4 and 5 at about -0.35 MPa pre-dawn. The lowest that the pre-dawn xylem pressure potentials of *Paranomus bracteolaris* reached was -1.69±0.22 MPa at site 4 and -1.48±0.18 MPa at site 5 in April. At the same time *Leucadendron pubescens* was -1.48±0.17 MPa at site 4 and -0.97±0.11 MPa at site 5. In February the pre-dawn xylem pressure potentials at site 5 were lower, reaching -1.26±0.11 MPa. The midday xylem

Table 4.2 The levels of the significance of the variations in the pre-dawn, midday, and midday depression in xylem pressure potential as given by either a two-way analysis of variance (site vs. date), or one-way analysis of variance (date). When a two-way analysis of variance was calculated the level of the significance of the interaction is given.

	Pre-dawn			Midday			Midday Depression		
Species	Site	Date	Int.	Site	Date	Int.	Site	Date	Int.
Karroid Species									
Ruschia sp.	n/a	.01	n/a	n/a	.01	n/a	n/a	.01	n/a
Rhus incisa	ns	.01	ns	ns	.01	ns	ns	.01	.01
Galenia africana	.01	.01	.01	ns	.01	.01	ns	.01	.01
Transitional species									
Nylandtia spinosa	.01	.01	.01	.01	.01	.01	.01	.01	.01
Eriocephalus africanus	.01	.01	.01	.01	.01	.01	.05	.01	.01
Rhus dissecta	.01	.01	.01	.01	.01	ns	ns	.01	.01
Fynbos understory species									
Elytropappus gnaphaloides	.01	.01	ns	.01	.01	.01	ns	.01	.01
Stoebe capitata	n/a	.01	n/a	n/a	.01	n/a	n/a	.05	n/a
Agathosma giftbergensis	.01	.01	.01	.01	.01	.01	.01	.01	.01
Fynbos overstory species									
Protea laurifolia	.01	.01	.05	.01	.01	.01	.05	.01	.01
Protea glabra	n/a	.01	n/a	n/a	.01	n/a	n/a	.01	n/a
Paranomus bracteolaris	ns	.01	ns	ns	.01	.01	ns	.01	.01
Leucadendron pubescens	.05	.01	.05	ns	.01	ns	ns	.01	.05

pressure potentials of *Paranomus bracteolaris* were -1.36 MPa at sites 4 and 5 in July 1982, and -1.95 MPa at their lowest which was in February at site 5 and in April at site 4. The midday values of *Leucadendron pubescens* dropped from -1.18±0.06 MPa at site 4 and -1.28±0.12 MPa at site 5 to -1.72±0.11 MPa at site 4 and -1.88±0.46 MPa at site 5. The lowest midday values at site 4 occurred in April, while at site 5 they occurred in December.

All four species had significant seasonal variations between pre-dawn values, but only *Protea laurifolia* showed significant inter-site differences at the 0.01 level. The inter-site difference between the pre-dawn values of *Leucadendron pubescens* was significant at the 0.05 level (Table 4.2). *Protea laurifolia* and *Leucadendron pubescens* had significant interactions between site and sampling data at the 0.05 level. The midday values for all 4 species differed significantly between sampling dates, and *Protea laurifolia* differed significantly between sites. Both *Protea laurifolia* and *Paranomus bracteolaris* had significant interactions between site and sampling date.

A Student-Newman-Keuls test of the significant differences between means showed that the yearly mean pre-dawn xylem pressure potentials of the fynbos overstory species were not significantly different (Table 4.3). The yearly average pre-dawn xylem pressure potentials of many of the other species were quite different over the range of their distributions, but only *Rhus dissecta* had a significant difference between the wettest and driest sites were it was sampled. The transitional species *Nylandtia*

Table 4.3 Species groups based on the ranges of the non-significant differences between the yearly mean values of the pre-dawn xylem pressure potential (Student-Newman-Keuls test).

Species	Type	Site	Yearly Mean Pre-dawn	Ranges of non-significant diffs.									
Leucadendron pubescens	FO	5	-0.652	│									
Protea laurifolia	FO	5	-0.727	│									
Protea glabra	FO	3	-0.728	│	│								
Leucadendron pubescens	FO	4	-0.733	│									
Protea laurifolia	FO	4	-0.774	│									
Paranomus bracteolaris	FO	5	-0.809	│									
Paranomus bracteolaris	FO	4	-0.874	│		│							
Protea laurifolia	FO	3	-0.970	│		│							
Stoebe capitata	FU	5	-1.277	│		│	│						
Elytropappus gnaphaloides	FU	4	-1.402	│		│	│	│					
Rhus dissecta	T	5	-1.565	│		│	│	│	│				
Ruschia sp.	K	1	-1.568	│		│	│	│	│				
Eriocephalus africanus	T	5	-1.717	│		│	│	│	│	│			
Agathosma giftbergensis	FU	5	-1.913		│	│	│	│	│		│		
Elytropappus gnaphaloides	FU	3	-2.140				│	│	│		│	│	
Rhus dissecta	T	4	-2.305				│	│	│		│	│	
Nylandtia spinosa	T	4	-2.307				│	│	│		│	│	│
Galenia africana	K	2	-2.374					│	│		│	│	│
Agathosma giftbergensis	FU	4	-2.553						│		│	│	│
Nylandtia spinosa	T	1	-2.555						│		│	│	│
Rhus incisa	K	1	-2.567						│		│	│	│
Rhus dissecta	T	2	-2.616						│		│	│	│
Rhus incisa	K	2	-2.803							│	│	│	│
Galenia africana	K	1	-2.911							│	│	│	│
Eriocephalus africanus	T	2	-2.930							│	│	│	│
Rhus dissecta	T	3	-2.982							│	│	│	│
Nylandtia spinosa	T	2	-3.078							│		│	│
Nylandtia spinosa	T	3	-3.253							│		│	│
Eriocephalus africanus	T	1	-3.261							│		│	│
Eriocephalus africanus	T	3	-3.487							│			│

Species types : K = Karroid
T = Transitional
FU = Fynbos understory
FO = Fynbos overstory

spinosa and Eriocephalus africanus at sites in the middle of the transect had the lowest yearly average pre-dawn xylem pressure potentials.

Although there was over a five fold spread in the yearly mean pre-dawn xylem pressure potentials, there was only half that range in the midday depressions (Table 4.4). Few of the means of the midday depression were significantly different. The fynbos overstory species had some of the smaller midday depressions in xylem pressure potential, and the fynbos understory species some of the larger values.

A seasonal mean xylem pressure potential, including both pre-dawn and midday values, separated the species into 3 general groups (Table 4.5). The fynbos overstory species were a distinct group, as were the understory species found at site 5, with the individuals at sites 1, 2, and 3 blending together, and those at site 4 having intermediate values. The fynbos overstory species had the highest yearly average xylem pressure potentials, and the transitional species the lowest yearly average xylem pressure potentials. The fynbos understory species had yearly average xylem pressure potentials which were generally higher than the karroid species. The Leucadendron pubescens found at site 5 had the highest yearly average xylem pressure potential, -0.99 MPa. The Eriocephalus africanus at site 3 had the lowest yearly average xylem pressure potential, -3.87 MPa. The yearly mean xylem pressure potentials in the fynbos overstory group decrease towards the drier sites, and Protea laurifolia sampled at site 3 had the lowest value of the group, -1.29 MPa. Below the fynbos overstory group there

Table 4.4 Species groups based on the ranges of the non-significant differences between the yearly mean values of the midday depression in xylem pressure potential (Student-Newman-Keuls test).

Species	Type	Site	Mean Midday Depression	Ranges of non-significant diffs.			
Eriocephalus africanus	T	1	-0.499	│			
Paranomus bracteolaris	FO	4	-0.614	│	│		
Paranomus bracteolaris	FO	5	-0.633	│	│	│	
Protea laurifolia	FO	3	-0.648	│	│	│	
Eriocephalus africanus	T	2	-0.679	│	│	│	
Leucadendron pubescens	FO	5	-0.684	│	│	│	│
Protea laurifolia	FO	5	-0.700	│	│	│	│
Eriocephalus africanus	T	5	-0.711	│	│	│	│
Leucadendron pubescens	FO	4	-0.712	│	│	│	│
Galenia africana	K	1	-0.730	│	│	│	│
Rhus dissecta	T	4	-0.738	│	│	│	│
Agathosma giftbergensis	FU	4	-0.767	│	│	│	│
Eriocephalus africanus	T	3	-0.771	│	│	│	│
Protea laurifolia	FO	4	-0.778	│	│	│	│
Ruschia sp.	K	1	-0.806	│	│	│	│
Rhus dissecta	T	3	-0.811	│	│	│	│
Rhus dissecta	T	2	-0.841	│	│	│	│
Protea glabra	FO	3	-0.857	│	│	│	│
Rhus dissecta	T	5	-0.887	│	│	│	│
Rhus incisa	K	2	-0.920	│	│	│	│
Nylandtia spinosa	T	2	-0.934	│	│	│	│
Rhus incisa	K	1	-1.029	│	│	│	│
Stoebe capitata	FU	5	-1.049	│	│	│	│
Agathosma giftbergensis	FU	5	-1.066	│	│	│	│
Nylandtia spinosa	T	3	-1.098		│	│	│
Galenia africana	K	2	-1.176		│	│	│
Elytropappus gnaphaloides	FU	3	-1.194		│	│	│
Elytropappus gnaphaloides	FU	4	-1.228			│	│
Nylandtia spinosa	T	1	-1.234			│	│
Nylandtia spinosa	T	4	-1.260				│

Species types : K = Karroid
T = Transitional
FU = Fynbos understory
FO = Fynbos overstory

Table 4.5 Species groups based the ranges of the non-significant differences between the yearly mean values (pre-dawn and midday) of the xylem pressure potential (Student-Newman-Keuls test).

Species	Type	Site	Yearly Mean	Ranges of non-significant diffs.								
Leucadendron pubescens	FO	5	-0.994	|								
Protea laurifolia	FO	5	-1.077	|	|							
Leucadendron pubescens	FO	4	-1.089	|								
Paranomus bracteolaris	FO	5	-1.125	|	|							
Protea glabra	FO	3	-1.156	|	|							
Protea laurifolia	FO	4	-1.163	|								
Paranomus bracteolaris	FO	4	-1.181	|								
Protea laurifolia	FO	3	-1.294	|								
Stoebe capitata	FU	5	-1.801			|						
Ruschia sp.	K	1	-1.971			|						
Rhus dissecta	T	5	-2.009			|						
Elytropappus gnaphaloides	FU	4	-2.016			|						
Eriocephalus africanus	T	5	-2.072	|		|	|					
Agathosma giftbergensis	FU	5	-2.446		|	|		|				
Rhus dissecta	T	4	-2.674				|	|				
Elytropappus gnaphaloides	FU	3	-2.737				|	|	|			
Agathosma giftbergensis	FU	4	-2.937				|	|	|	|		
Galenia africana	K	2	-2.962				|	|	|	|		
Nylandtia spinosa	T	4	-2.965				|	|	|	|		
Rhus incisa	K	1	-3.081				|	|	|	|	|	
Rhus dissecta	T	2	-3.166				|	|	|	|	|	|
Nylandtia spinosa	T	1	-3.173				|	|	|	|	|	|
Rhus incisa	K	2	-3.263				|		|	|	|	|
Eriocephalus africanus	T	2	-3.269				|		|	|	|	|
Galenia africana	K	1	-3.382				|		|	|	|	|
Rhus dissecta	T	3	-3.388				|		|	|	|	|
Eriocephalus africanus	T	1	-3.511						|	|	|	|
Nylandtia spinosa	T	2	-3.545							|	|	|
Nylandtia spinosa	T	3	-3.802								|	|
Eriocephalus africanus	T	3	-3.872									|

Species types :
K = Karroid
T = Transitional
FU = Fynbos understory
FO = Fynbos overstory

was a group which incuded *Stoebe capitata*, *Rhus dissecta*, *Eriocephalus africanus*, and *Agathosma giftbergensis* sampled at site 5, as well as *Elytropappus gnaphaloides* sampled at site 4 and *Ruschia sp.* sampled at site 1. The *Stoebe capitata* had the highest yearly mean xylem pressure potentials, -1.8 MPa, and the *Agathosma giftbergensis* at site 4 the lowest, -2.45 MPa. The transitional species, except where they occurred at sites 4 and 5 formed a group and had yearly average xylem pressure potentials between -3.17 MPa and -3.87 MPa.

4.3.5 Midday depressions in xylem pressure potential with decreasing pre-dawn xylem pressure potentials

Between July 1982 and April 1983 most species showed a regular pattern of decreasing pre-dawn xylem pressure potentials as a result of the progressive drying of the soil. The midday depressions in the xylem pressure potentials of the species that were sampled responded to the decreasing pre-dawn xylem pressure potentials following one of three possible patterns. The species either had smaller midday depressions with decreasing pre-dawn values, constant midday depressions with decreasing pre-dawn values, or larger midday depressions with decreasing pre-dawn xylem pressure potentials (Figure 4.14).

The fynbos overstory species, *Protea laurifolia*, *Protea glabra*, *Paranomus bracteolaris*, and *Leucadendron pubescens* as well as the karroid species *Ruschia sp.* all had decreasing midday depressions in xylem pressure potential as the pre-dawn xylem pressure potentials dropped

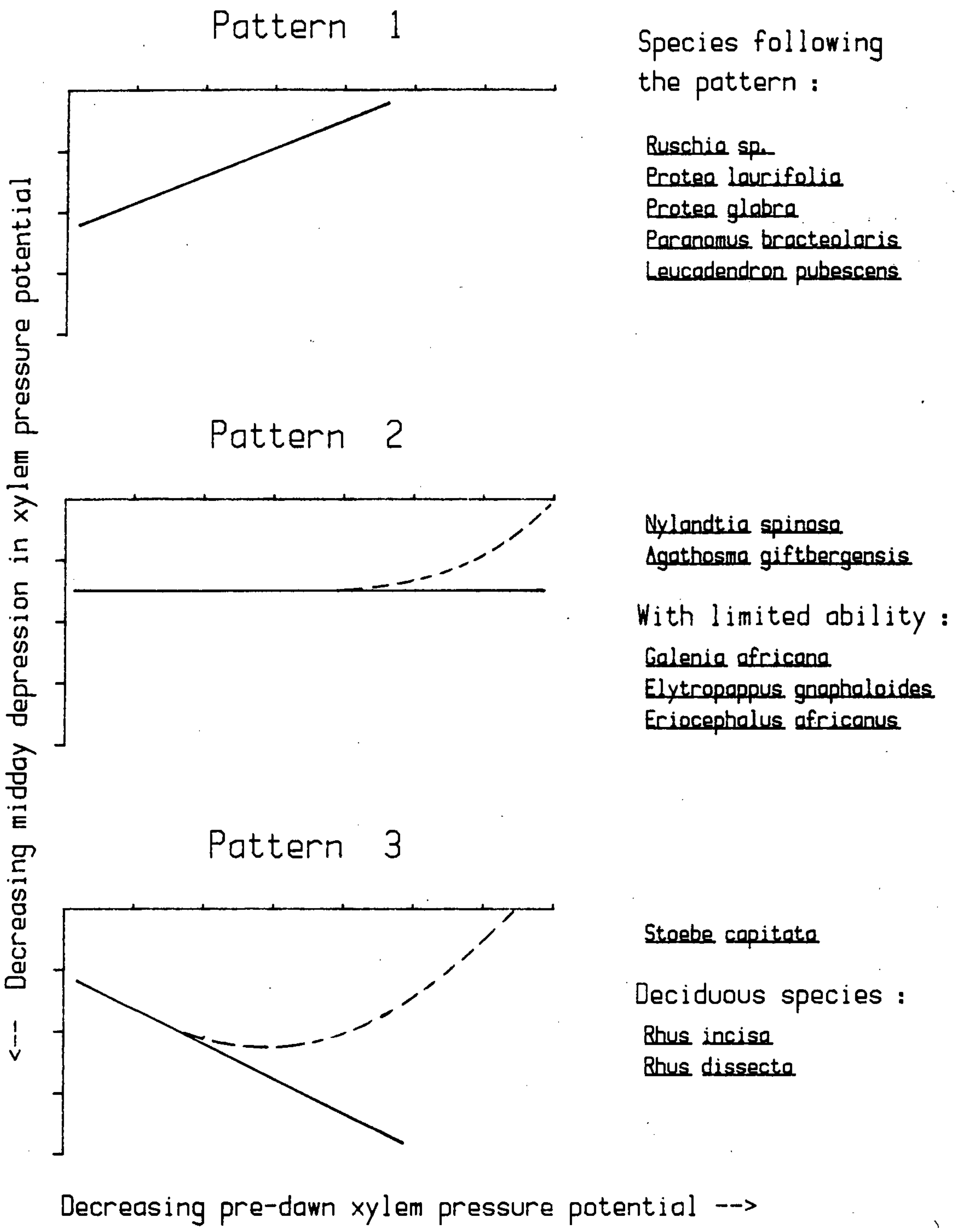


Figure 4.14 The three possible responses of the midday depression in the xylem pressure potential to decreasing pre-dawn xylem pressure potentials during a drought period. The top pattern shows passive stomatal control, and a seasonally fixed xylem pressure potential corresponding to the point of turgor loss. The middle pattern shows active stomatal control, and a changing xylem pressure potential corresponding to the point of turgor loss. The bottom pattern shows no stomatal control to limit water loss. The dashed line on the bottom pattern includes leaf shedding.

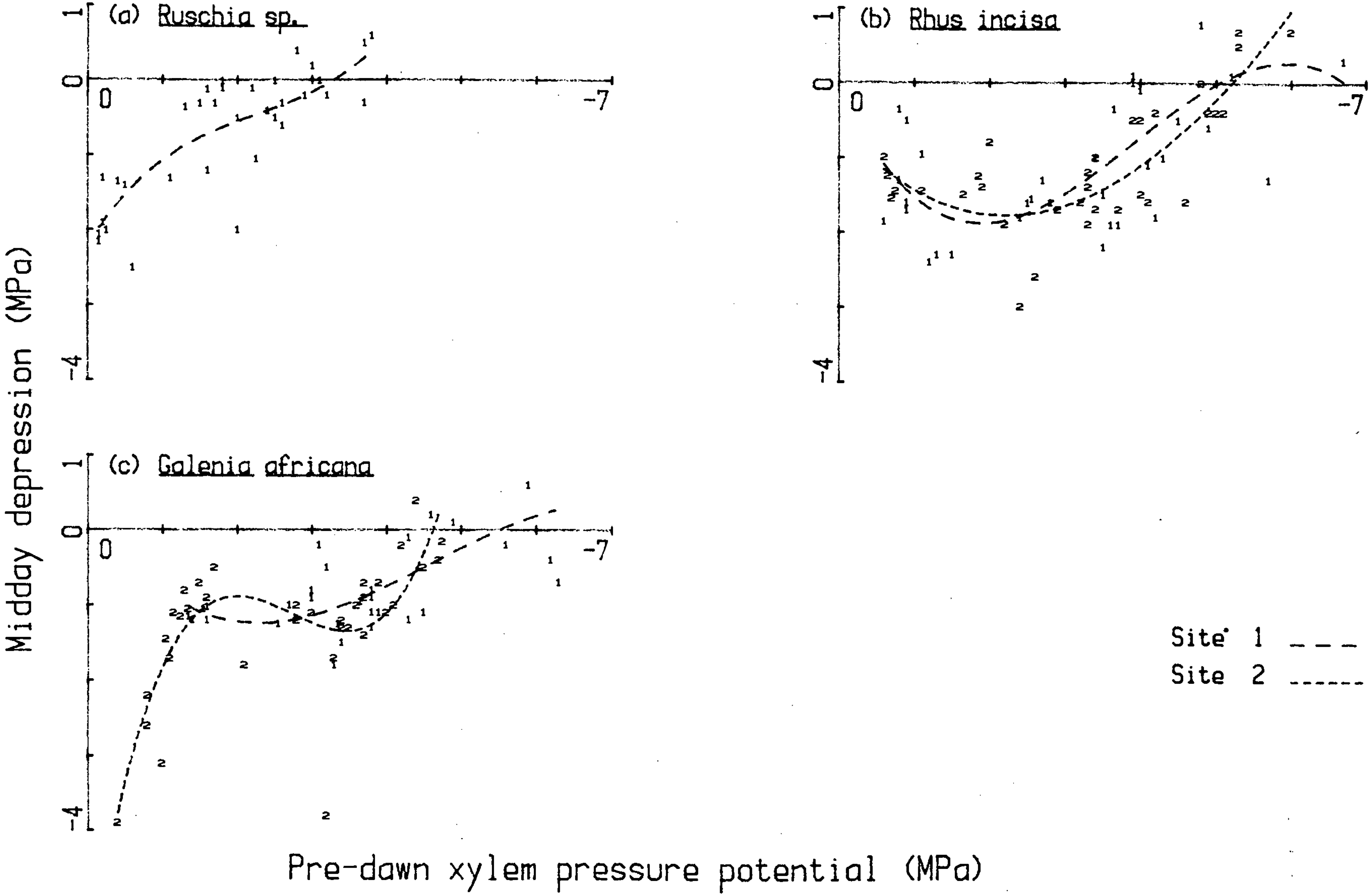


Figure 4.15 The midday depression in xylem pressure potential as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for the karriod species. The numbers refer to the data points at that site. The equations for the 3rd order regression lines show are in Table 4.6.

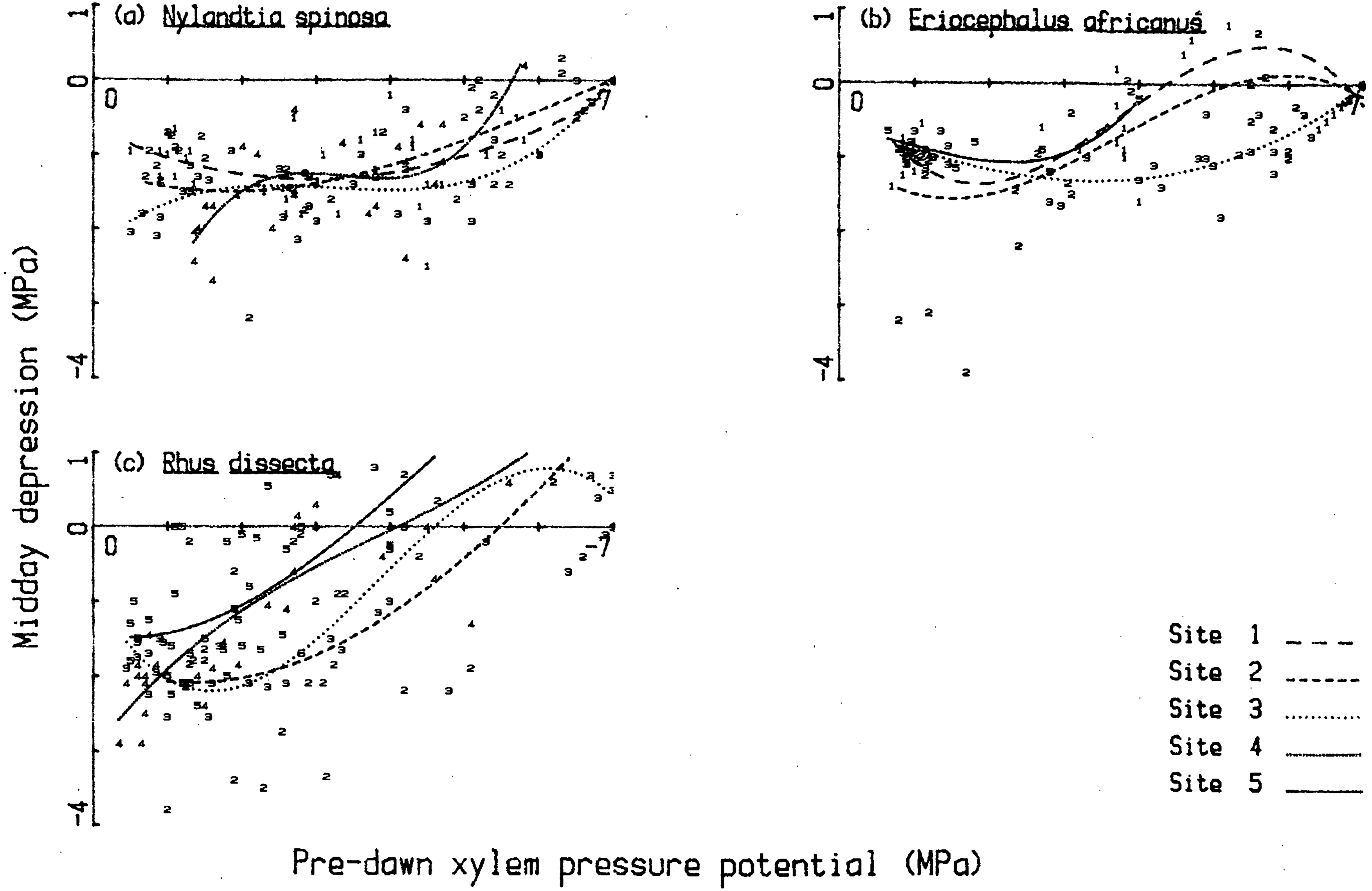


Figure 4.16 The midday depression in xylem pressure potential as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for the transitional species. The numbers refer to the data points at that site. The equations for the 3rd order regression lines show are in Table 4.6.

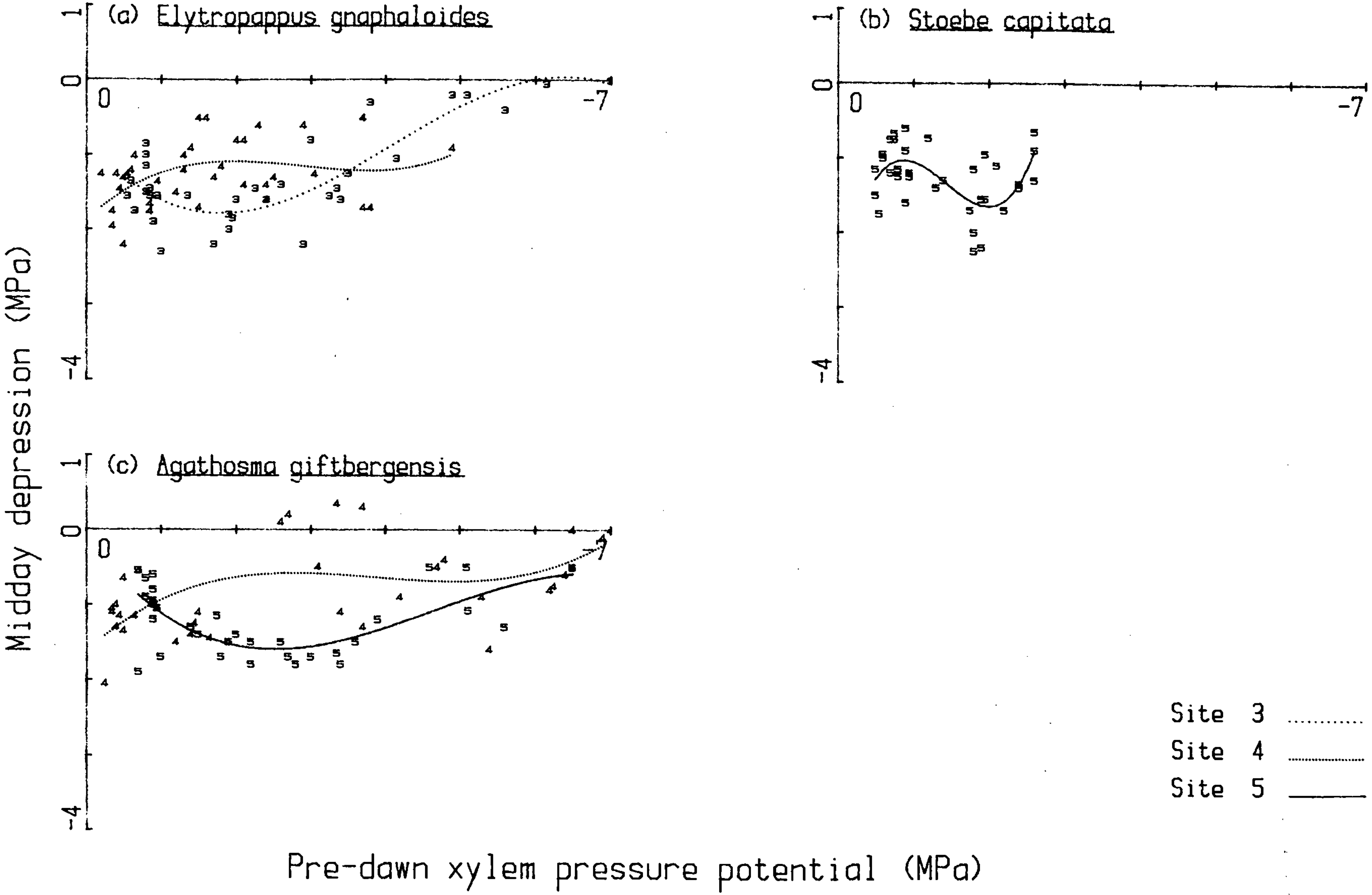


Figure 4.17 The midday depression in xylem pressure potential as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for the fynbos understory species. The numbers refer to the data points at that site. The equations for the 3rd order regression lines show are in Table 4.6.

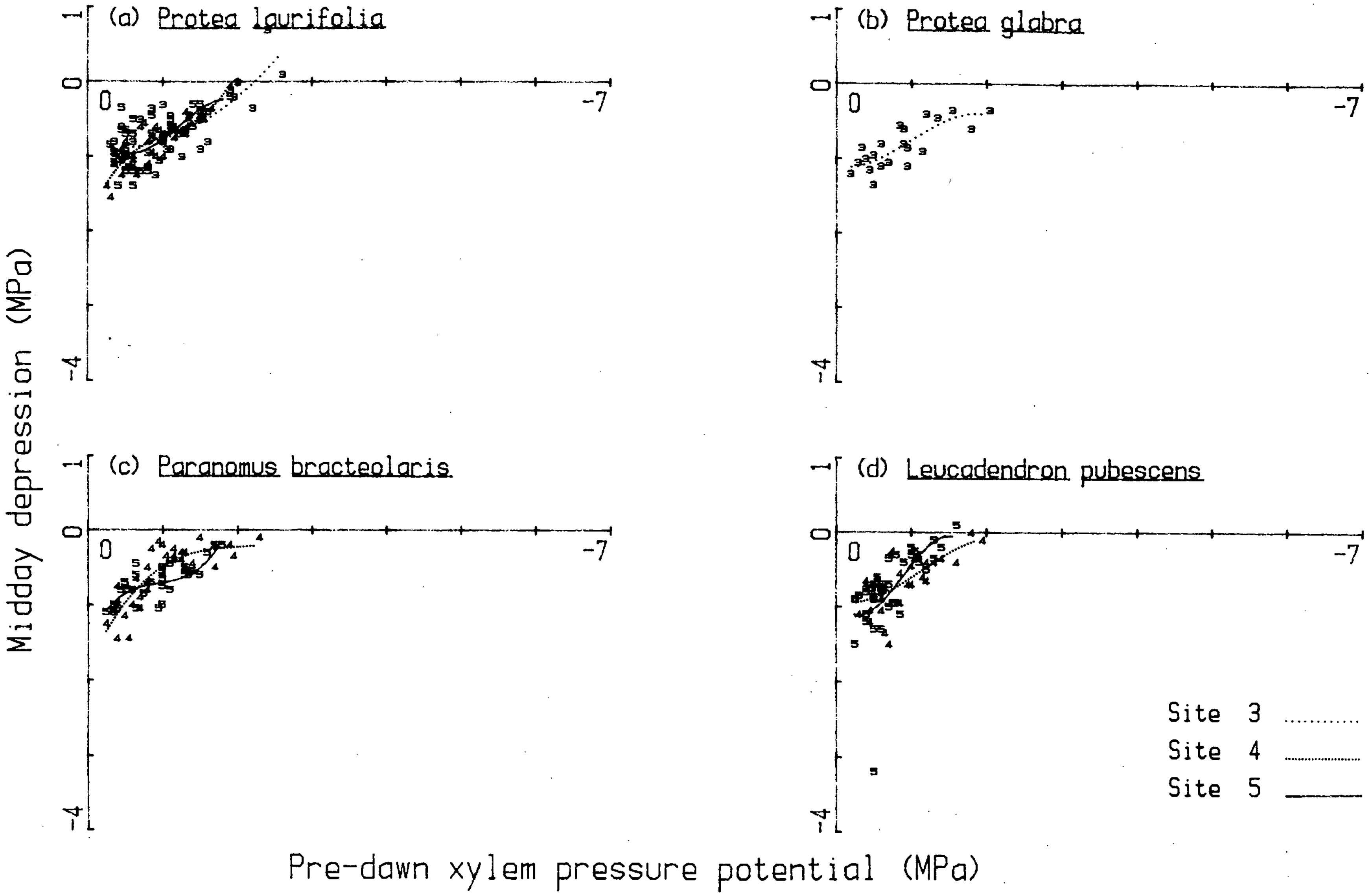


Figure 4.18 The midday depression in xylem pressure potential as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for the fynbos overstory species. The numbers refer to the data points at that site. The equations for the 3rd order regression lines show are in Table 4.6.

Table 4.6 The parameters of the 3rd order regression equations of midday depression in xylem pressure potential as a function of the pre-dawn xylem pressure potential in Figures 4.15 to 4.18. The coefficient of determination (r2) is of the regression equation.

omit

$$\text{Midday depression} = A + B{*}\text{Pre-dawn} + C{*}\text{Pre-dawn}^2 + D{*}\text{Pre-dawn}^3$$

Species	Site	Regression equation parameters A	B	C	D	r2
Karroid species						
Ruschia sp.	1	-2.20	-1.60	-0.55	-0.08	0.61
Rhus incisa	1	-0.04	2.18	0.76	0.06	0.41
	2	-0.59	1.11	0.28	0.008	0.77
Galenia africana	1	0.28	1.50	0.44	0.03	0.45
	2	-5.87	-6.17	-2.44	-0.30	0.56
Transitional species						
Nylandtia spinosa	1	-0.65	0.49	0.09	0.002	0.21
	2	-1.17	0.38	0.12	0.006	0.31
	3	-2.29	-0.89	-0.30	-0.03	0.78
	4	-6.04	-4.41	-1.33	-0.13	0.51
Eriocephalus africanus	1	0.32	2.05	0.74	0.07	0.50
	2	-0.88	0.99	0.42	0.04	0.40
	3	-0.51	0.43	0.04	-0.004	0.75
	5	-0.64	0.11	-0.15	-0.05	0.76
Rhus dissecta	2	-1.83	0.39	0.16	0.005	0.42
	3	-0.86	1.86	0.74	0.06	0.66
	4	-3.01	-1.30	-0.21	-0.02	0.80
	5	-1.43	0.21	0.23	0.01	0.46
Fynbos understory species						
Elytropappus gnaphaloides	3	-0.76	1.27	0.46	0.04	0.74
	4	-1.88	-0.98	-0.38	-0.04	0.19
Stoebe capitata	5	-2.76	-4.64	-3.81	-0.88	0.36
Agathosma giftbergensis	4	-1.64	-0.94	-0.27	-0.02	0.34
	5	-0.09	1.37	0.37	0.03	0.47
Fynbos overstory species						
Protea laurifolia	3	-0.95	-0.04	0.11	-0.03	0.63
	4	-1.89	-2.52	-1.96	-0.60	0.70
	5	-0.42	2.15	2.48	0.68	0.46
Protea glabra	3	-1.10	0.19	0.83	0.28	0.63
Paranomus bracteolaris	4	-1.86	-2.28	-1.07	-0.17	0.72
	5	-1.48	-2.10	-2.02	-0.71	0.65
Leucadendron pubescens	4	-0.92	0.29	0.85	-0.25	0.48
	5	-0.87	1.72	3.38	1.24	0.38

(Figures 4.18a, 4.18b, 4.18c, 4.18d, and 4.15a). The xylem pressure potentials of the four fynbos overstory species were never much below -2 MPa, either pre-dawn or midday, and there is therefore a characteristic relationship between pre-dawn xylem pressure potentials and midday depressions in xylem pressure potential for the group. At high pre-dawn values there were midday values of about -2 MPa, and at pre-dawn values of -2 MPa there was practically no midday depression. *Ruschia sp.* had a similar pattern, but with a limit of -3 MPa. ~~The coefficients of determination of the third-order regression lines for the 5 species averaged 0.58~~ (~~Table 4.6~~).

The midday depressions in xylem pressure potential of transitional species *Nylandtia spinosa*, and the fynbos understory species *Agathosma giftbergensis* were relatively constant as the pre-dawn xylem pressure potentials decreased (Figures 4.16a and 4.17c). At all four sites where *Nylandtia spinosa* was sampled there was a constant midday depression of -1.0 to -1.5 MPa until the limit of the pressure chamber was reached, which then caused a truncation in the curves. ~~The coefficients of determination of the regression lines of *Nylandtia spinosa* were 0.21 at site 1, 0.31 at site 2, 0.78 at site 3, and 0.51 at site 4 (Table 4.6~~). The coefficients of determination of the regression lines of *Agathosma giftbergensis* were 0.34 at site 4 and 0.47 at site 5. In December the midday xylem pressure potentials of *Agathosma giftbergensis* at site 4 where not much lower than the pre-dawn values (about -3 MPa), and this caused the regression lines of sites 4 and 5 in Figure 4.17c to separate.

The karroid species *Galenia africana*, the transitional species *Eriocephalus africanus*, and the fynbos understory species *Elytropappus gnaphaloides* maintained nearly constant midday depressions until the midday xylem pressure potentials reached about -5 MPa, after which the midday depression began to decrease (Figures 4.15c, 4.16b, and 4.17a). The midday depressions in xylem pressure potential of *Galenia africana* were between -1 and -1.5 MPa, except for those values at site 2 resulting from the sampling after the rain in December. ~~The coefficients of determination for the regression lines for *Galenia africana* were 0.45 at site 1 and 0.56 at site 2 (Table 4.6)~~. The *Eriocephalus africanus* sampled at site 3 had constant midday depressions as the pre-dawn xylem pressure potentials dropped, while at sites 1 and 2 the midday depressions decreased when xylem pressure potentials dropped below a threshold of -5 MPa. ~~The coefficients of determination averaged 0.6 including site 5 (Table 4.6)~~. The midday depressions of *Elytropappus gnaphaloides* were between -1 and -2 MPa, and were constant at site 4, while at site 3 they decreased, with decreasing pre-dawn xylem pressure potentials. The r^2 value at site 3 was 0.74, while that at site 4 was 0.19.

The midday depressions in xylem pressure potential of *Rhus incisa* increased from about -1 MPa to -2 MPa until the midday values reached -5 MPa, and then decreased (Figure 4.15b). At sites 2 and 3 *Rhus dissecta* followed the same pattern and had similar values (Figure 4.16c). At sites 4 and 5 the midday depressions of *Rhus dissecta* decreased uniformly with decreasing pre-dawn xylem pressure potential. Even though the Rhus dissecta at sites 4 and 5 were never under as much stress as those at sites 2 and 3 they still shed their leaves. Stoebe capitata never reached xylem pressure potentials as low as the other fynbos understory species, but seemed to show a continuing increase in midday depression with decreasing pre-dawn xylem pressure potential (Figure 4.17b). ~~The coefficients of determination for the regression lines of the 3 species averaged 0.56 (Table 4.6)~~.

4.3.6 Patterns of pre- and post-drought xylem pressure potentials

There was much more rain than normal in May 1983, and the sampling took place soon after the major storm that marked the end of the summer drought. As a result of this rain the pre-dawn xylem pressure potentials at the end of the summer drought period, in May 1983, were higher than at the beginning, in October 1982 (Table 4.7). Most species had smaller midday depressions in xylem pressure potential in May 1983 than in October 1982 (Table 4.8).

The smaller midday depressions in xylem pressure potential following the drought period could result from the plants acquired ability to control water loss. Root growth following the re-wetting of the soil could have occurred before leaf growth, resulting in higher pre-dawn values and smaller midday depressions. The stomata could have become blocked by waxes, which would also contributing to smaller midday depressions. However, in most cases the higher pre-dawn xylem pressure potentials, and the smaller midday

Table 4.7 The direction and level of significance of the differences between the pre-dawn xylem pressure potentials in October 1982, before the summer drought, and May 1983, after the summer drought. The double asterisk signifies the 0.01 level, and the sin, and May 1983, after the summer drought. The double asterisk signifies the 0.01 level, and the single asterisk the 0.05 level.

Species	Site 1	2	3	4	5
Karroid species					
Ruschia sp.	Dec				
Rhus incisa	Inc*	Inc**			
Galenia africana	Inc**	Dec			
Transitional species					
Nylandtia spinosa	Inc**	Dec*	Inc	Inc**	
Eriocephalus africanus	Inc*	Dec**	Inc**		
Rhus dissecta		Inc**	Inc	Dec	Inc**
Fynbos understory species					
Elytropappus gnaphaloides			Inc**	Inc	
Stoebe capitata					Inc
Agathosma giftbergensis				Inc*	Inc**
Fynbos overstory species					
Protea laurifolia			Inc	Inc**	Inc**
Protea glabra			Inc		
Paranomus bracteolaris				Inc	Inc
Leucadendron pubescens				Inc**	Inc*

Table 4.8 The levels of significance of the differences between the midday depressions in xylem pressure potential in October 1982, before the summer drought, and May 1983, after the summer drought. The double asterisk signifies the 0.01 level, and the single asterisk the 0.05 level.

			Site		
Species	1	2	3	4	5
Karroid species					
Ruschia sp.	Dec**				
Rhus incisa	Dec*	Dec**			
Galenia africana	Inc*	Inc**			
Transitional species					
Nylandtia spinosa	Inc	Dec	Dec	Inc*	
Eriocephalus africanus	Dec*	Dec**	Dec		
Rhus dissecta		Dec*	Dec*	Dec**	Inc
Fynbos understory species					
Elytropappus gnaphaloides			Dec	Inc	
Stoebe capitata					Dec*
Agathosma giftbergensis				Dec	Dec
Fynbos overstory species					
Protea laurifolia			Dec	Inc	Dec
Protea glabra			Inc		
Paranomus bracteolaris				Inc	Equal
Leucadendron pubescens				Inc	Inc

depressions, are probably just a reflection on the abundance of soil moisture in May 1983, and ease at which the plants could extract it.

Larger midday depressions, such as those of Galenia africana, could have been the result of a lack of root growth. A small root area would allow over night recovery, but might not be able to sustain the demand during the day. The fynbos overstory species had larger midday depressions because of the higher pre-dawn values and their seasonally constant midday minimum value.

4.3.7 Spatial and temporal patterns of community xylem pressure potentials

The seasonal course of the site average pre-dawn xylem pressure potentials, calculated without biasing based on some parameter of species abundance or cover, show that with the decreasing rainfall along the transect the three fynbos communities, sites 5, 4, and 3 had consistently longer periods of water stress and lower minimum values (Figure 4.19). Following the vegetation switch between sites 3 and 2 the length of the period the plants were under stress, and the minimum values reached, were similar. Even though site 2 was between sites 1 and 3, it received less rain than site 1, and had the lowest yearly average pre-dawn xylem pressure potentials. The yearly mean pre-dawn xylem pressure potentials at sites 1 and 2 were not significantly different, as were the means at sites 1 and 3 (Table 4.9). Had the site averages of the pre-dawn xylem pressure potential been biased by including biomass or percent cover,

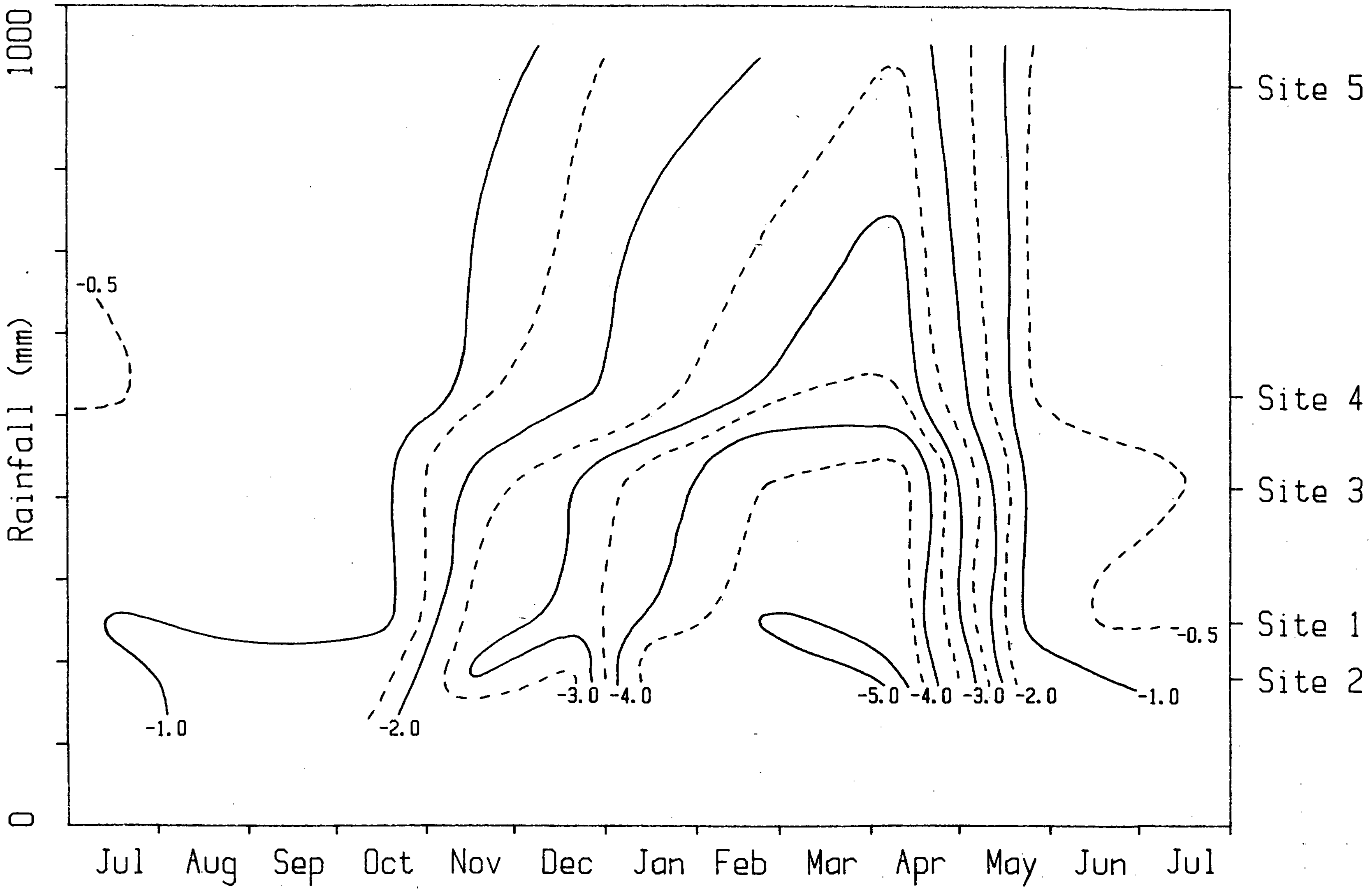


Figure 4.19 Isolines of the site average pre-dawn xylem pressure potential along the transect during the period July 1982 to July 1983. The sites are located according to the rainfall during the sample period.

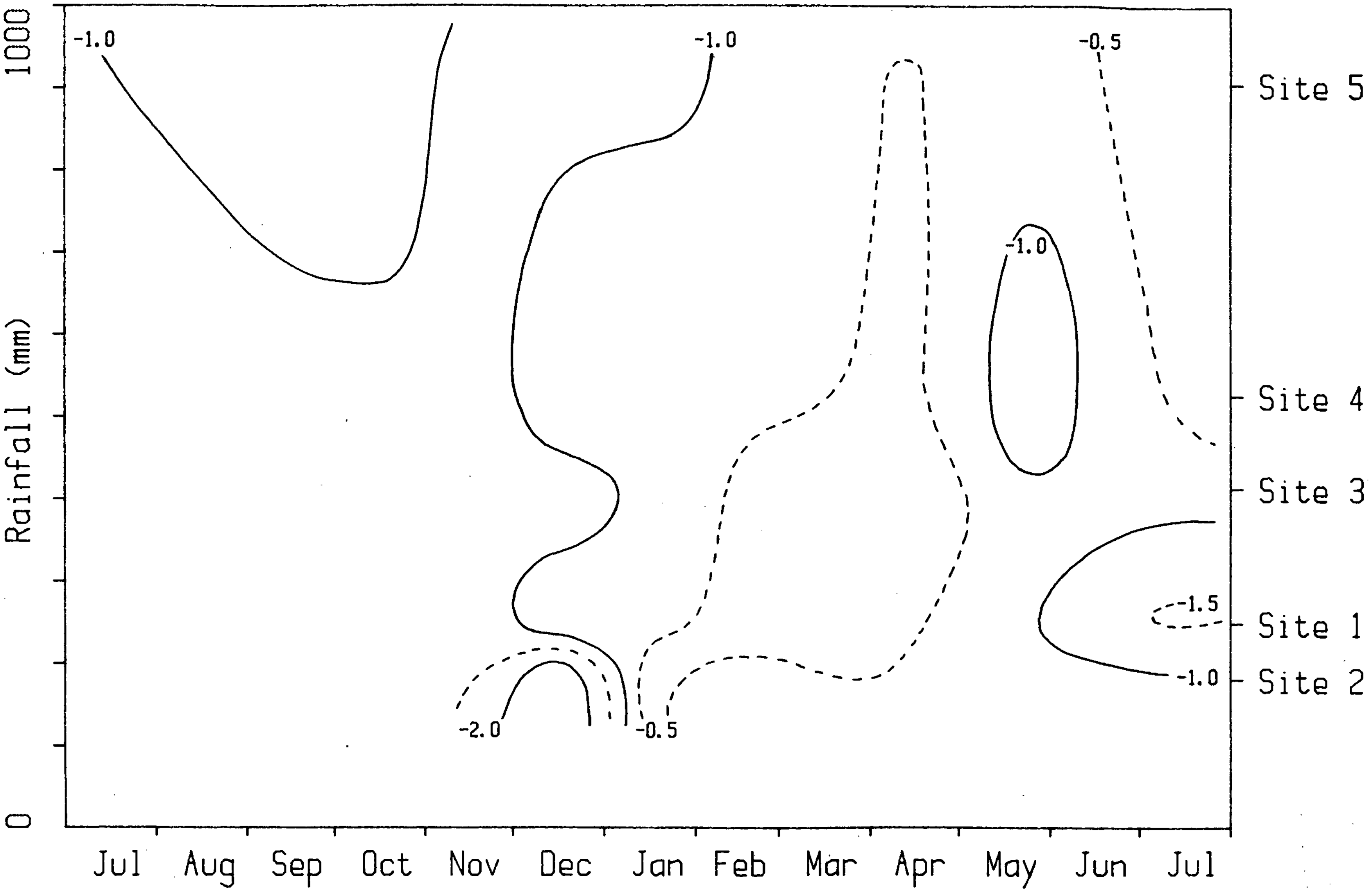


Figure 4.20 Isolines of the site average midday depression in xylem pressure potential along the transect during the period July 1982 to July 1983. The sites are located according to the rainfall during the sample period.

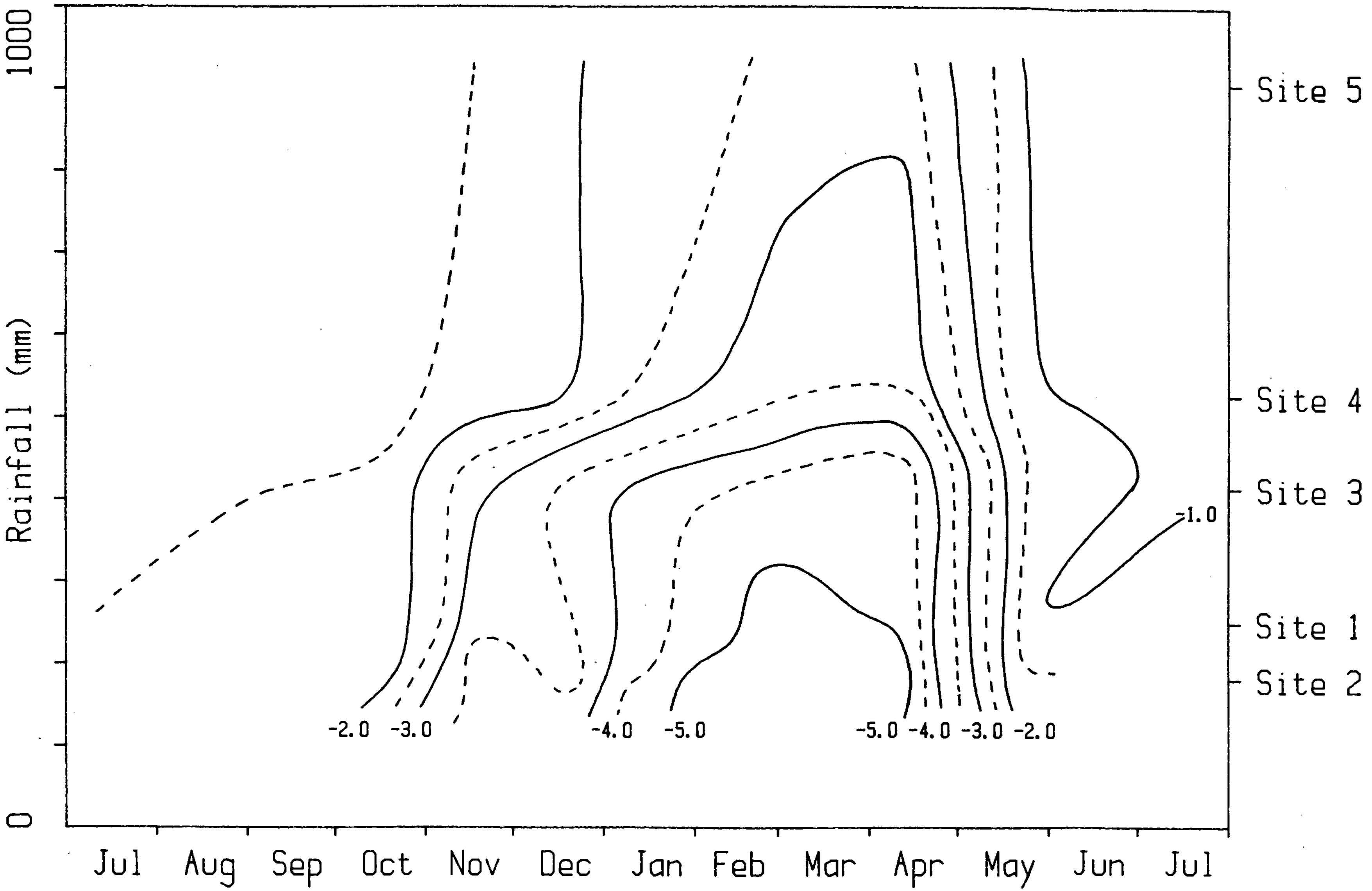


Figure 4.21 Isolines of the average (pre-dawn and midday) xylem pressure potential along the transect during the period July 1982 to July 1983. The sites are located according to the rainfall during the sample period.

Table 4.9 The ranges of the non-significant differences between the seasonal means of the site average pre-dawn xylem pressure potential, the site average midday depression in xylem pressure potential, and the site average (pre-dawn and midday) xylem pressure potential (Student-Newman-Keuls test).

	Pre-dawn			Midday depression		Average		
Site	Mean	Ranges of nonsig. diffs.		Mean	Ranges of nonsig. diffs.	Mean	Ranges of nonsig. diffs.	
5	-1.18			-0.83	│	-1.59		
4	-1.54			-0.87	│	-1.98		
3	-2.37	│		-0.90	│	-2.82	│	
1	-2.56	│	│	-0.90	│	-3.01	│	│
2	-2.76		│	-0.95	│	-3.24		│

then there would have been an even stronger trend of decreasing water stress up the transect. At site 5 the fynbos understory species would then have had a practically insignificant contribution to the site average, whereas at site 3 their contribution is probably presently accurately reflected.

The December rain event which elevated the pre-dawn xylem pressure potentials at site 2, while leaving the midday values untouched, created a noticeable hole in the otherwise constant pattern of site average midday depressions in xylem pressure potential (Figure 4.20). The midday depressions in winter were below 1.0 MPa at the wetter end of the transect, while they were above 1.0 MPa at the drier end. In the summer site 5 experienced a brief period when midday depressions were restricted, whereas below site 3 the midday depression were below 0.5 MPa for almost 3 months. The annual means of the midday depressions at all of the sites along the transect were not significantly different (Table 4.9).

The site average xylem pressure potentials, including both the pre-dawn and the midday values, show that if a value such as -3.0 MPa is used, there was an approximately 6 month period when the xylem pressure potentials were lower at sites 1 and 2, between a 5 and a 6 month period at site 3, a 2.5 month period at site 4, and at site 5 the xylem pressure potentials were never that low (Figure 4.21). The step between site 4 and site 3 corresponds to disappearance of many of the species that characterize Mesic Mountain Fynbos, and may show the maximum period of summer drought that these species can tolerate.

Between April and May the isolines should actually be closer together, as the re-wetting occurred during one large rain event of 8 days. As with the isolines of pre-dawn xylem pressure potential, the importance of the fynbos understory species at site 5 is being over represented in these "community average" xylem pressure potentials. Between sites 1 and 2, and sites 1 and 3 there were not significant differences in the yearly means of the site average xylem pressure potentials (Table 4.9).

4.4 Discussion

Low xylem pressure potentials, and significant periods of water stress have not been previously measured in fynbos plants. In a survey of midsummer xylem pressure potentials Miller _et_ _al._ (1984) rarely found pre-dawn xylem pressure potentials below -2 MPa at seven fynbos sites that had annual rainfalls between 550 and 1600 mm/year. Studies of the seasonal progressions of xylem pressure potentials have never found more than 1 month in the middle of the summer when low xylem pressure potentials indicated that water stress was an important phenomenon in the fynbos (Miller _et_ _al._ 1983; Moll and Sommerville 1985). This lack of a period of water stress in the summer is not unexpected since these areas receive more rainfall than the approximately 600-900 mm/year which is considered as the upper limit for mediterranean-type climates (Aschmann 1973).

The water relations of only six of the thirteen species in this study, *Rhus incisa*, *Stoebe capitata*, *Agathosma giftbergensis*, *Protea laurifolia*, *Paranomus bracteolaris*, and *Leucadendron pubescens* have been previously measured. During the summer of 1981 to 1982 Miller *et al.* (1983), who also worked at the site 5 of this study, found little water stress in these five species. The pre-dawn xylem pressure potentials of *Rhus incisa* (reported as *Rhus dissecta* in Miller *et al.* 1983, and Miller *et al.* 1984) were -2.0 ± 0.1 MPa in February of the 1981/82 season, and the midday values were -3.2 ± 0.2 MPa. During the same month in the 1982/83 season the pre-dawn values of *Rhus incisa* were -2.91 ± 0.48 MPa, and the midday values were -3.57 ± 0.25 MPa. The fynbos understory species *Stoebe capitata* and *Agathosma giftbergensis* (reported as *Elytropappus gnaphaloides* and *Diosma hirsuta* in Miller *et al.* 1983, and Miller *et al.* 1984) had minimum pre-dawn xylem pressure potentials in 1981/82 of about -1.0 and -2.5 MPa respectively. At the end of the summer of 1982/83 *Stoebe capitata* was about -2.0 MPa, and *Agathosma giftbergensis* was -5.5 MPa. In 1981/82 the pre-dawn xylem pressure potentials of *Protea laurifolia*, *Paranomus bracteolaris* and *Leucadendron pubescens* were between 0.5 and 1.0 MPa throughout the year, whereas in 1982-83 they dropped below 1.0 MPa. The spring of 1981 (July, August, and September) received more rain than the spring of 1982, and the Algeria Forestry Station received 510.2 mm of rainfall in 1981 compared to the 164.4 mm received in 1982. The average rainfall for the three month period is 268 mm. The summer of 1981-82 also received 68.5 mm of rainfall in January, which is 5 times the monthly average of 13.5 mm. The exceptionally wet spring resulted in a total of 1000.4 mm for the 13 month period of July 1981 to July 1982, and was probably the reason why a summer drought, with low xylem pressure potentials and leaf conductances, was not found.

The seasonal patterns of xylem pressure potentials found along the transect between Clanwilliam and the Algeria were similar to those reported by Poole and Miller (1981) for a transect through the chaparral zone in California except that many of the plants seemed to experience a longer period of water stress. Whereas the xylem pressure potentials of the plants in California dropped for a period of about 3 months, those in the fynbos were depressed for 6 months. Roberts *et al.* (1981) found a period of about 6 months in the chaparral when xylem pressure potentials were depressed. In both the chaparral and the fynbos the magnitude of the depressions were similar, with some species reaching -6 to -7 MPa pre-dawn. In the matorral of Chile Giliberto and Estay (1978) found a similar 6 month period with depressed xylem pressure potentials, but minimum values of only -4 MPa. Margaris (1977) also found a period of about 6 months in the drought-deciduous phrygana of Greece (annual rainfall of 400 mm) when the plants xylem water potentials were less than -3.5 MPa.

The species found along the transect in the fynbos followed one of the three successful life forms in areas with limited water, succulence, drought-deciduousness, or evergreen-sclerophylly (Morrow and Mooney 1974). At both the dry and the wet ends of the transect some of the species maintained high xylem pressure potentials throughout the year. At the dry end of the transect _Ruschia sp._ maintained high xylem pressure potentials throughout the season because of its succulent nature. Members of the Mesembryanthemaceae have been reported to show signs of Crassulacean acid metabolism (Schütte _et al._ 1967). Even if _Ruschia sp._ was a CAM plant, it still showed the diurnal variations in xylem pressure potential of a plant that was losing water during the day. At the mesic end of the transect the sclerophyllous proteoid overstory species maintained high xylem pressure potentials throughout the year probably because they were deep rooted and had low rates of water loss (Miller _et al._ 1983). In the middle of the transect many of the species were deciduous or semi-deciduous, and also underwent large seasonal fluctuations in xylem pressure potential. Many of the species that were found at more than one site along the transect showed increased water stress toward the dryer areas which would seem to show the importance of water in limiting their distributions.

The pre-dawn xylem pressure potentials of most of the species continued to decline as the summer progressed, probably reflecting the decreasing soil moisture availability. During the same time the increasing air temperatures and resulting vapor pressure deficits presented the plants with an increasingly xeric aerial environment. Most of the plants along the transect responded to this gradient in ways that show physiological adaptation to water stress.

Of the thirteen species only _Stoebe capitata_ seemed to show increasing midday depressions in xylem pressure potential with decreasing pre-dawn xylem pressure potentials. Throughout the year the pre-dawn xylem pressure potentials of *Stoebe capitata* remained relatively constant, possibly as the result of a deep root system which allowed overnight recovery, even in late summer. As the summer progressed the midday depressions in xylem pressure potential continued to increase. *Stoebe capitata* did not seem to have the stomatal control necessary to limit water loss and maintain a balance with the root uptake. This pattern shows little physiological adaptation to drought, and may be the reason why *Stoebe capitata* was limited to the wettest site of the transect.

The two completely deciduous *Rhus* species, and some of the semi-deciduous species also had slightly increasing midday depressions in xylem pressure potential with decreasing pre-dawn values, until they began to shed their leaves. As the leaf areas of these species declined the rate of water loss from the individuals may have declined, while the root area remained the same, allowing smaller midday depressions in xylem pressure potential. Instead of showing a seasonal physiological modification in response to water stress these species showed morphological adaptations.

The fynbos overstory species *Protea laurifolia*, *Protea glabra*, *Paranomus bracteolaris*, and *Leucadendron pubescens*, and the karroid species *Ruschia sp.* responded to the increasing drought by limiting water loss through stomatal closure. As the pre-dawn xylem pressure potentials dropped, the midday depressions in the xylem pressure potential also decreased, showing a decreasing rate of water loss, or increasing rates of water uptake which is unlikely (Boyer 1974). These species, especially the fynbos overstory species, exhibited little seasonal shift in the xylem pressure potential that probably corresponded to the point of turgor loss. The response of the stomata seems to have been effective in controlling water loss, and the species maintained high midday xylem pressure potentials throughout the year. It is probably because of their conservative pattern of water use that the fynbos overstory species were limited to the more mesic areas where there was enough water to allow the stomates to stay open for a period long enough to maintain a positive carbon balance for the year. *Protea glabra*, which was only found at the dryer edge of the distribution of *Protea laurifolia*, had higher pre-dawn xylem pressure potentials, higher midday xylem pressure potentials, and also had larger midday depressions in xylem pressure potential than *Protea laurifolia*. *Protea glabra* must have had a more effective root system which allowed better recovery during the night, and then possibly greater transpiration, assuming both species had similar leaf water content to leaf water potential relationships. This may have then allowed greater carbon gain during the day.

Ruschia sp. was able to maintain this conservative response to water stress because the community was too sparse to experience shading. The distribution of *Ruschia sp.* probably did not continue into areas of the transect with higher rainfalls because the low growing species would have been overgrown by other taller species which could withstand lower xylem pressure potentials and continue growing. The proteoid overstory species have low light requirements for photosynthesis (Mooney _et al._ 1983), and can therefore slowly grow out of understory species in a post fire community.

In the middle areas of the transect, where the strategy of the fynbos overstory species may not have allowed sufficient photosynthesis to meet the demands of respiration and growth, species that could withstand low xylem pressure potentials seem to have displaced the succulents. As the pre-dawn xylem pressure potentials of many of the transitional species decreased the midday depressions in xylem pressure potential remained relatively constant. These species may have stomata that are sensitive to the rates of water loss, since as the summer progressed, and the evaporative conditions increased, most of the species did not have increasing diurnal fluctuations in xylem pressure potential resulting from increasing rates of water loss. The ability to maintain stomatal functioning, and diurnal fluctuations in xylem pressure potential, must be the result of seasonal adjustments in the osmotic potentials of the leaves.

During the period when _Rhus dissecta_ was leafless the xylem pressure potentials were higher in the middle of the day than pre-dawn. This "inverted" pattern was also found to a lesser degree in _Rhus incisa_ when it was leafless, and in _Eriocephalus africanus_. Syvertsen _et al._ (1975) reports that in _Larrea tridentata_ in New Mexico a similar pattern was found and could possibly have been the result of diurnal patterns of vertical water vapor movement in the soil in response to the changing temperature gradients of the soil. They found that midday xylem pressure potentials could be up to 3.5 MPa higher than the pre-dawn values, when the pre-dawn xylem pressure potentials were between -8 and -9 MPa. During the time that the diurnal pattern of xylem pressure potentials was inverted, Larrea tridentata was also actively transpiring. This pattern should be even more pronounced in a plant that was not actively transpiring, such as the leafless Rhus dissecta, but was in equilibrium with the soil through bi-directional root exchanges.

Both Rhus incisa and Rhus dissecta dropped their leaves when the xylem pressure potentials reached about -5 MPa. At site 5 the xylem pressure potentials did not reach this level, but leaf shedding still occurred. Before Rhus dissecta shed its leaves at site 2 they showed signs of burning, possibly because they where not able to maintain the necessary transpirative cooling. The switch from the shiny dark-green leaves of Rhus dissecta found at the mesic end of the transect, to the glaucous grey-green leaves of Rhus incisa found at the xeric end of the transect follows the patterns Ehleringer (1980) found with several species of Encilia in the Sonoran desert.

The minimum xylem pressure potentials of many of the fynbos understory species, and the transitional species must have been sensitive to the soil moisture levels near the surface of the soil. The fynbos understory species Elytropappus gnaphaloides, and Agathosma giftbergensis both had much lower xylem pressure potentials at the more xeric site of their distribution. Even at site 5 Agathosma giftbergensis reached xylem pressure potentials of -6 MPa when the nearby proteoid overstory species where -2 MPa, which must reflect the shallow rooting of Agathosma giftbergensis.

The xylem pressure potentials of many of the transitional species were lowest at site 3, and increased toward site 1. The increased rainfall at site 3 may have been offset by an increase in leaf area, and competition for water. The Nylandtia spinosa and Eriocephalus africanus that occurred at sites 4 and 5 were usually overtopped by a member of the proteoid overstory, or overgrown by some other understory shrub, and the wetter limit of the distribution of these species may be determined by shading.

Of the three responses to increasing drought; increasing midday depressions in xylem pressure potential with decreasing pre-dawn xylem pressure potential, decreasing midday depressions with decreasing pre-dawn xylem pressure potential, and constant midday depression in xylem pressure potential with decreasing pre-dawn xylem pressure potential, the last group should show the most hardening and permanent physiological changes. Unfortunately, the higher than average autumn rainfall raised the pre-dawn xylem pressure potentials and made comparisons of the pre-drought and post-drought midday depressions in xylem pressure potential difficult. The increased soil moisture was probably responsible for the generally smaller post-drought midday depressions in xylem pressure potential.

5. DIURNAL PATTERNS OF LEAF CONDUCTANCE, TRANSPIRATION, AND XYLEM PRESSURE POTENTIAL IN SELECTED KARROID AND FYNBOS PLANTS DURING THE SEASON

5.1 Introduction

The production rates of most communities are either limited by some environmental parameter, or by the genetically determined maximum. Where community production is limited by the genetic potentials of the species involved, there should be a gradual shift in species composition until an environmental limit is reached. In an isolated community, with limited immigration and where the existing species have a limited ability to modify inheritable characteristics through time, or exhibit little nonheritable plasticity, this pattern of resource optimization may not occur. Areas with rapidly shifting environments or repeated disturbances may also not follow a pattern of resource optimization.

The evergreen sclerophyllous shrublands of the five disjunct mediterranean-type ecosystems are structurally similar to the evergreen sclerophyllous heathlands that occur in many areas of the world (Specht 1979). The environmental factors which have been hypothesized to control these two types of ecosystems are quite different.

The vegetation of the mediterranean-type ecosystems is thought to primarily result from the seasonality and amount of rainfall the areas receive, which results in a characteristic period of summer drought, and the winter temperatures cold enough to inhibit growth (Miller 1979; Mitrakos 1980). Heathlands occur in areas with a wide range of seasonal patterns and amounts of rainfall, but are usually in areas where soil nutrients are limited. Heathlands are therefore thought to primarily be a response to the low soil nutrient levels rather than a response to the moisture levels (Specht 1979). The five mediterranean-type ecosystems also have relatively low levels of soil nutrients and may, because of the additional factor of the moisture regime, represent a special case, or subset, of the heathlands (Specht 1980).

The water relations of fynbos plants at several sites in the winter rainfall region of the western Cape which received more than approximately 600 mm/year rainfall exhibited little evidence of a significant period of water stress during the summer (Miller et al. 1983). In the mediterranean-type ecosystems of Chile and California the evergreen sclerophyllous shrubs receiving similar levels of rainfall also showed little water stress, but were also near the mesic edge of their distribution, and with slightly higher rainfalls would be replaced by forest species (Di Castri 1981). Unlike in the chaparral in California and the matorral in Chile, where the distribution of the evergreen sclerophyllous shrub vegetation type, and the total biomass, has closely linked to the precipitation levels, the distribution and the total biomass of the fynbos seems to be governed by some other environmental factor.

The fynbos, which is characterized by the presence of a high proportion of species endemic to the western Cape, South Africa, especially members of the Proteaceae, Restionaceae, and Ericaceae (Taylor 1978; Kruger 1979), is bounded by three general switches in environmental conditions. As the rainfall levels decrease, without a switch from the Table Mountain Sandstone soil type, fynbos is replaced by karroid communities of succulents and drought-deciduous species. At intermediate rainfall levels, between 300 and 600 mm/year, the switch from Table Mountain Sandstone soils to the heavier and more nutrient rich shale soils brings a switch to Rhenosterveld, which is characterized by fine-leaved and semi-deciduous species, and the characteristic *Elytropappus rhinocerotis* (Rhenosterbos) (Moll *et al.* 1984). In the southern Cape there is a switch from fynbos to forests in areas which generally have high annual rainfalls with little seasonality but with no clear environmental differences from nearby areas that are covered with fynbos (van Daalen 1981). Forests also occur in isolated pockets, usually in drainage areas with high rainfall, throughout the range of the fynbos where topographic factors seem to allow protection from fire.

It is the lack of a consistent replacement of the evergreen sclerophyllous shrublands by a forest community when rainfall levels are above 600 to 900 mm/year that is the main physiognomic difference between the fynbos and the other four mediterranean-type ecosystems, and the main link to the heathlands of the world. The performance of pine plantations in areas that were previously covered by fynbos, and the escape of pines and other introduced tree species into undisturbed areas of fynbos, would seem to negate the idea that the soils are too nutrient impoverished to support forests. It would rather seem that there is a lack of indigenous temperate forest species (Campbell et al. 1979; Moll et al. 1980), or a lack of some component of a forest ecosystem such as ectomycorrhizal associations as opposed to endomycorrhizal associations (Read and Mitchell 1983; Day 1983), in southern Africa that seems to have allowed the fynbos to invade into areas that, based on the environmental conditions, could be forested.

The fynbos includes many endemic species which are rare or endangered. Much of the fynbos is also found in the Mountain Catchment Areas of the Directorate of Forestry of the Department of Environment Affairs whose mandate is to maintain water yield and quality from these areas, as well as the conservation of the areas. An understanding of the basic environmental controls on the vegetation type may improve the understanding of the ecosystem, and assist with the active management policy presently practiced. Linking the physiology of the plants in the fynbos to plants in either the hypothetical mediterranean-type ecosystem, which is water limited, or the hypothetical heathland, which is nutrient limited, will provide a basic framework for the understanding of the ecosystem.

It may be possible to interpret the functioning of the fynbos, as equivalent to either a mediterranean-type ecosystem or a heathland, from seasonal pattern of water relations at the arid boundary of its distribution. The boundary of the fynbos defined by the switch in soil type is complicated by the differing soil water properties of the two soils, as well as their different nutrient levels. The heavier shales may have soil water potentials similar to a coarse Table Mountain Sandstone derived soil receiving much lower rainfall, and may therefore also represent a switch to a more xeric environment. The seasonal pattern of the water relations of fynbos species, and of species from the communities which replace fynbos, at a series of sites with rainfalls similar to where the drought-deciduous and evergreen sclerophyll communities are found in the other mediterranean-type ecosystems, i.e. sites with rainfalls between approximately 200 and 700 mm/year and all on the same soil type, should show whether there is the characteristic period of water stress and how the species respond to a seasonal drought.

Plants with xeromorphic characteristics resulting from nutrient deficiency rather than adaptation to xeric environments do not necessarily have an ability to endure water stress. Such species may, however, be able to survive in semi-arid areas because the nutrient limited biomass does not transpire sufficiently to cause water stress. In order to survive in an arid environment a plant must either have a life cycle that allows dormancy, and avoidance of the drought period, or be able to continue photosynthesis. In order to maintain the necessary turgor for stomatal functioning a species must either be able to absorb as much water as it transpires, and therefore maintain high water potentials, or be able to adjust its cellular osmotic potential as the water potential drops.

The boundary of the distribution of a xeromorphic species, which is not a true xerophyte, along a gradient of decreasing rainfall will be where the period of water stress induced stomatal closure is too long to ensure a positive carbon balance for the year. If the species is not sufficiently cutinized, which limits the water loss except that under stomatal control, then the plant may be restricted to even wetter areas which offset the continuing loss of water. If a plant is unable to maintain transpirative cooling and is also receiving large energy loads, then the leaves may overheat causing tissue damage or death. The species may therefore be restricted to areas where there is never a period of water stress.

Areas with mediterranean-type climates, unlike deserts, are only seasonally arid and the plants do not have to be adapted to "exist" in arid conditions, but merely "survive" them. As the rainfall levels decrease, and the length of the summer drought increases, there will be a switch in the dominant growth strategy. When there is a short period of water stress plants may be able to have a fixed osmotic potential which will then cause, as the water potential drops, the leaves to loose turgor and the stomata to close. As long as the period of drought is short the plants will be able to survive the lack of photosynthesis. Species following this pattern may have to have leaf life spans longer than a single year in order to recover the costs of growth, and should be sclerophyllous in order to limit water loss other than through the stomata.

As the length of the summer drought increases plants will have to minimize the length of time without sufficient turgor to maintain photosynthesis by either having large osmotic potentials or adjusting the osmotic potential during the course of the season. The rigid cell walls of the sclerophyllous leaf form may be important in resisting the low water potentials that will develop, following the ability to continue water loss due to the adjustment of the osmotic potential. As the period of water stress continues to increase plants with high photosynthetic rates, and high rates of water loss, which are then seasonally deciduous will become more successful. Seasonally deciduous species will also have to endure water stress, especially on a diurnal time scale, if they are going to be able to maximize their carbon uptake while they have their leaves. At very low rainfall levels the seasonality of the rainfall is minimal. There is instead a pattern of isolated events, with the length of time between events becoming the most important factor. Plants with very short life cycles, or those with internal water reserves such as succulents, or plants with Crassulacean acid metabolism will become dominant.

5.2 Methods

The diurnal patterns of leaf conductance to water loss and xylem pressure potential were measured at sites 1, 3, and 5. When the weather permitted the measurements were made on three successive days. The measurements were made on the same individuals as were used in the measurement of the seasonal patterns of pre-dawn and midday xylem pressure potential. Measurements were made in July, October, November and December of 1982, and in January, April, and July in 1983. At site 3 measurements were also made in May 1983.

Leaf conductance was measured with a null balance porometer (Beardsell *et al.* 1972; Roberts *et al.* 1981). Except for *Protea laurifolia* and *Protea glabra*, where individual leaves were measured, shoot tips were sampled. The same tissue was sampled throughout the day, unless it was damaged during sampling. When this occurred tissue from a nearby branch was used for the remainder of the day. At the end of the day all the material was collected and leaf area was determined by either tracing and digitizing the areas, or by the measurement of appropriate dimensions. The leaves of *Rhus incisa*, *Rhus dissecta*, *Protea laurifolia*, *Protea glabra* and *Leucadendron pubescens* were traced and the area doubled so conductance could be expressed as a function of total leaf area (both sides). The leaves of *Ruschia sp.*, *Eriocephalus africanus*, *Agathosma giftbergensis* and *Paranomus bracteolaris* were treated as cylinders, as were the photosynthetic stems of *Nylandtia spinosa*. The leaves of *Nylandtia spinosa* (when they were present), *Galenia africana*, *Elytropappus gnaphaloides*, and *Stoebe capitata* were treated as rectangles whose areas were doubled to include both sides.

Xylem pressure potentials were measured as in section 4.2. The measurements of the xylem pressure potential were made on tissue of the same age and location on the plant as that used for the measurement of leaf conductance. Xylem pressure potentials were sampled at the same time as each leaf conductance measurement. The photosynthetically active photon flux (PAR) in a vertical direction was measured at each leaf just before the measurement of leaf conductance using a Lambda Co. model LI 185 quantum sensor.

Following Jarvis (1976) the responses of leaf conductance to the controlling variables; xylem pressure potential, photosynthetically active photon flux, vapor pressure deficit, and temperature were calculated. The potential maximum leaf conductance in response to each controlling variable was described by a function which formed the upper limit of the distribution of the field data. A Michaelis-Menten equation, with an offset to move the origin to the minimum xylem pressure potential observed and the K_m adjusted to reflect the distance from this offset was used to describe the potential maximum leaf conductance in response to decreasing xylem pressure potentials. An unmodified Michaelis-Menten equation was used to describe the maximum potential leaf conductance in response to increasing levels of photosynthetically active photon flux. A linear equation was used to describe the response of leaf conductance to increasing vapor pressure deficits, and a sinusoidal function was used for temperature. The sinusoidal function for temperature was split in half, because the curve below the temperature with the highest leaf conductances was often different than the curve above the maximum point.

5.3 Results

Throughout the year the leaf conductances to water loss of most species were highest early in the morning and then continuously declined throughout the day. Because the vapor pressure deficits were highest in the afternoon, the transpiration rate often increased until midday and then declined in the late afternoon. The leaf conductances of many of the species tended to increase with the onset of the drought in early summer, and then drop to low values for the 4 month period between January and April. In many cases leaf conductances where higher in July 1983 than they where July 1982, which may have been the result of the higher rainfall in the winter of 1983. The xylem pressure potentials of most species were able to recover slightly in the late afternoon in winter, but by midsummer few species were able to recover before sundown. The xylem pressure potentials and the leaf conductances of some of the species, especially at site 1, increased in December. In December the sampling at site 1 was conducted the day after the site received 2.4 mm rainfall, and the sampling at site 5 was conducted three days after a 12.5 mm rainfall. In April most of the species had little, or no leaf conductance during the day.

5.3.1 Microclimate

The solar radiation, wind speed, air and soil surface temperatures, and relative humidity where recorded on the days when the diurnal patterns of xylem pressure potential and leaf conductance to water loss were sampled. The microclimate was not recorded in November 1982 and January 1983 because the equipment was either unavailable, or was not functioning. The diurnal patterns of leaf conductance were not measured in May 1983 at sites other than site 3 because of poor weather.

Based on the days when microclimate measurements are available, the three sites received similar amounts of solar radiation (Figures 5.1, 5.7, and 5.13). On the days sampling was conducted in the middle of winter, in July 1982, site 1 received 12.0 $MJ/m^2/day$ solar radiation, site 3 received 11.3 $MJ/m^2/day$, and site 5 received 10.7 $MJ/m^2/day$. On the sampling days in the middle of summer, in December 1982, site 1 received 29.6 $MJ/m^2/day$, and site 5 received 30.8 $MJ/m^2/day$. At site 3 the microclimatic record is incomplete on the sampling day in December.

At site 1 the wind speeds were usually about 5 m/s until noon, and then increased in the afternoon and evening to around 15 m/s (Figure 5.2). At site 3 the wind did not increase so noticeably in the afternoon, except during the October sampling trip (Figure 5.8). On 13 July 1982 there

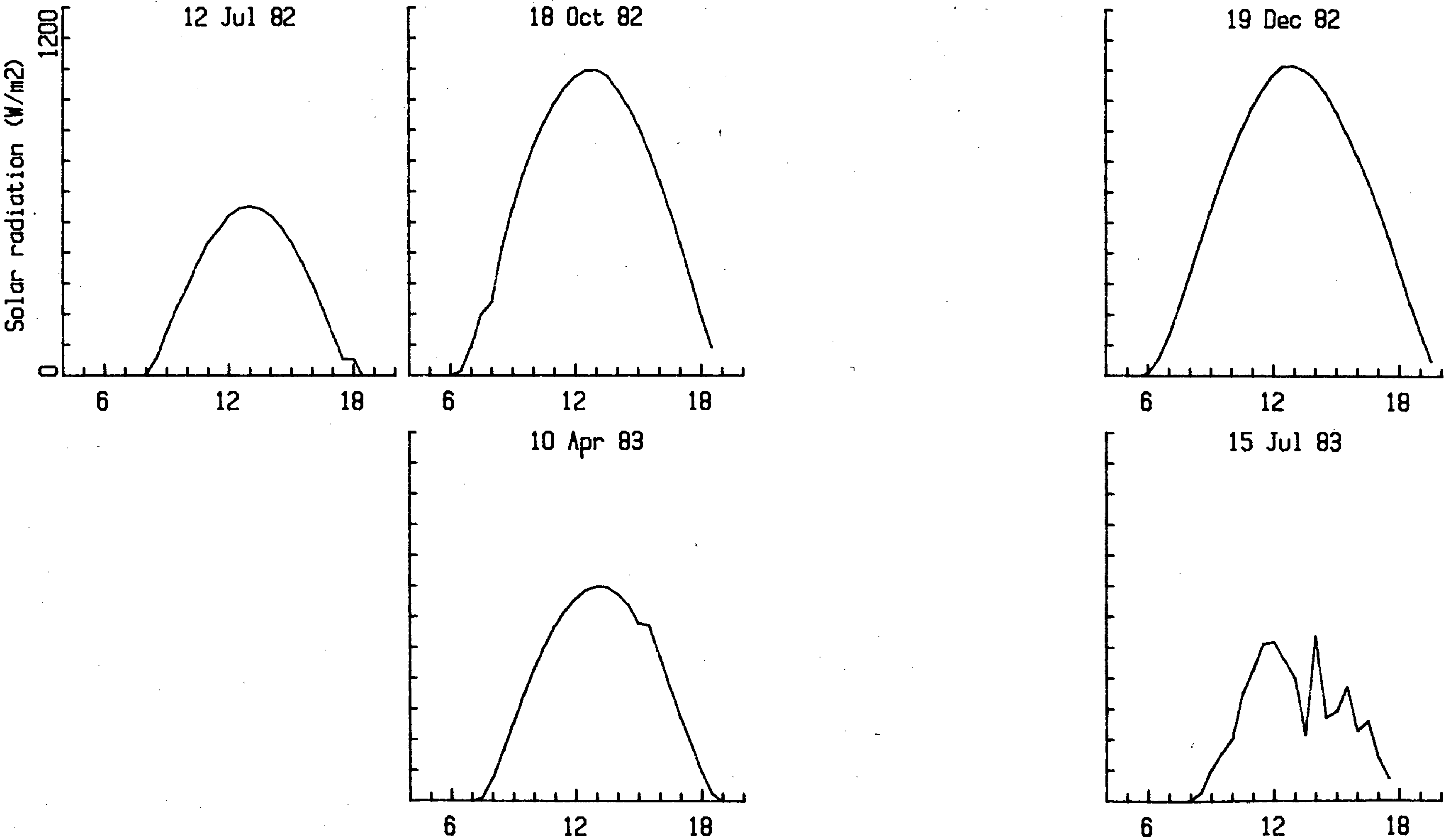


Figure 5.1 The diurnal pattern of solar radiation (W/m2) at site 1 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

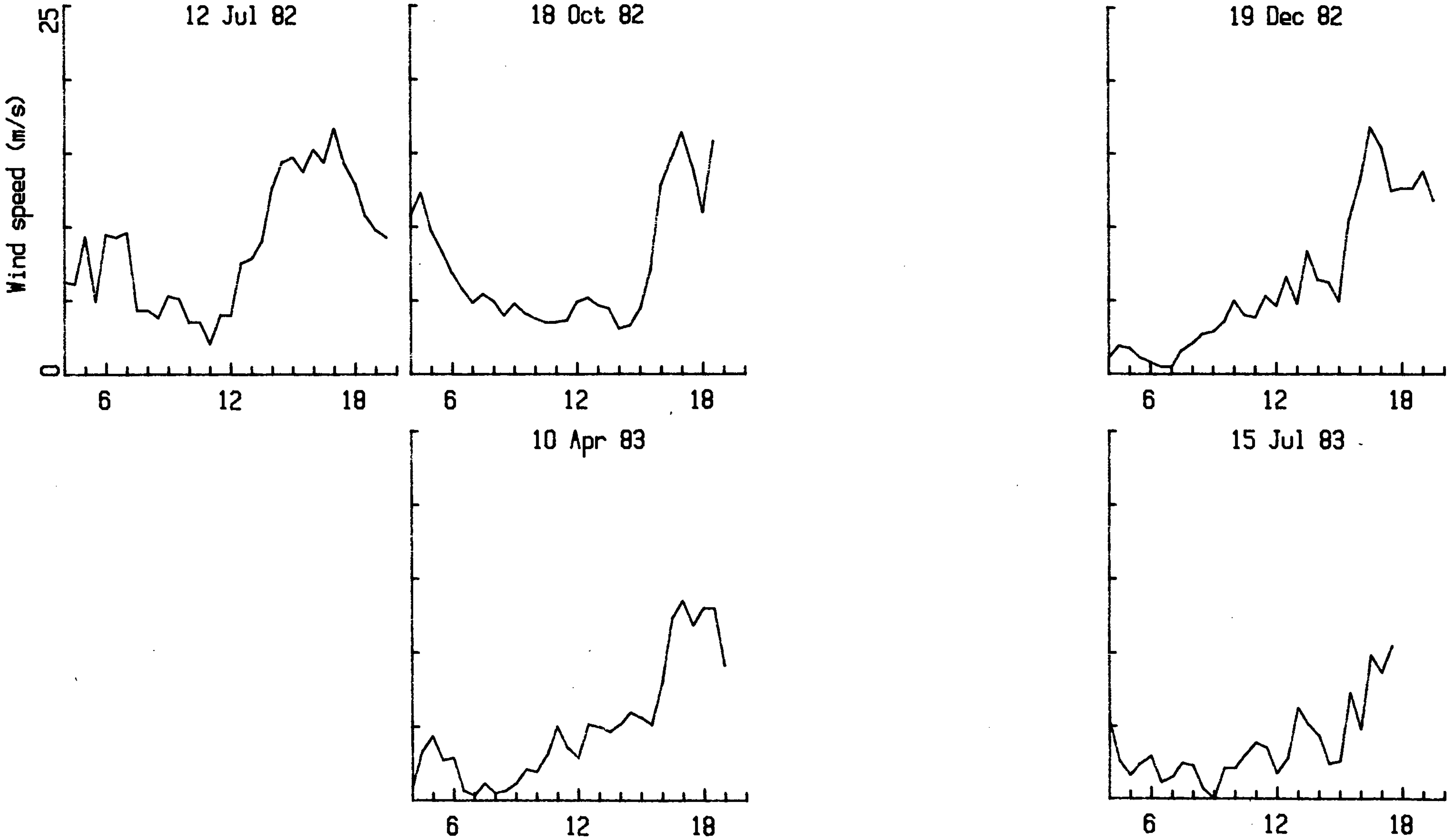


Figure 5.2 The diurnal pattern of wind speed (m/s) at site 1 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

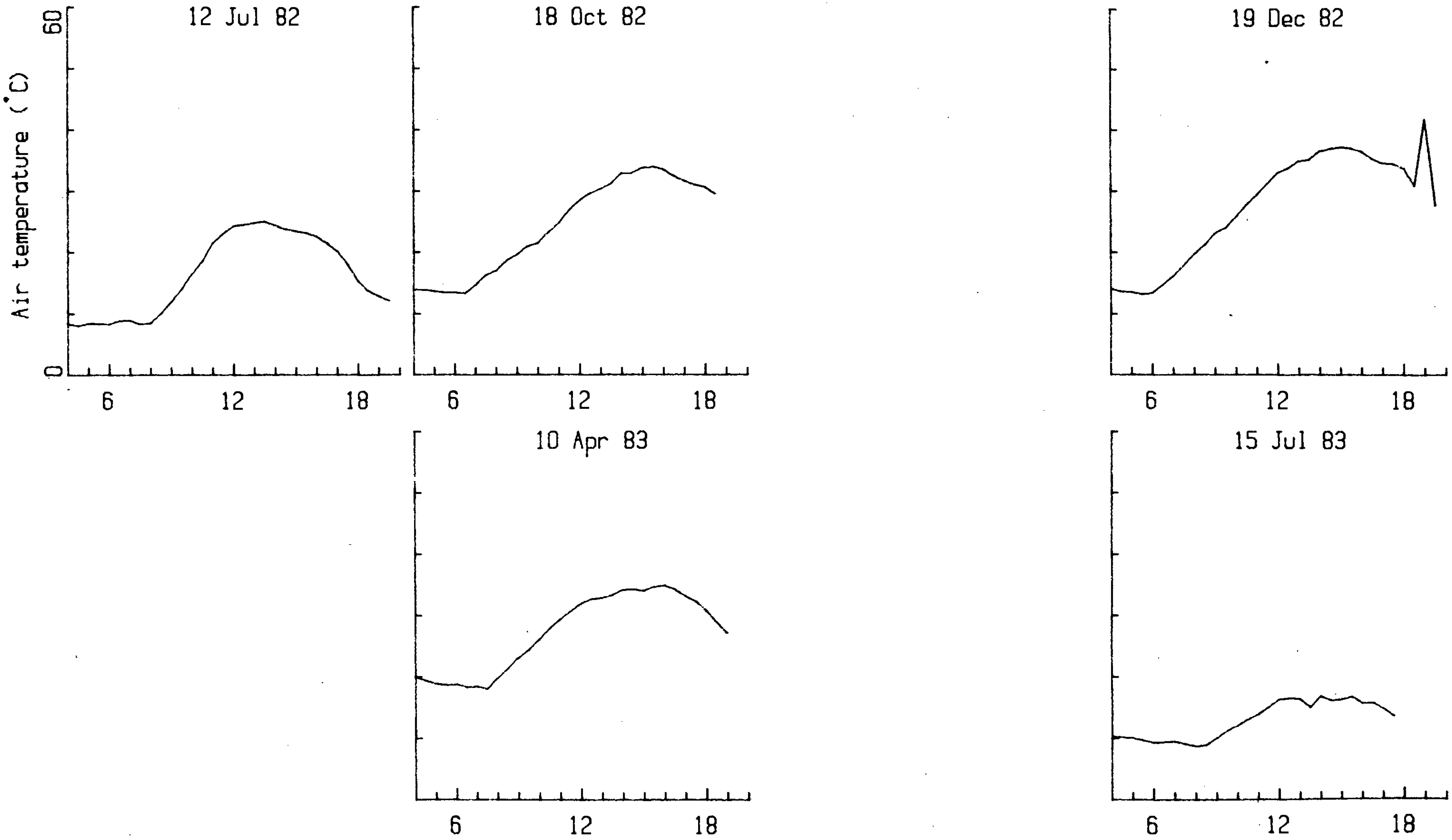


Figure 5.3 The diurnal pattern of air temperature (°C) at site 1 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

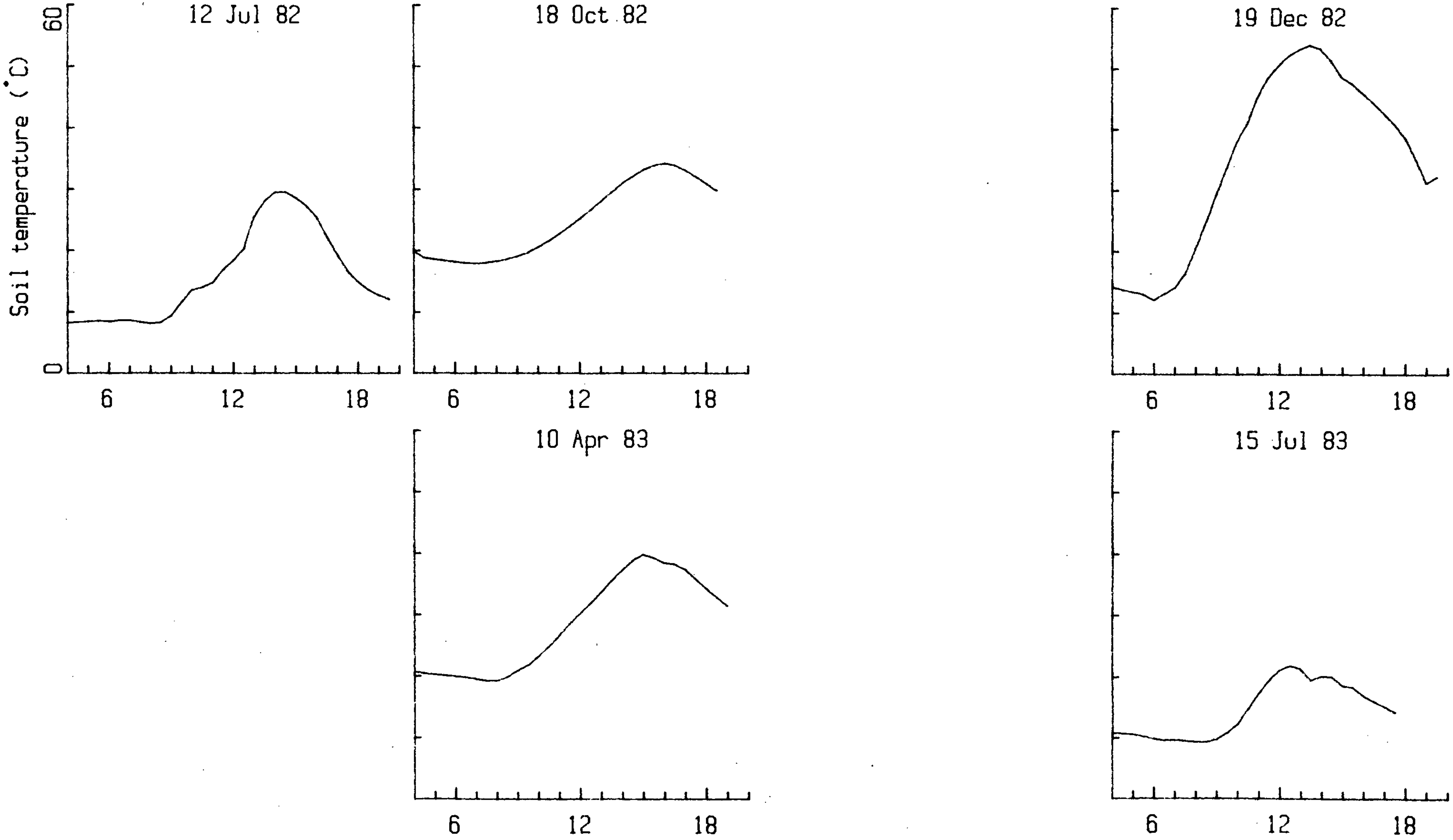


Figure 5.4 The diurnal pattern of soil surface temperature (°C) at site 1 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

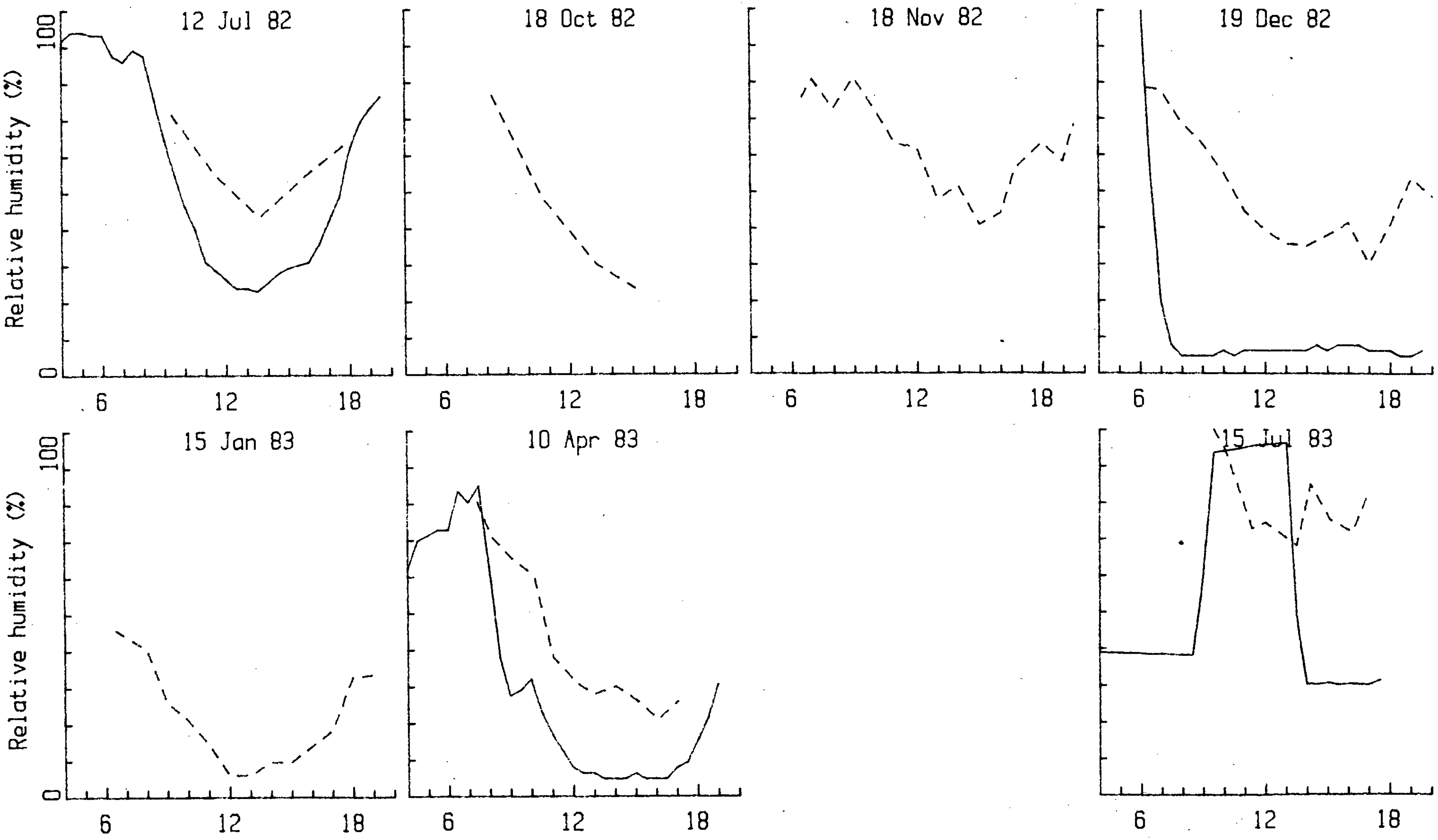


Figure 5.5 The diurnal pattern of relative humidity (%) at site 1 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours. (Solid line = Automatic weather station, Dash = Assmann psychrometer).

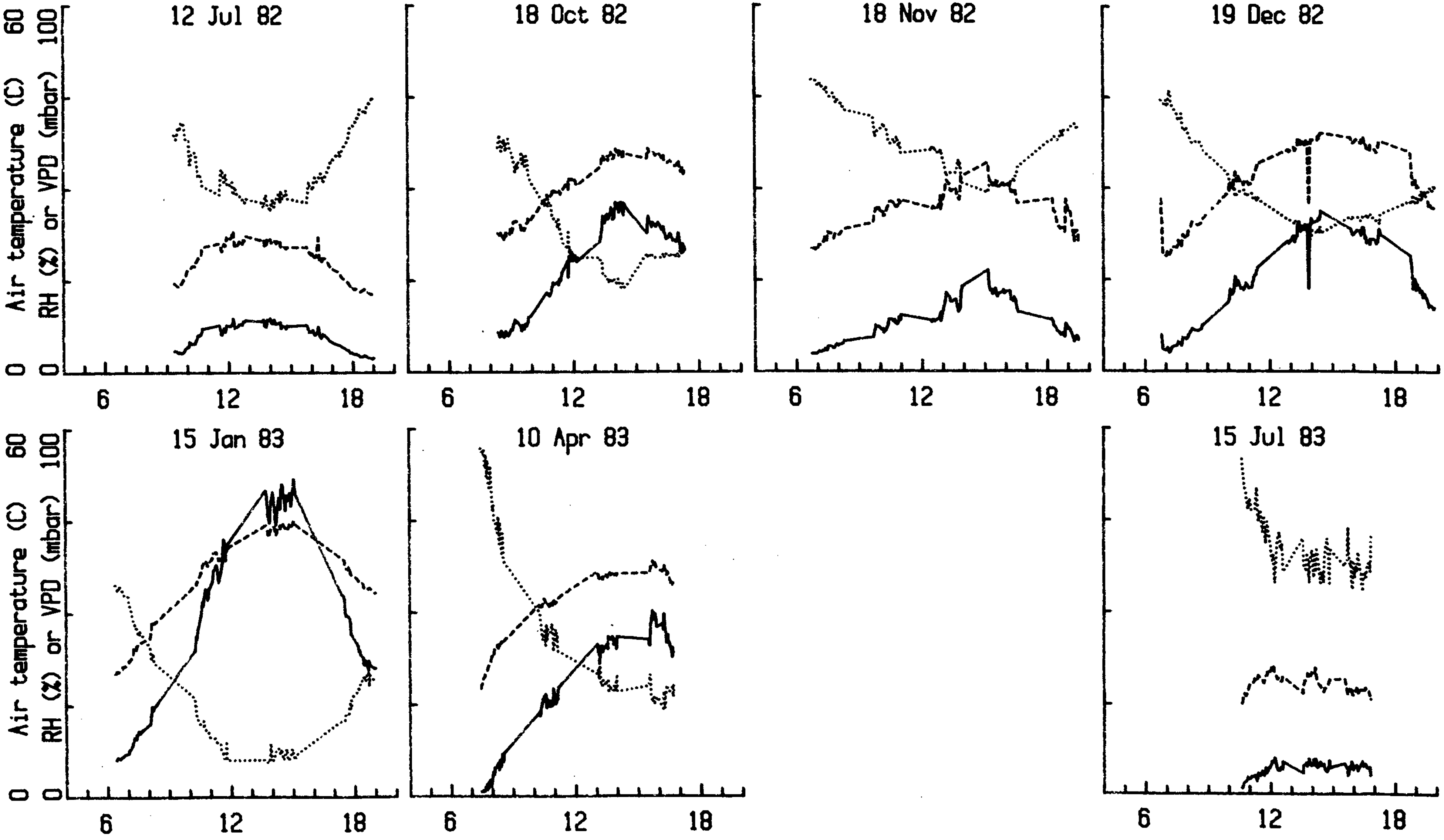


Figure 5.6 The diurnal pattern of relative humidity (%; dotted line), and air temperature (C; dashed line) measured by the porometer, and the calculated vapor pressure deficit (mbar; solid line) at site 1.

was a berg wind blowing while site 3 was being sampled, which also explains the high air temperatures found at site 5 on 14 July 1982. On the days when measurements were made at site 3 in April, May, and July 1983, the wind speeds were usually below 5 m/s. The anemometer at the permanent automatic weather station at site 5 was not very reliable. In July 1982 the wind speeds recorded at site 5 were slightly lower than those recorded at sites 1 and 3 (Figure 5.14). This pattern may have continued throughout the year, as site 1 was on top of a ridge and was exposed to strong diurnal winds, and site 3 was in a constriction in the valley.

The maximum air temperatures on the sampling days in December, in the middle of the summer, reached 37.3 °C at site 1, and 29.5 °C at site 5 (Figures 5.3, 5.9, and 5.15). The maximum air temperatures on the days of sampling in July 1982, 25.0 °C at site 1, 28.3 °C at site 3, and 31.8 °C at site 5, where higher than in July 1983, when they were 16.8 °C at site 1, 16.5 °C at site 3, and 14.9 °C at site 5. There were larger diurnal variations in the temperature of the surface of the soil than in the air temperatures at all three sites throughout the year. On the December sampling trips the temperature of the surface of the soil reached a maximum of 53.9 °C at site 1, and 38.7 °C at site 5 (Figures 5.4, 5.10, 5.16). As with the air temperatures, the soil surface temperatures in July 1982; 29.5 °C at site 1, 16.9 °C at site 3, and 20.1 °C at site 5 where higher than those in July 1983; 21.8 °C at site 1, 15.3 °C at site 3, and 11.5 °C at site 5. The incoming energy loads in July

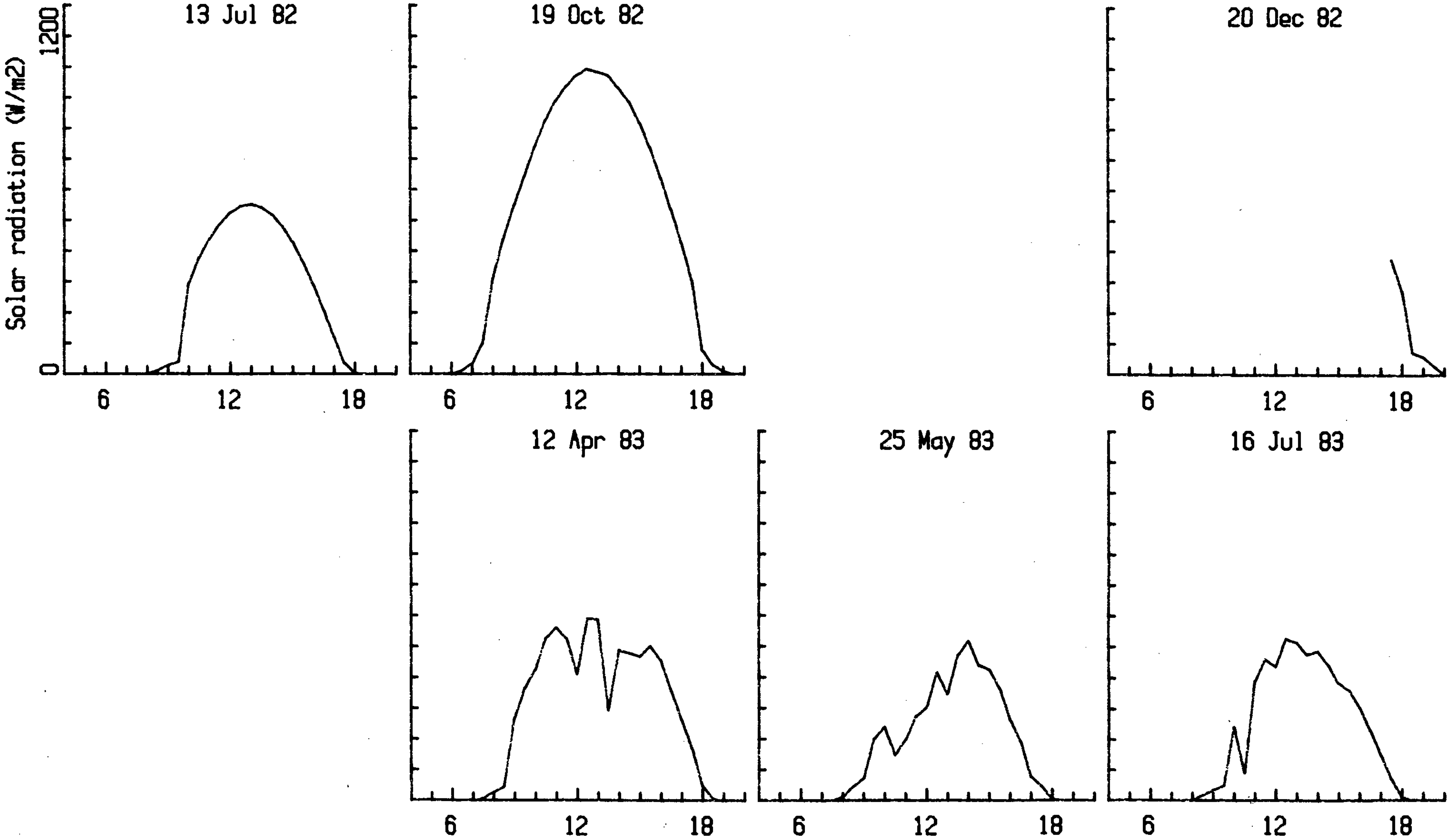


Figure 5.7 The diurnal pattern of solar radiation (W/m2) at site 3 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

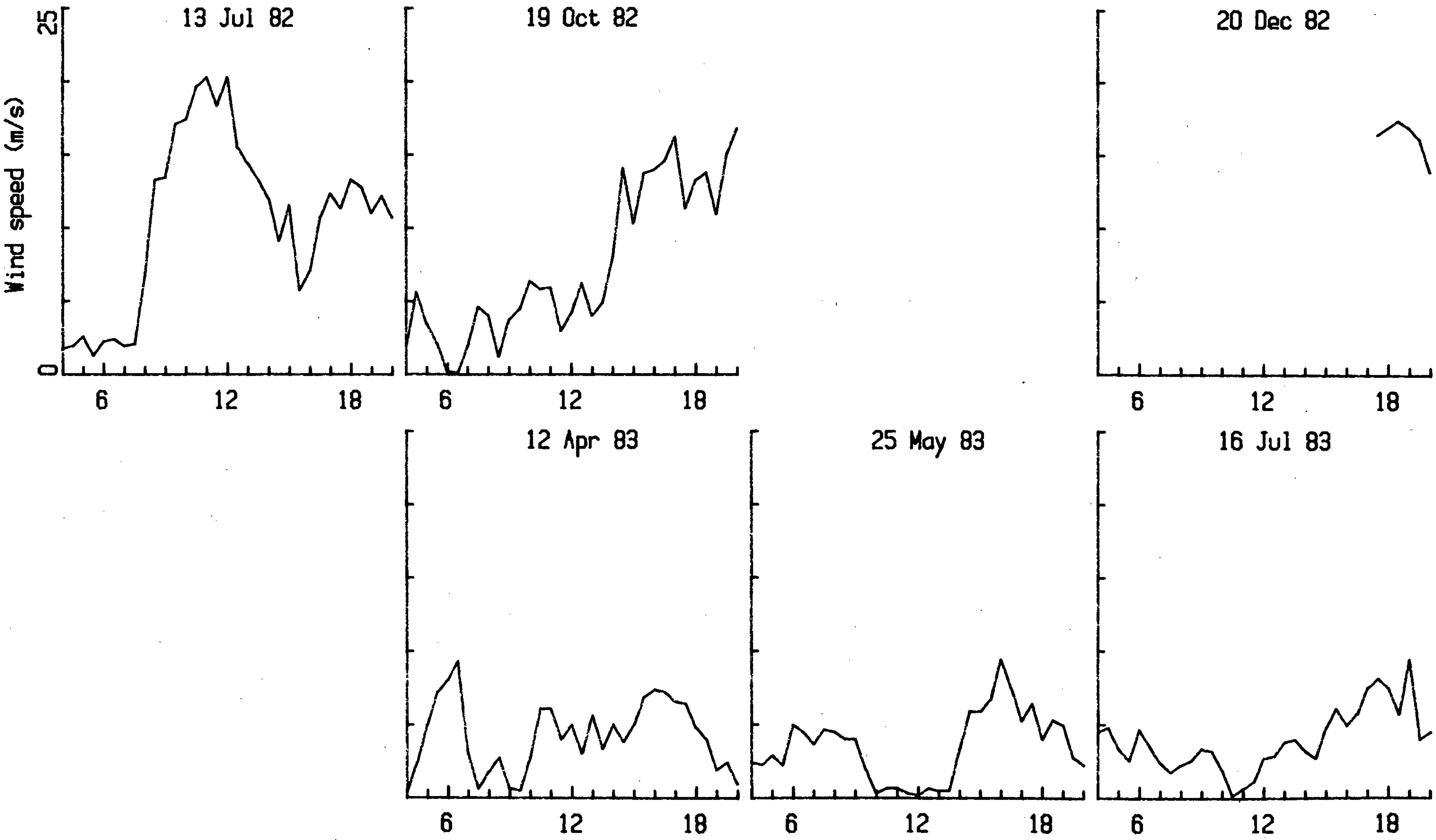


Figure 5.8 The diurnal pattern of wind speed (m/s) at site 3 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

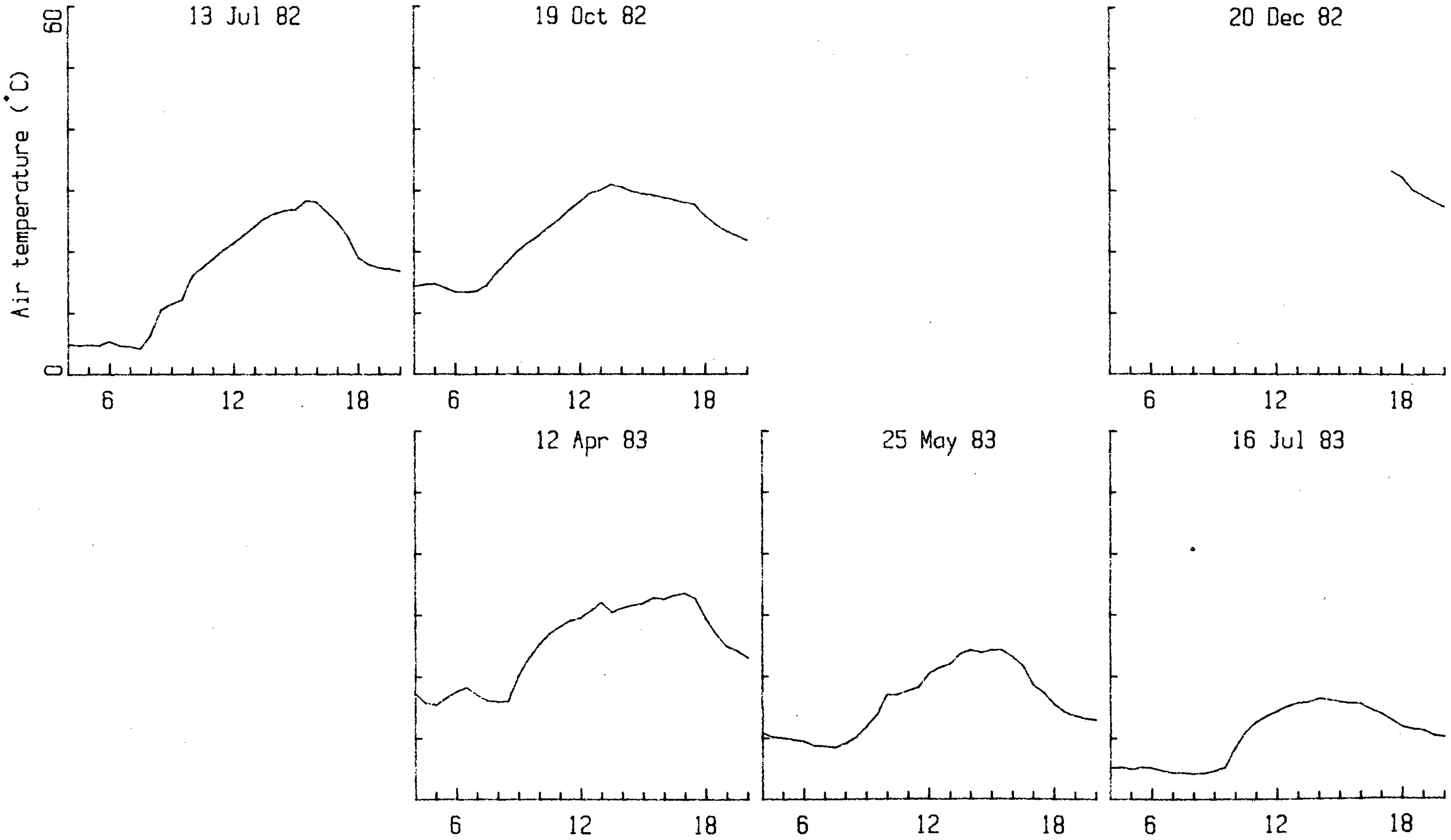


Figure 5.9 The diurnal pattern of air temperature (°C) at site 3 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

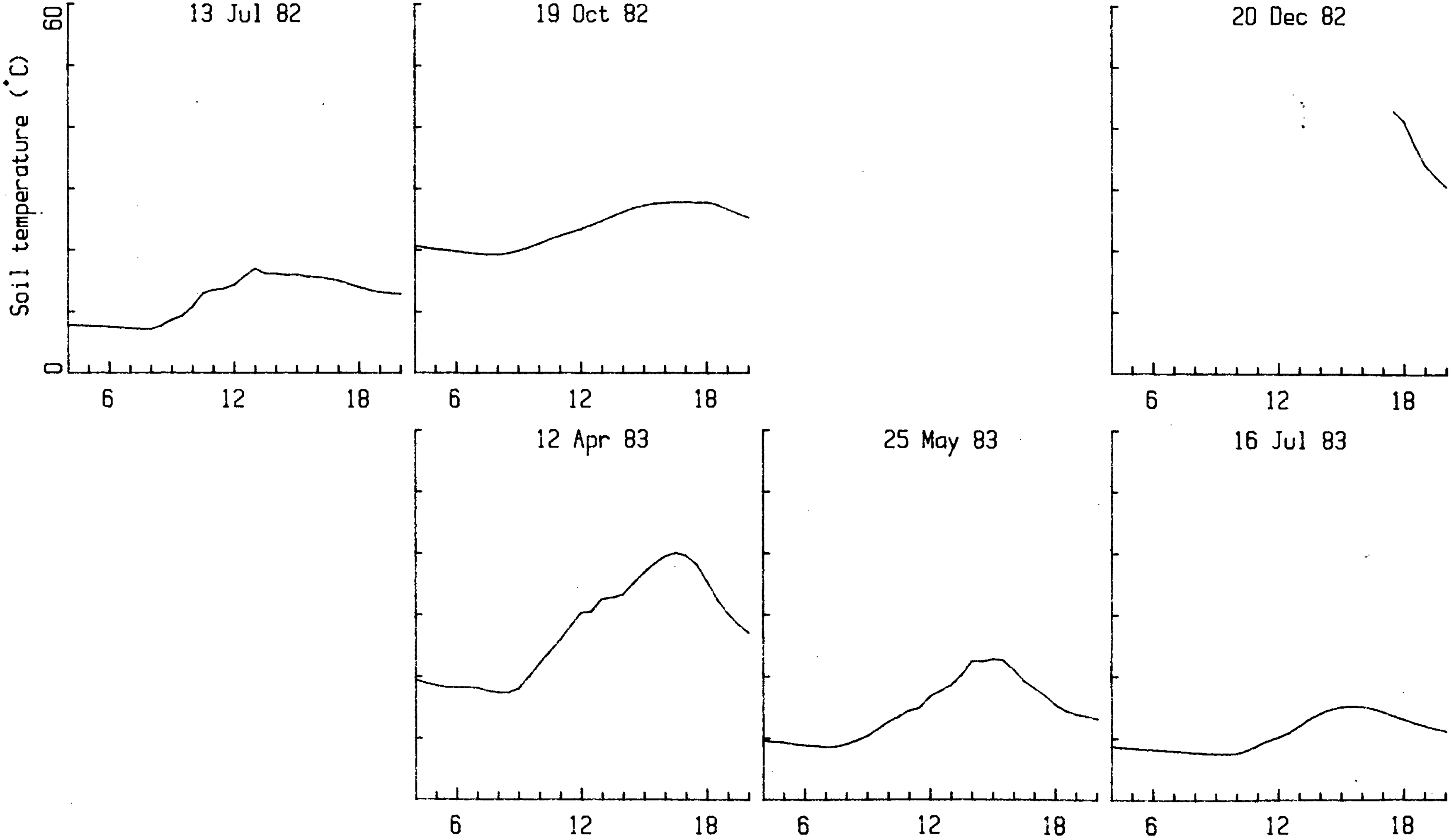


Figure 5.10 The diurnal pattern of soil surface temperature (°C) at site 3 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

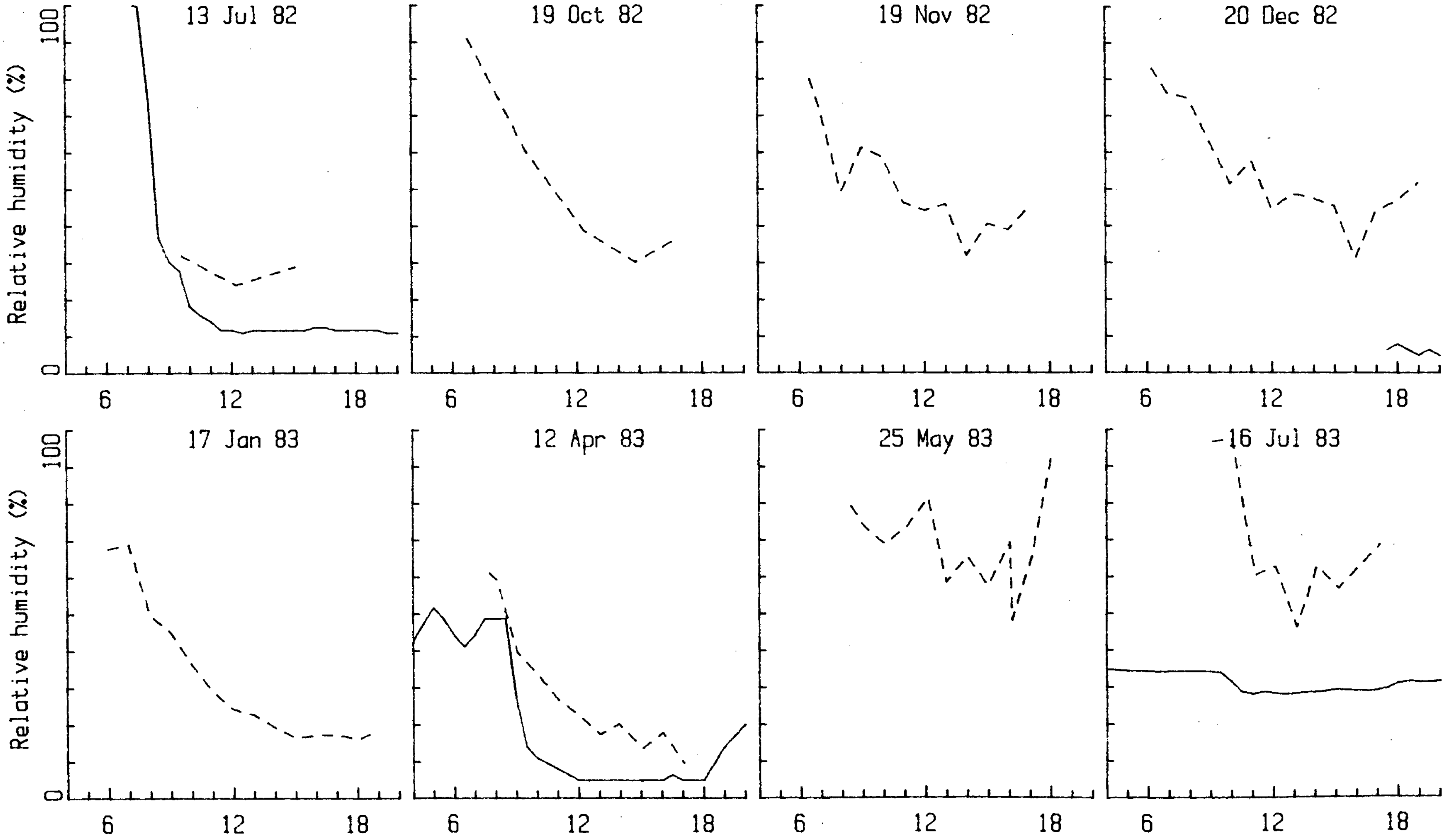


Figure 5.11 The diurnal pattern of relative humidity (%) at site 3 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours. (Solid line = Automatic weather station, Dash = Assmann psychrometer).

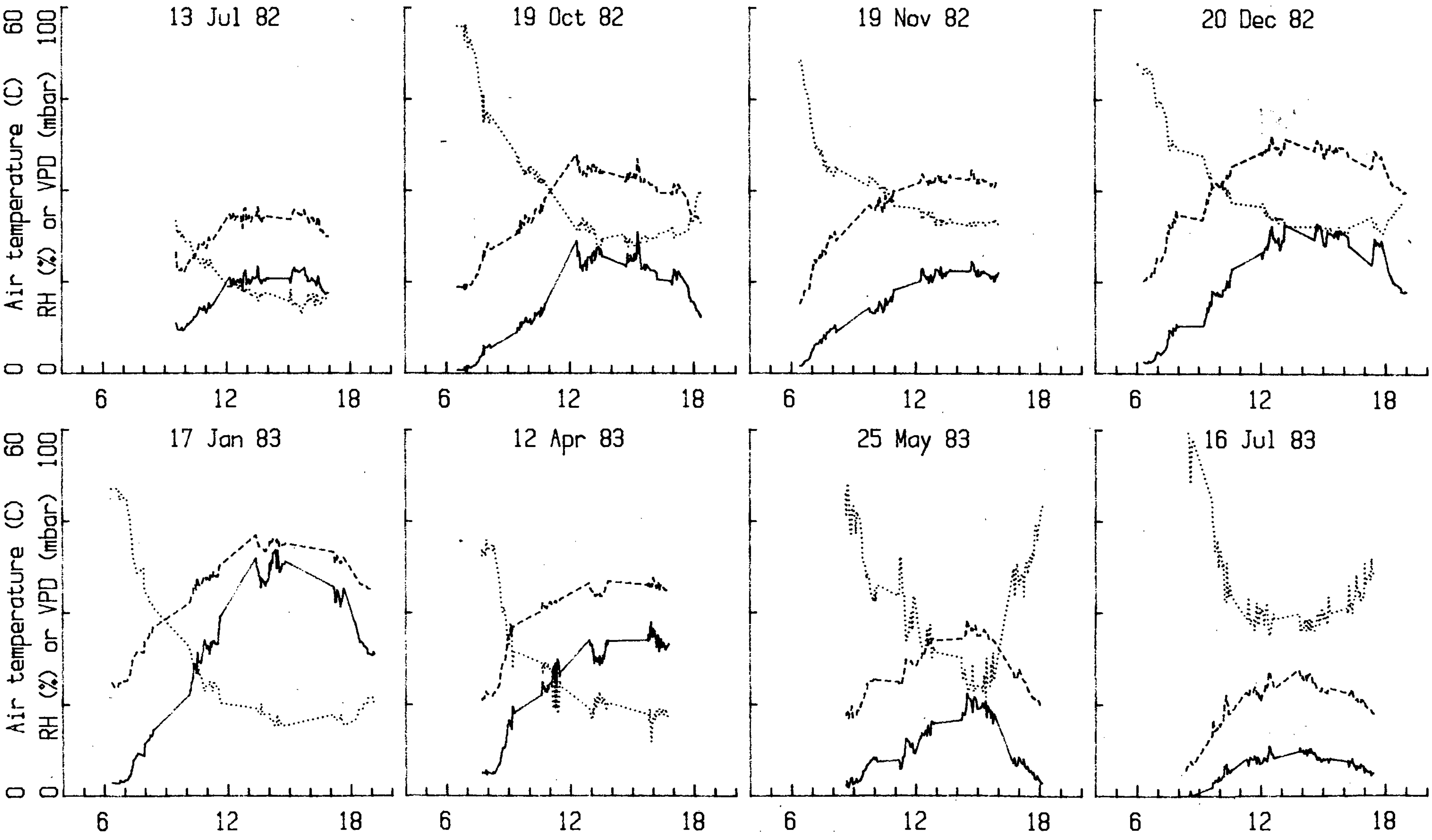


Figure 5.12 The diurnal pattern of relative humidity (%; dotted line), and air temperature (C; dashed line) measured by the porometer, and the calculated vapor pressure deficit (mbar; solid line) at site 3 .

1983 where slightly lower than in July 1982 at sites 1 and 3 because of cloud cover, which probably caused the lower soil surface temperatures. The rainfall during the winter of 1983 was greater than in the winter of 1982, and there was probably more moisture in the soil in July 1983 than in July 1982, which would also have contributed to the smaller diurnal fluctuations in the temperature of the surface of the soil.

The relative humidity sensors used with the automatic data loggers had to be protected from 100% condensing relative humidity. The sensor that was used at sites 1 and 3 was protected by a cubic, opaque plastic container. This container seems to have acted as a green-house, and heated the air inside the container, or allowed poor exchange with the ambient air even though the bottom side of the container was completely open. This caused the sensor to give very low, and probably erroneous, relative humidities during the day. The sensor used in the permanent automatic weather station at site 5 was not replaced after it had broken, since it could not be protected and yet still accurately measure the relative humidity. The Assmann psychrometer readings, especially at site 5, were variable and depended on whether they were made in the closed canopy or in clearings. Relative humidities were generally high at night and in the early morning (80 - 100 %), and then decreased sharply to values of about 50% in winter and 20-30 % in summer (Figures 5.5, 5.11, and 5.17). Based on the measurements of the ambient relative humidity and temperature made by the porometer, the midday vapor pressure deficits were about 10

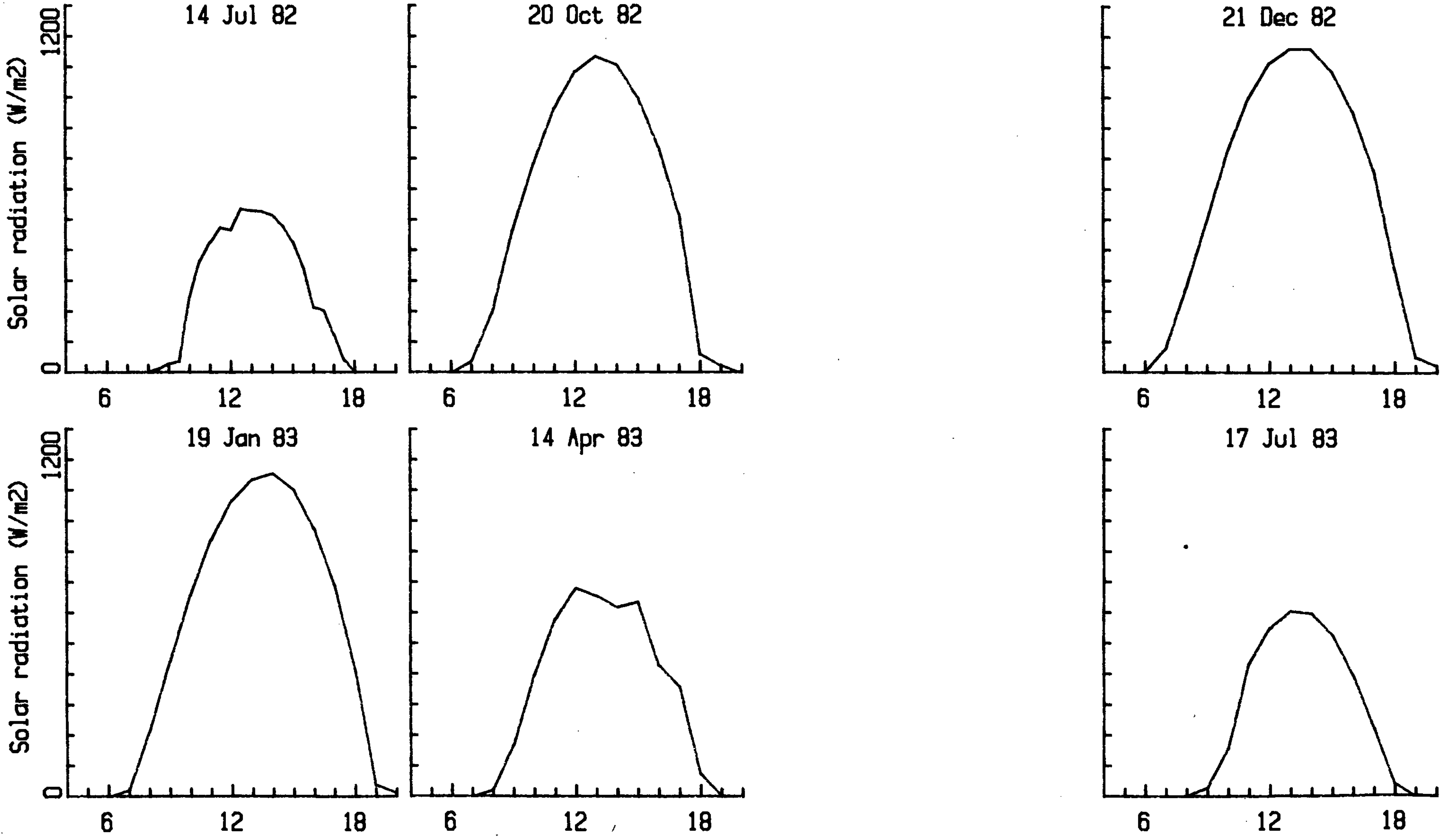


Figure 5.13 The diurnal pattern of solar radiation (W/m2) at site 5 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

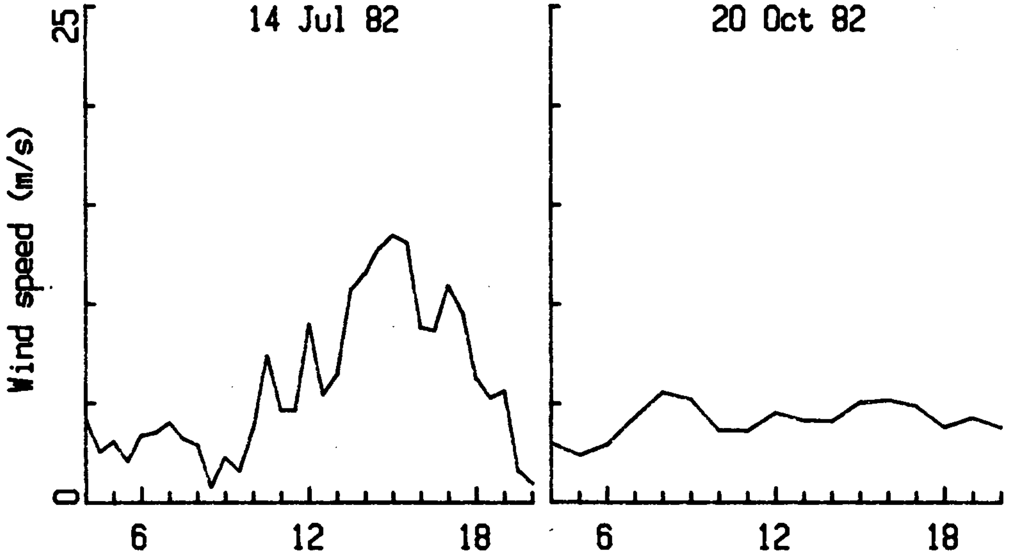


Figure 5.14 The diurnal pattern of wind speed (m/s) at site 5 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

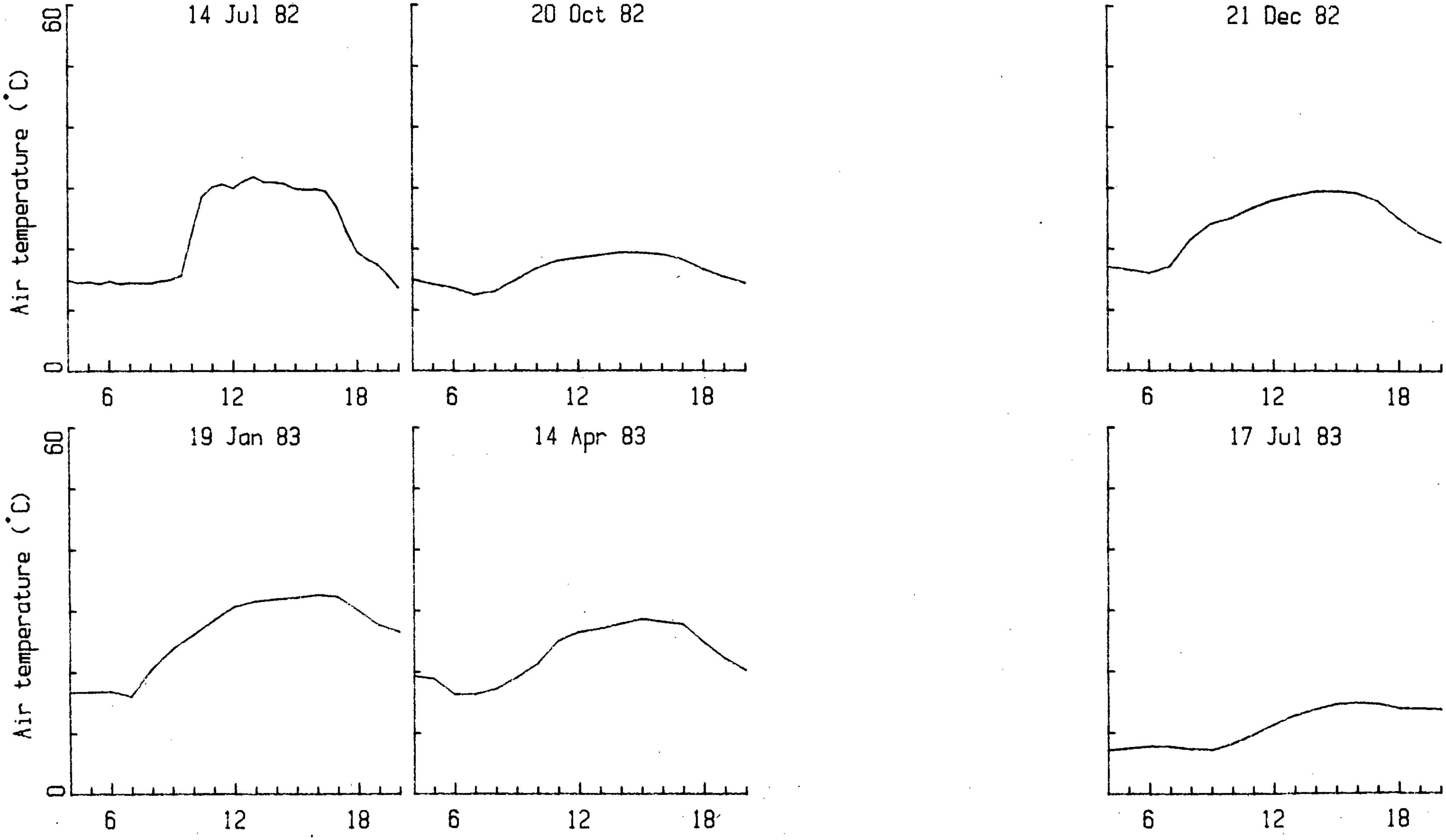


Figure 5.15 The diurnal pattern of air temperature (°C) at site 5 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours.

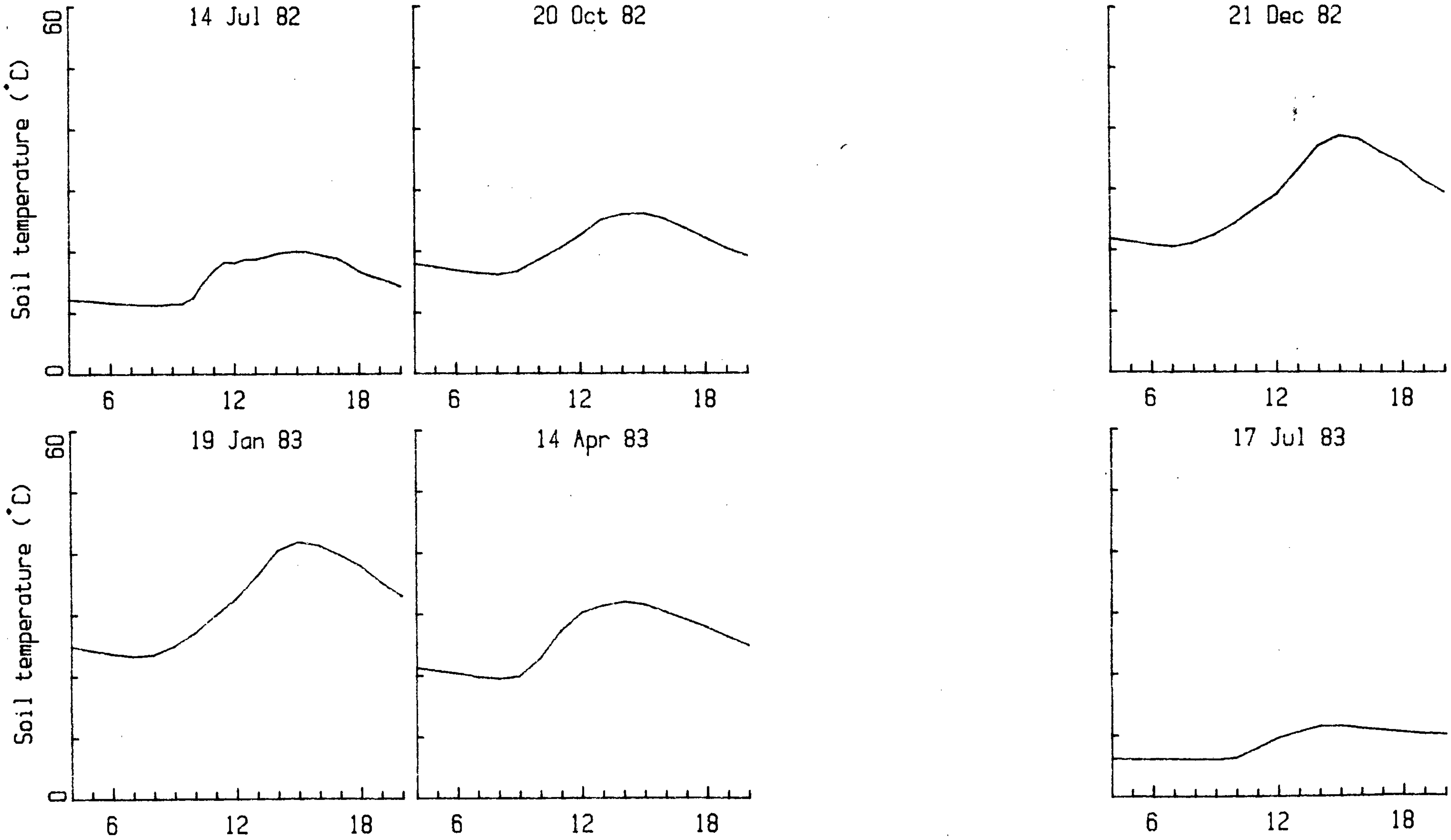


Figure 5.16 The diurnal pattern of soil surface temperature (°C) at site 5 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured.
The time scale is in hours.

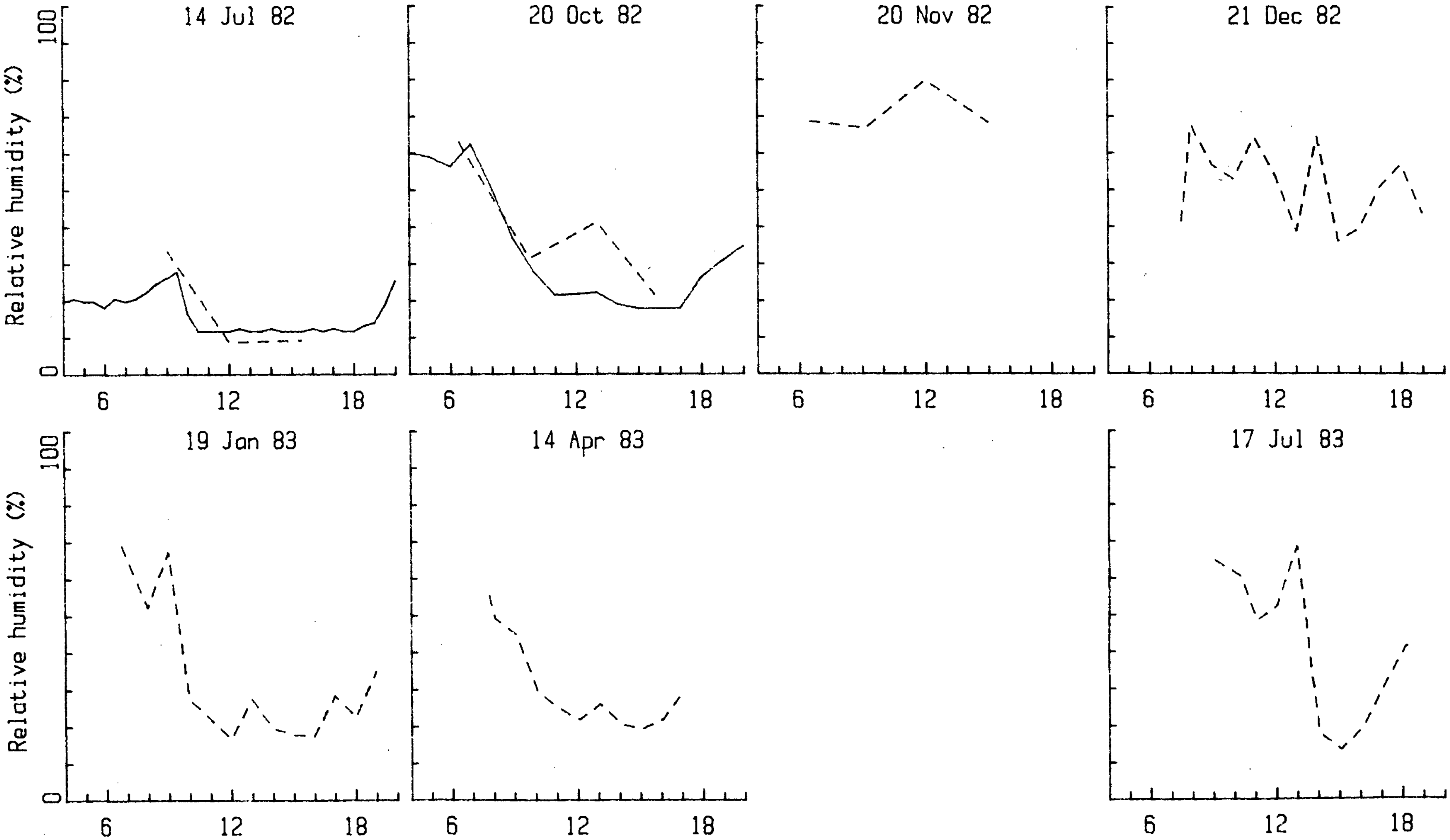


Figure 5.17 The diurnal pattern of relative humidity (%) at site 5 on some of the days when the diurnal patterns of leaf conductance and xylem pressure potential were measured. The time scale is in hours. (Solid line = Automatic weather station, Dash = Assmann psychrometer).

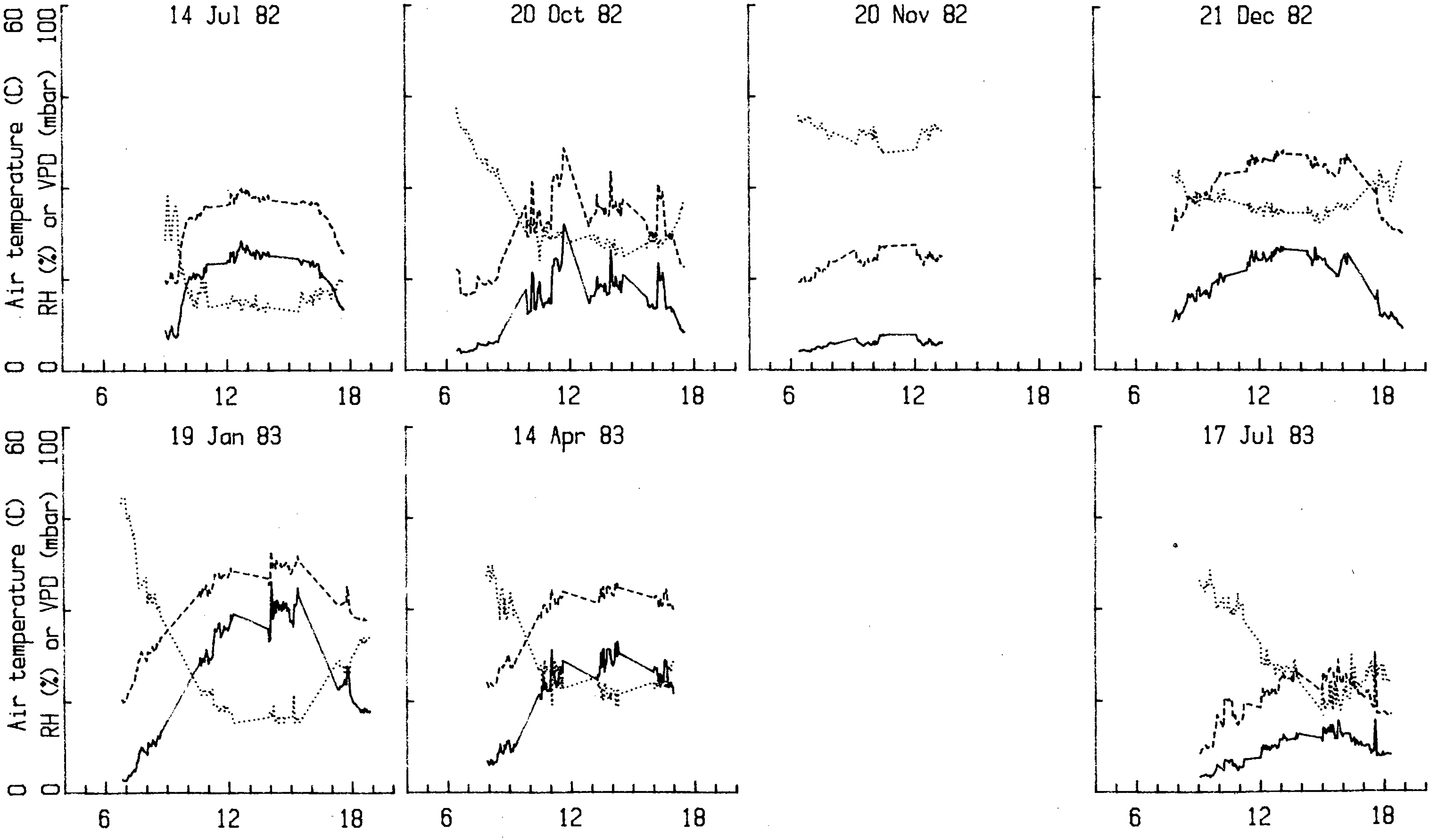


Figure 5.18 The diurnal pattern of relative humidity (%; dotted line), and air temperature (C; dashed line) measured by the porometer, and the calculated vapor pressure deficit (mbar; solid line) at site 5 .

to 15 mbar at the three sites in the middle of the winter, and reached about 80 mbar at site 1, 60 mbar at site 3, and 50 mbar at site 5 in the middle of the day in midsummer (Figures 5.6, 5.12, and 5.18). The berg wind that occurred in July 1982 when the sampling was conducted at sites 3 and 5 created a vapor pressure deficit of 25 to 30 mbar.

5.3.2 Species at site 1

Of the 5 species sampled at site 1, Ruschia sp. had the lowest leaf conductances to water loss and the highest xylem pressure potentials throughout the year (Figure 5.19). Except for the measurements in July 1983, the leaf conductances were highest in the early morning and decreased throughout the day. In July 1982 the highest leaf conductances occurred in the morning, 1.92±0.23 mm/s, and declined to 0.21±0.16 mm/s. The xylem pressure potentials were -1.13±0.20 MPa before dawn, -1.64±0.07 MPa in the morning, and then showed a slight midday recovery before falling to -1.99±0.09 MPa in the evening. The transpiration rates were highest in the middle of the afternoon, and reached 13.5±3.2 $mg/m^2/s$. Early morning conductances in October, November and December were about twice the midday values. In October the xylem pressure potentials dropped from -0.19±0.02 MPa before dawn to -2.07±0.15 MPa in the afternoon. The leaf conductances dropped from 2.98±0.33 mm/s in the morning to 0.45±0.13 mm/s in the afternoon and then recovered to 1.36±0.16 mm/s, which also caused the transpiration to drop in the afternoon and then recover. In November the xylem pressure potentials also

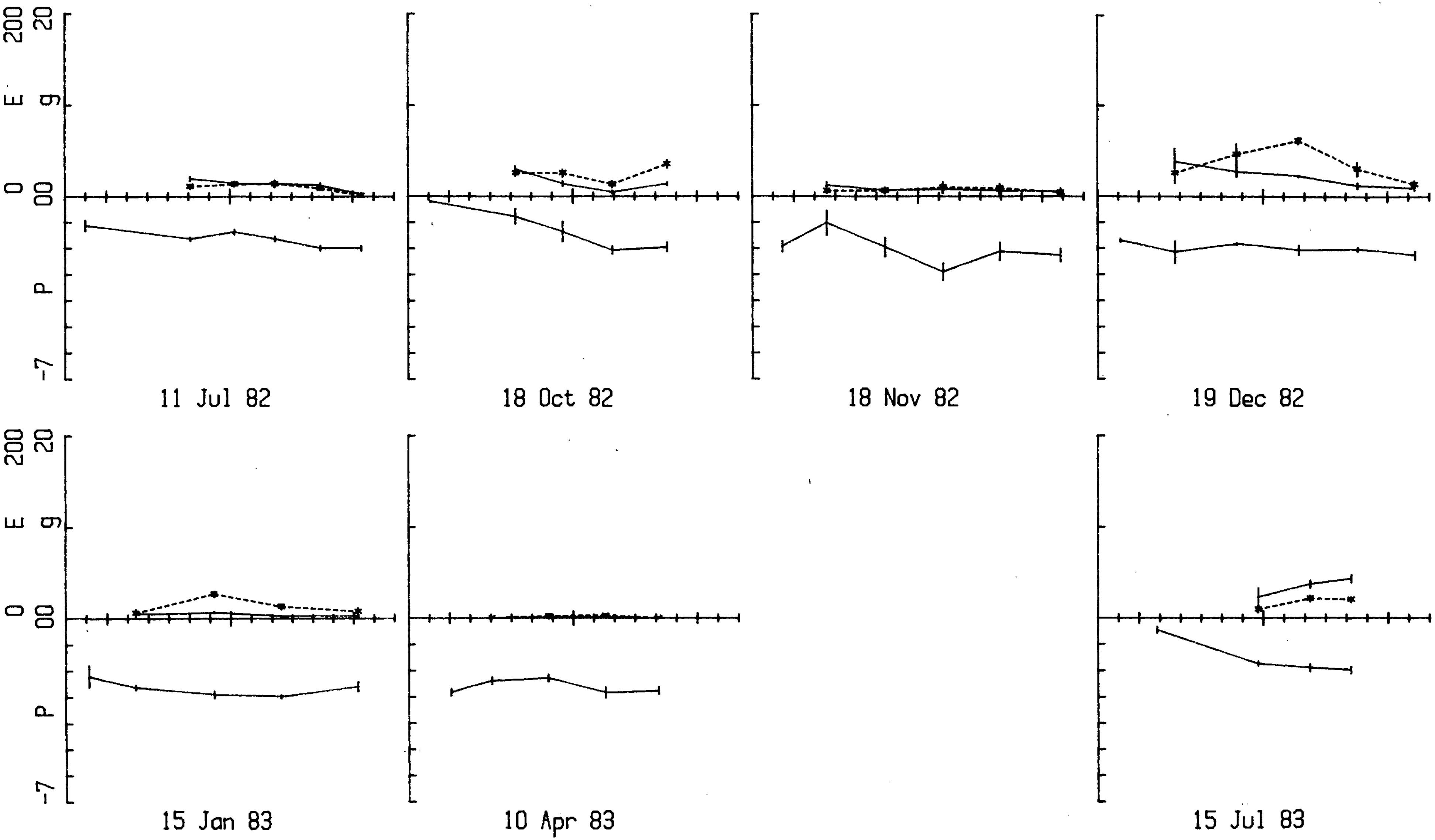


Figure 5.19 The diurnal pattern of the leaf conductance (g: mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of Ruschia sp. at site 1 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

showed large diurnal variations, while the leaf conductances were below 1 mm/s, and rather uniform, except in the early morning. The rains immediately before the December sampling slightly raised the pre-dawn xylem pressure potentials from what they were the month before, and increased the midday leaf conductances to 3.87±1.44 mm/s at their highest in the morning. The transpiration rates reached 61.7±3.4 $mg/m^2/s$, while there was only a 0.38 MPa depression in xylem pressure potential from the pre-dawn value to the lowest values of the day. In January the xylem pressure potentials were between the pre-dawn value of -2.20±0.41 MPa and the afternoon value of -2.98±0.06 MPa, and leaf conductances where below the 0.68 mm/s of midday, while the transpiration rate reached 27.2±3.0 $mg/m^2/s$. In April 1983 the pre-dawn xylem pressure potentials were -2.82±0.13 MPa, and were higher for most of the rest of the day. There was no leaf conductance for most of the day. In July 1983 there was again a large diurnal variation in xylem pressure potential, from 0.44±0.13 MPa to -2.00±0.13 MPa, and high leaf conductances (4.31±0.41 mm/s in the afternoon), with relatively low rates of transpiration (21.5±3.2 $mg/m^2/s$ in the middle of the day).

In July, October, and November 1982 the xylem pressure potentials of Rhus incisa at site 1 showed decreasing ability to recover in the late afternoon, and during the rest of the season did not recover before sundown (Figure 5.20). Throughout the year the leaf conductances declined during the day, while the transpiration rates increased until midday before declining. In July 1982 the xylem

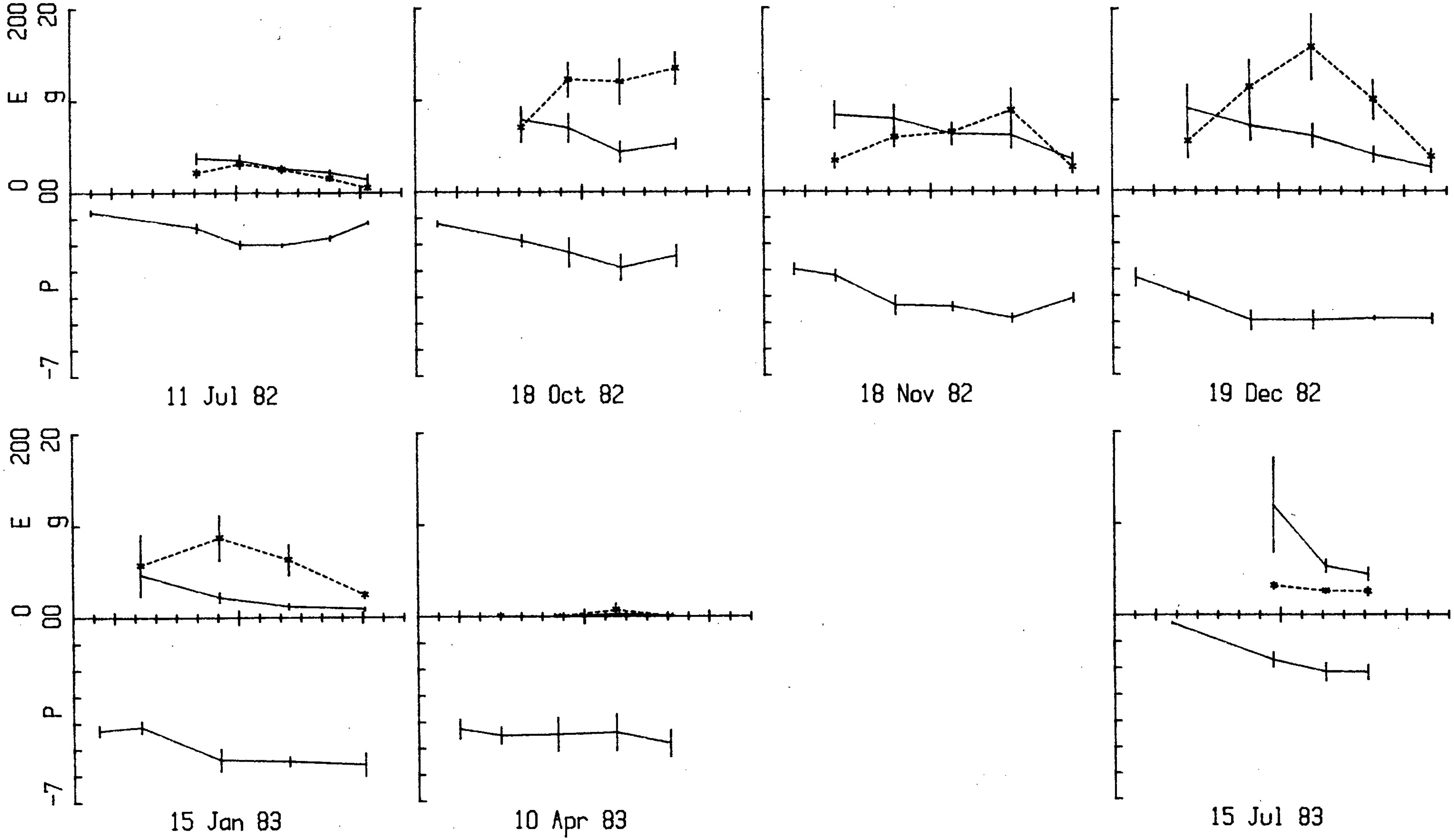


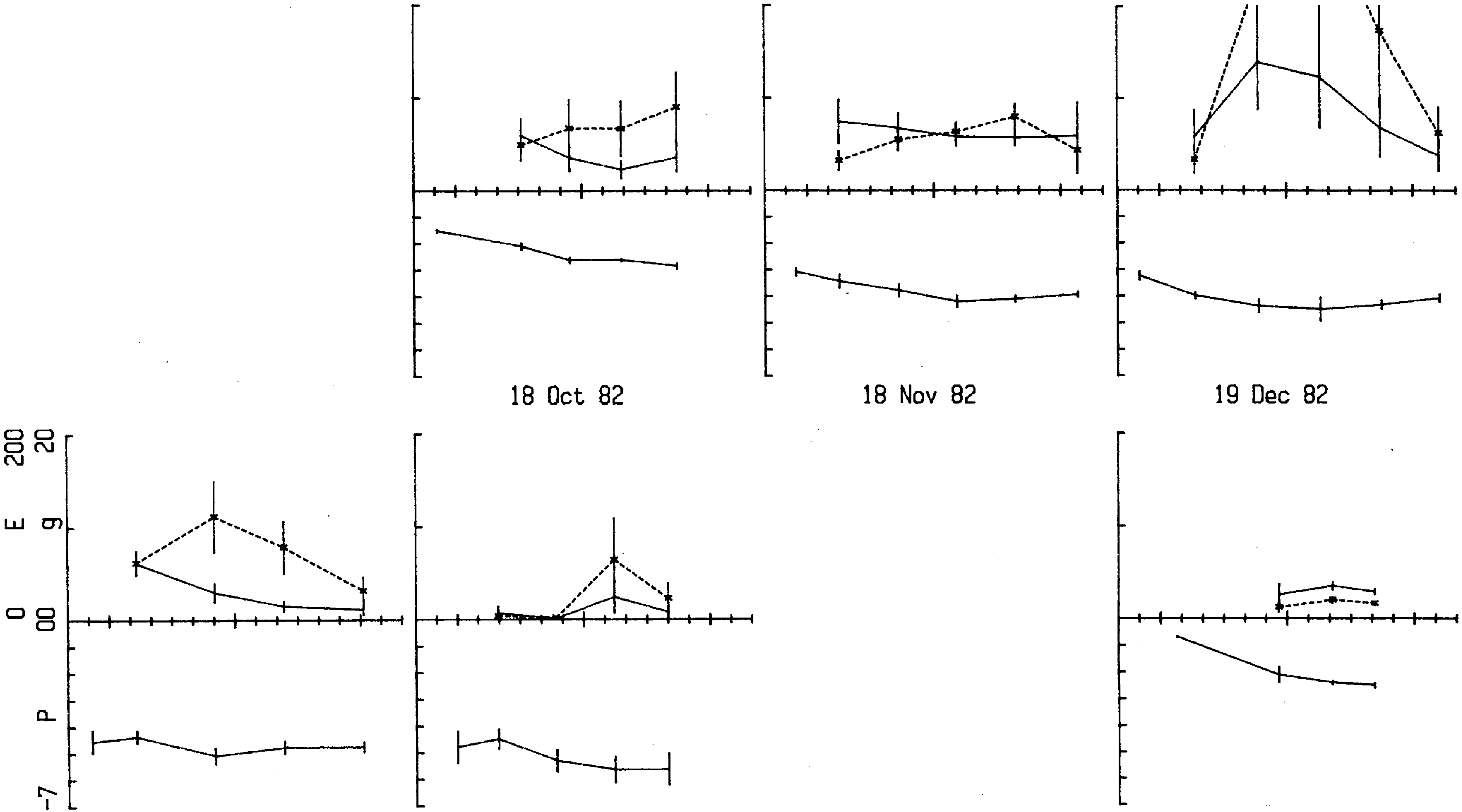
Figure 5.20 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of Rhus incisa at site 1 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

pressure potentials dropped from the pre-dawn value of -0.76±0.08 MPa to -2.01±0.05 MPa before recovering to -1.15±0.04 MPa. The leaf conductances dropped from 3.75±0.59 mm/s to 1.38±0.55 mm/s, and the transpiration rate reached 31.5±5.2 mg/m^2/s midday. During the next three months, October, November, and December the xylem pressure potentials steadily decreased to near -5 MPa, while the leaf conductances followed nearly identical diurnal paths, starting at up to 9.09±2.52 mm/s in the morning, and dropping to 2.59±0.58 mm/s late in the afternoon. The transpiration rates where up to 134.3±17.5 mg/m^2/s in October, and 157.7±3.58 mg/m^2/s in October and December, and were lower in November because of the lower vapor pressure deficits. In January the xylem pressure potentials were between -4.28±0.20 MPa and -5.58±0.44 MPa, and leaf conductances quickly dropped from the morning value of 4.68±2.07 mm/s to 2.22±0.54 mm/s midday, and were 0.91±0.17 mm/s by the end of the day. Transpiration was still high, and reached 86.7±24.3 mg/m^2/s midday. In April the xylem pressure potentials were above -5 MPa, and there was effectively no leaf conductance.

The transpiration rates of *Rhus incisa* were sensitive to both the leaf conductances and the vapor pressure gradients. Even though the leaf conductances were similar in November and December, the maximum transpiration rates doubled because of the increase in the vapor pressure deficit. In November and January the maximum transpiration rates were similar, while the leaf conductances in November were twice those in January. The rains in December may have slightly raised the pre-dawn xylem pressure potentials, but did not increase the midday xylem pressure potentials, or increase midday leaf conductances. When the xylem pressure potentials dropped below -5 MPa *Rhus incisa* no longer seemed to be able to continue transpiration.

The last 3 species measured at site 1, *Galenia africana*, *Nylandtia spinosa*, and *Eriocephalus africanus* all exhibited similar diurnal patterns of xylem pressure potentials and leaf conductances during the course of the season (Figures 5.21, 5.22, and 5.23). In July and October leaf conductances were moderate, and then in November and December, as the xylem pressure potentials dropped, the leaf conductances increased dramatically. In January the xylem pressure potentials were low, and leaf conductances were slowing in the late afternoon, and then in April the stomata were closed.

Galenia africana was not sampled at site 1 in July 1982. In July 1982 the xylem pressure potentials of *Nylandtia spinosa* and *Eriocephalus africanus* dropped from pre-dawn values of -1.00±0.07 and -0.95±0.03 MPa to -1.94±0.14 MPa and -1.91±0.07 MPa before recovering to -1.32±0.09 MPa and -1.39±0.10 MPa. The leaf conductances of *Nylandtia spinosa* dropped from a morning high of 5.29±1.35 mm/s, and those of *Eriocephalus africana* dropped from 8.16±1.89 mm/s. Midday transpiration rates of *Nylandtia spinosa* and *Eriocephalus africanus* were 34.9±10.9 $mg/m^2/s$ and 52.3±14.2 $mg/m^2/s$ and then declined with the falling leaf conductances. In October the xylem pressure potentials of all three species did not recover before



18 Oct 82

18 Nov 82

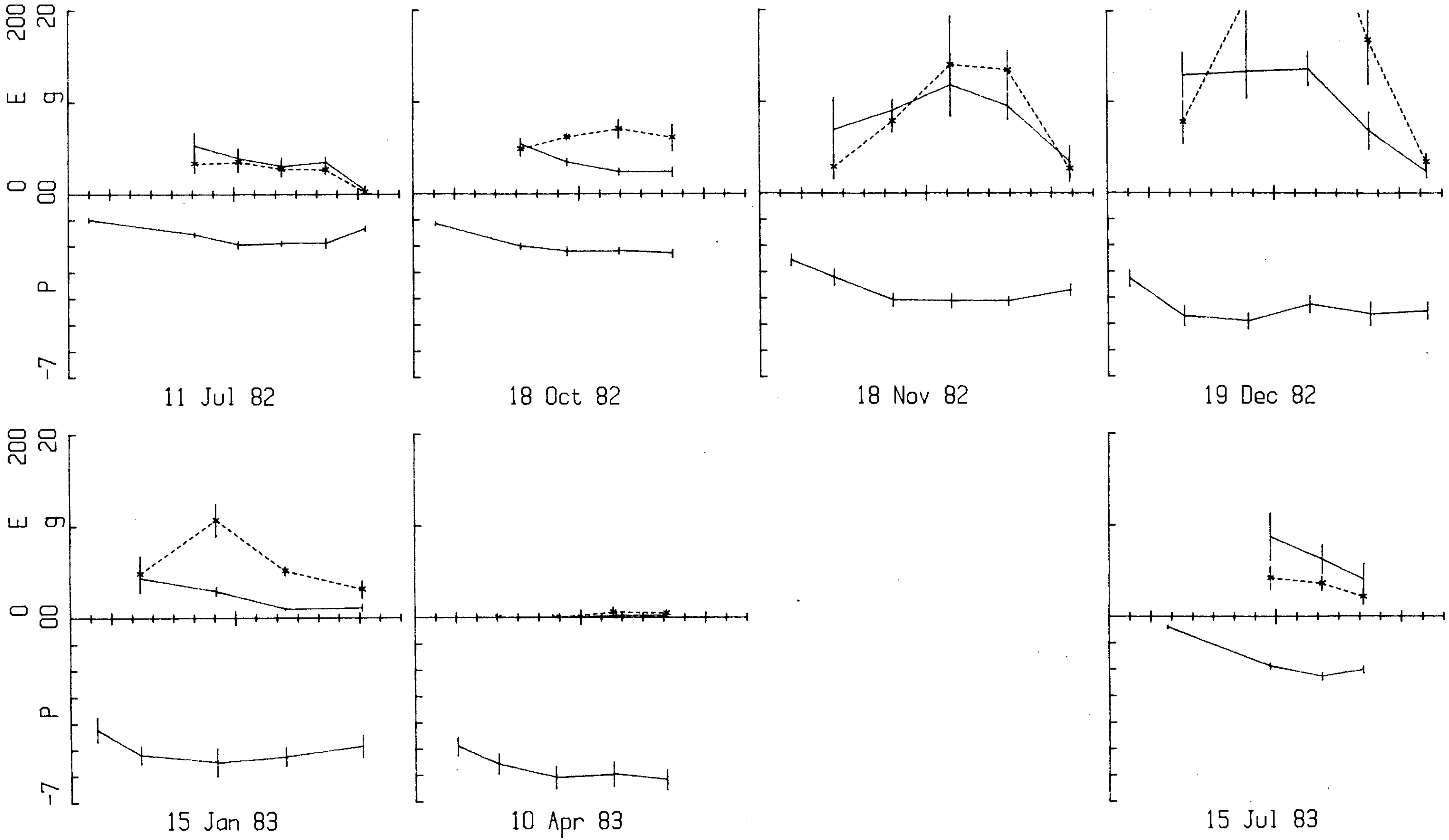
19 Dec 82

15 Jan 83

10 Apr 83

15 Jul 83

Figure 5.21 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of Galenia africana at site 1 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.



11 Jul 82

18 Oct 82

18 Nov 82

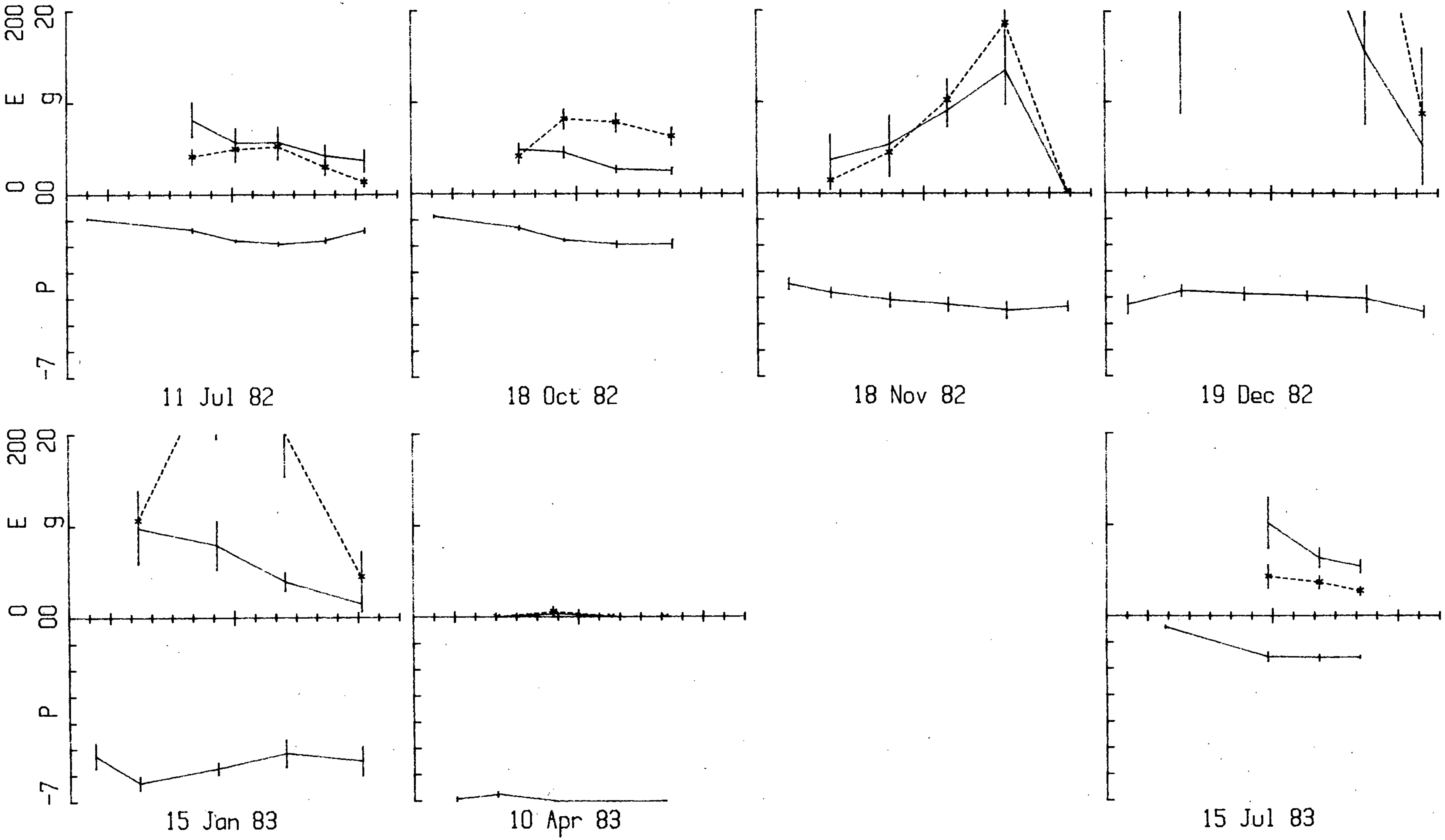
19 Dec 82

15 Jan 83

10 Apr 83

15 Jul 83

Figure 5.22 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of Nylandtia spinosa at site 1 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.



11 Jul 82
18 Oct 82
18 Nov 82
19 Dec 82
15 Jan 83
10 Apr 83
15 Jul 83

Figure 5.23 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of Eriocephalus africanus at site 1 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

sundown. The xylem pressure potentials of *Galenia africana* reached -2.85±0.09 MPa, those of *Nylandtia spinosa* reached -2.29±0.14 MPa, and those of *Eriocephalus africanus* reached -1.93±0.17 MPa. Leaf conductances dropped from morning highs of 5.92±1.81 mm/s for *Galenia africana*, 5.43±0.59 mm/s for *Nylandtia spinosa*, and 4.82±0.67 mm/s for *Eriocephalus africanus*. The highest transpiration rates of the day were 89.9±37.8 mg/m^2/s, 70.4±10.2 mg/m^2/s, and 81.5±1.10 mg/m^2/s respectively. In November and December the xylem pressure potentials of all three species were between -3 and -4.5 MPa during the day, and in November the maximum leaf conductances of *Galenia africana* reached 7.41±2.35 mm/s, those of *Nylandtia spinosa* reached 11.8±3.42 mm/s, and those of *Eriocephalus africanus* reached 13.42 mm/s. The leaf conductances of *Galenia africana* continued near the morning value during the day, while the highest conductances of *Nylandtia spinosa* were in the middle of the day, and those of *Eriocephalus africanus* were in the afternoon. Even though the leaf conductances were high, the transpiration rates of *Galenia africana*, *Nylandtia spinosa*, and *Eriocephalus africanus* only reached 79.4±14.0 mg/m^2/s, 140.0±53.5 mg/m^2/s, and 185.8±52.5 mg/m^2/s respectively. In December the leaf conductances of the three species peaked at 13.90±5.10 mm/s, 13.59±1.87 mm/s, and 43.12± 15.65 mm/s, and transpiration rates reached 306.3±154.6 mg/m^2/s, 353.8±50.7 mg/m^2/s, and 784.5±252.9 mg/m^2/s. In January the leaf conductances of *Galenia africana*, and *Nylandtia spinosa* dropped quickly following the high point early in the morning, while those of *Eriocephalus africanus* remained high, although decreasing, throughout the day. The xylem pressure potentials of Galenia africana and Nylandtia spinosa stayed above -5 and -5.5 MPa respectively, while those of Eriocephalus africanus dropped to -6.30±0.26 MPa. In April Galenia africana had leaf conductances of 2.44±1.74 mm/s in the afternoon, which caused a 0.3 MPa drop in the xylem pressure potentials in the afternoon. The stomata of Nylandtia spinosa and Eriocephalus africanus were closed for most of the day. Of the three species Nylandtia spinosa had largest average midday depression in xylem pressure potential for the year, 1.39 MPa, and Eriocephalus africanus the lowest, 0.81 MPa. The average midday depression in xylem pressure potential of Galenia africana for the year was 1.16 MPa. The average leaf conductances of Galenia africana and Nylandtia spinosa for the year were 4.56 mm/s and 4.94 mm/s, while that of Eriocephalus africanus was 8.5 mm/s.

Although the rain in December did not seem to affect the xylem pressure potentials of Galenia africana, the diurnal pattern of leaf conductance, which increased toward the middle of the day before declining, may have been the result of a good water supply in the soil. The pre-dawn xylem pressure potentials of Nylandtia spinosa were elevated, and there were high leaf conductances until the early afternoon when there was a sharp decline, possibly reflecting the exhaustion of the water supply. The xylem pressure potentials of Eriocephalus africanus, showed little response to the rain, except that they remained stable during the day while the conductance rates were very high.

5.3.3 Species at site 3

At site 3 the three transitional species sampled, *Nylandtia spinosa*, *Eriocephalus africanus*, *Rhus dissecta*, and the fynbos understory species *Elytropappus gnaphaloides*, with the exception of *Nylandtia spinosa*, all had diurnal patterns of water relations similar to those found at site 1 throughout the season. Unlike the *Nylandtia spinosa* at site 1, which had high leaf conductances at high xylem pressure potentials and then reduced leaf conductances as the xylem pressure potentials dropped, the *Nylandtia spinosa* at site 3 maintained uniformly low leaf conductances throughout the year. At site 3 the xylem pressure potentials of *Nylandtia spinosa* declined through the season, but did not exhibit large diurnal variations. The leaf conductances of *Eriocephalus africanus* increased in November and December, and the dropped in January and April as was the pattern at site 1. The *Rhus dissecta* at site 3, like *Rhus incisa* at site 1, maintained leaf conductances and had large diurnal fluctuations in xylem pressure potential until the leaves were shed. *Elytropappus gnaphaloides* followed the pattern of *Eriocephalus africanus* and had high leaf conductances and both large diurnal and large seasonal fluctuations in xylem pressure potential. Both of the *Protea* species sampled at site 3, *Protea laurifolia* and *Protea glabra*, had similar leaf conductances, but *Protea glabra* maintained slightly higher xylem pressure potentials, especially in the middle of the summer.

The diurnal courses of leaf conductance of *Nylandtia spinosa* at site 3 during the summer showed increasing stomatal reaction to water stress (Figure 5.24). In July, October, and November _Nylandtia spinosa_ maintained relatively uniform leaf conductances during the day. In July the leaf conductances were up to 4.09±0.23 mm/s, in October they were up to 3.83±0.74 mm/s, and in November up to 5.25±0.67 mm/s. During this time the diurnal variations in the xylem pressure potential were increasing. In July the midday depression in xylem pressure potential was 1 MPa, in October is was 1.46 MPa, and in October it was 1.87 MPa. In December, when the pre-dawn xylem pressure potentials were -4.34±0.34 MPa, _Nylandtia spinosa_ began to limit leaf conductance in order to stabilize the water potentials. Leaf conductances in December were 1.95 mm/s lower in the middle of the day than the morning and afternoon values of 4.13±0.79 mm/s and 4.15±0.46 mm/s. In January, when the pre-dawn xylem pressure potentials were -5.58±0.75 MPa, the leaf conductances were 1.67±0.65 mm/s in the morning, but then dropped to 0.34±0.08 mm/s in the afternoon. In April the pre-dawn xylem pressure potentials were -6.22 MPa, and after a conductance of 1.92± 0.92 mm/s in the morning, the stomata were closed for the rest of the day. The reaction of the stomata kept transpiration rates below 100 $mg/m^2/s$ throughout the year. Following the rain in May leaf conductances were high again, as were the diurnal fluctuations in xylem pressure potential.

The diurnal patterns of xylem pressure potential and leaf conductance of _Eriocephalus africanus_ at site 3 in July and October were similar to those during the same months at site 1 (Figure 5.25). In November the xylem pressure

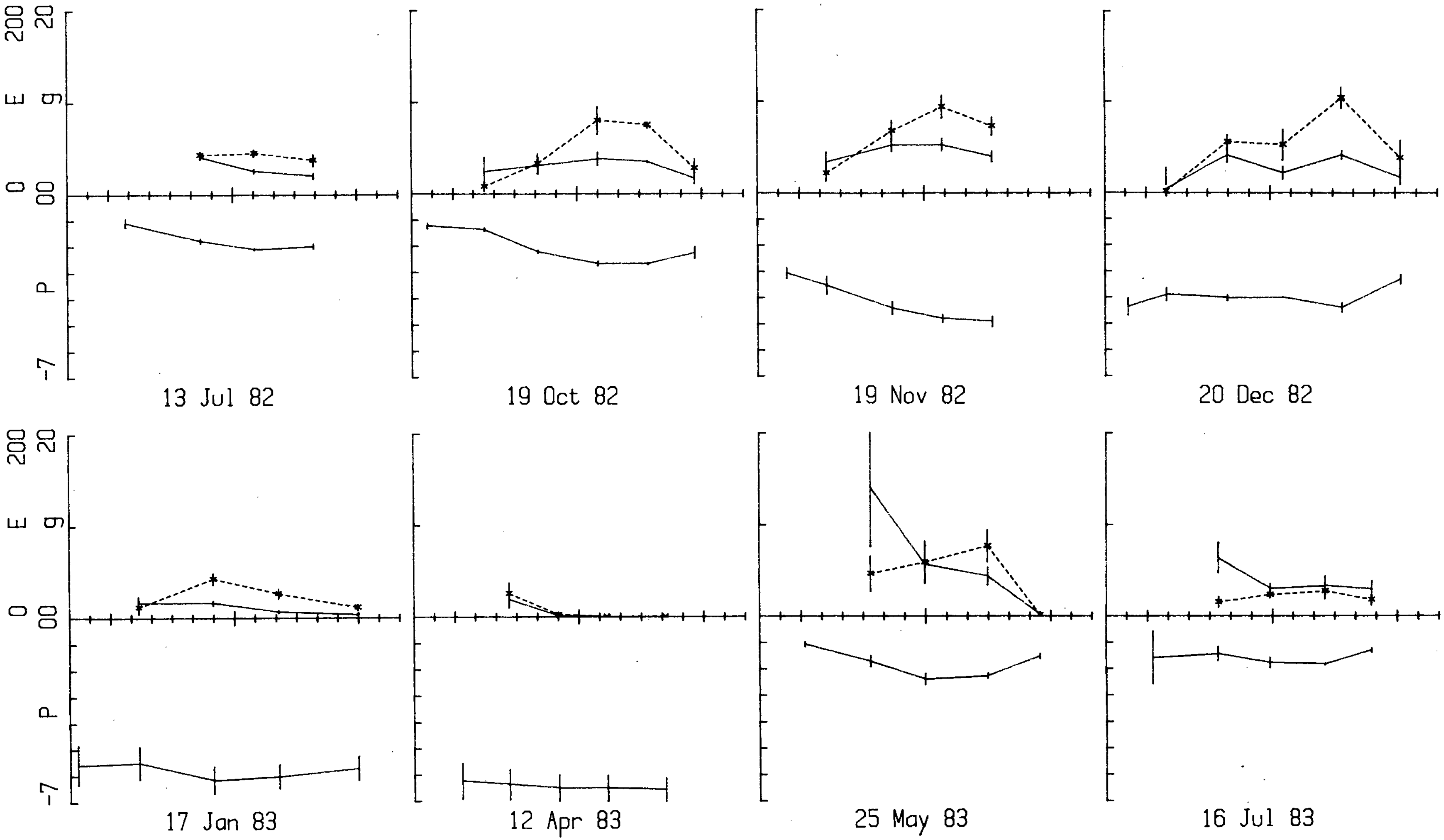


Figure 5.24 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of <u>Nylandtia spinosa</u> at site 3 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

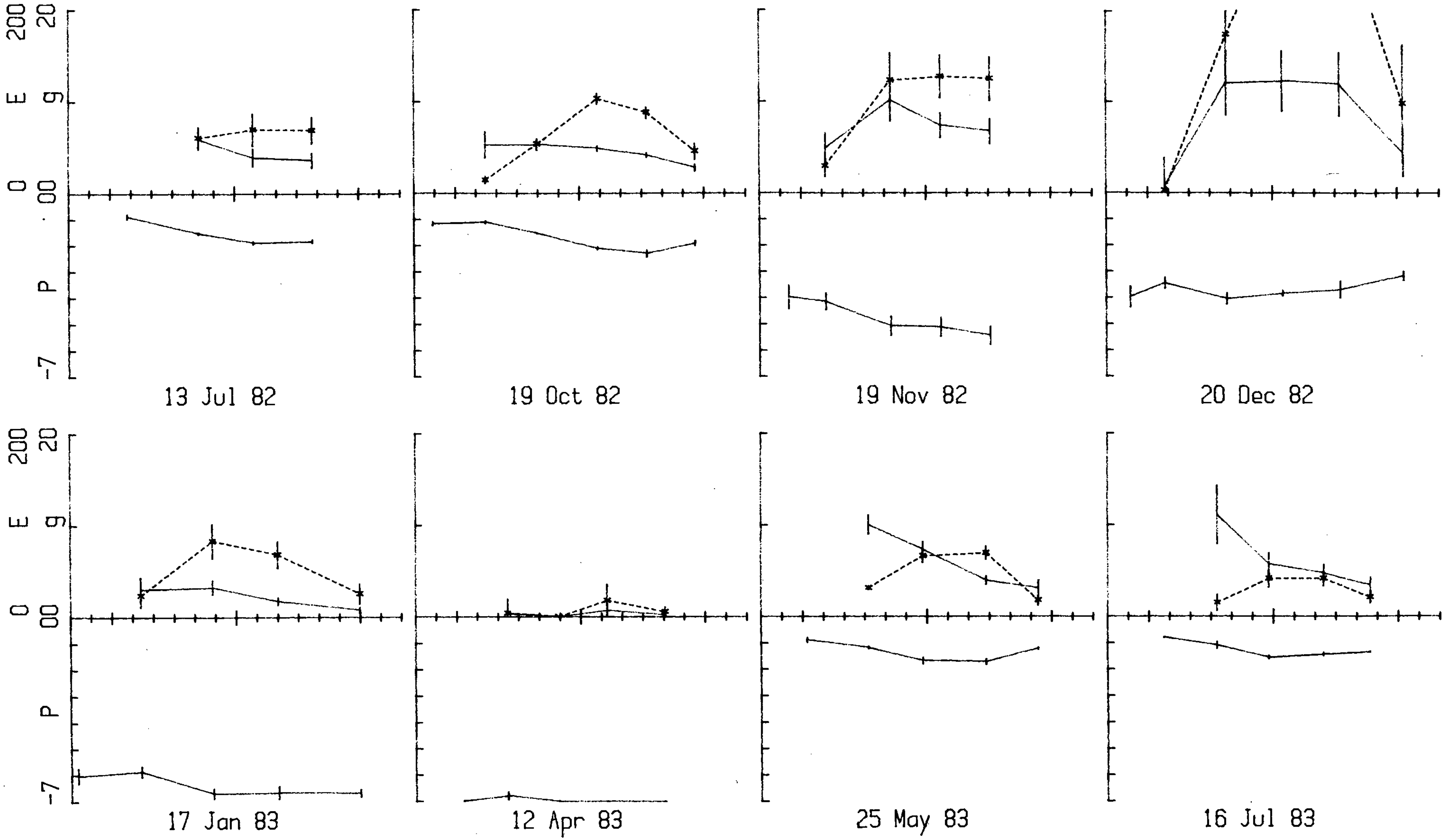


Figure 5.25 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of <u>Eriocephalus africanus</u> at site 3 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

potentials were lower at site 3, reaching -5.44±0.34 MPa, than they were at site 1. Unlike the pattern in November at site 1, the leaf conductances at site 3 reached a morning peak of 10.13±2.32 mm/s, and then declined. The transpiration rates stayed around 125 $mg/m^2/s$ for the rest of the day. In December the leaf conductances reached 12.29±3.29 mm/s, which is less than half the rate measured at site 1 for the month. The transpiration rate reached 307.6±87.7 $mg/m^2/s$ at site 3, which is also about half that at site 1. The xylem pressure potentials in January were lower at site 3 that at site 1, reaching -6.68±0.14 MPa, and the leaf conductances were about a third of those at site 1, being only 3.30±0.77 mm/s at their highest. As was found at site 1, in April the xylem pressure potentials were close to -7.0 MPa all day, and there was almost no leaf conductance. After the rain in May the xylem pressure potentials and leaf conductances were similar to what they had been the winter before.

Rhus dissecta maintained leaf conductances at the expense of stable xylem pressure potentials, and then shed its leaves to prevent further water loss (Figure 5.26). The pre-dawn xylem pressure potentials dropped from -0.56±0.04 MPa in July 1982, to -1.07±0.11 MPa in October, and then to -2.80±0.42 MPa in November. In December the pre-dawn xylem pressure potentials were -3.64±0.72 MPa. The midday depressions in xylem pressure potential reflect the seasonal course of the maximum daily leaf conductances. In July the midday depression in xylem pressure potential was 1.73 MPa and the maximum leaf conductances were

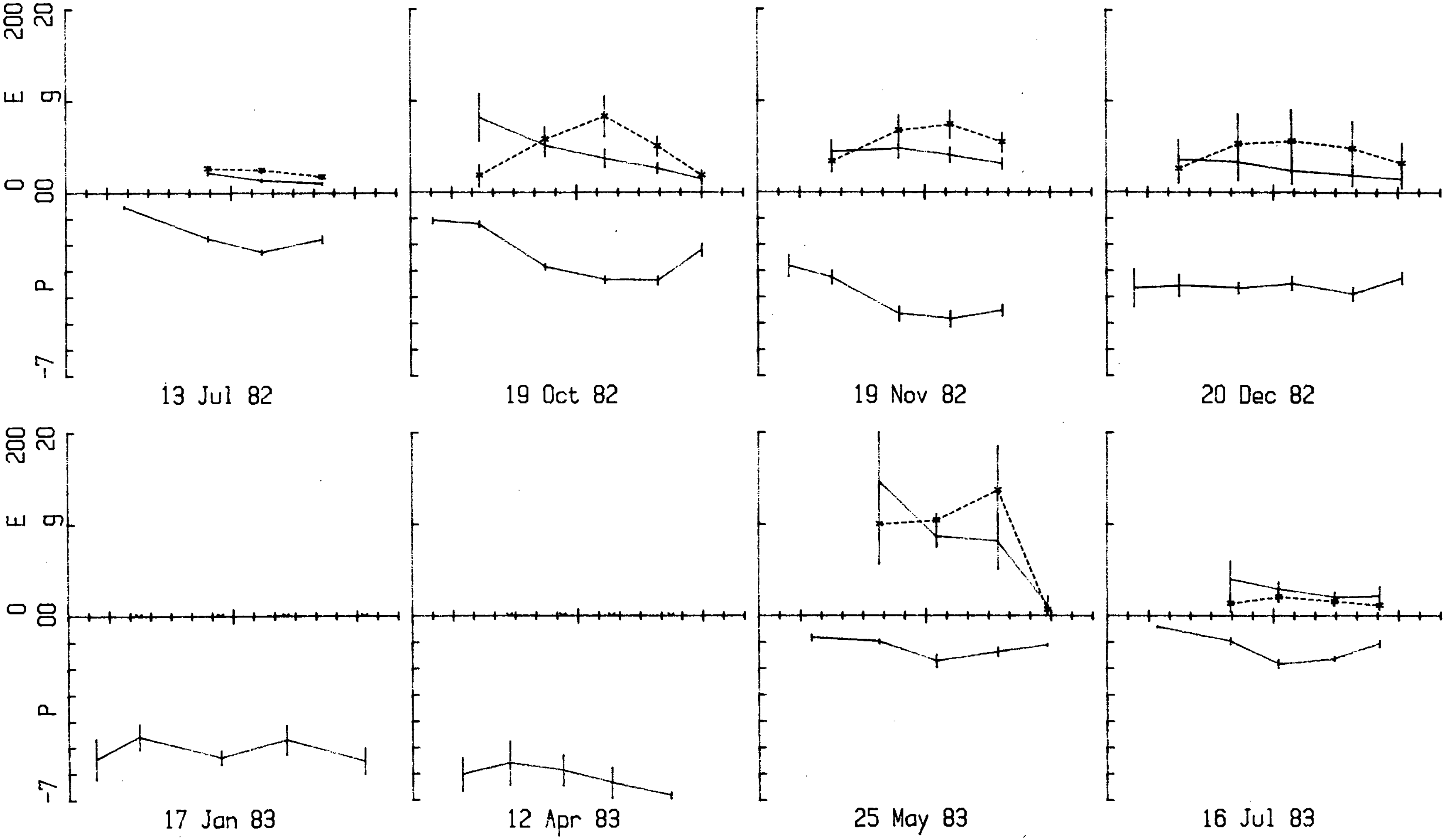
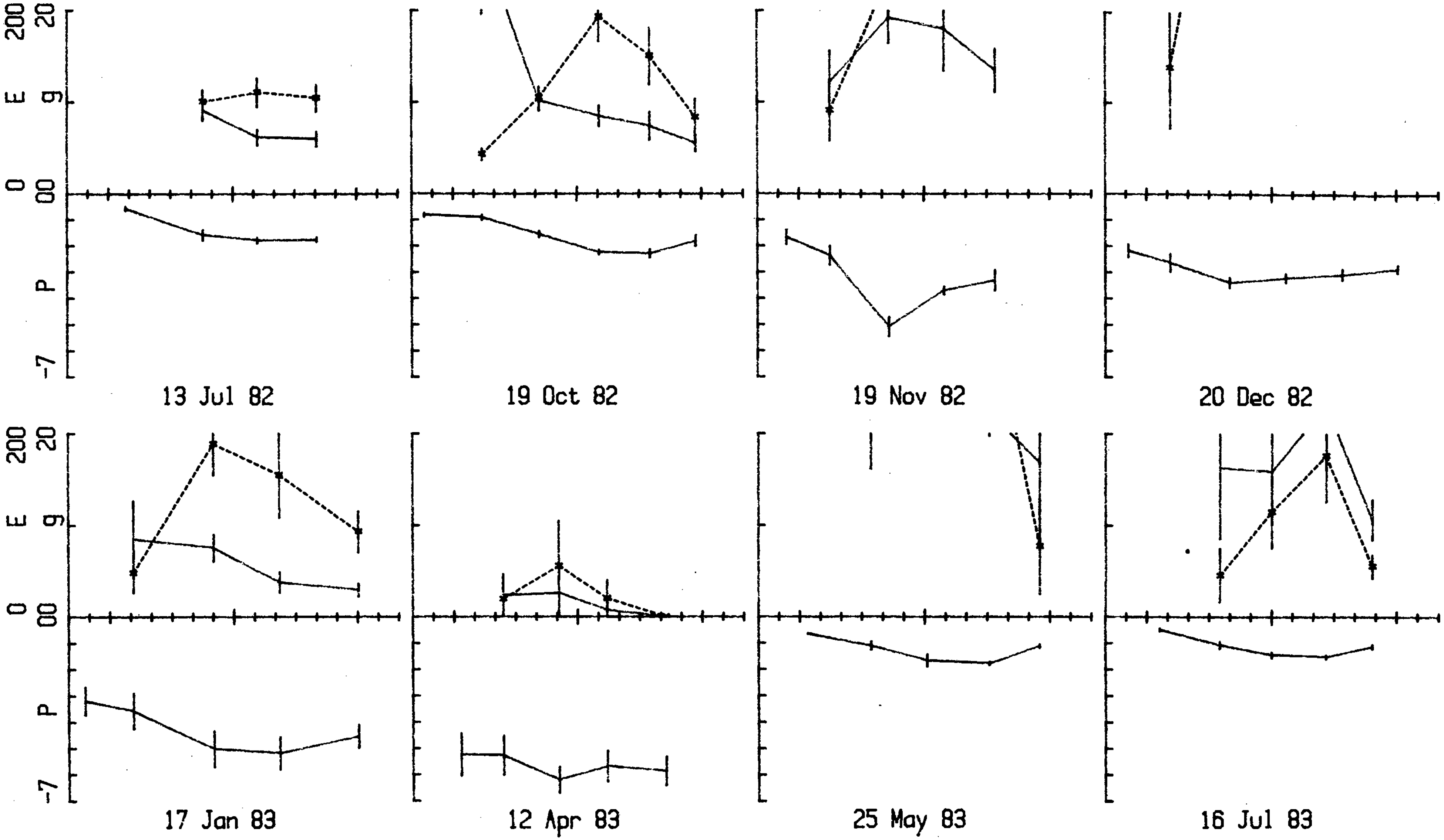


Figure 5.26 The diurnal pattern of the leaf conductance (g: mm/s), transpiration (E: mg/m2/s), and xylem pressure potential (P: MPa) of Rhus dissecta at site 3 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

2.14±0.22 mm/s. In October the midday depression increased to 2.3 MPa and the maximum leaf conductances were 8.17±2.56 mm/s. By November the midday depression in xylem pressure potential had begun to decrease, as the midday xylem pressure potentials approached -5 MPa, and was 2.04 MPa with a maximum leaf conductance for the day of 4.80±1.08 mm/s. In December the xylem pressure potentials no longer fluctuated, and the leaf conductances declined from the morning high of 3.56±2.18. Between October and December the average transpiration rates were consistently between 50 and 70 $mg/m^2/s$, although the individual values in December were higher, as the average included 3 individuals which had already shed their leaves and had no leaf conductance. In January and April the xylem pressure potentials varied during the day, even though there were no leaves and no transpiration. In May the soil must have been quite wet, and the leaf conductances of the new leaves were up to 14.62±6.37 mm/s, and the transpiration rates up to 136.8±48.1 $mg/m^2/s$, while the xylem pressure potentials only dropped to -1.73±0.24 MPa at their lowest.

The leaf area of _Elytropappus gnaphaloides_ was difficult to measure, and may have been systematically undervalued, which would explain the consistently high leaf conductances compared to other species (Figure 5.27). The diurnal patterns of xylem pressure potential and leaf conductance followed the pattern of _Eriocephalus africanus_, except that the xylem pressure potentials showed larger diurnal variations and the leaf conductances were much higher. Leaf conductances increased from July 1982 until



13 Jul 82

19 Oct 82

19 Nov 82

20 Dec 82

17 Jan 83

12 Apr 83

25 May 83

16 Jul 83

Figure 5.27 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of _Elytropappus gnaphaloides_ at site 3 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

December, when they were 41.33±11.12 mm/s in the middle of the day, and then dropped in January and were very low in April. In May the leaf conductances were again high. In July 1982 the pre-dawn xylem pressure potentials were -0.50±0.07 MPa, and in April they were -5.22±0.80 MPa.

Protea laurifolia and *Protea glabra* both had low leaf conductances and high xylem pressure potentials throughout the year, and showed little response to the rain in May (Figures 5.28, and 5.29). Their conservative behavior enabled them to maintain xylem pressure potentials above -2.5 MPa during the entire year, but did not allow them to increase leaf conductances when the conditions were more favorable. The highest leaf conductances of *Protea laurifolia* occurred in May 1983 and were 3.21±0.75 mm/s, while those of *Protea glabra* occurred in November 1982, before the height of the drought, and were 4.06±0.19 mm/s. The highest leaf conductances of *Protea glabra* usually occurred early in the morning, while those of *Protea laurifolia* occurred in the middle of the day. The lowest xylem pressure potentials of the year were -2.18±0.08 MPa for *Protea laurifolia*, and -2.10±0.21 MPa for *Protea glabra*. In November and January the differences between the xylem pressure potentials of the two species were greatest, and were about 0.25 MPa. The pattern of water relations of *Protea glabra* seemed to have a slight advantage over that of *Protea laurifolia*. *Protea glabra* maintained higher xylem pressure potentials than *Protea laurifolia* throughout the season. The highest leaf conductances of *Protea glabra* occurred in the mornings, when the vapor pressure deficits

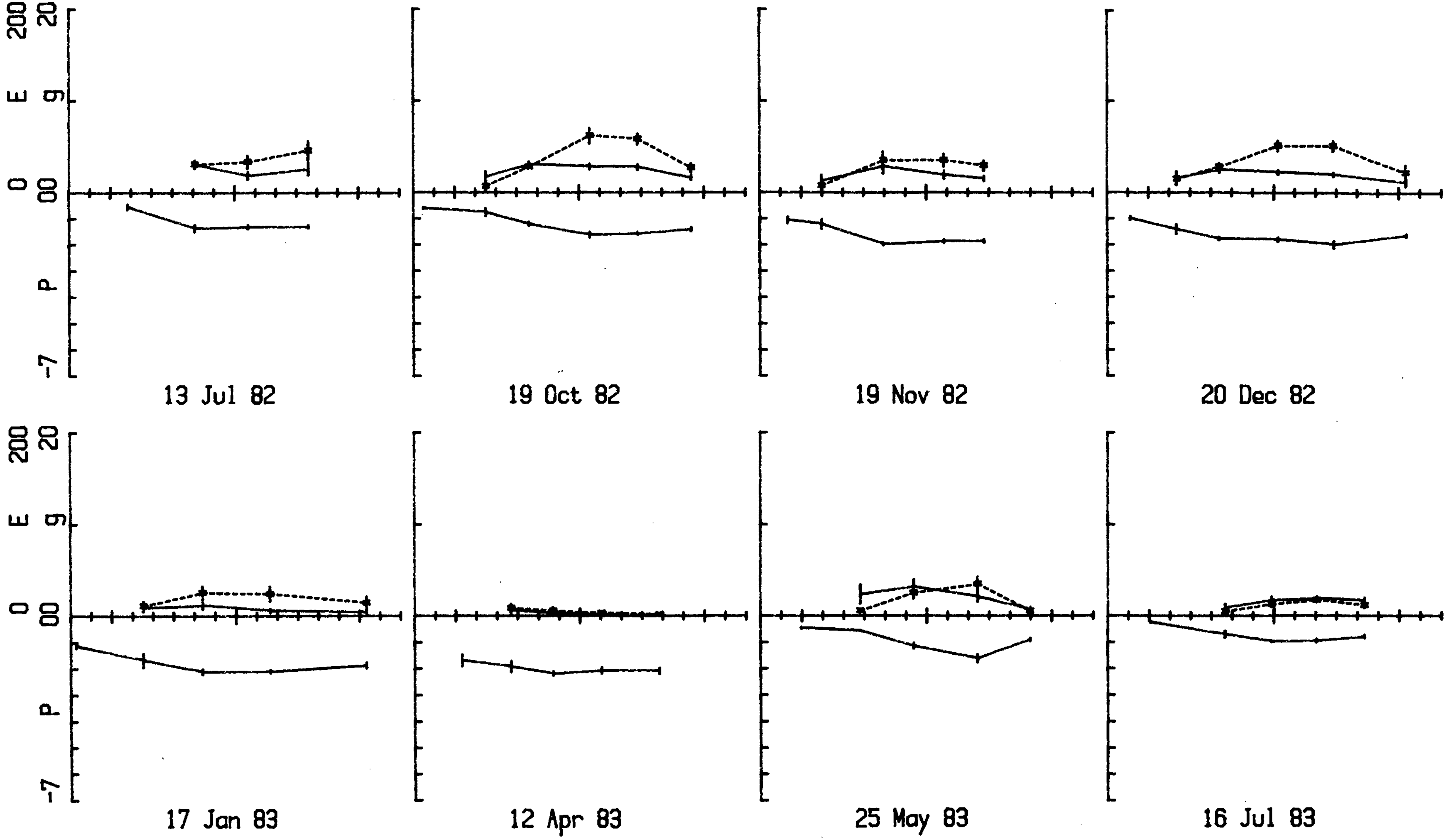
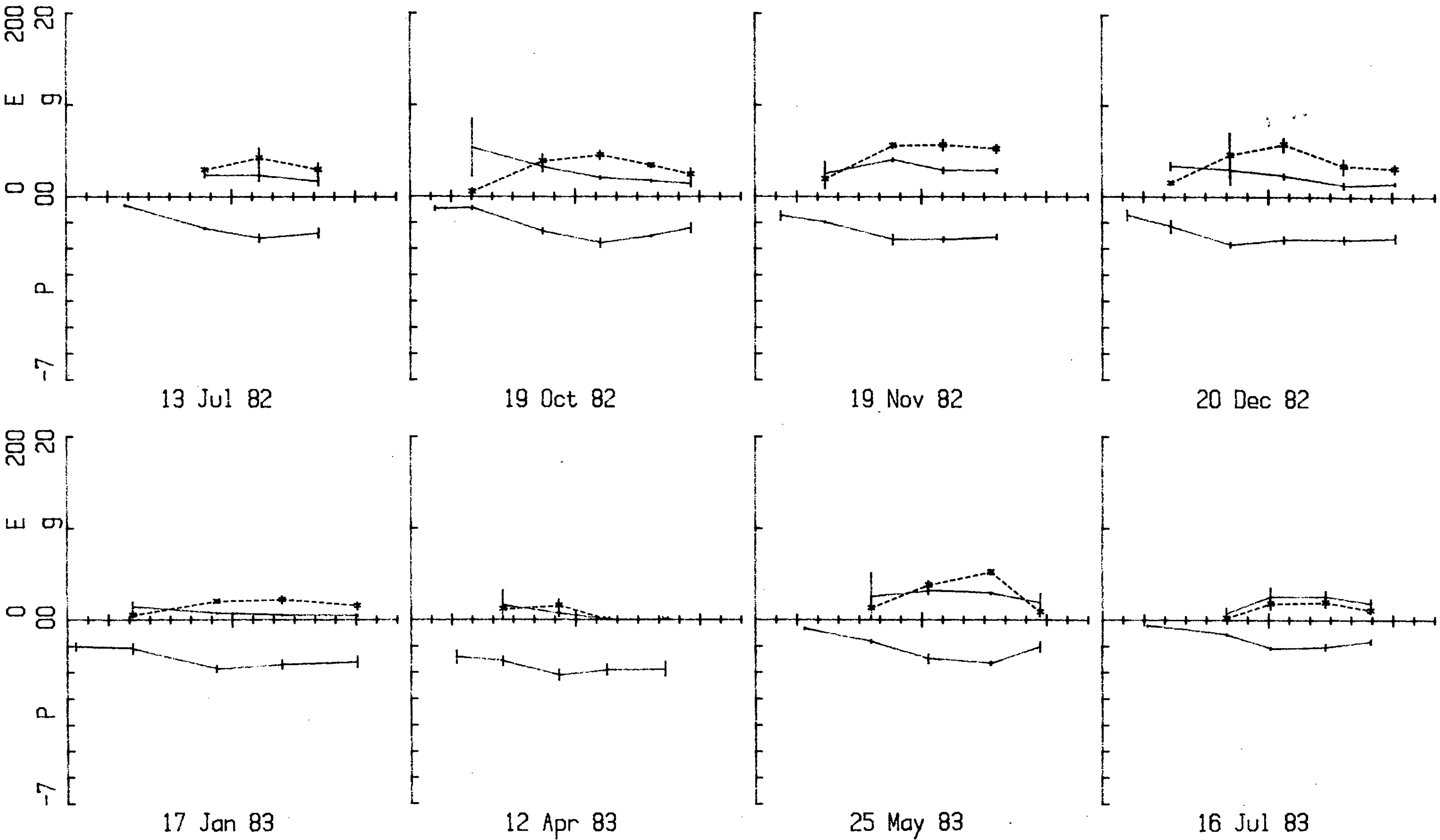


Figure 5.28 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of <u>Protea laurifolia</u> at site 3 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.



13 Jul 82

19 Oct 82

19 Nov 82

20 Dec 82

17 Jan 83

12 Apr 83

25 May 83

16 Jul 83

Figure 5.29 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of _Protea glabra_ at site 3 (mean and SE, n= 3). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

were low, rather than later in the day as was found in *Protea laurifolia*. However, the differences between the two species were small and not always clearly consistent.

5.3.4 Species at site 5

At site 5 the minimum xylem pressure potentials in the middle of the summer were not as low as those at sites 1 and 3, but all of the species had reduced leaf conductances during January and April. Unlike at the drier sites, as the leaf conductances at site 5 dropped in the afternoons, the xylem pressure potentials of most of the species managed some recovery before sundown all through the year.

Between July 1982 and December the single *Eriocephalus africanus* sampled maintained leaf conductances of around 10 mm/s throughout the day. In January and April the leaf conductances dropped after the morning highs of about 3.5 mm/s (Figure 5.30). In January leaf conductance continued into the afternoon, while in April there was little conductance during the rest of the day. The pre-dawn xylem pressure potential dropped from -0.95 MPa in winter to -4.60 MPa in April.

The *Rhus dissecta* at site 5 dropped their leaves several months after those at site 3. At site 3 some of the individuals had lost their leaves in December, and all were leafless from January to April. At site 5 the leaf conductances of *Rhus dissecta* were zero, because the plants were leafless, only in April (Figure 5.31). With the exception of April, the maximum leaf conductances were about 5 mm/s throughout the year. The highest transpiration

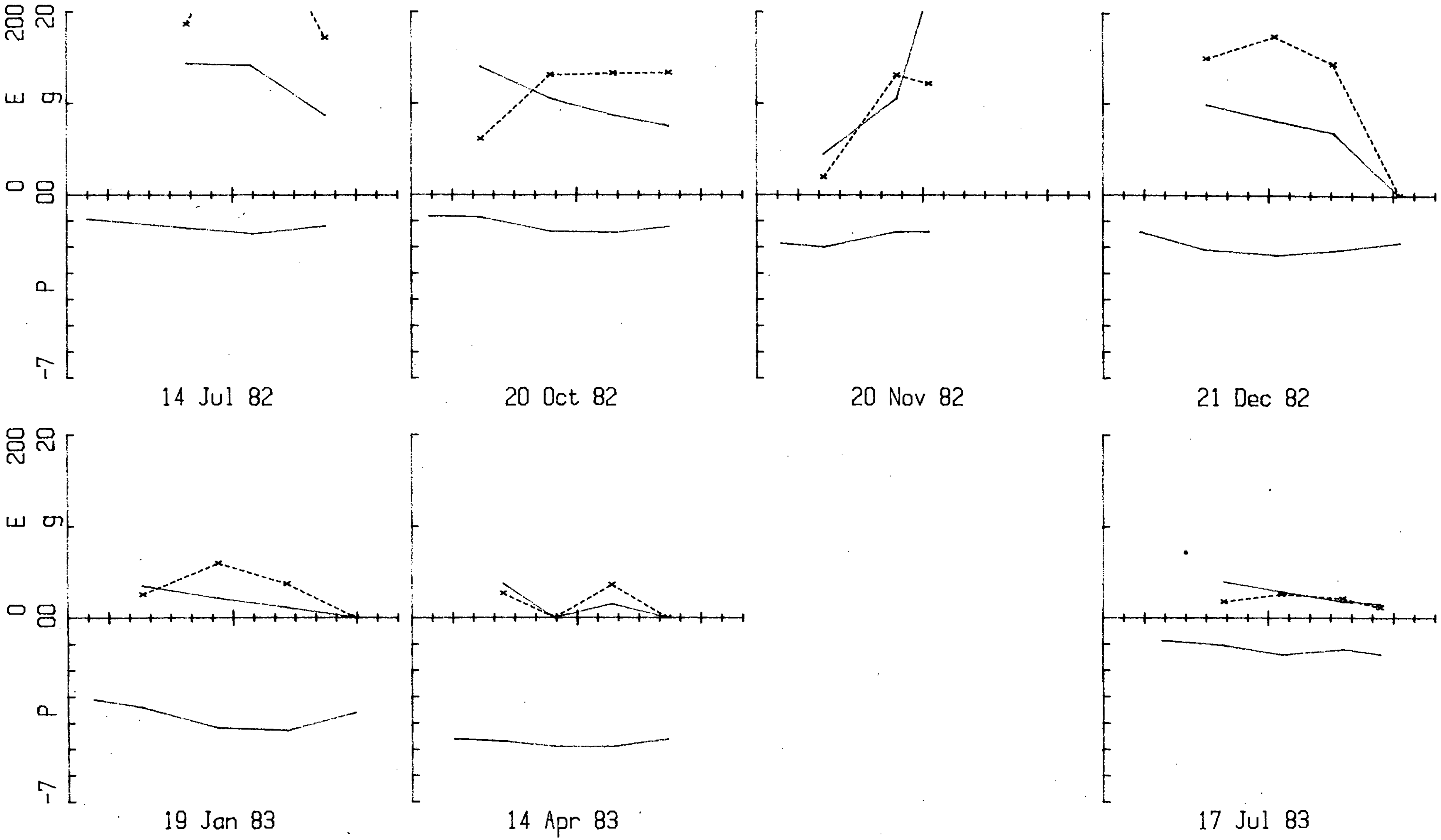


Figure 5.30 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of *Eriocephalus africanus* at site 5 (mean and SE, n= 1). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

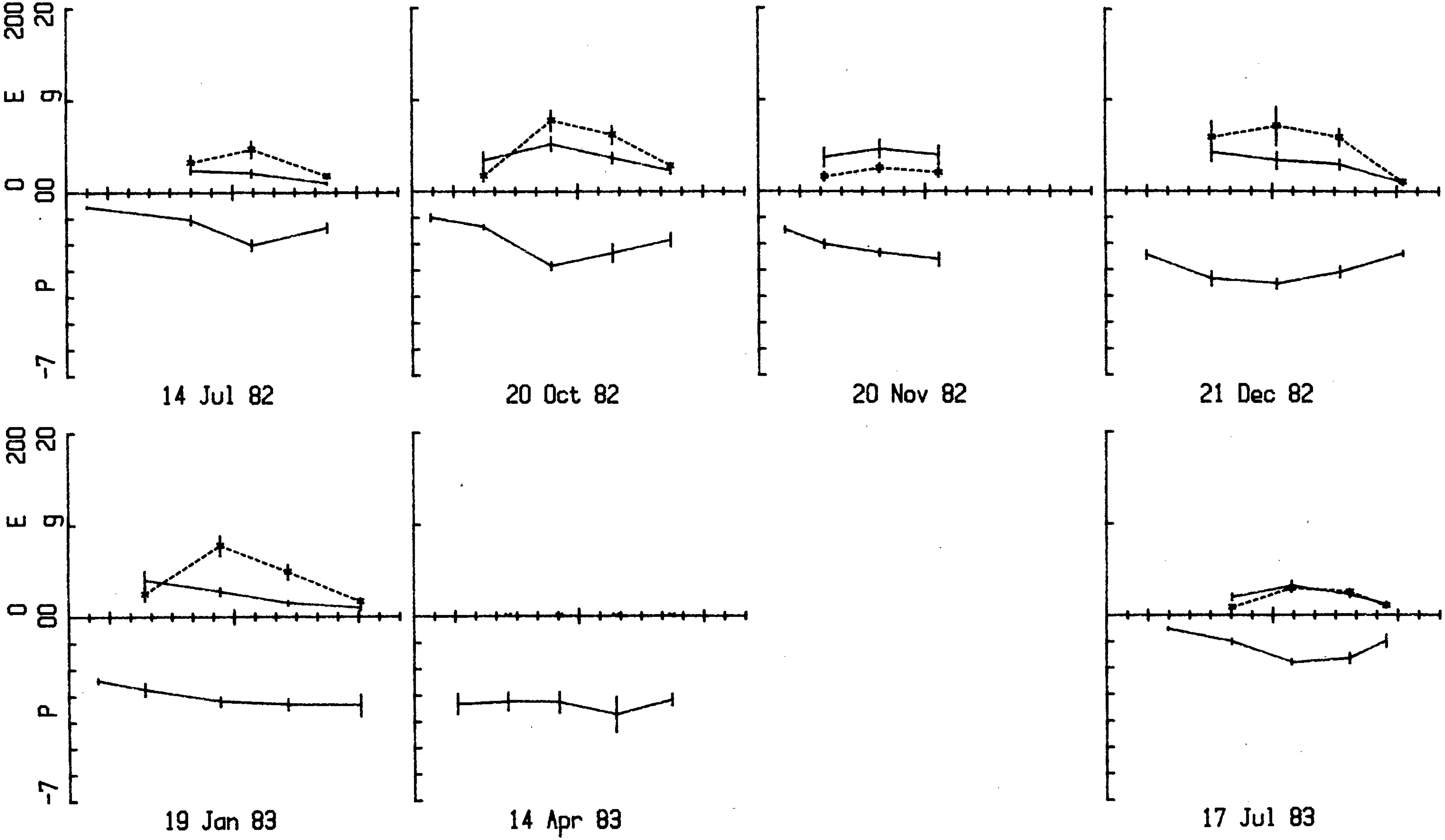


Figure 5.31 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of <u>Rhus dissecta</u> at site 5 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

rates, 77.9±10.6 $mg/m^2/s$, occurred in January, and were followed by the most noticeable reduction in leaf conductances in the afternoon. The pre-dawn xylem pressure potentials remained above 2.42±0.17 MPa until January. Unlike at site 3 where the leafless period corresponded to xylem pressure potentials of -5 to -6 MPa, at site 5 the xylem pressure potentials in April were between the pre-dawn value of -3.30±0.38 MPa and -3.72±0.67 MPa.

The leaf area measurements of <u>Stoebe capitata</u> were made by the same method as those of <u>Elytropappus gnaphaloides</u> and are also probably systematically low. As a result the leaf conductances of <u>Stoebe capitata</u> are high compared to the other species at site 3, but are similar to those of <u>Elytropappus gnaphaloides</u> (Figure 5.32). Between July and November the pre-dawn xylem pressure potentials fell from -0.79±0.04 MPa to -0.94±0.09 MPa and the leaf conductances were between 10 and 15 mm/s. The midday depressions in xylem pressure potential remained above 1 MPa. In December the pre-dawn xylem pressure potentials were -1.32±0.12 MPa, and the midday values down to -2.58±0.07 MPa. The conductances reached 22.70±5.68 mm/s. In January the pre-dawn values were even lower, -1.85±0.08 MPa, as where the minimum midday values, -3.76±0.11 MPa, and the leaf conductances were restricted following the morning high of 5.07±1.24 mm/s. In April, when pre-dawn xylem pressure potentials were -2.39±0.18 MPa, there was almost no leaf conductance.

Although <u>Agathosma giftbergensis</u> maintained leaf conductances, even in April, it seems to have had increasing

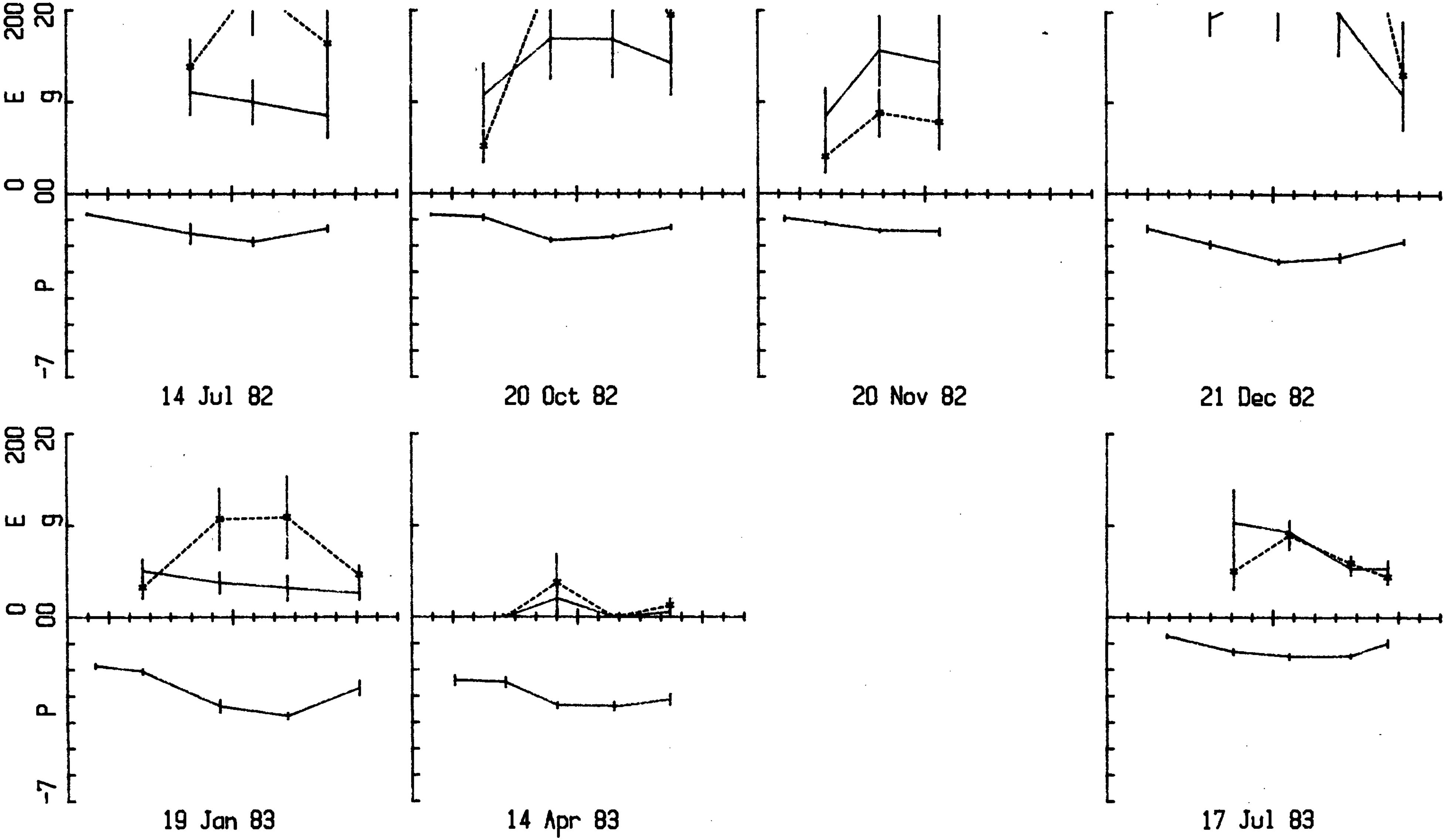
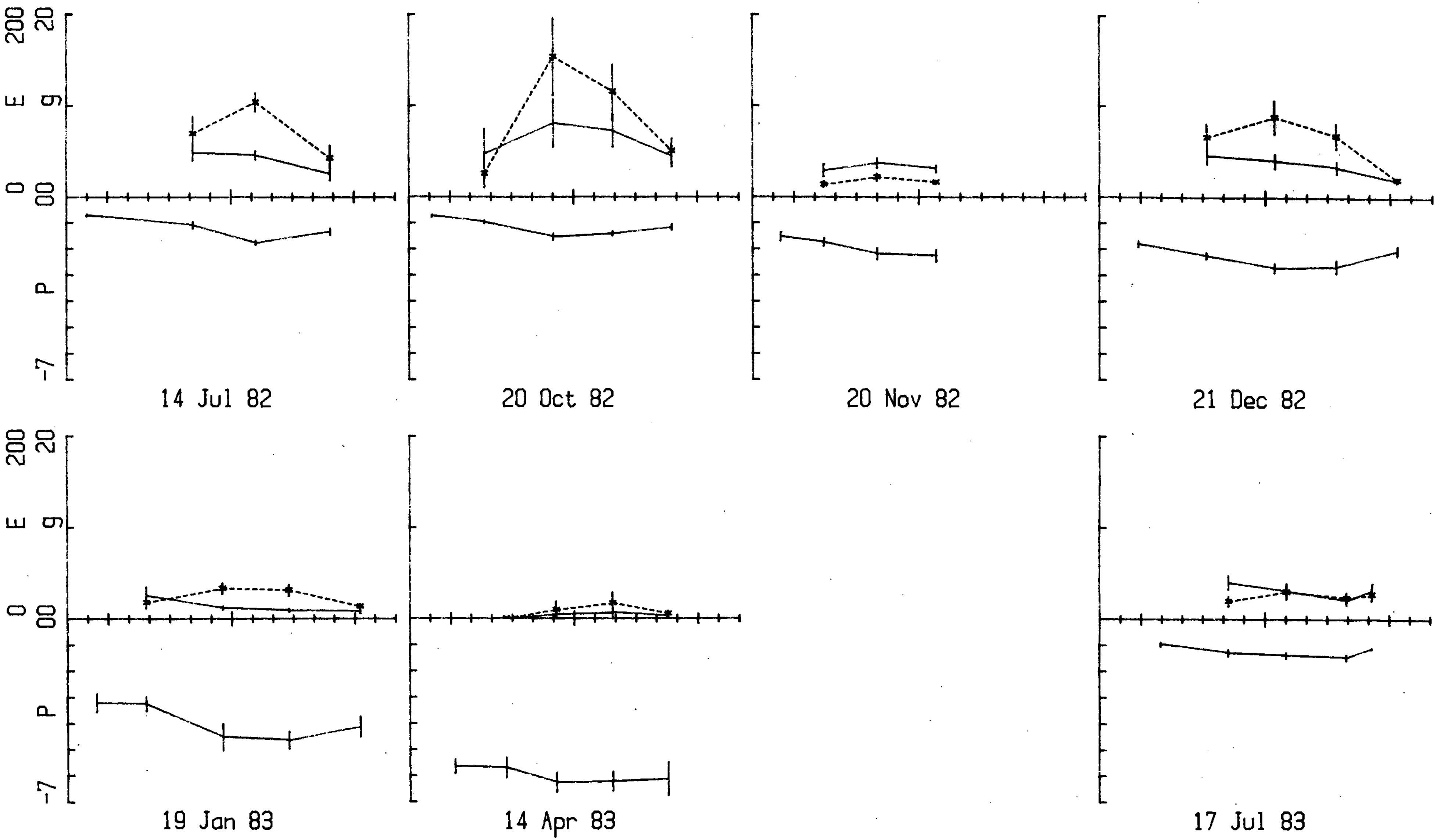


Figure 5.32 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of Stoebe capitata at site 5 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.



14 Jul 82

20 Oct 82

20 Nov 82

21 Dec 82

19 Jan 83

14 Apr 83

17 Jul 83

Figure 5.33 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of _Agathosma giftbergensis_ at site 5 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

difficulty in extracting water from the soil (Figure 5.33). In July and October the pre-dawn xylem pressure potentials were -0.72±0.05 MPa. The pre-dawn xylem pressure potentials then began to drop and were -1.51±0.17 MPa in November, -1.78±0.12 MPa in December, -3.20±0.34 MPa in January, and -5.62±0.27 MPa in April. The midday depressions in xylem pressure potential also increased, from 0.75 MPa in November, to 0.92 MPa in December, and then to 1.44 MPa in January, before becoming only 0.62 MPa in April when the leaf conductances were restricted. Leaf conductances were maintained at about 4.5 to 5 mm/s throughout the day, until January when they fell in the afternoon following the morning high of 2.55±0.91 mm/s.

The three overstory species sampled at site 5, Protea laurifolia, Paranomus bracteolaris, and Leucadendron pubescens all had similar xylem pressure potentials and leaf conductances, and followed the seasonal and diurnal patterns of the Protea laurifolia and Protea glabra at site 3 (Figures 5.34, 5.35, and 5.36). The xylem pressure potentials often immediately dropped from their pre-dawn values of between -0.5 and -1.0 MPa to the midday values of -1.5 to -2.0 MPa, and then quickly recovered at sundown. This pattern of xylem pressure potentials may reflect the presence of internal resistances to water movement, as the roots are probably still experiencing an adequate water supply. The stomata of these species are sensitive to xylem pressure potentials, and in January the leaf conductances dropped after the high values in the morning while in April there was very little leaf conductance in any of the three

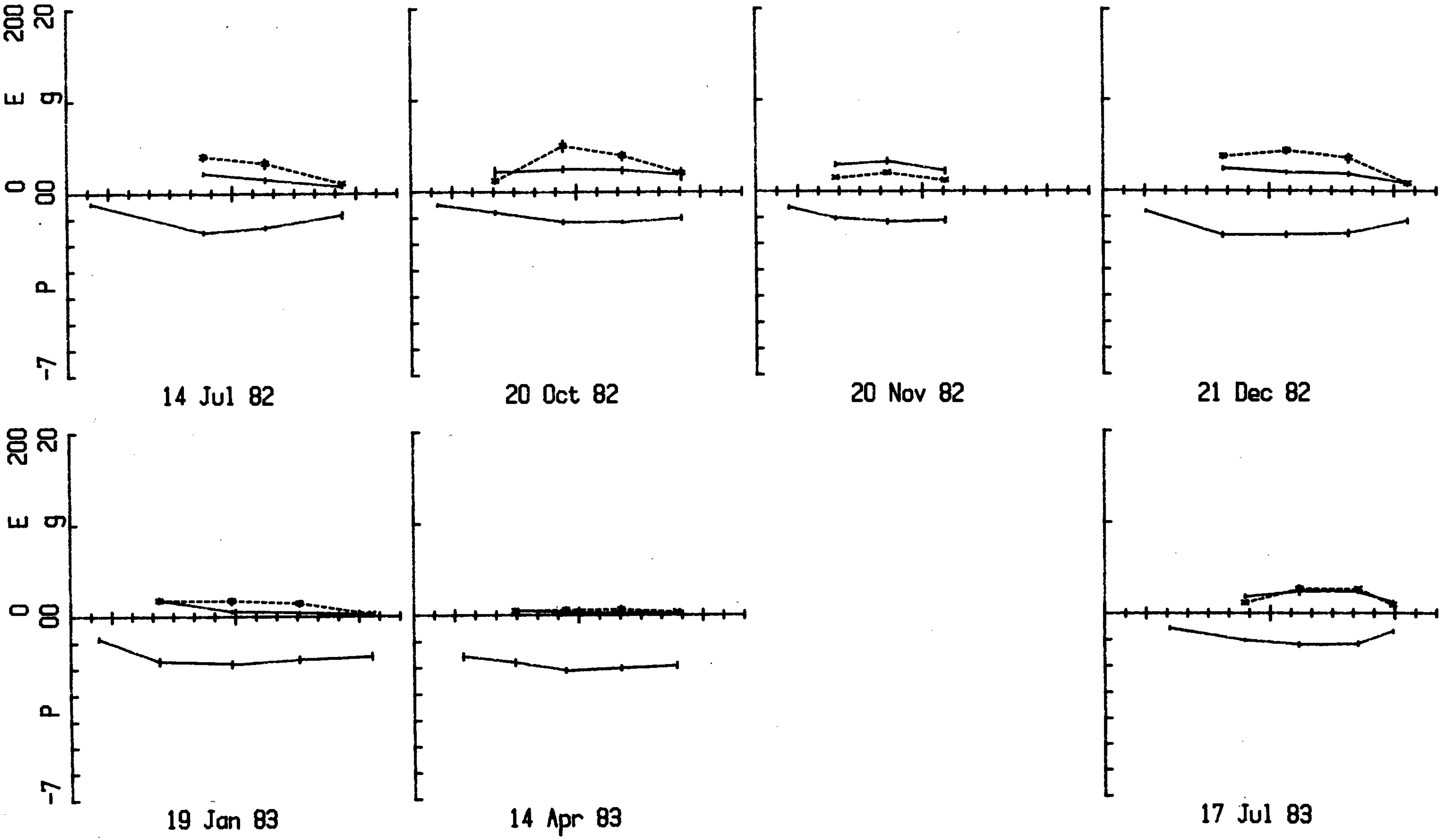
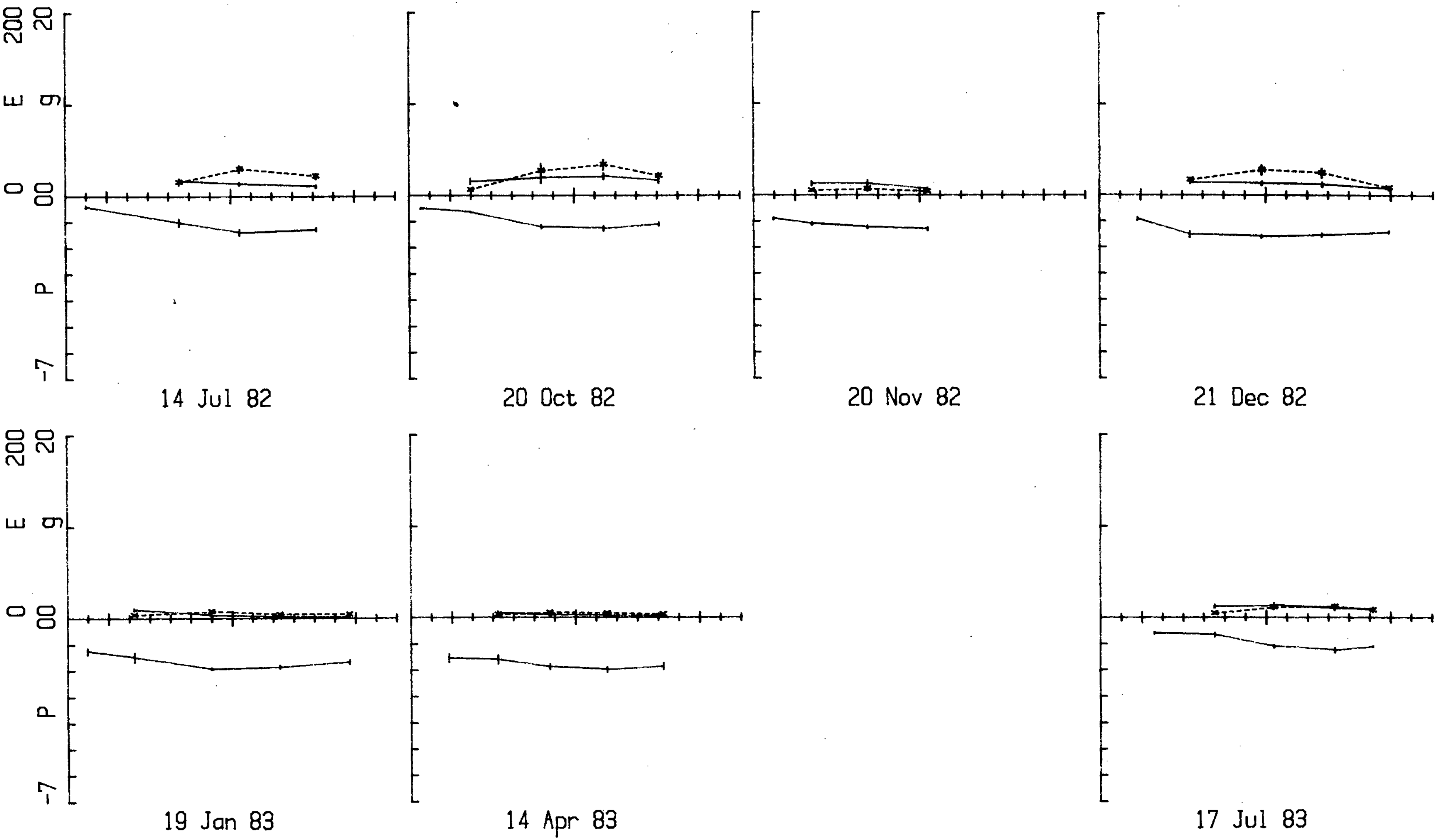


Figure 5.34 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of Protea laurifolia at site 5 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.



14 Jul 82

20 Oct 82

20 Nov 82

21 Dec 82

19 Jan 83

14 Apr 83

17 Jul 83

Figure 5.35 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of *Paranomus bracteolaris* at site 5 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

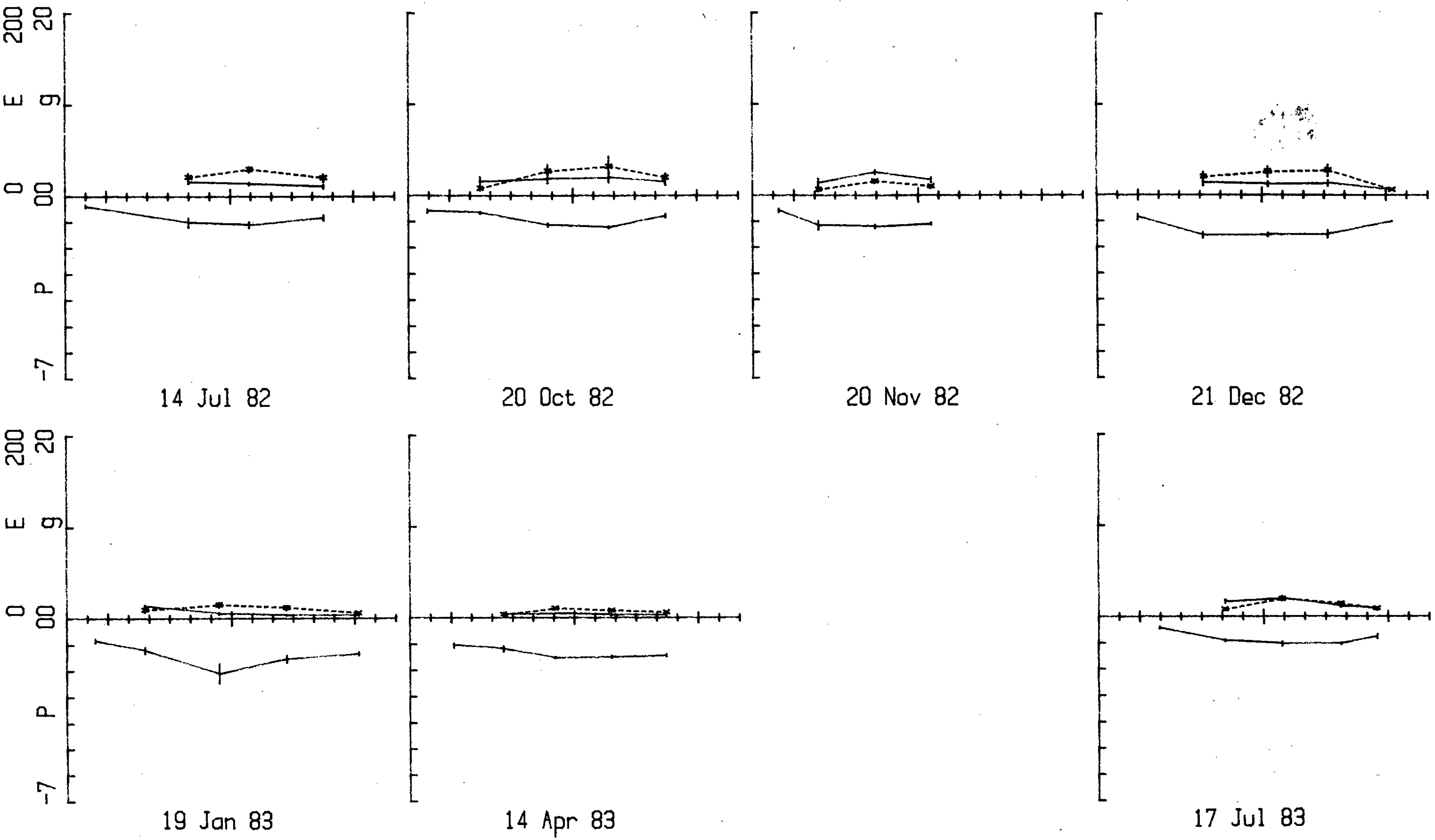


Figure 5.36 The diurnal pattern of the leaf conductance (g; mm/s), transpiration (E; mg/m2/s), and xylem pressure potential (P; MPa) of Leucadendron pubescens at site 5 (mean and SE, n= 5). Transpiration is the dashed line. The time scale is 04h00 - 20h00.

species. The maximum leaf conductances of Protea laurifolia were between 2.5 and 3.0 mm/s, while those of Paranomus bracteolaris were between 1.25 and 1.5 mm/s, and those of Leucadendron pubescens were between 1.5 and 2.0 mm/s. The lowest xylem pressure potentials of Protea laurifolia were -2.10 ± 0.08 MPa, while those of Paranomus bracteolaris were -1.92 ± 0.04 MPa, and those of Leucadendron pubescens were -2.10 ± 0.37 MPa.

5.3.5 Water relations of the dehydration postponing species with decreasing pre-dawn xylem pressure potentials

Between July 1982, in the middle of the winter, and April 1983, at the end of the summer, the conditions at all of the sites along the transect became more xeric as a result of the decreasing rainfall and the increasing vapor pressure deficits. From site 5 to site 1 both the period of time with low soil moisture, and the depth to which the soil dried, increased because of the lower total rainfall. During this time the declining pre-dawn xylem pressure potentials can be used as an index of the progression of the summer drought.

As the summer drought progressed plants followed one of three possible patterns of water relations. At the mesic end of the transect some species limited leaf conductance, and maintained high xylem pressure potentials by foregoing photosynthesis. At the dry end of the transect the probable switch to Crassulacean acid metabolism in Ruschia sp. also allowed the closure of the stomata during the day, and the maintenance of high xylem pressure potentials. The remaining species were either seasonally deciduous, or had to endure low xylem pressure potentials.

The species that had large seasonal fluctuations in xylem pressure potentials had varying ability to maintain leaf conductance. While some of the species continued leaf conductance at the lowest xylem pressure potentials that could be measured by the pressure chamber, others seemed to reach a minimum xylem pressure potential threshold below which leaf conductance stopped. The decrease in the leaf conductances could cuase a reduction in the transpiration rates and the diurnal fluctuations in xylem pressure potential. However, the increased vapor pressure deficits may offset the reduction in leaf conductance and maintain the transpiration rate. The non-linear relationship between soil water content and soil water potential makes extraction of equal amounts of water increasingly difficult as the soil water potentials drop, and may therefore not allow the diurnal fluctuations of xylem pressure potential to decrease.

With declining pre-dawn xylem pressure potentials, reflecting the development of the drought, the leaf conductances of Ruschia sp. decreased (Figure 5.37). In the middle of the summer, when the leaf conductances were low because of the low xylem pressure potentials, the vapor pressure deficits were high, and as a result the maximum transpiration rates did not decline. As the pre-dawn xylem pressure potentials decreased the midday depressions of the xylem pressure potential decreased, and were negligible at pre-dawn values of about -3.5 MPa. The midday xylem

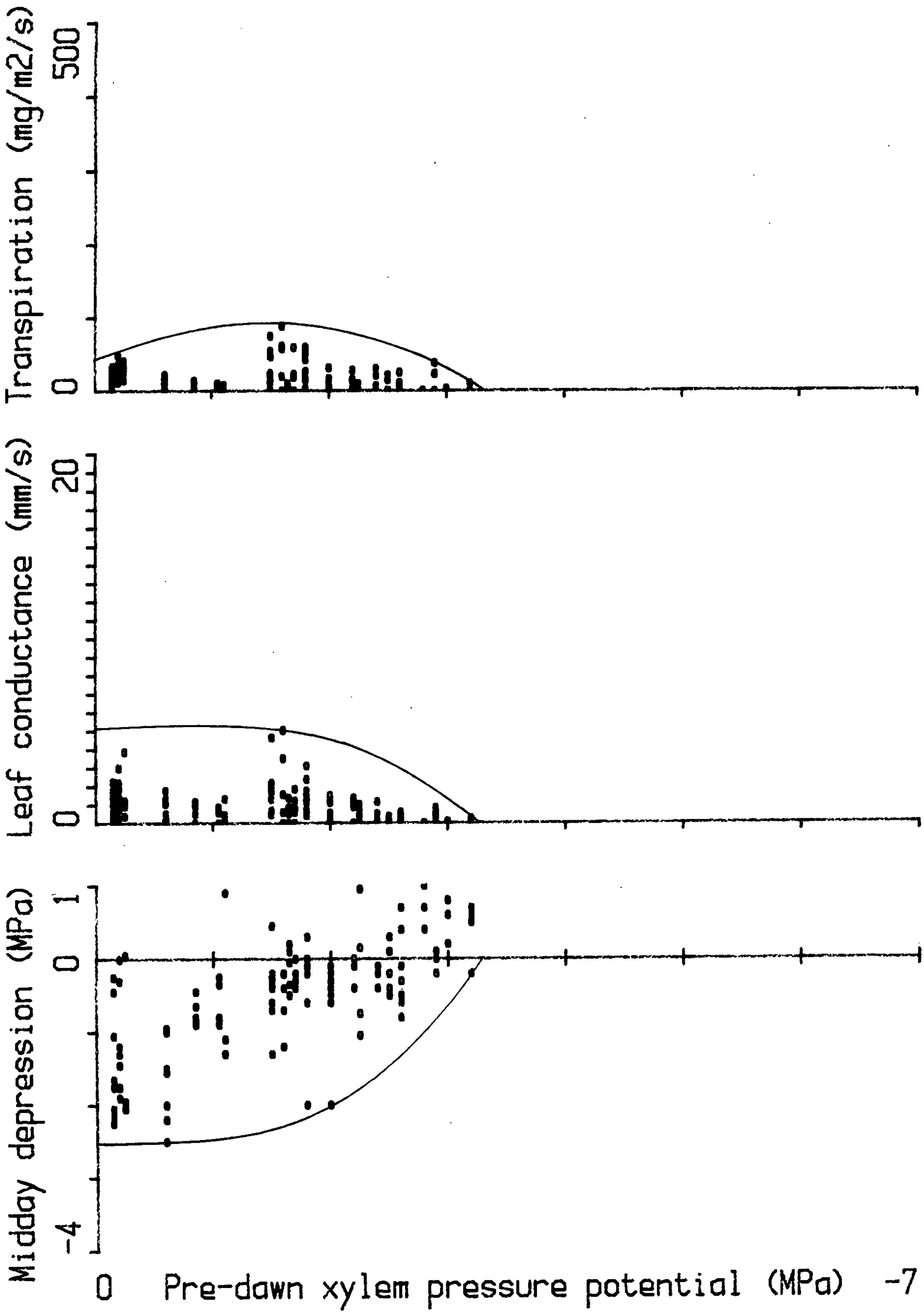


Figure 5.37 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Ruschia sp. at site 1.

pressure potential values were often higher than the pre-dawn values, especially in April, and this may reflect a shift to Crassulacean acid metabolism, when there could be water loss at night and recovery during the day.

The stomata of the overstory species Protea laurifolia, Protea glabra, Paranomus bracteolaris, and Leucadendron pubescens were very sensitive to decreasing xylem pressure potentials, and leaf conductances quickly dropped with decreasing pre-dawn xylem pressure potentials (Figures 5.38 to 5.42). The species were probably deep rooted, and in the winter months the xylem pressure potentials usually returned to near the pre-dawn values as soon as the sun went down. During these months the midday depressions in xylem pressure potential were probably more the result of a resistance to water transport than the result of a lack of water supply in the soil. These resistances dropped the midday xylem pressure potentials to between -1.5 and -2.0 MPa, which was the point at when the stomata began to close and reduce leaf conductance. The midday xylem pressure potentials in the middle of the summer at site 3 were only slightly lower than they were in the middle of the winter.

As the pre-dawn xylem pressure potentials of these five species declined there was first a period when the maximum leaf conductances were limited by the stomatal reaction to the water potentials developed from the internal resistances. This response created a ceiling on the leaf conductances and the midday depressions in xylem pressure potential. As the pre-dawn xylem pressure potentials continued to decrease there was a rapid reduction in the

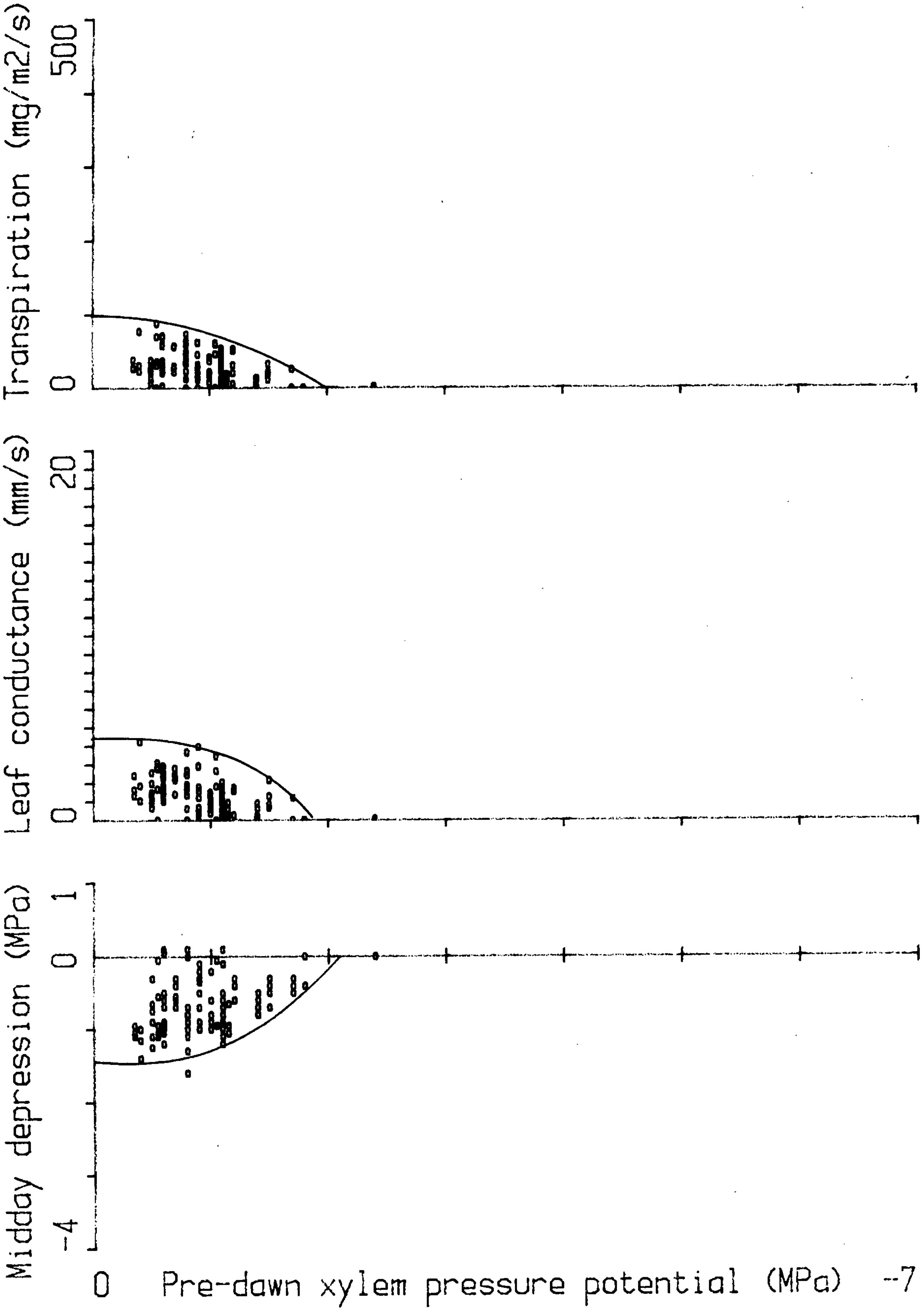


Figure 5.38 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Protea laurifolia at site 3.

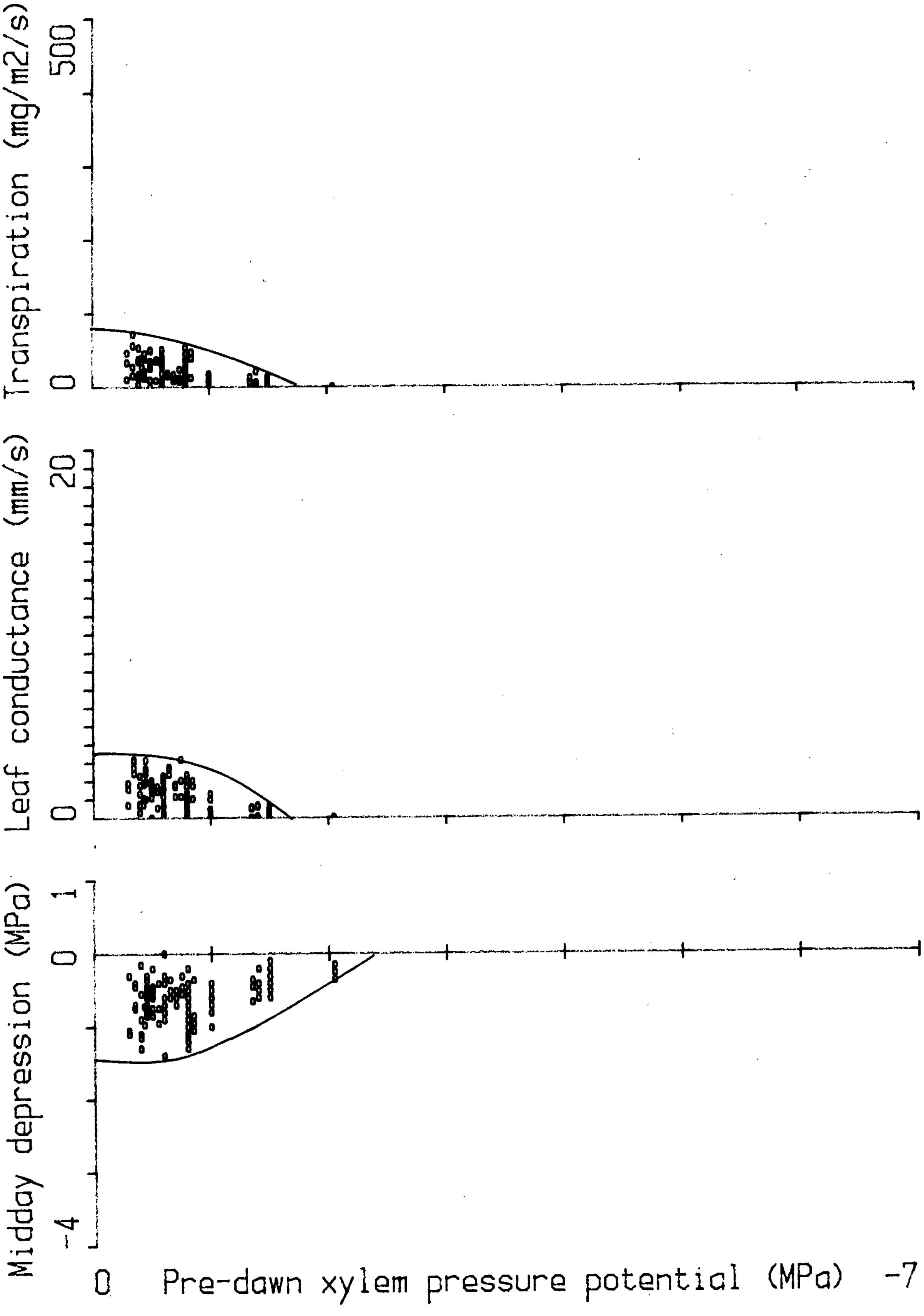


Figure 5.39 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Protea laurifolia at site 5 .

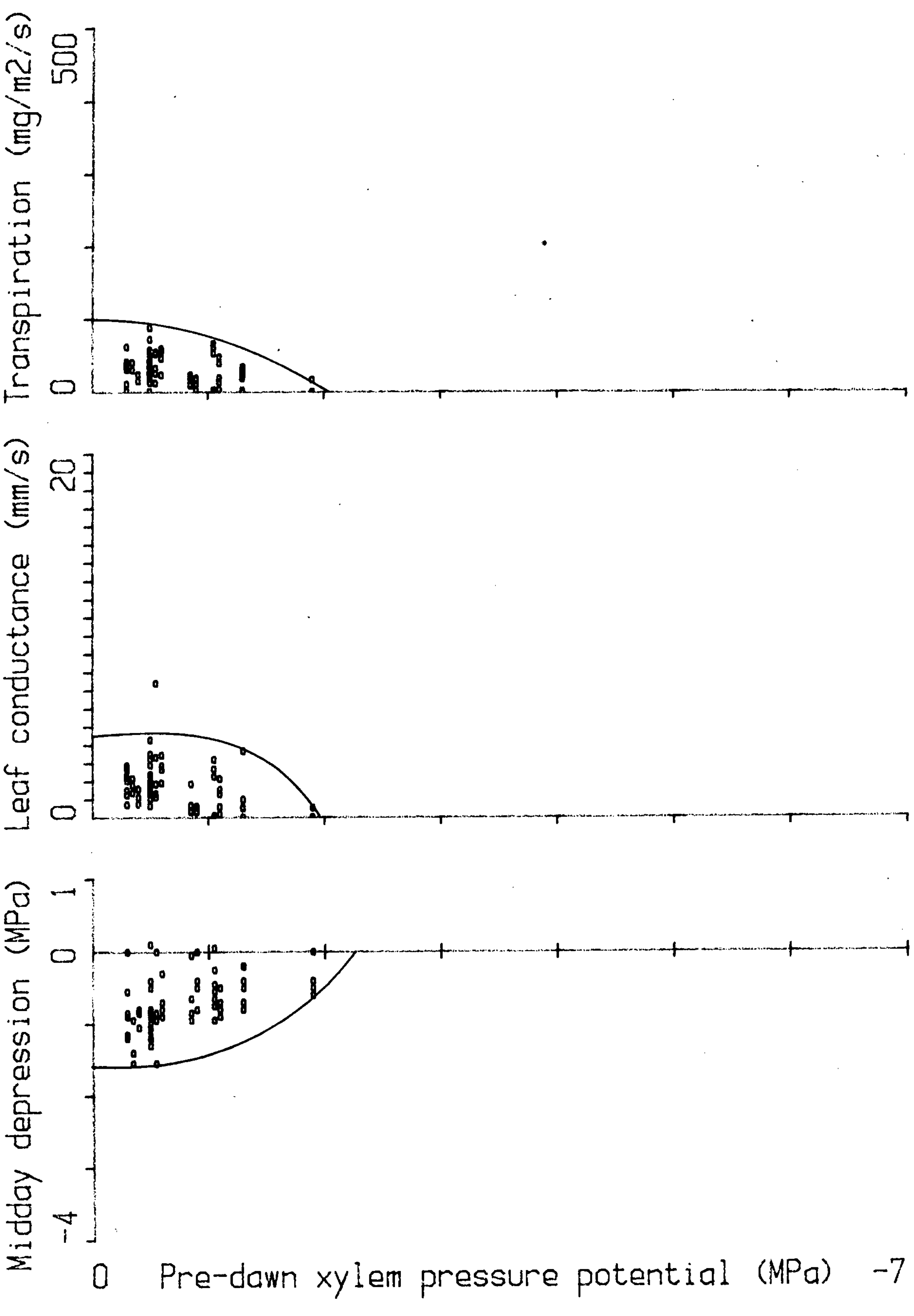


Figure 5.40 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Protea glabra at site 3.

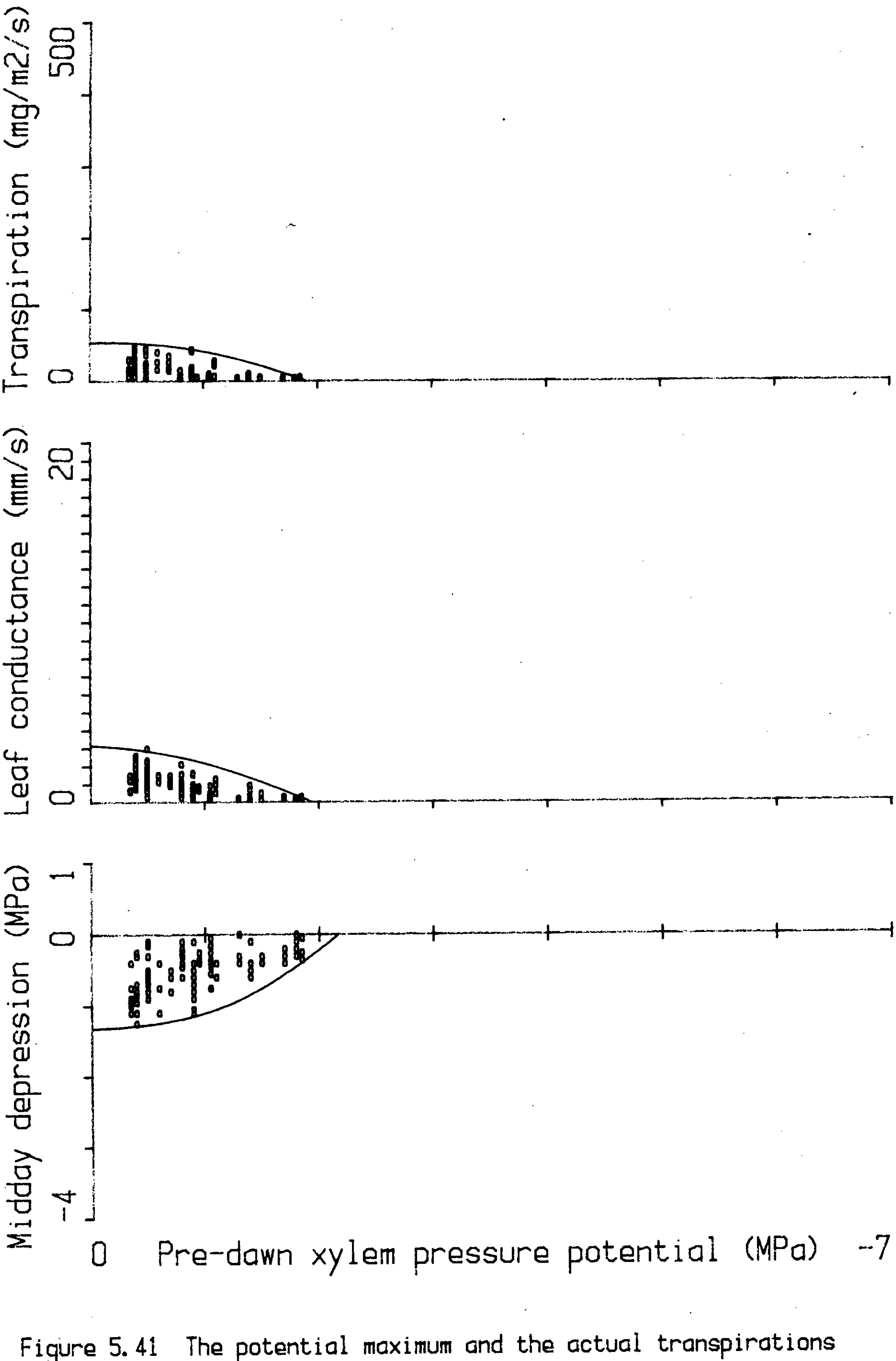


Figure 5.41 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for *Paranomus bracteolaris* at site 5.

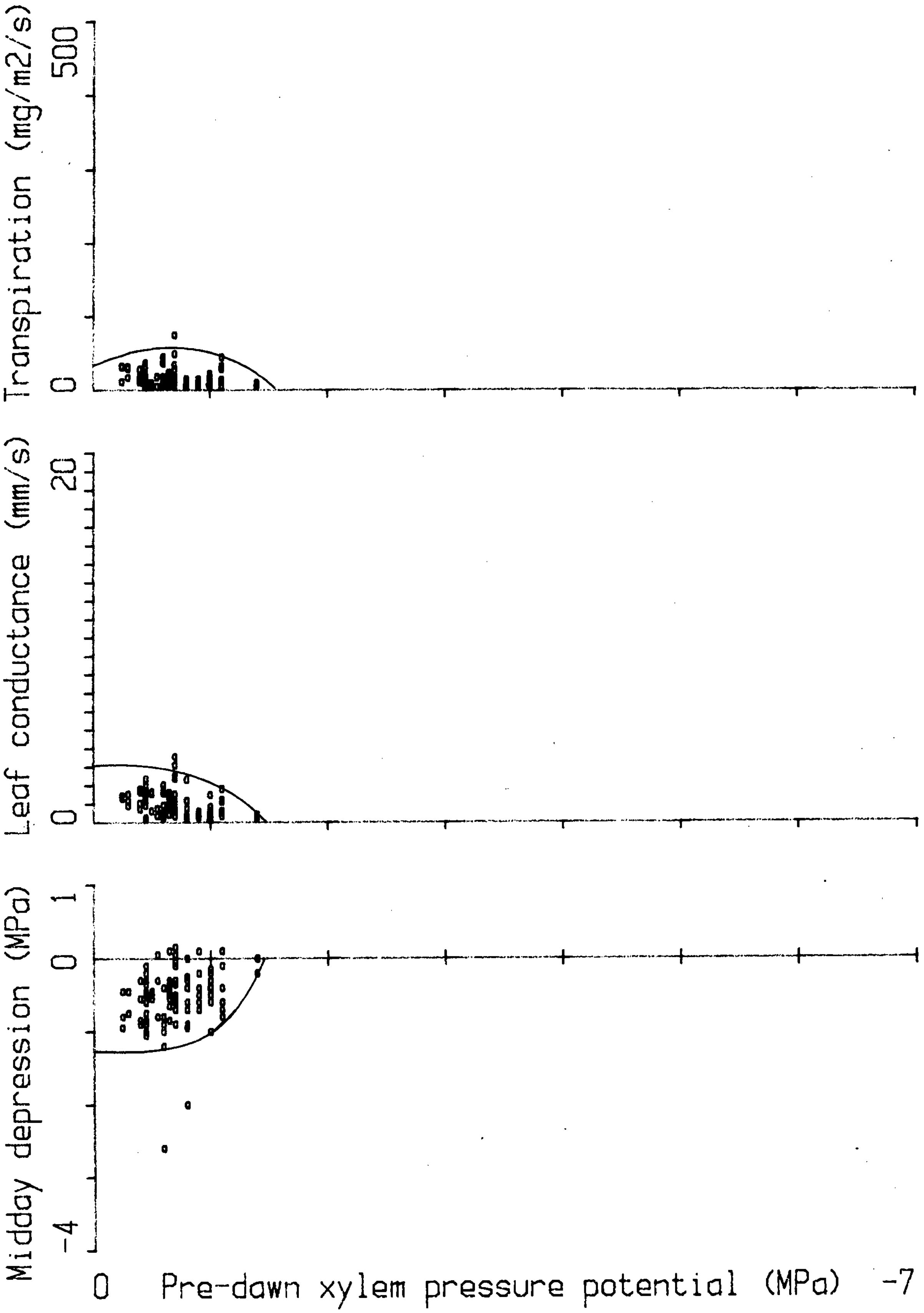


Figure 5.42 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Leucadendron pubescens at site 5.

leaf conductances which reduced the diurnal fluctuations in the xylem pressure potential. The response of the stomata of the fynbos overstory species was sufficient to limit transpiration, especially since the vapor pressure gradients were not as great as those experienced by Ruschia sp.

The Protea laurifolia at sites 3 and 5 had similar maximum rates of leaf conductance, and midday depressions in xylem pressure potential. The individuals at site 3 had a slightly lower xylem pressure potential threshold that governed when the reductions in leaf conductance occurred. As a result the leaf conductances of Protea laurifolia at site 3 continued at slightly lower pre-dawn xylem pressure potentials than at site 5. The response of the leaf conductances of Protea glabra to decreasing xylem pressure potentials was similar to the response of the Protea laurifolia at site 3. The concomitant diurnal fluctuations in xylem pressure potential, and transpiration rates of the two species were also nearly identical.

The patterns of leaf conductance with declining pre-dawn xylem pressure potentials of the last two species in the fynbos overstory group, Paranomus bracteolaris and Leucadendron pubescens were the extremes of the pattern of a plateau followed by a decline. Paranomus bracteolaris had the most sensitive stomata of the four overstory species. The leaf conductances never showed a plateau period, and began to drop as soon as the pre-dawn xylem pressure potentials began to decrease. The drop in leaf conductances decreased the transpiration rates which then reduced the diurnal fluctuations in xylem pressure potential.

The minimum midday xylem pressure potentials of Leucadendron pubescens were the most seasonally constant of the group, and the resistance to water transport seemed to be the highest. As a result there was a large plateau where the maximum leaf conductances and the diurnal fluctuations in xylem pressure potential were constant with decreasing pre-dawn xylem pressure potentials. This was followed by a sharp reduction in leaf conductance and midday depression in xylem pressure potential.

5.3.6 Water relations of the drought avoiding species with decreasing pre-dawn xylem pressure potentials

The second pattern of leaf conductance in response to decreasing pre-dawn xylem pressure potentials was that of the deciduous Rhus species (Figures 5.43, 5.44, and 5.45). Both Rhus incisa and Rhus dissecta exhibited little stomatal response to decreasing pre-dawn xylem pressure potentials and only through the reduction in transpiring surface area managed to prevent extremely low xylem pressure potentials. At low xylem pressure potentials there was a reduction in the leaf conductances of Rhus incisa at site 1, but the increased vapor pressure deficits prevented the slowing of transpiration. Rhus incisa maintained leaf conductances until the pre-dawn xylem pressure potentials reached -5 MPa, while the leaf conductances of Rhus dissecta at site 3 stopped at -4 MPa, and at site 5 at -3 MPa. The pattern in Rhus dissecta of increasing midday depressions in xylem pressure potential, reflecting constant transpirative demand from a drying soil, and then decreasing midday depressions,

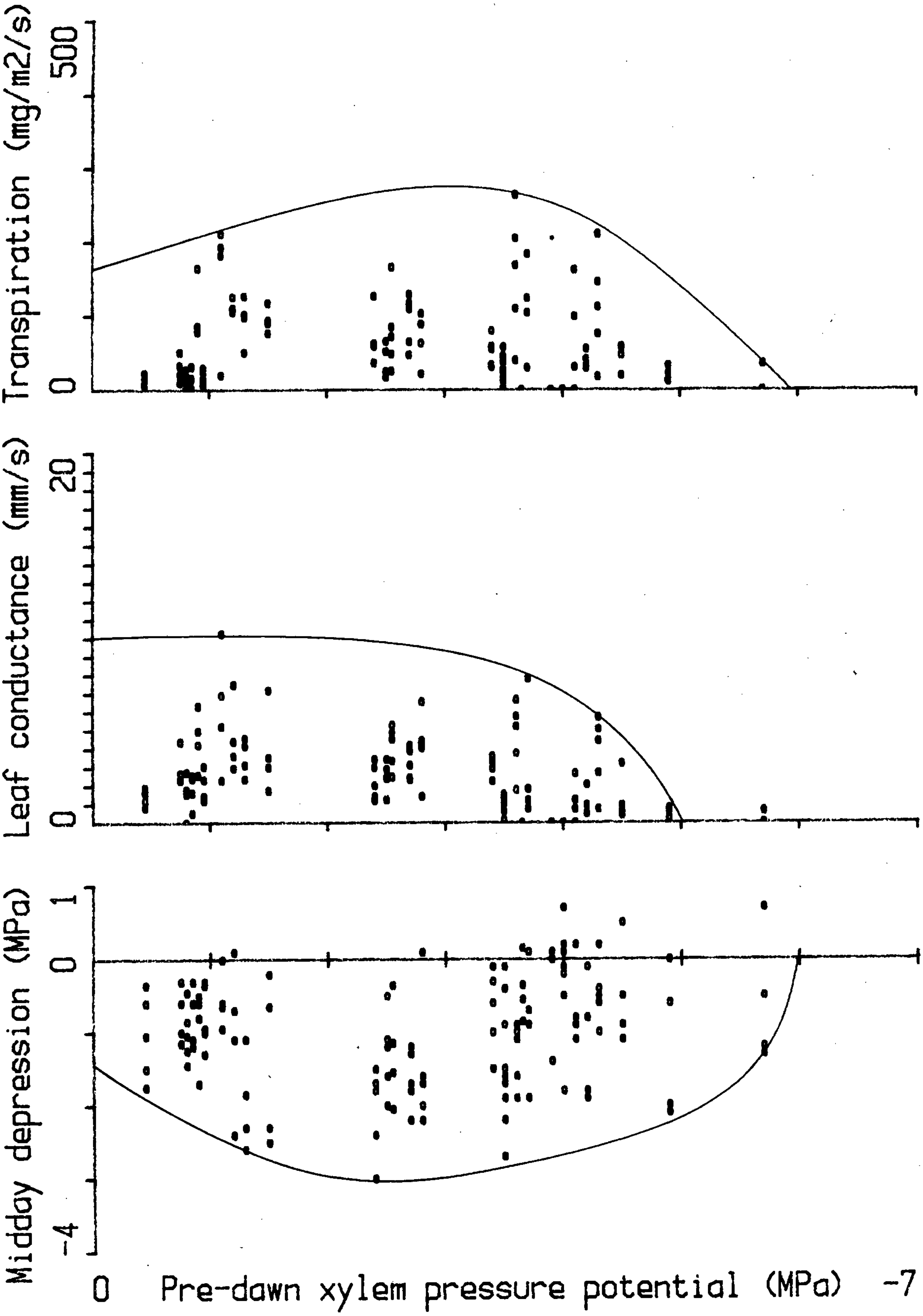


Figure 5.43 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Rhus incisa at site 1.

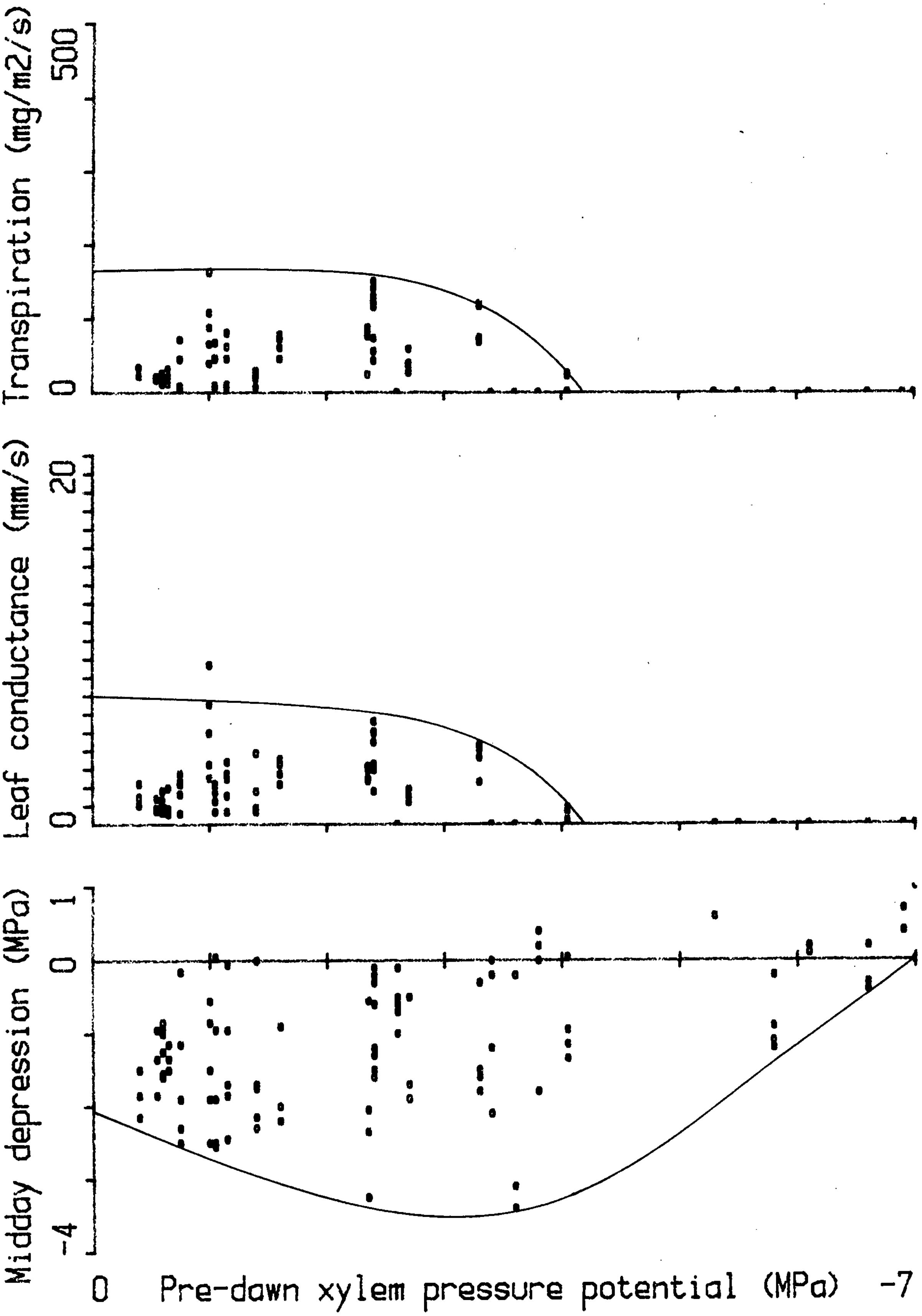


Figure 5.44 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Rhus dissecta at site 3.

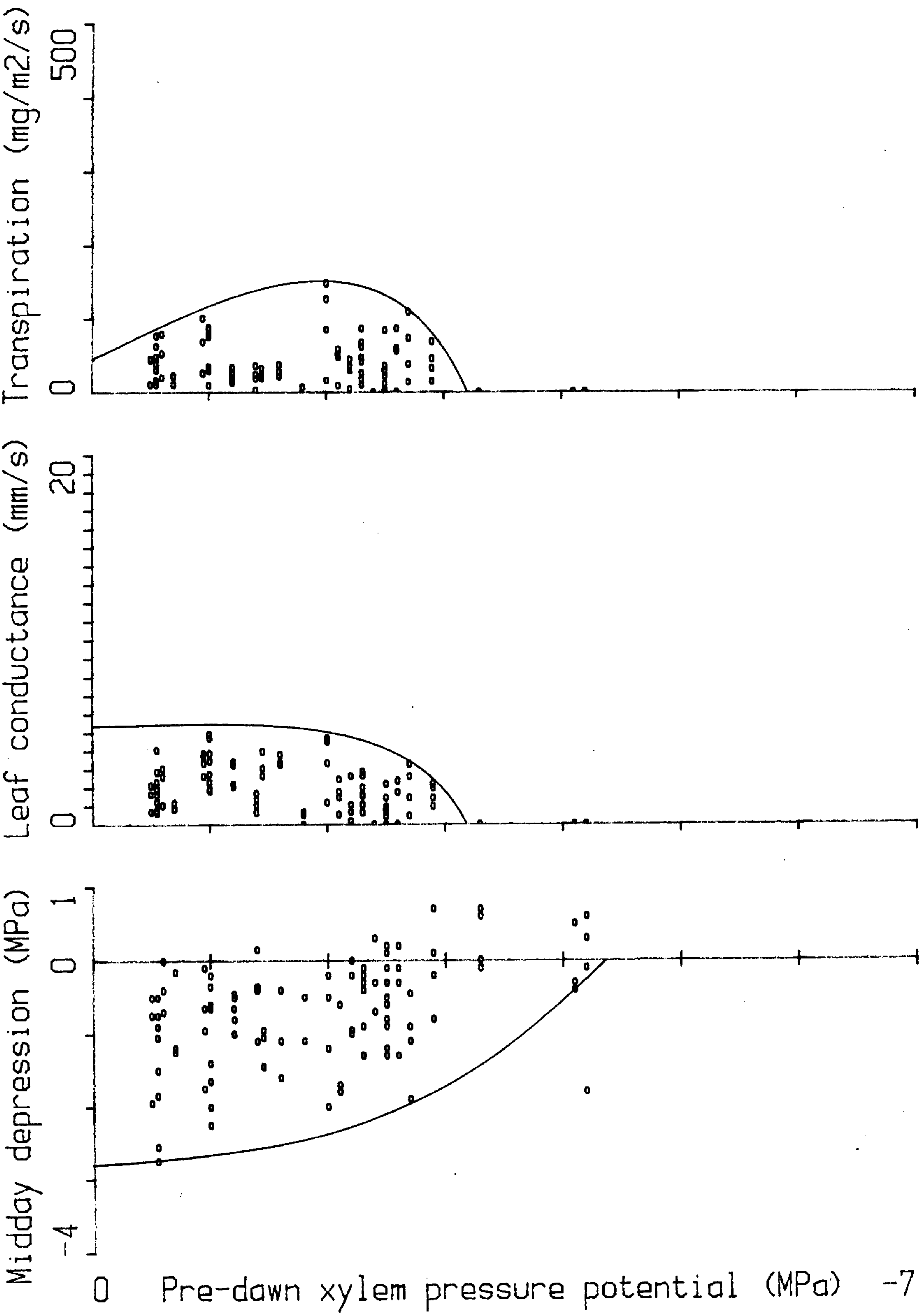


Figure 5.45 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for <u>Rhus dissecta</u> at site 5.

as there was a reduction in the leaf area, was strongest at site 3. At site 3 there were still diurnal fluctuations in the xylem pressure potential at pre-dawn values of -7MPa, whereas at site 5 they stopped when the pre-dawn xylem pressure potentials dropped below -4.5 MPa. The root system of Rhus incisa must be larger, or extend deeper than does the root system of Rhus dissecta, because Rhus incisa is the physically larger species, and yet maintained leaf conductances at a lower minimum xylem pressure potentials than Rhus dissecta. Both species had large diurnal variations in xylem pressure potential without reductions in leaf conductance and must have had high osmotic potentials which allowed the maintenance of turgor. The Rhus dissecta sampled at site 5 had lower leaf conductances, experienced a smaller range of pre-dawn xylem pressure potentials, and dropped their leaves at higher pre-dawn xylem pressure potentials than those sampled at site 3. The individuals at site 5 never experienced extremely low xylem pressure potentials because the site was never that dry, so there must either be a large amount of plasticity in the water stress cue for leaf shedding, or some other cue may also be involved.

5.3.7 Water relations of the dehydration tolerating species with decreasing pre-dawn xylem pressure potentials

The last pattern of water relations that some of the species followed, with varying degrees of success, while pre-dawn xylem pressure potentials dropped was to maintain leaf conductances and endure the resulting water stress.

Eriocephalus africanus was the most successful species of this group, and maintained leaf conductances at the lowest xylem pressure potentials. Stoebe capitata was the least successful species of the group, and quickly lost the ability to continue leaf conductance as the xylem pressure potentials fell.

At both site 1 and at site 3 Eriocephalus africanus had similar maximum rates of leaf conductance, and maintained leaf conductances until the pre-dawn xylem pressure potentials dropped to -7 MPa (Figures 5.46, and 5.47). In the middle and at the end of the summer, when the pre-dawn xylem pressure potentials were low, the increase in the vapor pressure deficits increased the transpiration rates. At the same time, since Eriocephalus africanus was a semi-deciduous species, there was a reduction in leaf area which seems to have offset the increased transpiration rates and allowed the midday depressions in xylem pressure potential to remain uniform during the drought. The single Eriocephalus africanus sampled at site 5 had decreasing leaf conductances with decreasing pre-dawn xylem pressure potentials (Figure 5.48). This may show that without the progressive hardening that probably occurred at sites 1 and 3 the species may have a more limited ability to endure low xylem pressure potentials.

Galenia africana, like Eriocephalus africanus, maintained leaf conductances at low xylem pressure potentials (Figure 5.49). The leaf conductances were lower, compared to the pattern of Eriocephalus africanus, when there were large vapor pressure deficits in the middle of

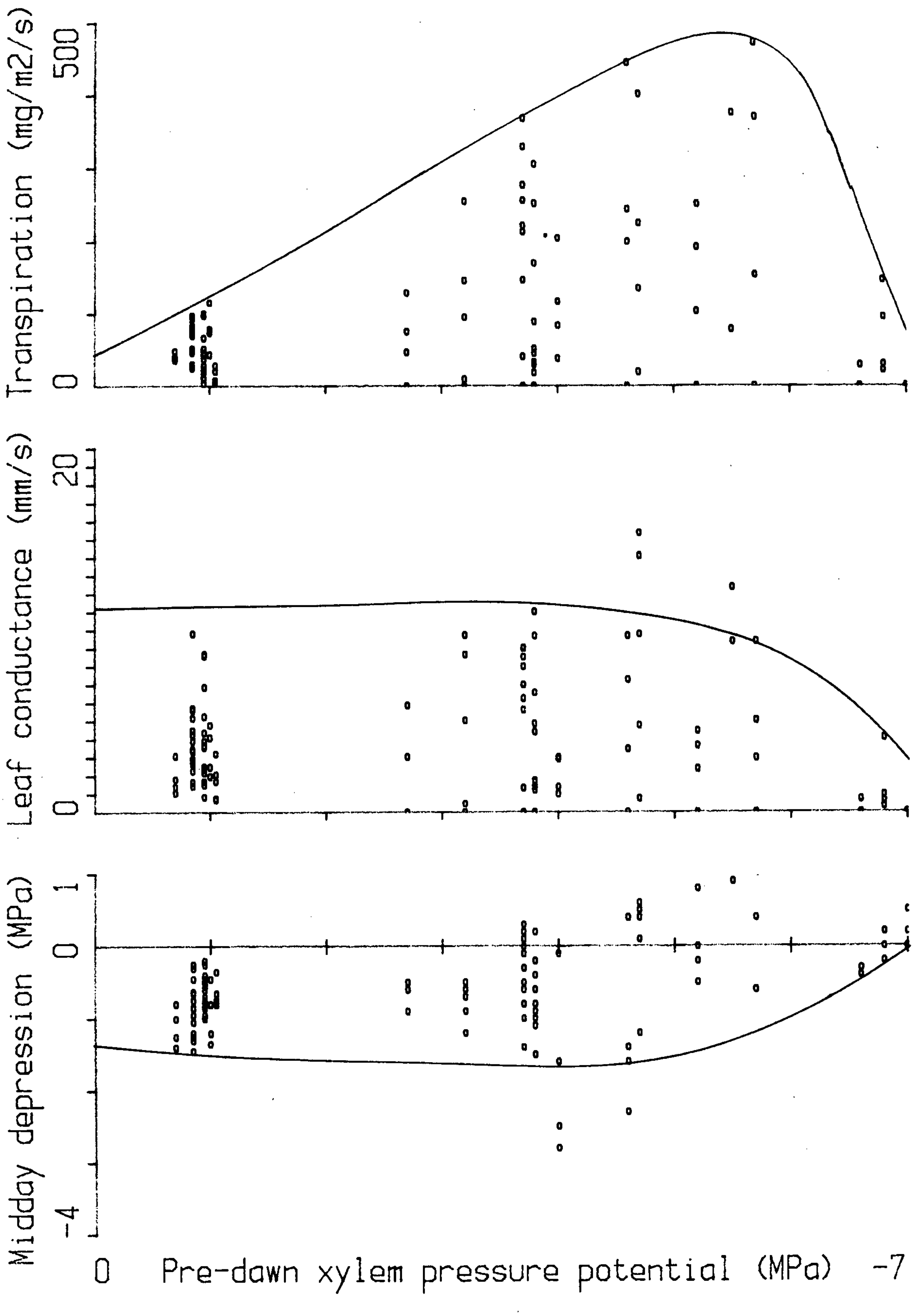


Figure 5.46 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for <u>Eriocephalus africanus</u> at site 1 .

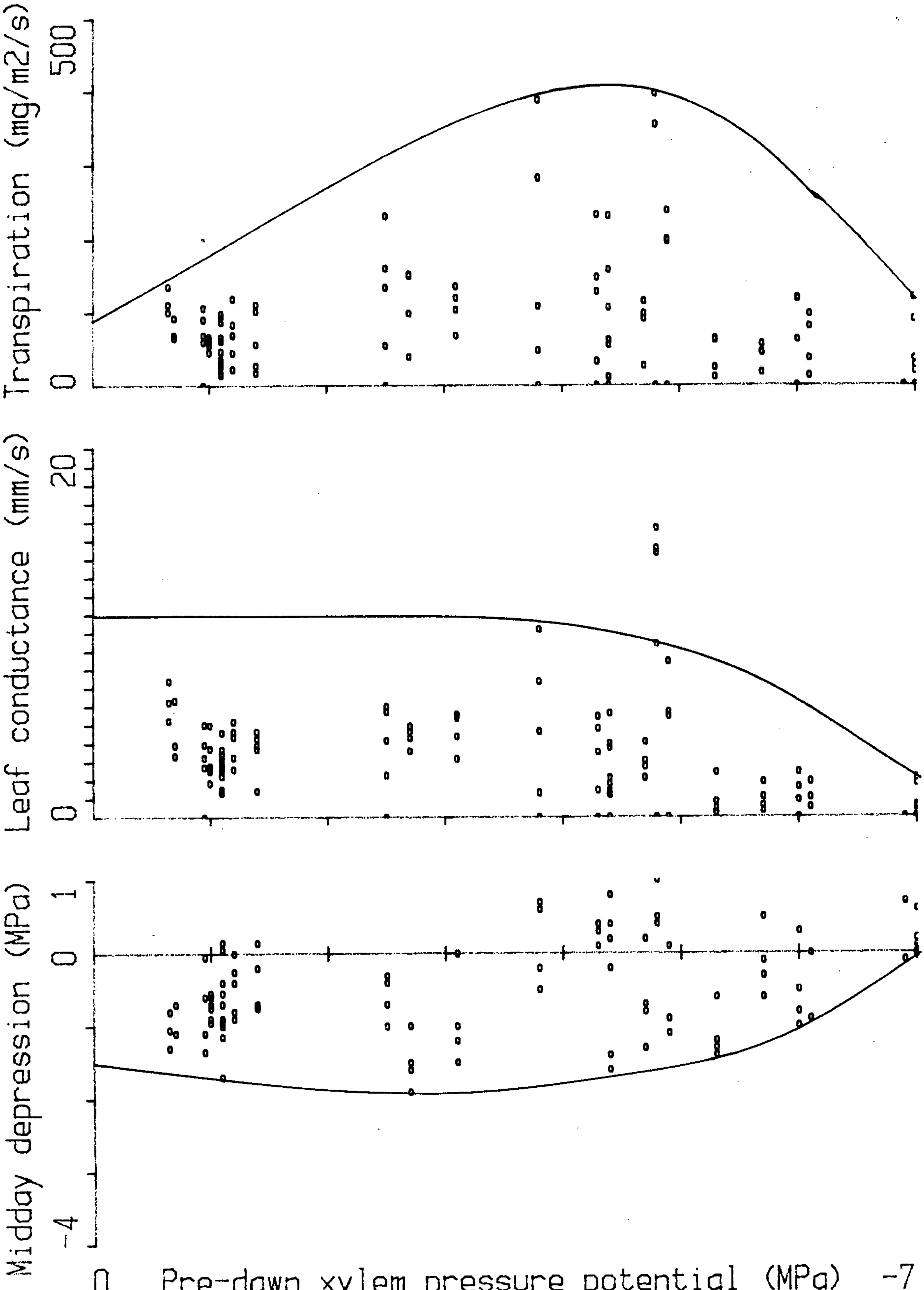


Figure 5.47 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for *Eriocephalus africanus* at site 3.

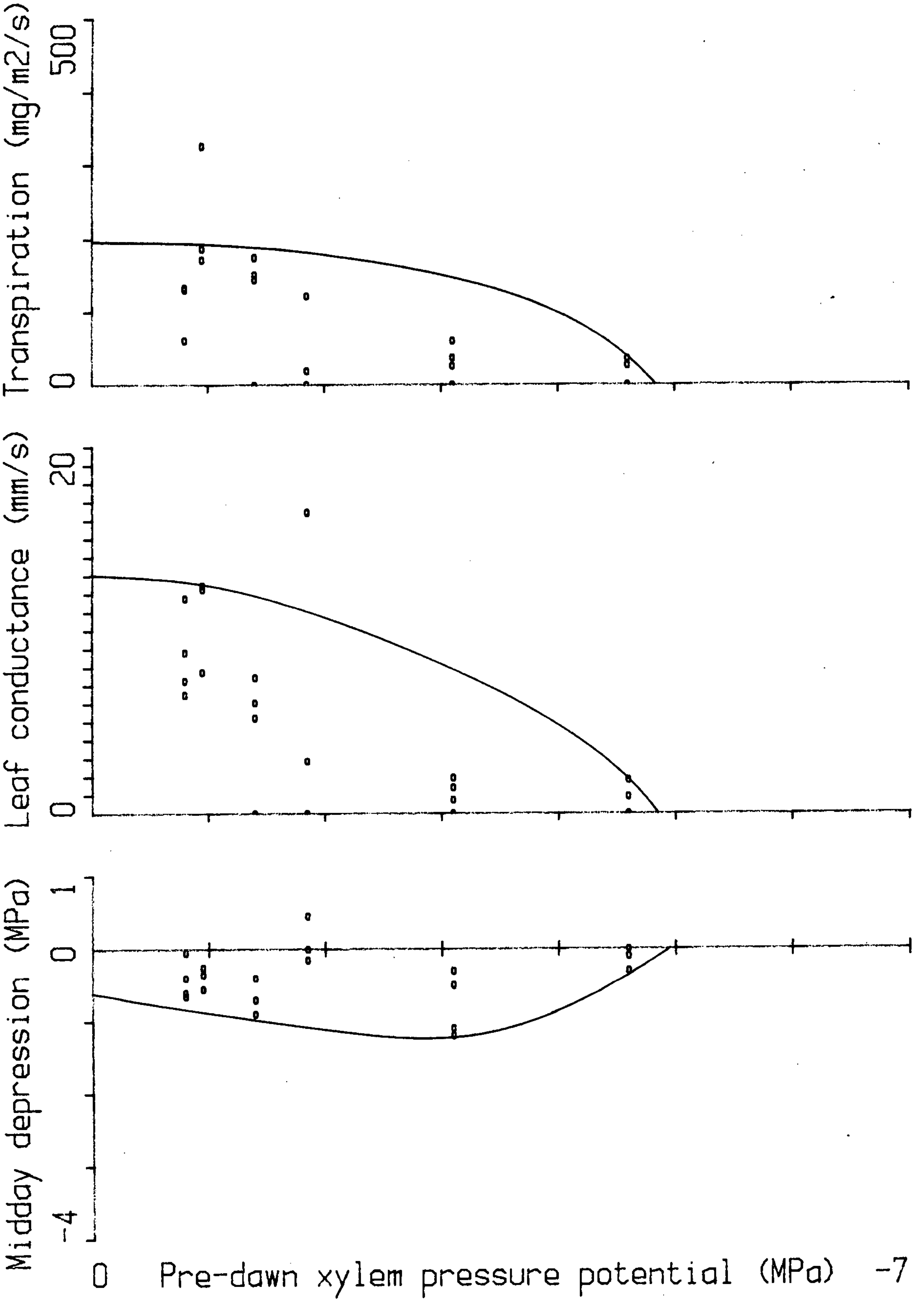


Figure 5.48 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Eriocephalus africanus at site 5.

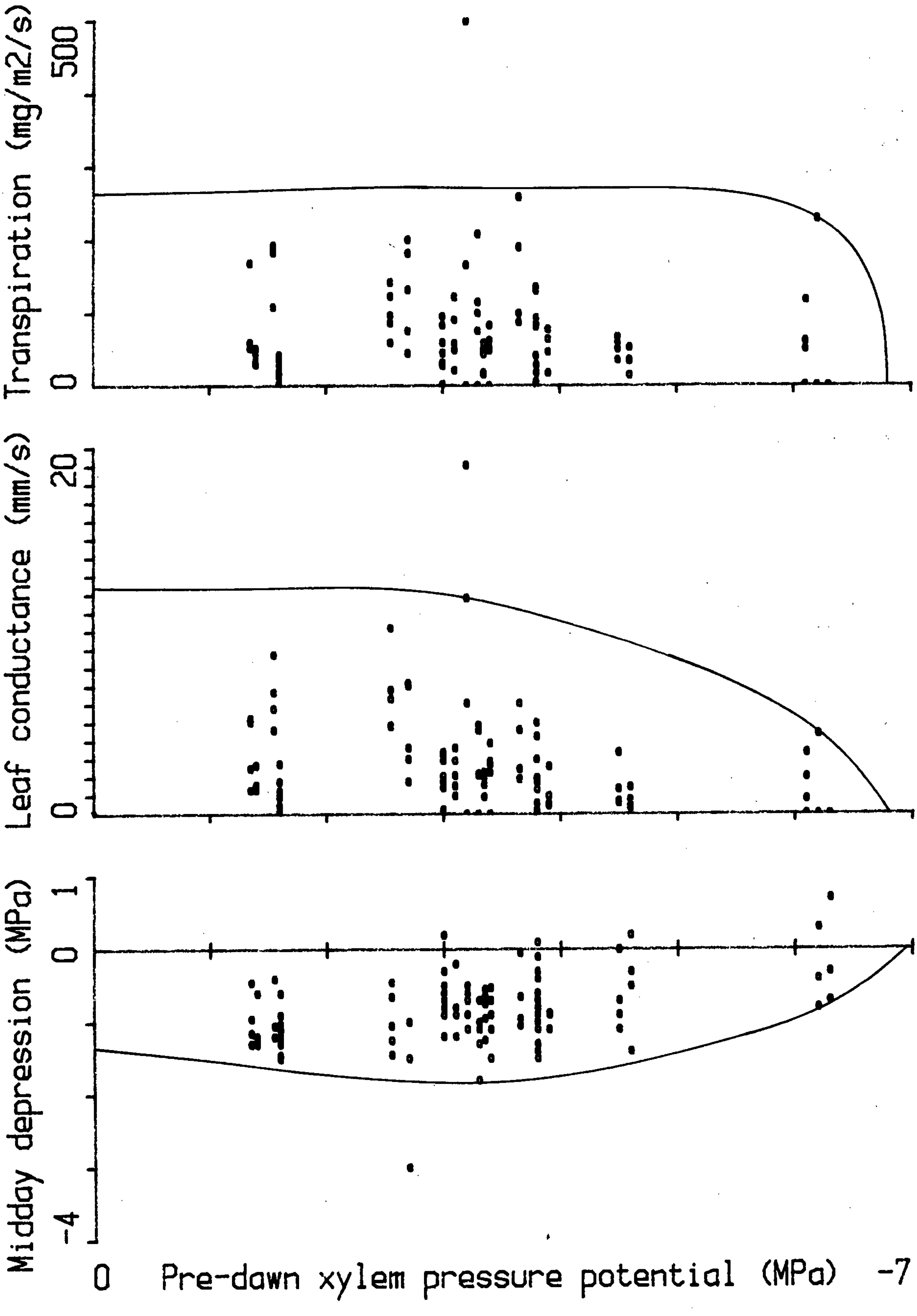


Figure 5.49 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for <u>Galenia africana</u> at site 1 .

the summer so there was a more uniform transpiration rate throughout the year. *Galenia africana* was also semi-deciduous, and may have relied on a reduction in total leaf area in order to reduce transpiration and the need to limit leaf conductances. By reducing leaf area the species did not have to reduce the rate of photosynthesis while still maintaining the respiratory costs of the tissue.

The *Nylandtia spinosa* at site 1 and at site 3 had different patterns of leaf conductance with falling xylem pressure potentials (Figures 5.50 and 5.51). As the pre-dawn xylem pressure potentials decreased at site 1, the species had high leaf conductances which caused increasing rates of water loss and increasing midday depressions in the xylem pressure potential. When the pre-dawn xylem pressure potentials dropped below -3.5 MPa the stomata began to close. At site 3 the species had low conductance rates, but maintained them at pre-dawn xylem pressure potentials as low as -7 MPa. There seems to have been considerable plasticity in the physiological controls on leaf conductance, and possibly two distinct ecotypes. The *Nylandtia spinosa* at site 1 exhibited a pattern of water use that would have maximized the amount of water used by the plant rather than lost to soil evaporation, before having to close the stomata until the next rain. At site 3, where the rainfall would have penetrated the soil more deeply and allowed a continuing reserve, the species seemed to have limited the maximum rates of water loss, but allowed water loss to continue. At site 1 the water may have been used to quickly to allow the gradual hardening that probably

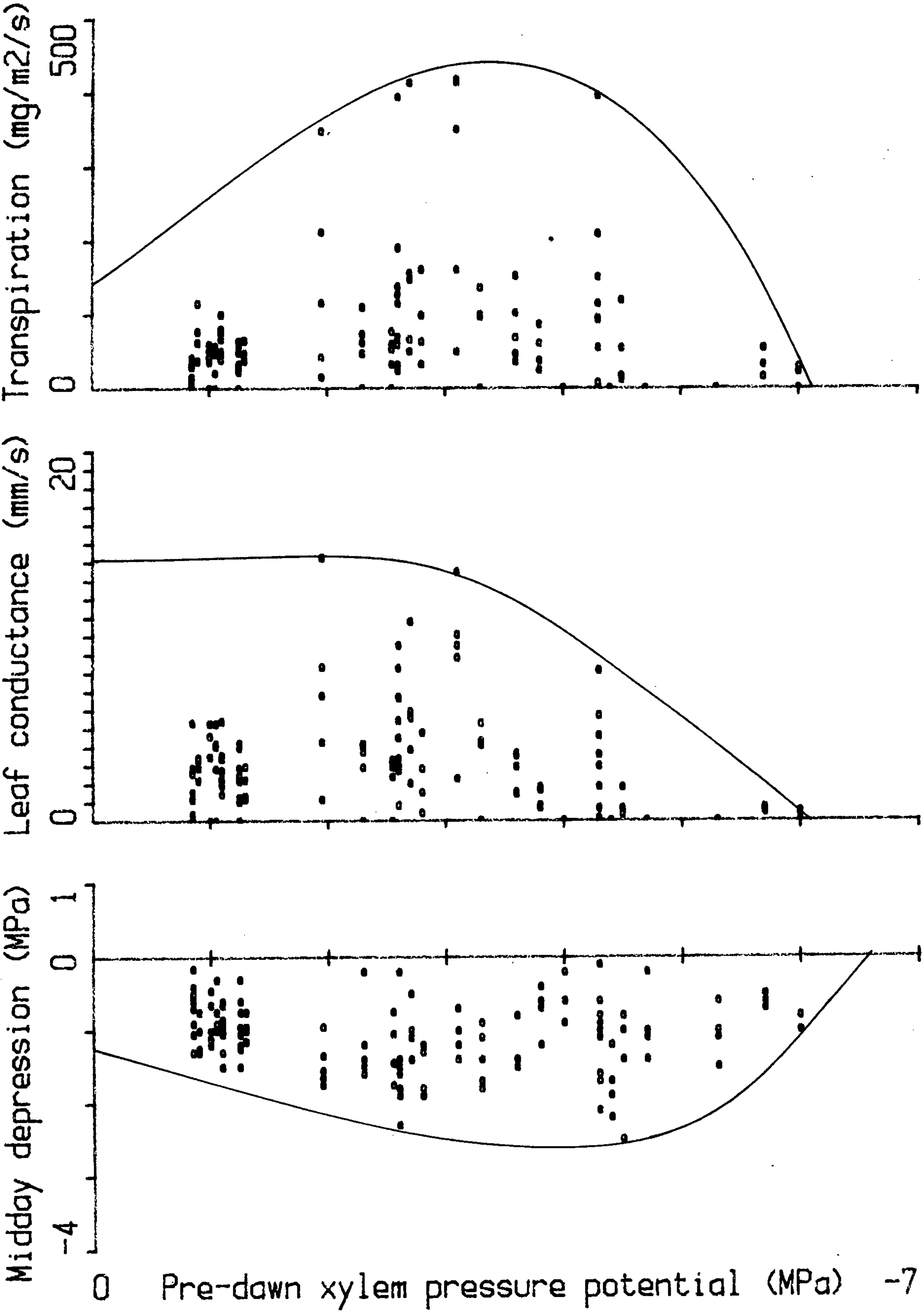


Figure 5.50 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for <u>Nylandtia spinosa</u> at site 1 .

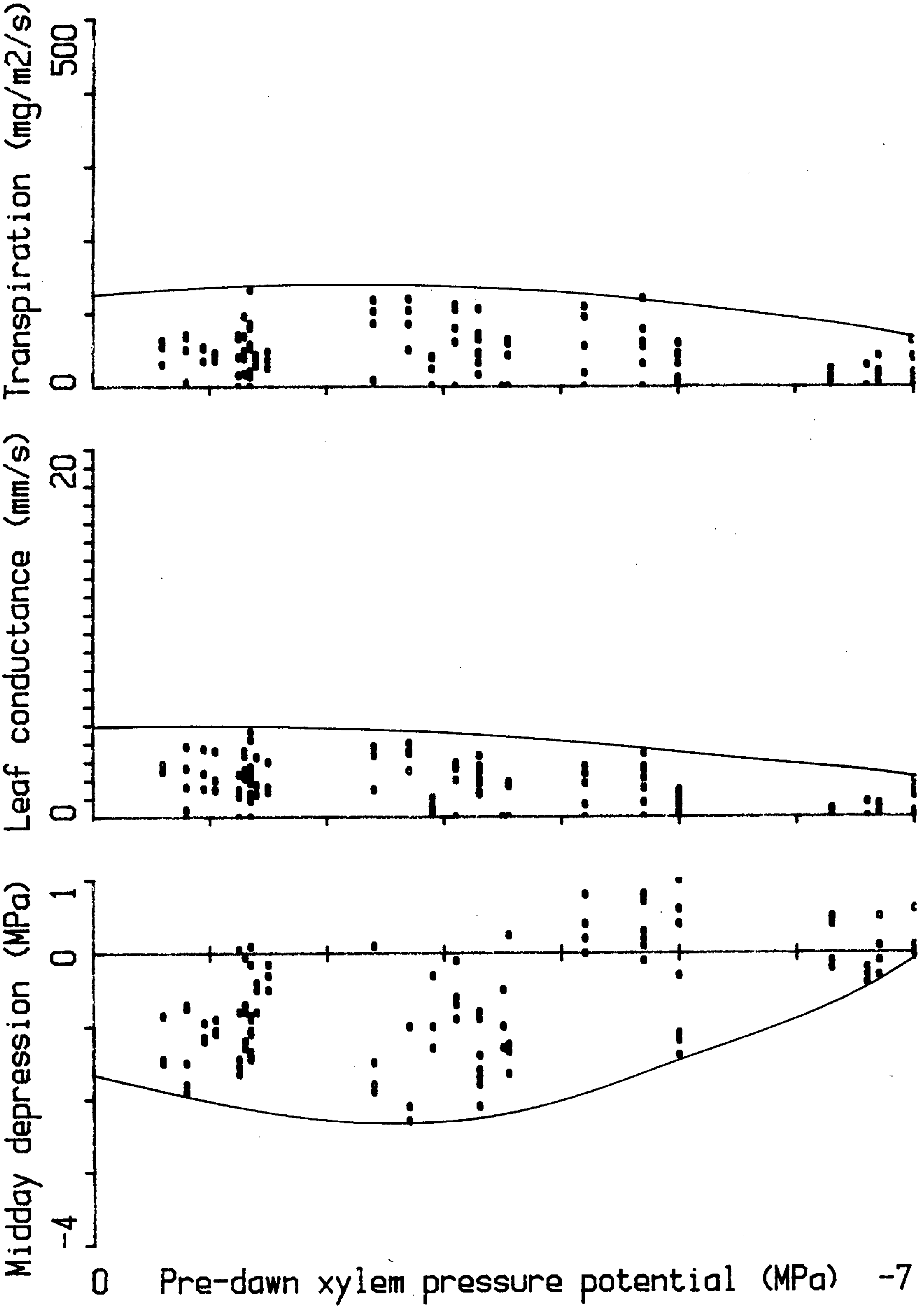


Figure 5.51 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for *Nylandtia spinosa* at site 3 .

occurred at site 3.

Elytropappus gnaphaloides and *Stoebe capitata* both maintained leaf conductances until the dropping pre-dawn xylem pressure potentials reached a threshold, after which there were reductions in the rates of water loss (Figures 5.52 and 5.53). *Elytropappus gnaphaloides*, which was sampled at site 3, and *Stoebe capitata*, which was sampled at site 5, were physiognomically identical, and were thought to be the same species when designing the experiment. The thresholds in xylem pressure potential of the two species, below which leaf conductances declined, were very different. Of the two, *Stoebe capitata* exhibited a more conservative pattern of water use. *Elytropappus gnaphaloides* had high leaf conductances until the pre-dawn xylem pressure potentials dropped below -3 MPa. Leaf conductance did not completely halt, even when the pre-dawn xylem pressure potentials reached -7 MPa. *Elytropappus gnaphaloides* experienced both large diurnal variations in xylem pressure potential, and also large seasonal variations.

Stoebe capitata also had high leaf conductances, but only half as high as those of *Elytropappus gnaphaloides*. When the pre-dawn xylem pressure potentials of *Stoebe capitata* dropped below -2 MPa the leaf conductances began to decrease, and although the species never experienced pre-dawn xylem pressure potentials lower than -3 MPa there was a complete halt in leaf conductance. The diurnal variations in the xylem pressure potential of *Stoebe capitata*, up to -2 MPa, were almost as large as the seasonal variation in pre-dawn xylem pressure potential.

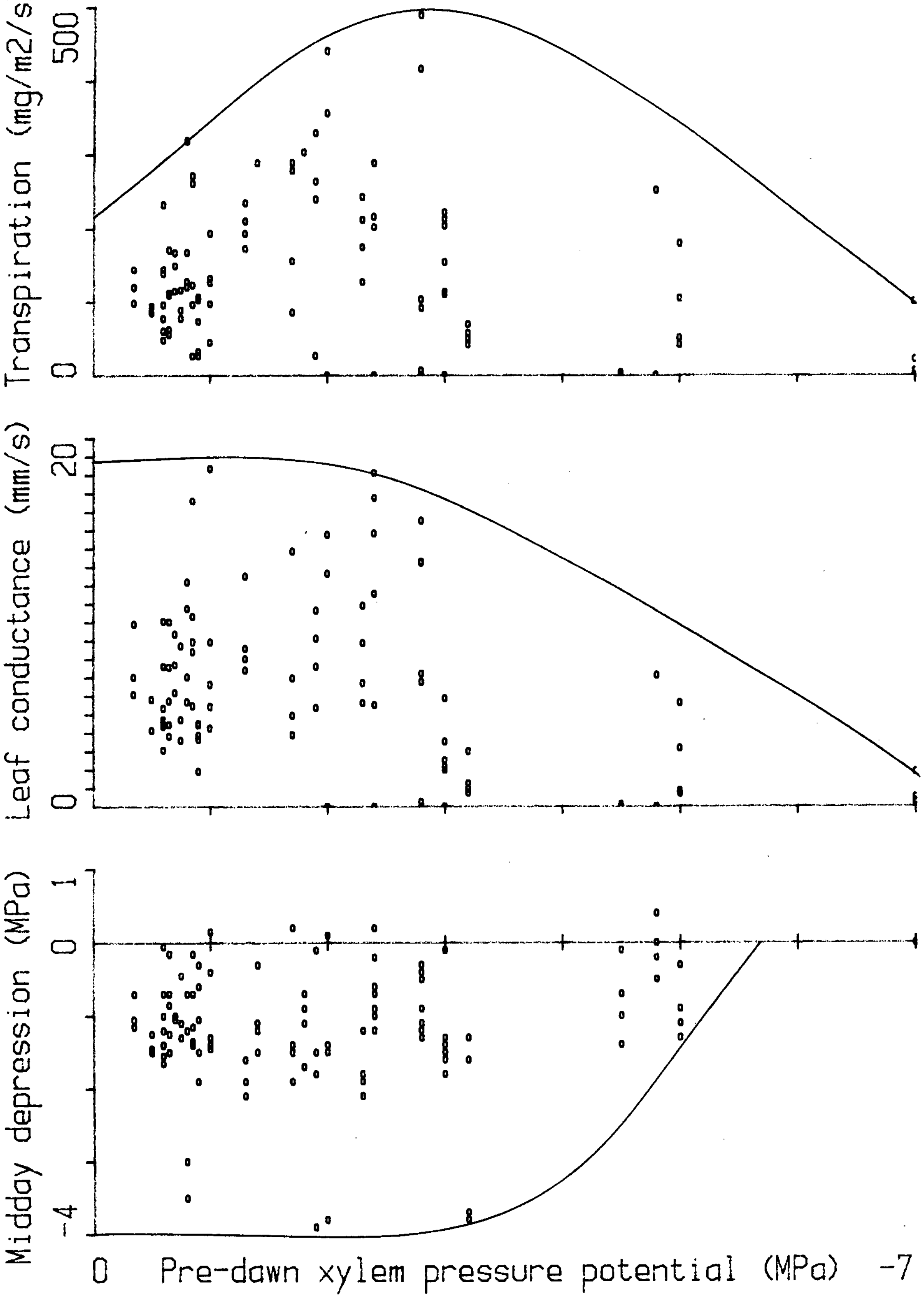


Figure 5.52 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Elytropappus gnaphaloides at site 3 .

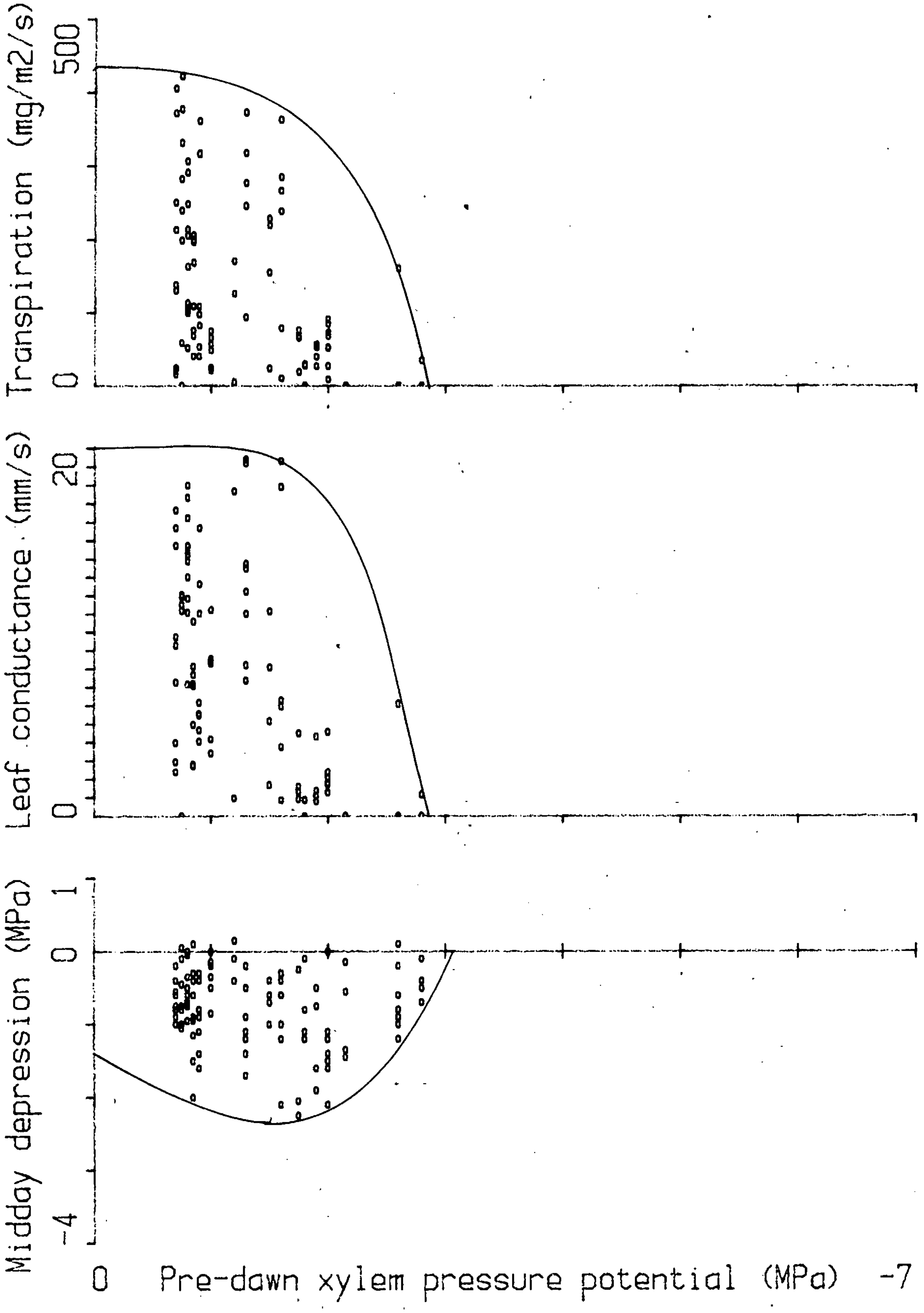


Figure 5.53 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Stoebe capitata at site 5.

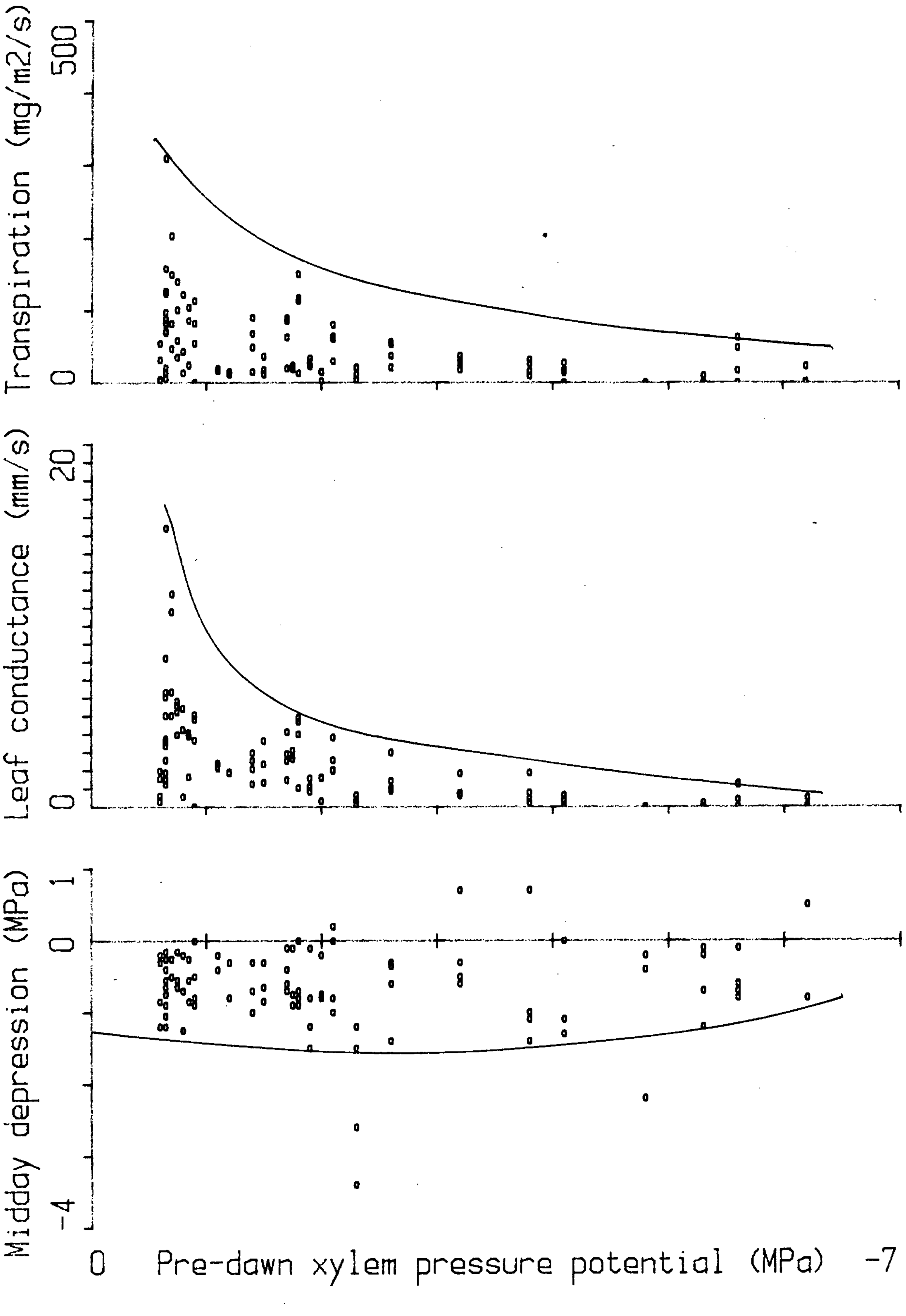


Figure 5.54 The potential maximum and the actual transpirations (mg/m2/s), leaf conductances (mm/s), and midday depressions in xylem pressure potential (MPa) as a function of the pre-dawn xylem pressure potential during the drying period July 1982 to April 1983 for Agathosma giftbergensis at site 5.

The last of the 13 species sampled, Agathosma giftbergensis, had a large seasonal variation in the pre-dawn xylem pressure potential, and must have been shallow rooted since the nearby fynbos overstory species had xylem pressure potentials almost 4 MPa higher in the middle of the summer. The leaf conductances declined as the pre-dawn xylem pressure potentials fell, but never completely prevented transpiration (Figure 5.54). The midday depressions in xylem pressure potential were uniform. As the plant adjusted the minimum xylem pressure potential that it could tolerate downwards though the year, the resulting gains in transpiration decreased since the quantities of water which caused an equal change in xylem pressure potential decreased.

5.3.8 The diurnal responses of leaf conductance to four controlling environmental parameters

During the course of a day the stomata of a plant respond to a variety of environmental cues, and the variations in stomatal aperture are the main control on the rate of leaf conductance. Transpiration is the product of leaf conductance and the vapor pressure gradient between the sub-stomatal cavity and the outside air. Because transpiration includes the environmental gradient it masks the physiological response of the plant, which is the variation in stomatal aperture. In controlling leaf conductance a plant is attempting to control transpiration while still maintaining photosynthesis. The response of transpiration to the variations in leaf conductance gauges the effectiveness of the stomatal control. During the course of the day different environmental factors limit leaf conductance at different times (Figure 5.55). In the early morning energy may be limiting, and at middle of the day water stress or excessively high rates of water loss. Between any single environmental factor and leaf conductance there is not usually a consistent relationship throughout the day, but rather a hysteresis curve as other variables become limiting (Figure 5.56). Throughout the season the shape of the diurnal hysteresis curve of leaf conductance as a function of a controlling environmental variable changes; as the pattern of the importance of the different environmental factors changes. When the hysteresis curve closes, and leaf conductances increase and decrease during the day along the same relationship, then the variable in question may be the most important variable controlling the rate of leaf conductance.

The seasonal courses of the relationships between leaf conductance and four controlling variables; xylem pressure potential, photosynthetically active photon flux, vapor pressure deficit, and temperature, and the relationships between transpiration and the same four variables are shown in Appendix 1. The leaf conductances of most species were higher in the morning and then declined in the afternoon. The four controlling variables also had a basic diurnal response of an increase until midday and then a decline. The resulting hysteresis curves therefore usually began with high rates of leaf conductance, and low levels of the controlling variable in question. The leaf conductances

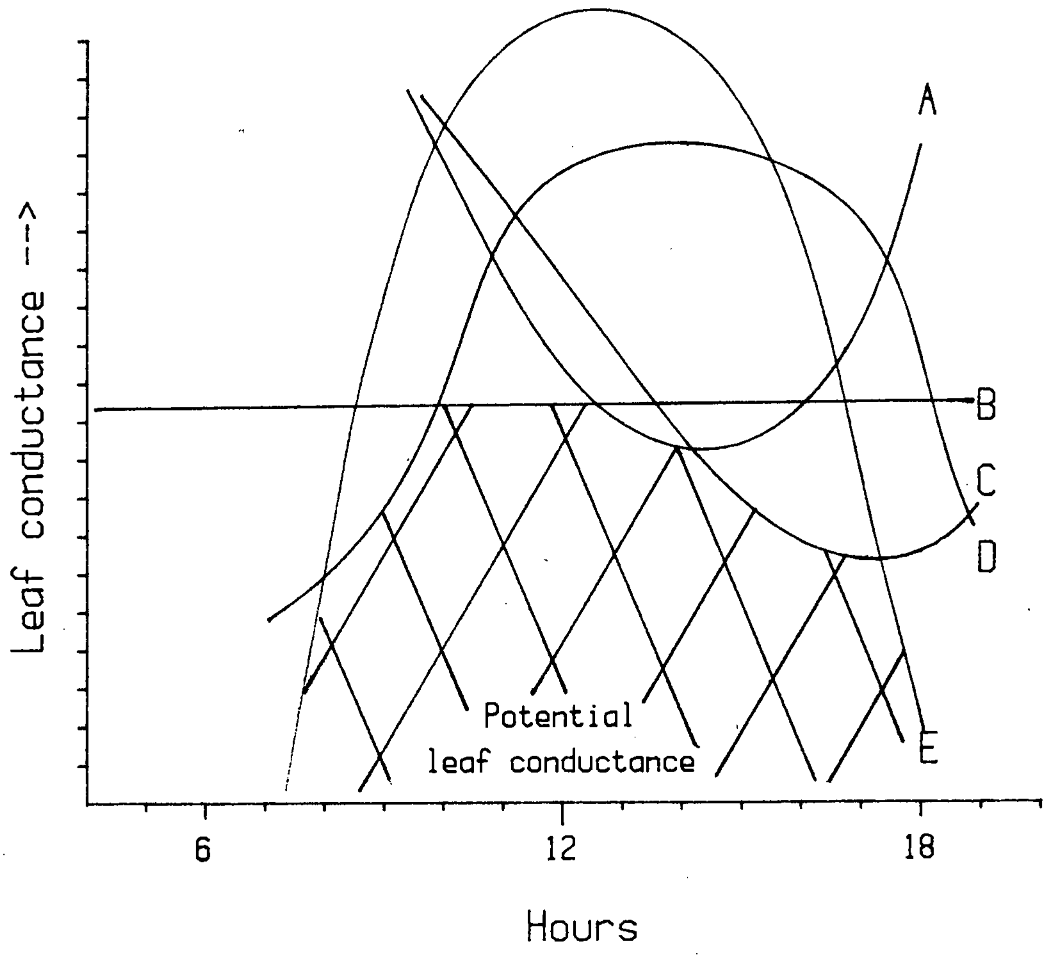


Figure 5.55 The potential maximum leaf conductance can be limited by various factors during the course of the day. In the early morning low light levels (E) or low temperatures (D) may be limiting. In the middle of the day a feedforward response to the vapor pressure deficit (A) may be limiting, and in the afternoon the depressed xylem pressure potentials (C) may cause a loss of turgor. In the morning leaf conductances may reach the genetically determined maximum rate (B).

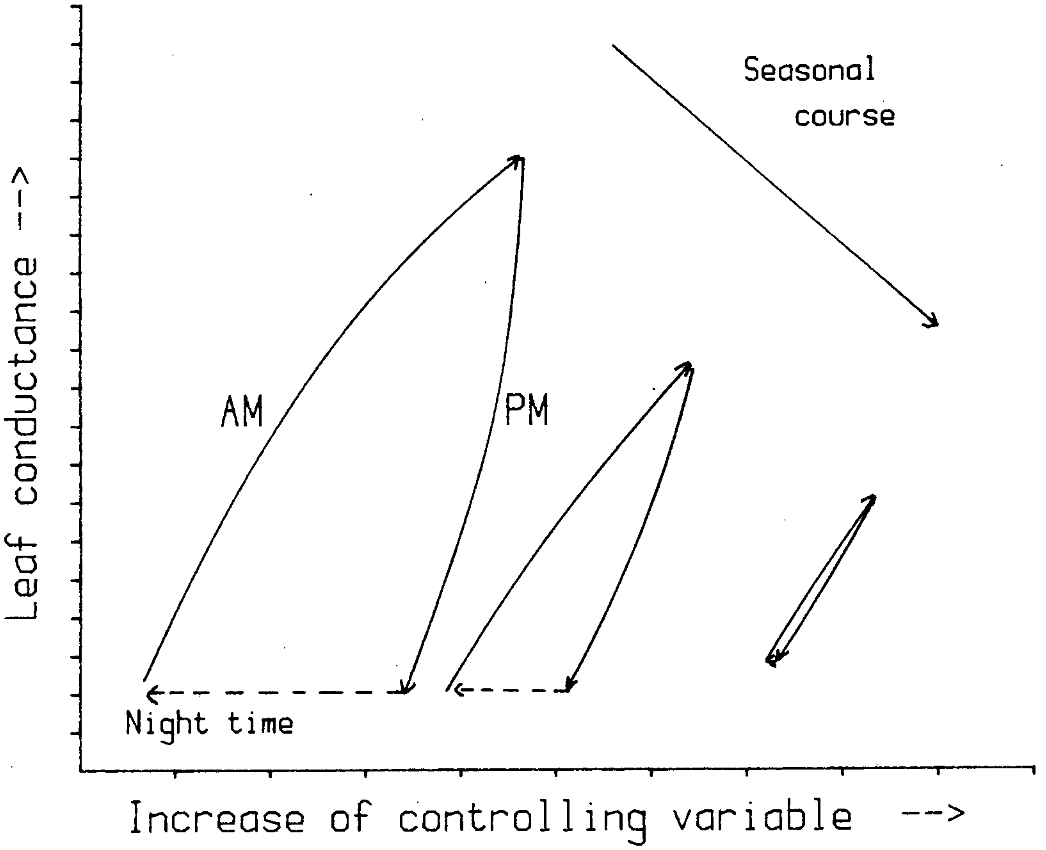


Figure 5.56 The potential seasonal course of the diurnal hysteresis of leaf conductance when expressed as a function of a controlling environmental variable. The diurnal hysteresis results when leaf conductances increase in the morning and decline in the afternoon following different relationships. During the course of the season the hysteresis loop may close, possibly showing that the variable in question has become the dominant factor controlling leaf conductance.

then began to decrease as the controlling variable increased, until midday. In the afternoon the leaf conductances continued to decrease as did the controlling variable. Even though the leaf conductances were lower in the middle of the day the transpiration rates usually increased until midday, and then declined.

In many species there was a drop in the xylem pressure potential as the transpiration rate increased, showing an inability to maintain root uptake at the same rate. When transpiration slowed in the afternoon some of the species showed little hysteresis in the relationship between transpiration and xylem pressure potential, and followed the same line during recovery as they had in the morning decline. This fixed relationship between leaf water content and xylem pressure potential would be expected, as long as there had not been significant diurnal changes in the other components of water potential. *Ruschia sp.*, *Rhus incisa*, *Rhus dissecta*, and *Eriocephalus africanus* seemed to have the largest diurnal hysteresis between xylem pressure potential and transpiration rate.

The slope of the relationship between transpiration and xylem pressure potential reflects the buffering capacity of the leaf, and the leaf water content to leaf water potential relationship. As the transpiration rate increased many of the species at the dryer end of the transect showed little change in xylem pressure potential, showing an ability to maintain root uptake, or a buffering capacity of water stored in the tissue. As the transpiration rates of many of the overstory species increased the xylem pressure potentials decreased, showing an inability to maintain root uptake. When the transpiration rates slowed the xylem pressure potentials of these overstory species recovered along the same line as they had dropped, with little diurnal hysteresis.

Rhus dissecta, *Protea glabra*, *Paranomus bracteolaris*, and *Leucadendron pubescens* all showed little diurnal hysteresis between the photosynthetically active photon flux (PAR) and transpiration. This might reflect stomatal action designed to maintain a constant photosynthesis to transpiration ratio. The direction that species followed the hysteresis curves between transpiration and PAR varied. When PAR was declining in the afternoon, the transpiration rates of most species were higher than they had been in the morning, except that of *Agathosma giftbergensis* which was lower.

The leaf conductances of none of the species exhibited a consistent response to either the vapor pressure deficit or the air temperature. There were usually large diurnal hystereses between the transpiration rates and these to parameters.

5.3.9 The potential maximum leaf conductance in response to four controlling variables

Even though the measurements of leaf conductance were made in the field, and there was no attempt to manipulate only one variable at a time, the potential maximum response of leaf conductance to decreasing xylem pressure potentials, increasing photosynthetically active photon flux, increasing vapor pressure deficits between the sub-stomatal cavity and the outside air, and increasing temperatures can be extrapolated. In most cases, lines following the theoretical shape of the potential response could be found which reasonably bounded the distribution of leaf conductances as a function of the respective variable, and these figures and the equations of the lines are in Appendix 2.

All of the species show abrupt declines in leaf conductance as a minimum xylem pressure potential was reached. Most of the species had low light saturation points for leaf conductance, and decreasing leaf conductances with increasing vapor pressure deficits. The responses of leaf conductance to vapor pressure deficit at the wetter sites, and to temperature are probably incomplete, as the extremes were never encountered. The responses of leaf conductances to low and high temperatures are probably the most incomplete, but many species do show declining leaf conductances at both high and low temperatures.

Where species were found at more than one site, the maximum conductance rates were higher at the drier site. The _Nylandtia spinosa_ at sites 1 and 3 have different responses to xylem pressure potential and PAR. At site 1 low xylem pressure potentials had a controlling influence on leaf conductance, whereas at site 3 they were not so important. At site 1 the species had a high light saturation point for leaf conductance, and a high maximum rate of leaf conductance, while at site 3 both are low.

Eriocephalus africanus also showed a decrease in the light saturation point for leaf conductance, and the maximum rate of leaf conductance, between sites 1 and 3. Between site 3 and site 5 the *Protea laurifolia* exhibited a decrease in the minimum xylem pressure potential at which leaf conductance could continue. All of the fynbos overstory species, *Protea laurifolia*, *Protea glabra*, *Paranomus bracteolaris*, and *Leucadendron pubescens* have very low light low saturation values, and low maximum rates of leaf conductance.

Other factors besides xylem pressure potential, photosynthetically active photon flux, vapor pressure deficit, and air temperature must play important roles in determining the rate of leaf conductance. One of these four factors rarely seem to be limiting, and the equations of the potential maximum leaf conductance therefore do not accurately predict leaf conductances. A Chi square test showed that for all of the species there were significant differences between the observed leaf conductances, and the leaf conductances calculated from the environmental conditions.

5.3.10 Community water and energy budgets

The yearly average transpiration rate was 65.71 $mg/m^2/s$ at site 1, 71.83 $mg/m^2/s$ at site 3, and 42.56 $mg/m^2/s$ at site 5. Assuming a 12 hour day this translates to a transpiration rate of 1036.1 mm/m^2 leaf/year at site 1, 1132.6 mm/m^2 leaf/year at site 3, and 671.1 mm/m^2 leaf/year. Based on the rainfall which occurred between 15 July 1982 and 15 July 1983, which was 247.9 mm at site 1, 411.9 mm at site 3, and 904.9 mm at site 5, the maximum leaf area index that could be supported would be 0.24 at site 1, 0.36 at site 3, and 1.35 at site 5. All three sites had a potential maximum energy input of about 7500 MJ/m^2 for the year. The calculated transpiration rate at site 1 uses 2530 MJ/m^2 leaf/year, or 34% of the incoming radiation. At site 3 the transpiration used 2760 MJ/m^2/year or 37% of the incoming radiation, and at site 5 the transpiration used 1640 MJ/m^2/year or 22% of the incoming radiation. The numbers are only rough approximations since the transpiration rates do not include the boundary layer resistance, soil evaporation and drainage have not been included, and no attempt has been made to adjust the community average transpiration rates to reflect the community composition.

5.4 Discussion

Previous measurements of the seasonal and diurnal patterns of the leaf conductances to water loss and the xylem pressure potentials of fynbos plants have not found a period when low xylem pressure potentials and restricted leaf conductances indicated water stress (Miller _et al._ 1983; Miller _et al._ in prep.). Diurnal measurements the water relations of representative species from the three characteristic components of the fynbos, the proteoid overstory, and the ericoid and restioid understory at Swartboschkloof in the Jonkershoek valley, which receives about 1600 mm/year rainfall, found relatively stable leaf conductances and xylem pressure potentials throughout the year. The xylem pressure potentials of some of the understory species were depressed for approximately one month in the middle of the summer but this had little effect on the rate of leaf conductance.

During the same summer the xylem pressure potentials of comparable species were sampled at the site 5, near the Algeria Forestry Station, of this study. The leaf conductances and xylem pressure potentials where higher at the Algeria Forestry Station than in the similar species at Swartboschkloof. This may have been because the amount and seasonal pattern of rainfall at Swartboschkloof during the 1981/82 season was closer to the long term average than the exceptionally wet spring and high rainfall in the middle of the summer which occurred at Algeria during the same period. The leaf area index was also higher at Swartboschkloof than at Algeria which could increase the transpirative losses and cause greater drying of the soil.

The leaf conductances and xylem pressure potentials of six of the thirteen species sampled in this study have been previously reported. *Rhus incisa*, *Stoebe capitata*, *Agathosma giftbergensis*, *Protea laurifolia*, *Paranomus bracteolaris*, and *Leucadendron pubescens* were measured during the summer of 1981/82. *Rhus incisa* was reported as *Rhus dissecta*, *Stoebe capitata* was reported as *Elytropappus gnaphaloides*, and *Agathosma giftbergensis* was reported as *Diosma hirsuta* in Miller *et al.* (1983) and Miller *et al.* (1984). The leaf conductances of *Stoebe capitata*, *Agathosma* *giftbergensis*, *Protea laurifolia*, and *Leucadendron pubescens* where highest in the mornings and then declined throughout the day during the 1981/82 season. All during the season the xylem pressure potentials of the four species exhibited diurnal fluctuations, but where able to recover to near the pre-dawn values before sundown (Miller *et al.* in prep.).

The late-morning leaf conductances of *Protea laurifolia* and *Leucadendron pubescens* declined slightly during the season, while those of *Stoebe capitata* and *Agathosma giftbergensis* increased from November to December, before dropping in January. In 1981/82 the pre-dawn xylem pressure potentials of *Protea laurifolia* and *Leucadendron pubescens* were nearly constant, as were those of *Stoebe capitata*, while those of *Agathosma giftbergensis* dropped in January (Miller *et al.* 1983). In December 1981 the midday leaf conductances of *Rhus incisa* were 15.1±2.1 mm/s, while those of *Agathosma giftbergensis* were 13.0±0.8 mm/s, those of *Protea laurifolia* were 2.3±0.4 mm/s, those of *Paranomus bracteolaris* were 2.9±0.5 mm/s, and those of *Leucadendron pubescens* were 1.4±0.1 mm/s. The xylem pressure potentials of *Rhus incisa* in December 1981 varied between the pre-dawn value of -1.2±0.1 MPa and the midday value of -3.2±0.2 MPa. The xylem pressure potentials of *Agathosma giftbergensis* were between -1.1±0.0 MPa and -1.8±0.0 MPa, while those of *Protea laurifolia* were between -0.4±0.0 MPa and -1.5±0.2 MPa, those of *Paranomus bracteolaris* were between -0.5±0.1 MPa and -1.5±0.1 MPa, and those of *Leucadendron pubescens* were between -0.3±0.0 MPa and -1.3±0.1 MPa (Miller *et al.* 1984).

The leaf conductances during the 1982/83 season were generally lower than those found in 1981/82, reflecting the lower, and closer to the long term average, rainfall in 1982/83. The xylem pressure potentials were also lower in 1982/83 than they were in 1981/82.

The leaf conductances reported for species from other mediterranean-type ecosystems have generally been slightly lower than those found in the fynbos. Poole and Miller (1978) found that the maximum leaf conductances of several evergreen sclerophyllous species in Chile were between 1.3 and 3.3 mm/s. Roberts (1982) found that in 5 matorral species in central Chile the leaf conductances at the height of the drought were between 1.5 mm/s and 4 mm/s in the morning, and then declined during the day. Gigon (1979) found similar leaf conductance rates on matorral plants that were growing at an experimental garden at Stanford, California. Maximum leaf conductances of chaparral species in southern California were below 3 to 5 mm/s throughout the year (Miller and Poole 1979). Leaf resistances (the inverse of leaf conductance) of these species were generally lowest in the morning and then increased during the day (Poole and Miller 1975). Leaf conductances below 4 mm/s were also found in three montane chaparral species in northern California (Conard and Radosevich 1979), and in plants near San Francisco (Mooney _et al._ 1975). In western Australia Hellmuth (1971) found transpiration rates of between 30 and 40 $mg/m^2/s$.

The seasonal range of the xylem pressure potentials found in this study were similar to those reported for other mediterranean- type ecosystems. Poole and Miller (1975) found that the minimum xylem pressure potentials of some of the species in the chaparral and coastal sage communities reached below -6.5 MPa, while others in the same community remained above -2.5 MPa. All through the year they found that the xylem pressure potentials would begin recovering before sunset, and in many cases almost attained the pre-dawn values. In the matorral Giliberto and Estay (1978) found minimum xylem pressure potentials in the late summer of at least the -4 MPa limit of their pressure chamber. Margaris (1977) found water potentials down to -3.5 MPa in the drought-deciduous phrygana of Greece, and Hellmuth (1971) reports osmotic potentials between -4 and -8 MPa for various species in Western Australia.

In order for the plants in mediterranean-type ecosystems to maintain the observed leaf conductances at the low xylem pressure potentials they must be able to maintain turgor and stomatal functioning. In order to maintain a positive leaf pressure potential the leaf osmotic potential must be lower than the xylem pressure potential. It is doubtful that the plants maintain these low osmotic potentials all during the year, since during the winter the large pressure potentials would require mediating in order to continue stomatal functioning. It is more likely that there is a downwards adjustment of the osmotic potential during the course of the summer drought, and then a recovery of the osmotic potential with the autumn rains. Many species in mediterranean-type ecosystems also experience large diurnal fluctuations in xylem pressure potential.

Measurements of the osmotic potential in the morning in chaparral species, and then the diurnal pattern of xylem pressure potential have found that leaf conductances were able to continue beyond the calculated point of turgor loss (Roberts *et al.* in press). Subsequent measurements of the diurnal course of osmotic potentials of chaparral species have found a diurnal shift in the water potential where turgor is lost of up to -0.4 to -0.6 MPa (Roberts and Bowman in press). Calkin and Pearcy (1982) found that the osmotic potentials of *Heteromeles arbutifolia*, an evergreen sclerophyllous chaparral species, underwent seasonal adjustments of about 2 MPa, which allowed the continuation of leaf conductance, while the osmotic potentials of *Aesculus californica*, a drought-deciduous species, did not adjust, and the species had to reduce the rate of leaf conductance. The third species they studied, *Cercis accidentalis* was able to continue leaf conductances even though the xylem pressure potential dropped below the point of turgor loss calculated from pressure-volume curves made on tissue sampled pre-dawn.

The differences in the ability of the plants in this study to modify the leaf osmotic potentials may explain many of the observed patterns of leaf conductance and xylem pressure potential. *Eriocephalus africanus* showed the greatest ability to continue leaf conductance at low xylem pressure potentials, and probably had the largest seasonal adjustments of the osmotic potential. The fynbos overstory species *Protea laurifolia*, *Protea glabra*, *Paranomus bracteolaris*, and *Leucadendron pubescens* and *Ruschia sp.*, and the fynbos understory species *Stoebe capitata* followed two different seasonal patterns of water relations resulting from having little ability to continue leaf conductance at low xylem pressure potentials.

From the magnitude of the diurnal fluctuations in the xylem pressure potential of *Eriocephalus africanus* it would seem that the species maintained the osmotic potential about 1.5 MPa below the pre-dawn xylem pressure potential. Somewhere between the pre-dawn xylem pressure potentials in January, which allowed leaf conductance to occur, and the pre-dawn xylem pressure potentials in April, which did not allow the stomata to open during the day, was the xylem pressure potential corresponding to the point of turgor loss, and the maximum ability of the osmotic potential to adjust on a seasonal basis. This pattern of a consistent adjustment of the osmotic potential until a minimum threshold, and then a sudden loss of turgor with slightly lower water potentials has also been found in wheat species (Morgan 1980). The xylem pressure potentials that triggered leaf shedding in *Rhus dissecta* and *Rhus incisa* probably corresponded to the point of turgor loss because without the transpirative cooling the leaves would probably overheat and suffer permanent damage.

In the middle of the summer, when the vapor pressure deficits were high, *Eriocephalus africanus* had high rates of transpiration and yet did not have larger midday depressions in the xylem pressure potential than occurred earlier in the season. With the higher transpiration rates there may have been a reduction in the root resistances to water uptake and the internal resistances to water movement (Oosterhuis 1983). A decrease in leaf area may also have allowed a higher rate of water loss for the remaining leaves. *Galenia africana* was also able to maintain leaf conductances at low xylem pressure potentials, but reduced the rates of leaf conductance in the middle of the summer in order to maintain constant rates of water loss.

Although most species exhibited some inter-site plasticity in the response to water stress none showed patterns as different as *Nylandtia spinosa*. The midday depressions in xylem pressure potential at site 1 were largest when the transpiration rates were highest, similar to the pattern of the two *Rhus* species. As with the two *Rhus* species, *Nylandtia spinosa* at site 1 then reduced the rates of water loss at low pre-dawn xylem pressure potentials, but through stomatal action rather than through the reduction of leaf area. At site 3 the pattern of water relations of *Nylandtia spinosa* was similar to that of *Eriocephalus africanus*, with continued low levels of leaf conductance at low xylem pressure potentials.

The overstory species, *Protea laurifolia*, *Protea glabra*, *Paranomus bracteolaris*, and *Leucadendron pubescens*, and *Ruschia sp.* all seemed to have a seasonally fixed xylem pressure potential which corresponded to the loss of leaf turgor. The maximum leaf conductances of these species had an almost linear relationship between the maximum rates found with high pre-dawn xylem pressure potentials and the minimum rates when the pre-dawn xylem pressure potentials approached -2 MPa. The restriction of leaf conductances when xylem pressure potentials dropped below -2 MPa will limit the four overstory species to mesic areas. The response of the stomata was sufficient to modulate the transpiration rates, and seasonal carbon balance studies would be necessary to determine how long of a period without photosynthesis (i.e. how long of a period of drought) the species could endure.

The overstory species maintained slight leaf conductances all during the year. The maintenance of low levels of leaf conductance, even during the night, has been observed in other members of the Proteaceae growing in green-houses (Schütte pers. comm.). This is thought to be advantageous since it allows the plant to maintain an internal water potential gradient. By maintaining an internal water potential gradient, and a low rate of transpiration, the plant may not have to subject the leaves to a period of stress in the morning before overcoming the lag of the transpirative stream through the plant. In an arid area, such as the area studied, the vapor pressure deficits develop very quickly in the morning. It would be advantageous for a plant to be able to keep up with the increasing evaporative demand, and not have to close the stomata because the lag in the transpirative stream had caused enough stress in the leaves to loose turgor. Part of the lack of an observed midday stomatal closure may be because of this pattern of maintaining a potential gradient.

The fynbos understory species Elytropappus gnaphaloides, Stoebe capitata, and Agathosma giftbergensis followed three different patterns of water relations.

Elytropappus gnaphaloides showed little moderation of leaf conductances until the pre-dawn xylem pressure potentials dropped below -3 MPa. Leaf conductances, transpiration rates, and midday depressions in xylem pressure potential then decreased and were near zero when the pre-dawn xylem pressure potentials were near -7 MPa. *Stoebe capitata*, like the fynbos overstory species, seemed to have had a fixed osmotic potential. Unlike the fynbos overstory species, *Stoebe capitata* maintained maximal leaf conductances until the point of turgor loss and then exhibited a sharp decline. The midday depressions in xylem pressure potential increased until the turgor loss point, after which transpiration stopped. This pattern, which usually leads to wilting, has been found in some crop plants (Turner 1974), and does not seem to be a pattern that would be particularly advantageous in an arid environment. *Agathosma giftbergensis* exhibited a pattern of water relations that may reflect an inability to limit water loss. The species had high leaf conductances when the pre-dawn xylem pressure potentials were low, and then continuing low levels of leaf conductance as the xylem pressure potentials dropped.

The leaf conductances of most of the species, except for *Rhus dissecta* which had shed its leaves several months earlier, only completely stopped, due to water stress, on the sampling trip in April. The midday xylem pressure potentials of most of the species were as low in January as as they were in April. The drop in the pre-dawn xylem pressure potentials of most of the species between January and April seems to have had the controlling roll in determining turgor, and therefore the possibility of leaf conductance, for the day. None of the species exhibited strong midday reductions in leaf conductance resulting from either the loss of turgor in the middle of the day and "wilting" or a feedforward mechanism sensing high rates of water loss. Instead there may have been diurnal shifts in osmotic potential similar to those measured in the chaparral, especially in those species which had large diurnal fluctuations in xylem pressure potential. The active production of photosynthates may have helped shift the osmotic potential. The increase in the osmotic potential due to the production of photosynthates would explain why some of the plants were able to continue leaf conductance at the midday xylem pressure potentials in January that were lower than the pre-dawn values in April, when the plants were unable to open the stomata in the morning or continue leaf conductance during the day.

Stomata respond to a variety of environmental phenomena, of which light and water stress are probably the most important, although the vapor pressure deficit, carbon dioxide concentrations, and temperature are also involved (Cowan 1978). Miller and Poole (1979) found nearly linear reductions in leaf conductance with decreasing xylem pressure potentials in seven species from the evergreen sclerophyllous chaparral and the seasonally deciduous coastal sage communities. Specht (1957) found that the transpiration of _Banksia ornata_ usually declined with decreasing relative humidities. Schulze _et al._ (1975) found that although the daily changes in water potential had little effect on the daily course of stomatal resistance there was a linear decline in water potential with increasing transpiration rates in Prunus armeniaca in the Negev desert of Israel.

Jarvis (1976) found, as in this study, that the equations describing leaf conductance developed from the upper bounds of field data plotted against concurrent environmental conditions did not account for a large percentage of the variability of the leaf conductance. However, Jarvis (1976) found that the residuals of the observed data against the calculated data were equally distributed around zero. The response of the fynbos overstory species to photosynthetically active photon flux follows the pattern of low light saturation values and low maximum rates of photosynthesis found by Mooney et al. (1983) for various Protea species at Jonkershoek. The higher light saturation values, and higher maximum rates of leaf conductance of the understory and drought deciduous species follows the patterns of photosynthesis found in the chaparral and coastal sage communities in California (Oechel et al. 1981).

Because the leaf conductances found in the study are higher than found in California, the transpiration rates are higher. The community average transpiration rates reported here are about twice the maximum values found in some species in the chaparral (Miller and Poole 1979). The energy requirements of the community average transpiration rates in this study are, on an annual basis, about four times that calculated for the chaparral (Miller et al. 1981).

6. GENERAL DISCUSSION

In other mediterranean-type ecosystems the presence and the length of a summer drought has been hypothesized to be critical for the development of the vegetation type (Miller and Mooney 1976; Miller 1979). In the mediterranean-type ecosystems of Chile and California the distribution of the drought-deciduous and evergreen sclerophyll communities has been explained by the differences in photosynthetic efficiencies, and patterns of drought avoidance and/or drought tolerance of the species involved. Where there is a summer drought longer than 90 days, which occurs with annual rainfalls below about 250 mm/year, drought-deciduous species should dominate the plant community. When there is a period of drought less than 90 days, which occurs with annual rainfalls of approximately 250 to 600 mm/year, evergreen shrubs should be dominate, and when there is not a period of summer drought, in areas with over 600 mm/year, there should be forests. Cowling and Campbell (1980) have hypothesized that in the western Cape of South Africa the low levels of nutrients in the soils preclude the viability of the drought-deciduous growth form. Just as the nutrient supplies are not sufficient to re-create new leaves each year, Cowling and Campbell (1980) also hypothesize that it is the lack of nutrients that prevents a forest from developing in the wetter areas. They found that as the annual rainfall levels dropped a community dominated by succulents replaced fynbos, and with high rainfall fynbos was not replaced by a forest, but rather continued since canopy development became nutrient limited rather than water limited.

As the summer drought progresses in the chaparral, Miller (1979) hypothesized that the deciduous communities should be the first to show symptoms of water stress, and that there should then be a pattern in the evergreen communities of stress developing at the dryer edges and working inwards towards the areas with higher rainfall. Poole and Miller (1981) found, however, that the length of the period of water stress was similar throughout the distribution of the chaparral, irregardless of the annual rainfall. They found that with increased annual rainfall the leaf area index of the chaparral community increased such that transpiration was reduced to 150-200 mm/year/unit leaf area. In the chaparral nutrient limitations do not seem to be as important as they are in the fynbos, and as the limitation by water decreases, the biomass can increase and the tree growth form become dominant.

Within the chaparral of southern California species with high leaf conductances, shallow roots, and seasonally variable water potentials were more common toward the arid edge, and species with low leaf conductances, deep roots, and seasonally stable water potentials were more common at the moist edge (Miller _et_ _al._ 1983). In the dryer areas the limited rainfall does not deeply penetrate the soil, and plants not only have to compete with their neighbors for water but also have to compete against soil evaporation since there is not a complete canopy cover. With increasing levels of rainfall, which can penetrate the soil further, and the development of a closed canopy, which limits soil evaporation, the more successful growth strategy is to have deep roots that will allow stable water potentials and photosynthesis on into the drought.

In the more mesic areas of the chaparral Poole and Miller (1981) found that some species underwent water stress while others did not. These differences are probably a reflection of the differences in the rooting depth of the species, with the deeper rooted species dropping the level of available water to below the rooting depth of the shallow rooting species. The seasonal course of water stress has been closely related to the depth and distribution of the roots of plants in the chaparral (Poole and Miller 1975), the Chilean matorral (Giliberto and Estay 1978), and has been hypothesized to be important in the fynbos (Miller *et al.* 1983).

Specht (1972) hypothesized that in a climax community the soil moisture is fully utilized, and that plants should moderate transpiration so that carbon uptake can continue throughout the year. The plants should be adapted to exhaust the soil moisture just before the next winter rains, thereby allowing the possibility of continuous photosynthesis and growth. Miller and Poole (1979) point out that a "cheater" would be benefited by the conservative nature of its neighbors, and that only in a mono-specific community would one expect to find water conservation. They found that the pure stands of Adenostoma fasciculatum showed slight water conservation, and that these pure stands could be found in areas that were too dry to support stands of mixed chaparral. Roberts et al. (1981) also reported that Adenostoma fasciculatum in pure stands had lower leaf conductances than Adenostoma fasciculatum in mixed stands, but that in pure stands the individuals had lower water potentials. This would seem to mean that the pure stands were not limiting their leaf conductance in order to conserve water, but were rather undergoing more water stress since the intraspecific pressures where stronger than the interspecific pressures. It would therefore seem that in areas with limiting water supplies it would never be beneficial for a plant to limit water use when competition for water is present.

Along the precipitation gradient studied by Poole and Miller (1981) in southern California there was a switch in the dominant vegetative growth form from drought-deciduous soft-leaved shrubs, through evergreen sclerophyllous shrubs, to evergreen and winter-deciduous trees. Along the rainfall gradient in this study the dominant plant growth forms followed the pattern found by Cowling and Campbell (1980). At the xeric extreme the community was dominated by succulents, and as the rainfall increased there was a small zone of predominantly drought-deciduous shrubs, which where heavily grazed, and then a community of evergreen sclerophyllous shrubs.

Comparisons between the spatial and temporal patterns of water stress of individuals and of the community in the fynbos and the chaparral indicate that different controls on canopy development may be present. The canopy development in the chaparral seems to be water-limited, and leaf area index increases with increasing rainfall such that the annual transpiration rate throughout the range of the chaparral is similar (Poole and Miller 1981).

The pattern of community average pre-dawn xylem pressure potentials along the transect between Clanwilliam and the Algeria Forestry Station show variations in both the length of the period of water stress, and the depth of water stress. The pattern of water stress follows the earlier hypothesis of seasonal patterns of water stress in the chaparral (Miller 1979). This hypothesis can only work if some factor other than water is limiting canopy development, and there is a relatively uniform leaf area with increasing levels of rainfall. This will result in longer periods of water stress in dryer areas and shorter periods of stress in wetter areas. Below site 3 the leaf area index seems to be changing, and there is a relatively uniform pattern of water stress. Above site 3 the leaf area index seems to become limited by some factor other than water, which explains the decreasing periods of water stress from site 3 to site 5. The patterns of stress at the community level are partly due to the replacement sequence of species which, although may not be "maximizing resource use efficiency", is inevitable, and partly due to the patterns of stress within each species. The presence of the fynbos overstory species, which are unable to grow in the drier areas and then shade out the understory species, and their contribution to the community average xylem pressure potentials cause must of the transition at site 3.

The patterns of midday depression in xylem pressure potential at the community level also show that the canopy at the mesic end of the transect does not seem to be as dense as it could be if water was the primary limiting agent. In the winter there is insufficient transpiration to cause midday depressions as large as occur in the drier areas. In summer the canopy does not dry the soil enough to cause the long periods of stress related reduction of midday depression found below site 3.

The species responded to the summer drought with one of three patterns of water relations. Species either postponed dehydration by limiting water loss and therefore maintaining high water potentials, endured dehydration and maintained the rates of water loss with the consequent seasonally variable water potentials, or escaped the drought by being either seasonally deciduous or succulent. From the mesic to the xeric end of the transect there was a pattern of species replacement to species with greater ability to endure water stress. Species that postponed dehydration were replaced by those that endured dehydration, and then by those that escaped the drought. Within each species there was also plasticity in the response to water stress, with the individuals at the drier sites maintaining leaf conductance at lower xylem pressure potentials those those at the wetter sites.

The pattern of water relations marked by seasonally stable xylem pressure potentials, limited leaf conductances, and stress sensitive stomata was found in the fynbos overstory species, *Protea laurifolia*, *Protea glabra*, *Paranomus bracteolaris*, and *Leucadendron pubescens*, and the succulent *Ruschia sp.* found only at the driest site. The xylem pressure potentials of the fynbos overstory species never dropped much below -2 MPa. As the pre-dawn xylem pressure potentials dropped to -2 MPa the maximum leaf conductance rates declined, and then stopped completely. *Ruschia sp.* had a similar pattern, but a minimum xylem pressure potential limit of about -3.5 MPa. The fynbos overstory species had low maximum rates of leaf conductance. Low metabolic rates would be advantageous for these species since the respiratory costs would be less during the period when the seasonal drought was sufficient to cause stomatal closure. In order for the overstory species to gain their stature they must shunt growth into stems instead of leaves and roots. In a post fire community this allocation pattern would cause these species to be shaded by the faster growing understory species, and the species exhibited low light saturation points for leaf conductance. It would also have been advantageous for the overstory species to have lower metabolic rates than the understory species in order to reduce the maintenance respiration costs of the stems. The light saturation point for photosynthesis and the maximum rates of photosynthesis presumably follow the pattern of the leaf conductances to water loss. The fynbos overstory species seemed to have high root resistances to water uptake, or internal resistances to water transport, which caused the leaves to experience sufficient water stress, in the middle of the winter when the soils were wet, to close the stomata and limit the maximum rate of water loss.

Ruschia sp. exhibited the diurnal patterns of water relations of a non-CAM plant when there was sufficient water so that the species was not stressed. Towards the end of the summer, when the stomata were closed during the day, the midday xylem pressure potentials were often higher than the pre-dawn values, possible reflecting a switch to Crassulacean acid metabolism and water loss during the night.

At least one of the two seasonally deciduous species, *Rhus incisa* and *Rhus dissecta* was found at each site along the transect. Both species only occurred at site 2. The glaucous-leaved *Rhus incisa* was found at the driest two sites along the transect, and the dark-green leaved *Rhus dissecta* at the wettest four sites. At site 2 *Rhus dissecta* shed its leaves several months earlier than *Rhus incisa*. *Rhus incisa* had both larger diurnal variations in xylem pressure potential and larger seasonal variations than *Rhus dissecta*. *Rhus incisa* exhibited considerable plasticity in the response to water stress. At site 5 the species reduced the diurnal fluctuations in xylem pressure potential, and shed its leaves, at much higher pre-dawn xylem pressure potentials than at site 2. The individuals at the dryer sites were able to endure more water stress than those at wetter sites. As with many of the species found at the more open xeric sites, the two *Rhus* species did not seem to be able to tolerate shading. The most vigorous *Rhus dissecta* occurred at site 3, and the individuals in the understory at site 5 were rather etiolated.

The remaining species, *Galenia africana*, *Nylandtia spinosa*, *Eriocephalus africanus*, *Elytropappus gnaphaloides*, *Stoebe capitata*, and *Agathosma giftbergensis* showed varying abilities to maintain leaf conductance with decreasing xylem pressure potentials. The ability to retain turgor and stomatal functioning probably resulted from osmotic adjustment during the season. *Eriocephalus africanus* showed the greatest ability to maintain leaf conductance, and had consistent diurnal fluctuations in xylem pressure potential of about 1.5 MPa. This may represent the approximate magnitude of the leaf pressure potential as the leaf osmotic potential decreased during the season. Because *Eriocephalus africanus* maintained the rate of leaf conductance, while the vapor pressure gradients increased in the middle of the summer, the species had increasing transpiration rates at low pre-dawn xylem pressure potentials. The species must have been able to reduce the root resistances to water uptake, or reduce the leaf area, with higher transpiration rates since the diurnal fluctuations in xylem pressure potential did not increase.

Nylandtia spinosa had higher transpiration rates, more reactive stomata, and higher xylem pressure potentials at site 1, the driest site, than at site 3. This pattern of high rates of water use, and then stomatal closure would have increased the amount of moisture utilized by the plant instead of lost to soil evaporation. At the wetter site, where the rain more deeply penetrated the soil and allowed a continuing water supply, the species had low rates of leaf conductance, but continued leaf conductance at very low xylem pressure potentials.

The three fynbos understory species sampled exhibited three different patterns of water relations. Elytropappus gnaphaloides and Stoebe capitata were physiognomically identical, and both had high leaf conductances probably due to the under measurement of the leaf area. Elytropappus gnaphaloides had large seasonal variations in the xylem pressure potential, but at low pre-dawn xylem pressure potentials reduced the leaf conductances and limited the diurnal fluctuations in xylem pressure potential. Stoebe capitata did not seem to be able to regulate the rate of water loss during the day. As the pre-dawn xylem pressure potentials decreased there were increasing diurnal fluctuations in the xylem pressure potential, until its stomata were no longer able to open and the plant effectively "wilted". Agathosma giftbergensis had high leaf conductances when the xylem pressure potentials were high, and then continued low levels of water loss during the rest of the drought. The individuals at site 4 had much lower xylem pressure potentials than those at site 5. Agathosma giftbergensis did not seem to be able to limit water loss on a seasonal time scale in order to maintain the xylem pressure potentials.

The fynbos overstory species Protea laurifolia, Protea glabra, Paranomus bracteolaris, and Leucadendron pubescens were unable to make seasonal adjustments in the osmotic potential, and lost turgor on a seasonal basis as the pre-dawn xylem pressure potentials fell. The presence of photosynthates may have modified the osmotic potential on a diurnal basis, as the plants were able to continue leaf conductance at midday xylem pressure potentials that prohibited it when they occurred pre-dawn. The high xylem pressure potentials corresponding to the point of turgor loss would limit these species to mesic areas where the period without turgor sufficient to continue photosynthesis would be short enough to allow a positive carbon balance. *Stoebe* capitata did not seem to be able to regulate water loss on a diurnal basis, resulting in a loss of turgor, and *Agathosma giftbergensis* did not seem to be able to regulate water loss on a seasonal basis, resulting in very low xylem pressure potentials.

The evergreen sclerophyllous fynbos species, which were limited to the wetter end of the transect, had increasing periods of water stress and decreasing minimum xylem pressure potentials at the drier sites of their distribution. From this pattern, and the lack of a switch in soil type, it would seem probable that the boundary of the distribution of these species was determined by water. These species did not extend along the transect below rainfalls of about 400 mm/year, which is similar the the boundary that has been calculated and found for the evergreen sclerophyllous species in the mediterranean-type ecosystems of Chile and California.

The transect in this study did not extend towards the coast as did the transect studied California, and should rather be compared to the inland gradients in those studies.

The evergreen sclerophyllous shrub community in this study was replaced by a community of drought-deciduous and succulent species, which is the same pattern as occurs at the inland boundary of the chaparral in California. The gradient toward the drier communities along the coast in Chile and California have fewer succulents and more drought-deciduous species as a result of the maritime influence bringing lower temperatures and vapor pressure deficits.

The seasonal patterns, and the annual totals, of the rainfall at the five sites along the transect in this study were similar to that found in drought-deciduous and evergreen sclerophyllous communities of the mediterranean-type ecosystems of Chile and California. The period of water stress, and the boundaries of the drought-deciduous and the evergreen sclerophyllous communities, in relation to the rainfall levels, were similar in the fynbos to the distributions found in chaparral and the matorral. It would therefore seem probable that there are similar selective pressures present. The responses of the fynbos species do not, however, seem to be particularly adaptive to arid conditions. At the wetter three sites, that had fynbos vegetation, the decreasing patterns of water stress at both the species and the community level does not seem to follow the hypothesized pattern in mediterranean-type ecosystems of a vegetation responding to water limitation.

With increasing total rainfall there was a distinct reduction in length of the period of water stress and the minimum xylem pressure potentials at both the community level, which included species replacement, and at the species level. In the chaparral of California the biomass, and the leaf area index, increased with increasing rainfall so that the community transpiration caused a uniform period of water stress throughout the distribution of the vegetation type. Whereas the chaparral responded to water as the primary control on biomass throughout its distribution, the biomass in the fynbos seems to quickly become limited by some other factor. This second limitation does not allow the transpiration rate, which is fixed per unit leaf area, to increase with increasing leaf area and does not dry the soil enough to cause water stress. At the community level there is a discontinuity in the pattern of water stress at the boundary between evergreen sclerophyllous fynbos community and the drought-deciduous and succulent communities. The lack of the fynbos overstory species below site 3 creates a large decrease in the community average xylem pressure potentials.

Although xerophyllic characteristics such as high resistances to water loss may not hinder growth in nutrient deficient areas where there are low photosynthetic rates because of low rates of carbon fixation at the cellular level, xeromorphy resulting from nutrient deprivation does not necessarily preadapt a species for arid environments. The distribution of the fynbos in the western Cape follows the distribution of the Table Mountain Sandstone derived soils, rather than the mediterranean-type climate. Because of this, and the observed patterns of water relations of the fynbos species that did not seem to be adaptive to survival in arid areas, and the lack of a consistent period of water stress with increasing rainfall it would seem that fynbos may be functionally more similar to heath vegetation, whose xeromorphic characteristic have resulted from nutrient deficiency, than to the vegetation of a mediterranean-type ecosystem, which is truly xerophytic. The low levels of the soil nutrients limit the biomass, and therefore the community water use, and allows fynbos to extent into relatively arid areas.

The performance of pine plantations, and the escape of various introduced forest species into fynbos areas would seem to negate the idea that the soils are too impoverished to support more biomass. The pattern of water relations found in this study would also exist in vegetation that was restricted to a narrow band of rainfall levels, between about 400 and possibly 700 mm/year, above which a forest occurred with a very short, or no period of summer drought. Unlike in the northern hemisphere and to some extent in South America, where there are land masses towards the poles, there is not a refuge from global climatic changes for temperate forest species in southern Africa and Australia. In Australia the eucalyptus seems to have enough plasticity in growth form to fill the tree "niche". In southern Africa the potential for adaptive radiation seems to be limited, and an indigenous version of the various pines, which must have higher nutrient uptake abilities than fynbos plants, does not seem to exist.

A better understanding of the selective pressures that exist in the fynbos could improve the management of these ecosystems. Short rotation burning cycles may be able to reduce the biomass accumulation in a mediterranean-type ecosystem before it becomes water limited, and increase the water yield without destroying the nutrient supplies. However, shorter burning cycles in the fynbos are only going to cause a switch from a slow growing, low transpiration _Protea_ community to a faster recovering, higher transpiration restio and understory species community. The area with a short burning cycle may show more water yield for a short period following fire, but because of the fast regrowth, and high transpiration rates will soon show less water yield than and area with a long burning cycling covered with slow growing _Proteas_. In both of the "mature" communities there should be similar biomass and leaf area indices, since production is nutrient limited. Because of the vertical structure of they _Protea_ overstory species there may be slightly higher biomass and water use in old vegetation with long burning cycles.

7. CONCLUSION

The plants sampled at the five sites along the transect between the town of Clanwilliam, which had an average annual rainfall of about 225 mm/year, and the Algeria Forestry Station, which received about 675 mm/year rainfall, experienced a period of water stress in the summer sufficient to cause stomatal closure. From the mesic end of the transect, at site 5, to site 3 the plants showed increasing periods of water stress, and decreasing seasonal minimum xylem pressure potentials. Many of the evergreen sclerophyllous overstory species that characterize fynbos did not extend to site 3, and none of the fynbos species continued past site 3. Following the switch in vegetation type at site 3, from the evergreen sclerophyllous fynbos to the drought-deciduous and succulent dominated communities, the period of water stress and the minimum xylem pressure potentials during the season remained similar along the rest of the transect.

The fynbos overstory species had seasonally stable xylem pressure potentials, and reduced leaf conductances and the rates of water in the middle of the summer. Because the species were unable to continue leaf conductance when the pre-dawn xylem pressure potentials approached -2 MPa the species were limited to the wetter areas of the transect.

The fynbos understory species either exhibited an inability to limit the rate of water loss resulting in a loss of turgor in the middle of the summer, or an inability to stop water loss resulting in very low xylem pressure potentials but with only minimal leaf conductance rates.

The species which replaced fynbos at the more xeric sites were able to continue leaf conductances at very low xylem pressure potentials, probably through the adjustment of the osmotic potential. Other species in the more arid communities were either seasonally deciduous, or possibly switched to Crassulacean acid metabolism during the season.

Because there was not a consistent pattern of water stress all along the transect, which would result from water being the primary limit on the biomass, it would seem that some other factor becomes limiting at high levels of rainfall, where fynbos is found. Fynbos species did not exhibit patterns of water relations that were clearly adaptive to survival in arid climates.

It it therefore proposed that fynbos should be considered as being functionally more similar to heath vegetation responding to a nutrient limitation than to vegetation of a mediterranean-type ecosystem responding to a water limitation. Fynbos vegetation can extend into arid areas because the low biomass does not require much water to support. This conclusion is in keeping with the broader distribution of the fynbos, which follows the distribution of the low nutrient Table Mountain Sandstone derived soils, rather than the distribution of the mediterranean-type climate.

LITERATURE CITED

Acocks, J.P.H., 1975. Veld types of South Africa. Memoirs of the Botanical Survey of South Africa. No. 40. pp. 128.

Aschmann, H., 1973. Distribution and Peculiarity of Mediterranean Ecosystems. In: di Castri, F., and H.A. Mooney (eds), 1973. Mediterranean Type Ecosystems. Springer-Verlag. New York. pp. 405.

Beadle, N.C.W., 1966. Soil phosphate and its role in molding segements of the Austalian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology 47: 992-1007.

Beard, J.S., 1983. Ecological control of the vegetation of southwestern Australia: Moisture versus nutrients. pp. 66-73. In: Kruger, F.J., D.T. Mitchell, and J.U.M. Jarvis (eds), 1983. Mediterranean-type ecosystems: The role of nutrients. Springer-Verlag. Berlin. pp. 552.

Beardsell, M.F., P.G. Jarvis, and B. Davidson, 1972. A null-balance diffusion porometer suitable for use with leaves of many shapes. Journal of Applied Ecology 9: 677-690.

Bell, C.J., and G.R. Squire, 1981. Comparative Measurements with two water vapour diffusion porometers (dynamic and steady state). Journal of Experimental Botany 32(131): 1143-1156.

Bond, P., and P. Goldblatt, 1984. Plants of the Cape Flora: A descriptive catalogue. Journal of South African Botany. Supplementary volume no. 13. National Botanic Gardens, South Africa. pp. 455.

Boyer, J.S., 1967. Leaf water potentials measured with a pressure chamber. Plant Physiology 42: 133-137.

Boyer, J.S., 1974. Water transport in plants: Mechanism of apparent changes in resistance during absorption. Planta 117: 187-207.

Calkin, H.W., and R.W. Pearcy, 1982. Seasonal progressions in the water relations of deciduous and evergreen perennials in the northern California chaparral. p. 591. In: Conrad, C.E., and Oechel, W.C. (eds), 1982. Proceedings of the symposium on dynamics and management of mediterranean-type ecosystems. Gen. Tech. Rep. PSW-58. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. pp. 637.

Campbell, B.M., B. McKenzie, and E.J. Moll, 1979. Should there be more tree vegetation in the mediterranean climate region of South Africa? Journal of South African Botany 45(4): 453-457.

Chabot, F.A., and D.J. Hicks, 1982. The ecology of leaf life spans. Anual Review of Ecology and Systematics 13: 229-259.

Cheung, Y.N.S., M.T. Tyree, and J. Dainty, 1975. Water relations parameters on single leaves obtained in a pressure bomb and some ecological interpretations. Canadian Journal of Botany. 53: 1342-1346.

Cody, M.L., and H.A. Mooney, 1978. Convergence versus nonconvergence in mediterranean-climate ecosystems. Annual Review of Ecology and Systematics 9: 265-321.

Conard, S.G., and S.R. Radosevich, 1981. Photosynthesis, xylem presure potential, and leaf conductance of three montane chaparral species in California. Forest Science 27(4): 627-639.

Cowan, I.R., 1978. Stomatal behaviour and environment. Advances in Botanical Research 4: 117-228.

Cowling, R.M., and B.M. Campbell, 1980. Convergence in vegetation structure in the mediterranean communities of California, Chile, and South Africa. Vegetatio 43: 191-197.

Day, J.A. (ed), 1983. Mineral nutrients in mediterranean ecosystems. South African National Scientific Programmes Report No. 71. pp. 165.

Di Castri, F., 1981. Mediterranean-type shrublands of the world. pp. 1-52. In: Di Castri, D.W. Goodall, and R.L. Specht (eds), 1981. Ecosystems of the world 11: Mediterranean-type shrublands. Elsevier Scientific Publishing Company, Amsterdam. pp. 643.

Ehleringer, J., 1980. Leaf morphology and reflectance in relaiton to water and temperature stress. In: Turner, N.C., and P.J. Kramer (eds), 1980. Adaptation of plants to water and high temperature stress. John Wiley & Sons, New York. pp. 482.

Fuggle, R.F., 1981. Macro-climatic patterns within the fynbos biome. National Programme for Environmental Sciences. Fynbos Biome Project. Finial Report. pp. 116.

Geological Survey, 1973. 3218 Clanwilliam 1:250000 Geological Map Series, Geological Survey, Pretoria.

Gigon, A., 1979. CO2-gas exchange, water relations and convergence of mediterranean shrub-types from California and Chile. Oecolgia Plantarum 14: 129-150.

Giliberto, J., and H. Estay, 1978. Seasonal water stress in some Chilean matorral shrubs. Botanical Gazette 139(2): 236-240.

Hellmuth, E.O., 1971. Eco-physiological studies on plants in arid and semi-arid regions in Western Australia III. Comparative studies on photosynthesis, respiration and water relations of ten arid zone and two semi-arid zone plants under winter and late summer climatic conditions. Journal of Ecology 59: 225-259.

Hsiao, T.C., 1973. Plant responses to water stress. Annual Review of Plant Physiology 24: 519-570.

Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. Phil. Trans. Roy. Soc. London. Ser. B. 273: 593-610.

Jacobson, M.B., W.A. Stoner, and S.P. Richards, 1981. Models of plant and soil processes. pp. 287-368. In: Miller, P.C. (ed), 1981. Resource use by chaparral and matorral. Springer-Verlag. Berlin. pp. 455.

Kramer, P.J., 1980. Drought, Stress, and the Origin of Adaptations. pp. 7-20. In: Turner, N.C., and P.J. Kramer (eds), 1980. Adaptation of Plants to Water and High Temperature Stress. John Wiley & Sons. New York. pp. 482.

Kruger, F.J., 1979. South African heathlands. pp. 19-80. In: Specht, R.L. (ed), 1979. Ecosystems of the world 9A: Heathlands and related shrublands, Descriptive studies. Elsevier Scientific Publishing Co., New York. pp. 497.

Kruger, F.J., D.T. Mitchell, and J.U.M. Jarvis (eds), 1983. Mediterranean-type ecosystems: The role of nutrients. Springer-Verlag. Berlin. pp. 552.

Larcher, W., 1980. Physiological plant ecology. 2nd ed. Springer-Verlag. Berlin.

le Maitre, D.C., 1984. Aspects of the structure and phenology of two fynbos communities. Msc Thesis. University of Cape Town, Cape Town, South Africa.

Levitt, J., 1980. Responses of plants to environmental stresses. II. Water, radiation, salt, and other stresses. Academic Press. New York. pp. 607.

Margaris, N.S., 1977. Water relations in plants dominating phryganic ecosystems. Biologia Plantarum (Praha) 19(6): 442-447.

Merino, J., 1982. Growth and maintenance costs of chaparral leaves. p. 619. In: Conrad, C.E., and Oechel, W.C. (eds), 1982. Proceedings of the symposium on dynamics and management of mediterranean-type ecosystems. Gen. Tech. Rep. PSW-58. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. pp. 637.

Milewski, A.V., 1979. A climatic basis for the study of convergence of vegetation structure in mediterranean Australia and southern Africa. Journal of Biogeography 6: 293-299.

Miller, J.M., P.C. Miller, and P.M. Miller, 1984. Leaf conductances and xylem pressure potentials in fynbos plant species. South African Journal of Science 80: 381-385.

Miller, J.M., P.M. Miller, and P.C. Miller, in prep. Diurnal patterns of leaf conductance and water potentials in selected fynbos plant species.

Miller, P.C., 1979. Quantitative plant ecology. pp. 179-232. In: Horn, D., G.R. Stairs, and R.D. Mitchell (eds), 1979. Analysis of Ecosystems. Ohio State University. Columbus.

Miller, P.C. (ed), 1981. Resource use by chaparral and matorral. Springer-Verlag. Berlin. pp. 455.

Miller, P.C., J.M Miller, and P.M. Miller, 1983. Seasonal progression of plant water relations in fynbos in the western Cape Province, South Africa. Oecologia 56: 392-396.

Miller, P.C., E. Hajek, D.K. Poole, and S.W. Roberts, 1981. Microclimate and energy exchange. pp. 97-121. In: Miller, P.C. (ed), 1981. Resource use by chaparral and matorral. Springer-Verlag. Berlin. pp. 455.

Miller, P.C., and H.A. Mooney, 1976. The origin and structure of American arid-zone ecosystems. The producers: Interactions between environment, form, and function. pp. 38-56. In: de Wit, C.T., and G.W. Arnold (eds.), 1976. Critical evaluation of systems analysis in ecosystems research and management. Centre for Agricultural Publishing and Documentation. Wageningen.

Miller, P.C., and D.K. Poole, 1979. Patterns of water use by shrubs in southern California. Forest Science 25(1): 84-98.

Milthorpe, F.L., and J. Moorby, 1979. An introduction to crop physiology (2nd ed.). Cambridge University Press. Cambridge. pp. 243.

Mitrakos, K., 1980. A theory for mediterranean plant life. Acta Oecological/Oecologia Plantarum 1[15](3): 245-252.

Moll, E.J., and L. Bossi, 1983. Vegetation of the Fynbos Biome (1:1000000 map). Chief Director of Surveys and Mapping, Mobray, South Africa.

Moll, E.J., B.M. Campbell, R.M. Cowling, L. Bossi, M.L. Jarman, and C. Boucher, 1984. A description of major vegetation categories in and adjacent to the Fynbos biome. South African national scientific Programmes Report No. 83. pp. 29.

Moll, E.J., and M.L. Jarman, 1984. Is fynbos a heathland? South African Journal of Science 80: 352-355.

Moll, E.J., B. McKenzie, and D. McLachlan, 1980. A possible explanation for the lack of trees in the fynbos, Cape Province, South Africa. Biological Conservation 17: 221-228.

Moll, E.J., and J.E.M. Sommerville, 1985. Seasonal xylem pressure potentials of two South African coastal fynbos species in three soil types. South African Journal of Botany 51(3): 187-193.

Monk, C.D., 1966. An ecological significance of evergreenness. Ecology 47: 504-505.

Mooney, H.A., 1980. Seasonality and gradients in the study of stress adaptation. pp. 279-294. In: Turner, N.C., and P.J. Kramer (eds), 1980. Adaptation of plants to water and high temperature stress. John Wiley & Sons. New York. pp. 482.

Mooney, H.A., C. Field, S.L. Gulmon, P. Rundel, and F.J. Kruger, 1983. Photosynthetic characteristic of South African sclerophylls. Oecologia 58: 398-401.

Mooney, H.A., and S.L. Gulmon, 1982. Constraints on leaf structure and function in reference to herbivory. BioScience 32: 198-206.

Mooney, H.A., A.T. Harrison, and P.A. Morrow, 1975. Environmental limitations of photosynthesis on a California evergreen shrub. Oecologia 19:293-301.

Mooney, H.A., and P.W. Rundel, 1979. Nutrient relations of the evergreen shrub _Adenostoma fasciculatum_, in the California chaparral. Botanical Gazette 140(1): 109-113.

Monteith, J.L, 1973. Principles of environmental physics. Eward Arnold. Great Britain. pp. 241.

Morgan, J.M., 1980. Differences in adaptation to water stress within crop species. pp. 369-382. In: Turner, N.C., and P.J. Kramer (eds), 1980. Adaptation of plants to water and high temperature stress. John Wiley & Sons. New York. pp. 482.

Morrow, P.A., and H.A. Mooney, 1974. Drought adaptations in two Californian evergreen sclerophylls. Oecologia 15: 205-222.

Nobel, P.S., 1980. Leaf anatomy and water use efficiency. pp. 43-55. In: Turner, N.C., and P.J. Kramer (eds), 1980. Adaptation of plants to water and high temperature stress. John Wiley & Sons. New York. 482 p.

Odening, W.R., B.R. Strain, and W.C. Oechel, 1974. The effects of decreasing water potentail on net CO2 exchange of intact desert shrubs. Ecology 55: 1086-1095.

Oechel, W.C., W. Lawrence, J. Mustafa, and J. Martinez, 1981. Energy and carbon aquisition. pp. 151-183. In: Miller, P.C. (ed), 1981. Resource use by chaparral and matorral. Springer-Verlag. Berlin. pp. 455.

Oosterhuis, D.M., 1983. Resistances to water flow through the soil-plant system. South African Journal of Science 79: 459-465.

Parkinson, K.J., and B.J. Legg, 1972. A continuous flow porometer. Journal of Applied Ecology 9: 677-690.

Poole, D.K., and P.C. Miller, 1975. Water relations of selected species of chaparral and coastal sage communities. Ecology 56(5): 1118-1128.

Poole, D.K., and P.C. Miller, 1978. Water related characteristics of some evergreen sclerophyll shrubs in central Chile. Oecologia Plantarum 13(4): 289-299.

Poole, D.K., and P.C. Miller, 1981. The distribution of plant water stress and vegetation characteristics in southern California chaparral. American Midland Naturalist 105(1): 32-43.

Rabinovitch-Vin, A., 1983. Influence of nutrients on the composition and distribution of plant communities in mediterranean-type ecosystems of Israel. pp. 74-85. In: Kruger, F.J., D.T. Mitchell, and J.U.M. Jarvis (eds), 1983. Mediterranean-type ecosystems: The role of nutrients. Springer-Verlag. Berlin. pp. 552.

Roberts, S.W., 1982. Some recent aspects and problems of chaparral plant water relations. pp. 351-357. In: Conrad, C.E., and Oechel, W.C. (eds), 1982. Proceedings of the symposium on dynamics and management of mediterranean-type ecosystems. Gen. Tech. Rep. PSW-58. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. pp. 637.

Roberts, S.W., and W. D. Bowman, in press. Osmotic and turgor relations in selected chaparral shrub species.

Roberts, S.W., P.C. Miller, and A. Valamanesh, 1981. Comparative field water relations of four co-occurring chaparral shrub species. Oecologia 48: 360-363.

Roberts, S.W., S. Oberbauer, R. Kendall, and P.C. Miller, in press. Properties of internal leaf water relations in chaparral shrubs, measured by pressure volume analysis.

Ritchie, G.A., and T.M. Hinckley, 1975. The pressure chamber as an instrument for ecological research. Advances in Ecological Research 9: 165-254.

Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen, 1965. Sap pressure in vascular plants. Science. 148: 339-346.

Schülze, E.-D., O.L. Lange, M. Evenari, L. Kappen, and U. Buschbom, 1975. The role of air humidity and leaf temperature in controlling stomatal resistance of Prunus armeniaca L. under desert conditions II. the significance of leaf water status and internal carbon dioxide concentration. Oecologia 18: 219-233.

Schütte, K.H., R. Steyn, and M. van der Westhuizen, 1967. Crassulacean acid metabolism in South African succulents: A preliminary investigation into its occurrence in various families. Journal of South African Botany 33(2): 107-110.

Shields, L.M., 1950. Leaf xeromorphy as related to physiological and structural influences. Botanical Review 8: 399-447.

Seddon, G., 1974. Xerophytes, xeromorphs and sclerophylls: The history of some concepts in ecology. Biol J. Linn. Soc. 6: 65-87.

Slatyer, R.O., 1967. Plant-water relationships. Academic Press. New York. pp. 366.

Small, E., 1973. Xeromorphy in plants as a poossible basis for migration between arid and nutritionally-deficient environments. Bot. Notiser. 26: 534-539.

Spain, J.D., 1982. BASIC Microcomputer Models in Biology. Addison-Wesley. Massachusetts. pp. 354.

Specht, R.L., 1957. Dark island heath (Ninety-mile plain, South Australia) IV. The water relationships in heath vegetation and pastures on the Makin sand. Australian Journal of Botany 5: 151-172.

Specht, R.L., 1972. Water use by perennial evergreen plant communities in Australia and Papua New Guinea. Australian Journal of Botany 20: 273-299.

Specht, R.L., 1979. Preface. In: Specht, R.L. (ed), 1979. Ecosystems of the world 9A: Heathlands and related shrublands, Descriptive studies. Elsevier Scientific Publishing Co., New York. pp. 497.

Specht, R.L., 1981. Preface. In: Specht, R.L. (ed), 1981. Ecosystems of the world 9B: Heathlands and related shrublands, Analytical studies. Elsevier Scientific Publishing Co., New York. pp. 385.

Specht, R.L., and R. Jones, 1971. A comparison of the water use by heath vegetation at Frankston, Victoria, and Dark Island Soak, South Australia. Australian Journal of Botany 19: 311-326.

Specht, R.L., and E.J. Moll, 1983. Mediterranean-type heathlands and sclerophyllous shrublands of the world: An overview. pp. 41-65. In: Kruger, F.J., D.T. Mitchell, and J.U.M. Jarvis (ed), 1983. Mediterranean-type ecosystems: The role of nutrients. Springer-Verlag. Berlin. pp. 552.

Syvertsen, J.P., G.L. Cunningham, and T.V. Feather, 1975. Anomalous diurnal patterns of stem xylem water potentials in Larrea tridentata. Ecology 56: 1423 - 1428.

Taylor, H.C., 1978. Phytogeography and ecology of Capensis. pp 171-229. In: Werger, M.J.A., 1978. The biogeography and ecology of southern Africa. W. Junk. The Hague.

Turner, N.C., 1974. Stomatal behavior and water status of maize, sorghum, and tobacco under field conditions II. At low soil water potential. Plant Physiology 53: 360 - 365.

Turner, N.C., and G.J. Burch, 1983. The role of water in plants. pp. 73-126. In: Teare and Peet, 1983. Crop - water relations. John Wiley. New York.

Turner, N.C., and M.M. Jones, 1980. Turgor maintenance by osmotic adjustment: A review and evalutaion. pp. 87-103. In: Turner, N.C., and P.J. Kramer, 1980. Adaptation of Plants to Water and High Temperature Stress. John Wiley & Sons, New York. pp. 482.

Tyree, M.T., and H.T. Hammel, 1972. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. Journal of Experimental Botany. 23(74): 267-82.

van Daalen, J.C., 1981. The dynamics of the indigenous forest-fynbos ecotone in the Southern Cape. South African Forestry Journal 119: 14-23.

Waring, R.H., and B.D. Cleary, 1967. Plant moisture stress: evaluation by pressure bomb. Science. 155: 1248-1254.

Walter, H., 1973. Vegetation of the earth in relation to climate and eco-physiological conditions. (Trans. from 2nd German edition by Joy Wieser). Springer-Verlag. New York. pp. 237.

Appendix 1

The diurnal response of the leaf conductances of the 13 species to the controlling variables; xylem pressure potential, photosynthetically active photon flux, vapor pressure deficit, and air temperature during the course of the season.

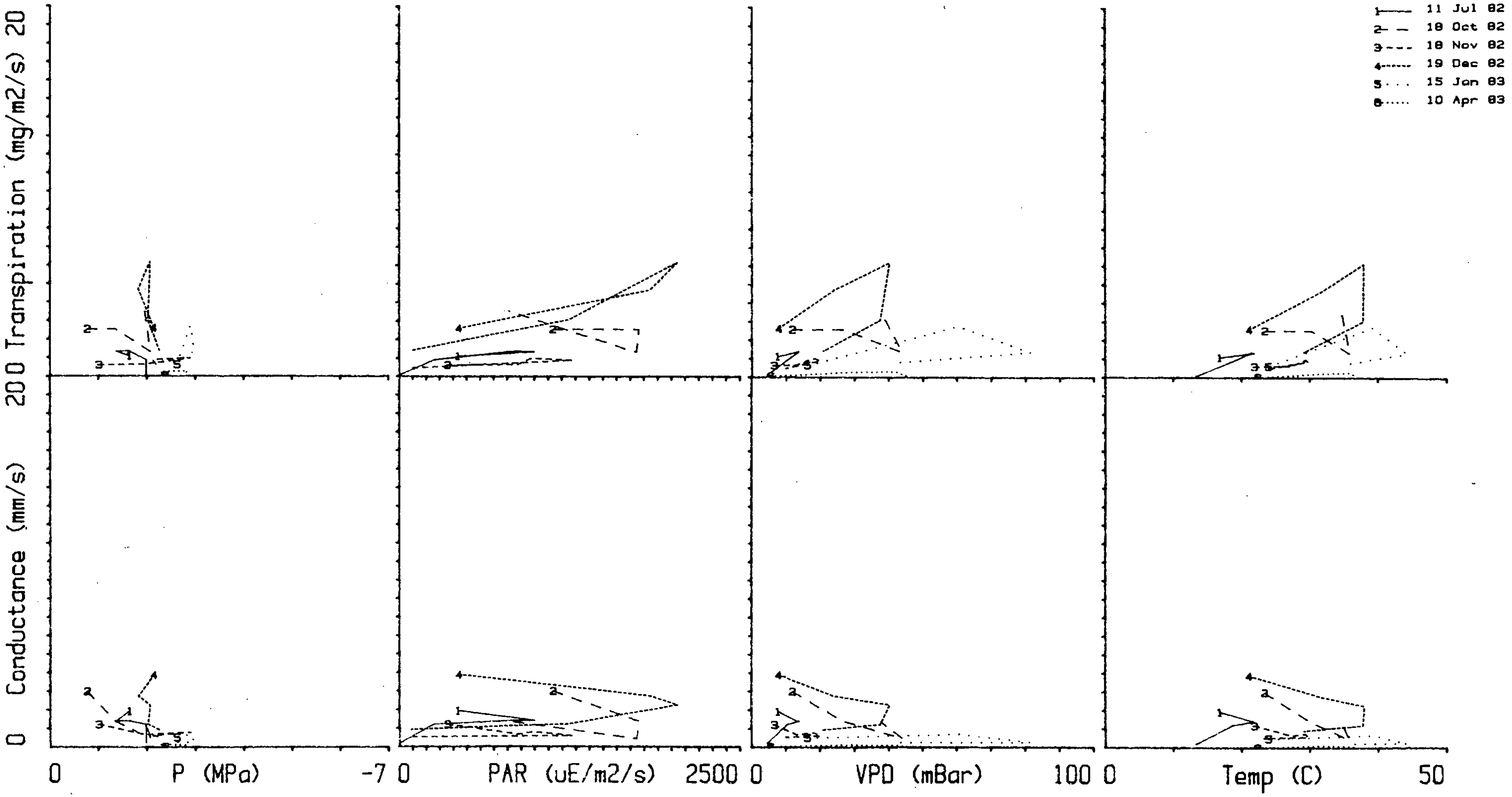


Figure A1.1 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for Ruschia sp. at site 1 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

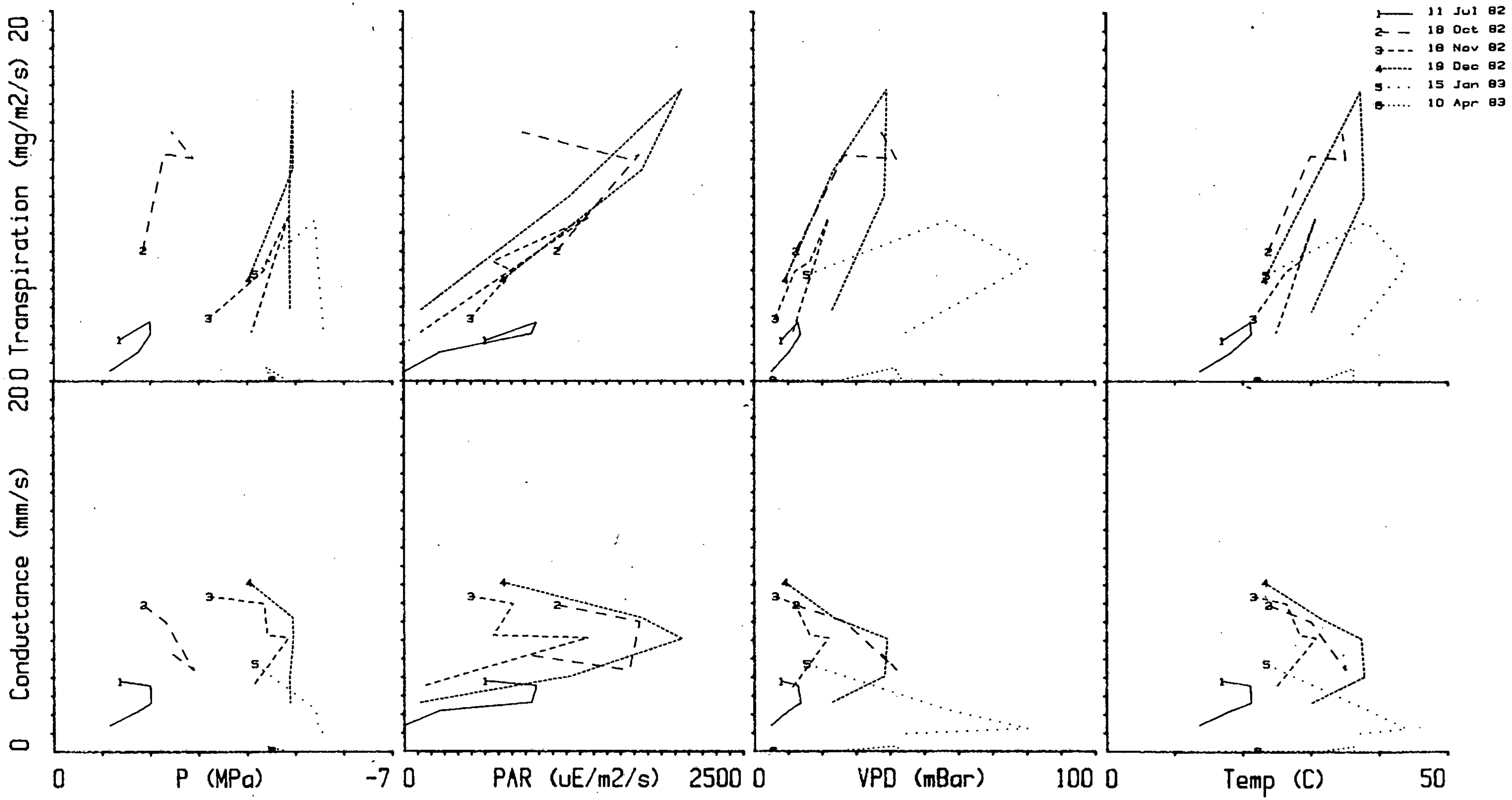


Figure A1.2 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for _Rhus incisa_ at site 1 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

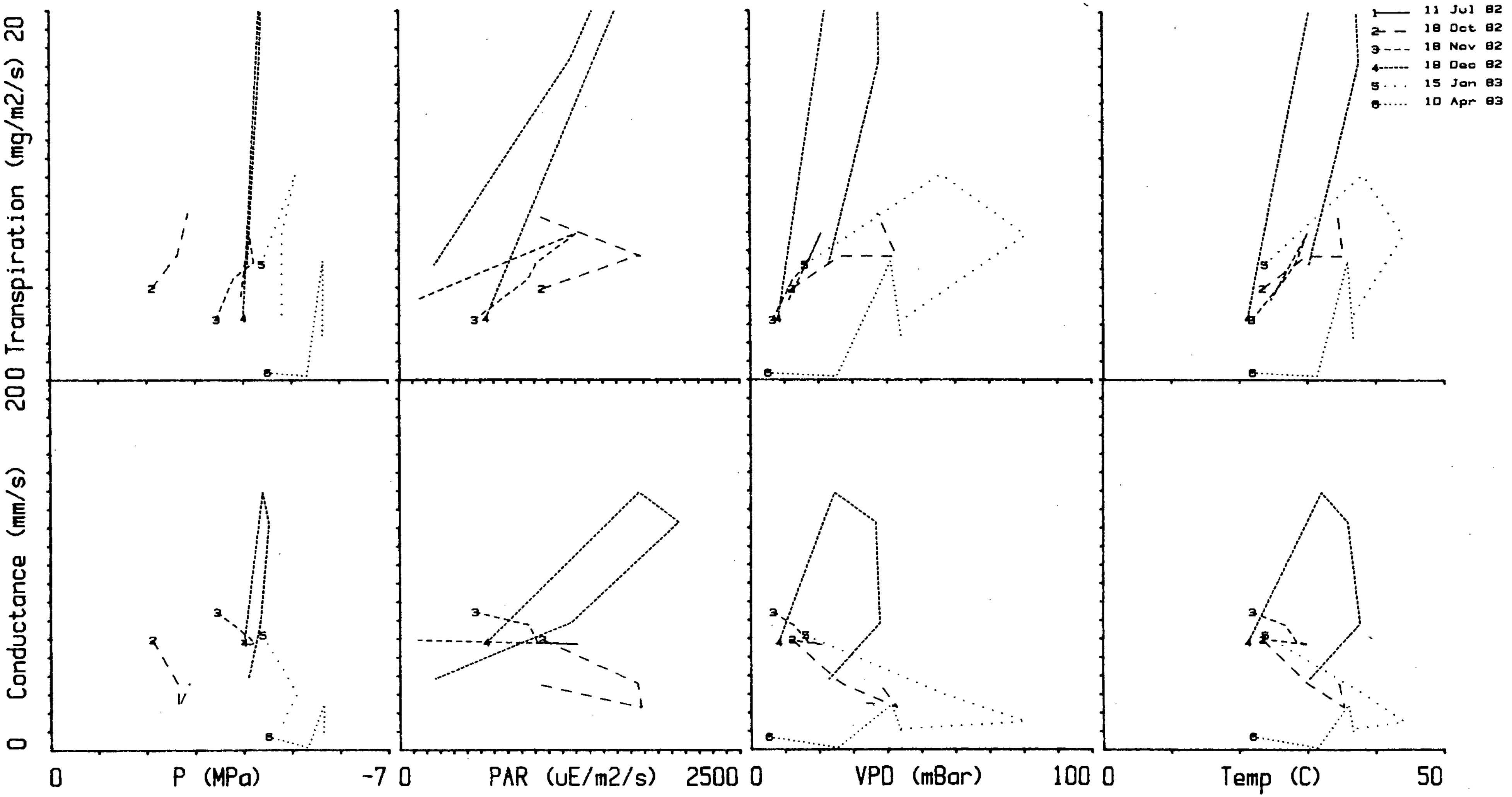


Figure A1.3 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for <u>Galenia africana</u> at site 1 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

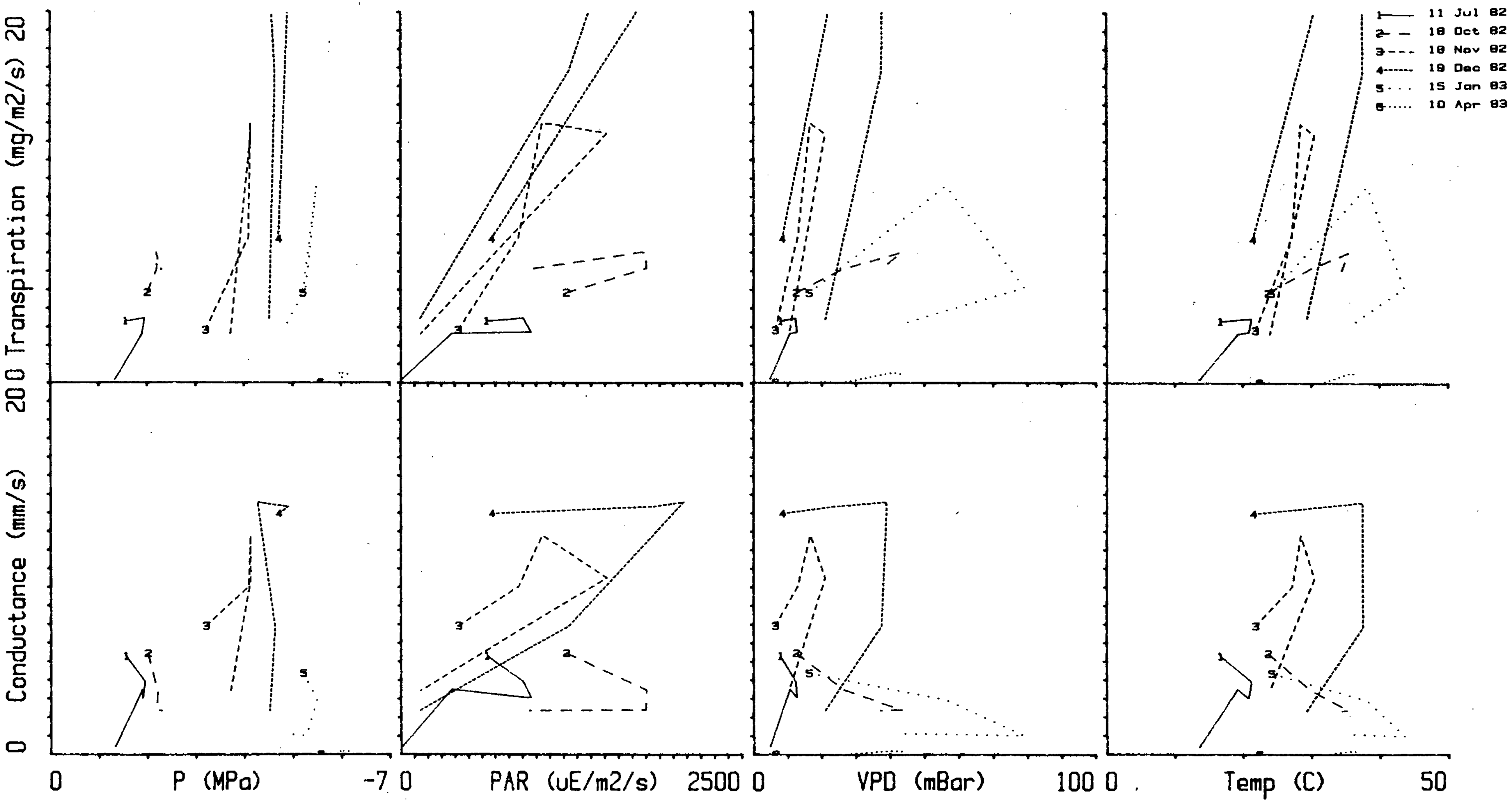


Figure A1.4 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for Nylandtia spinosa at site 1 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

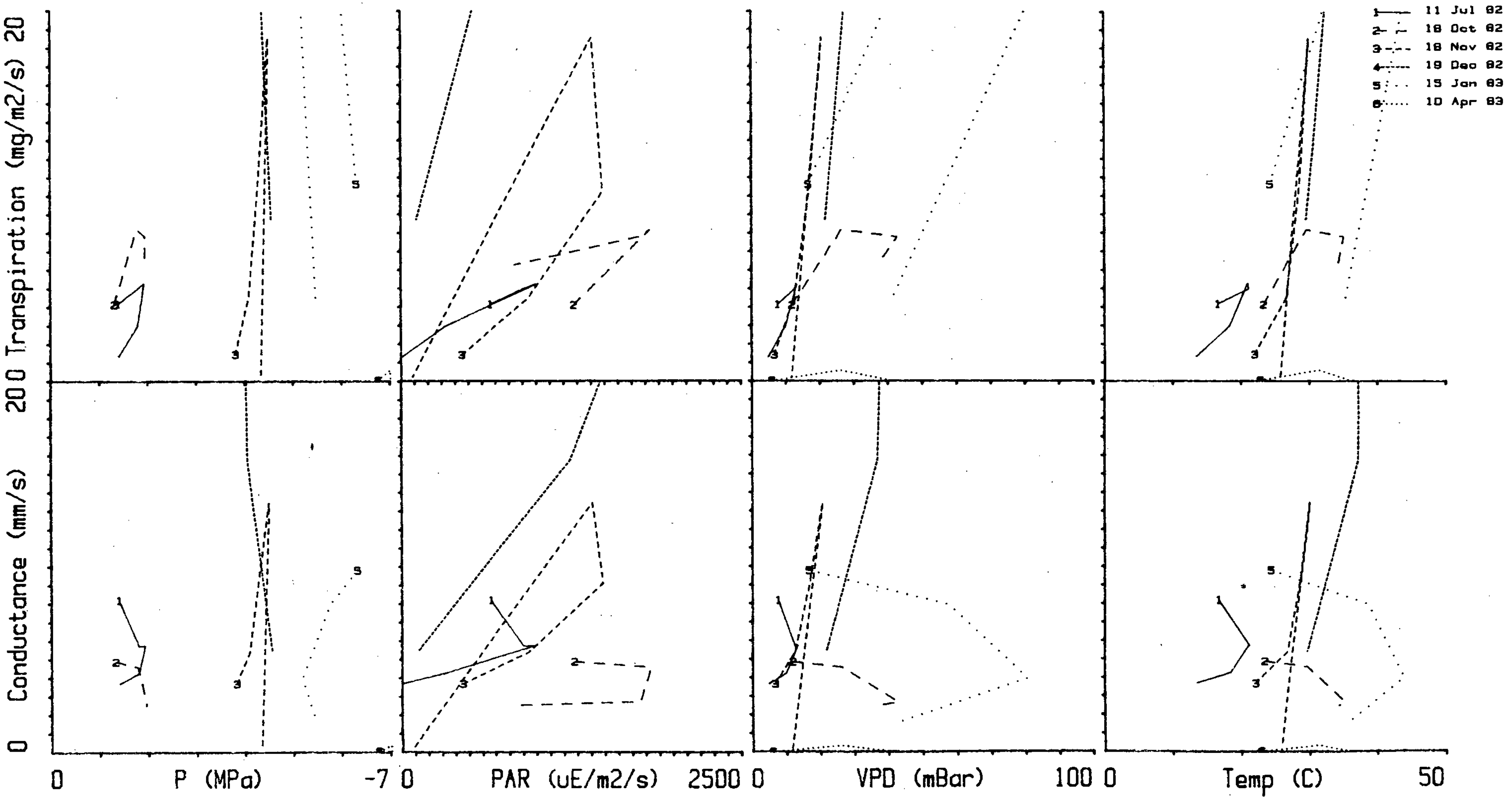


Figure A1.5 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for *Eriocephalus africanus* at site 1 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

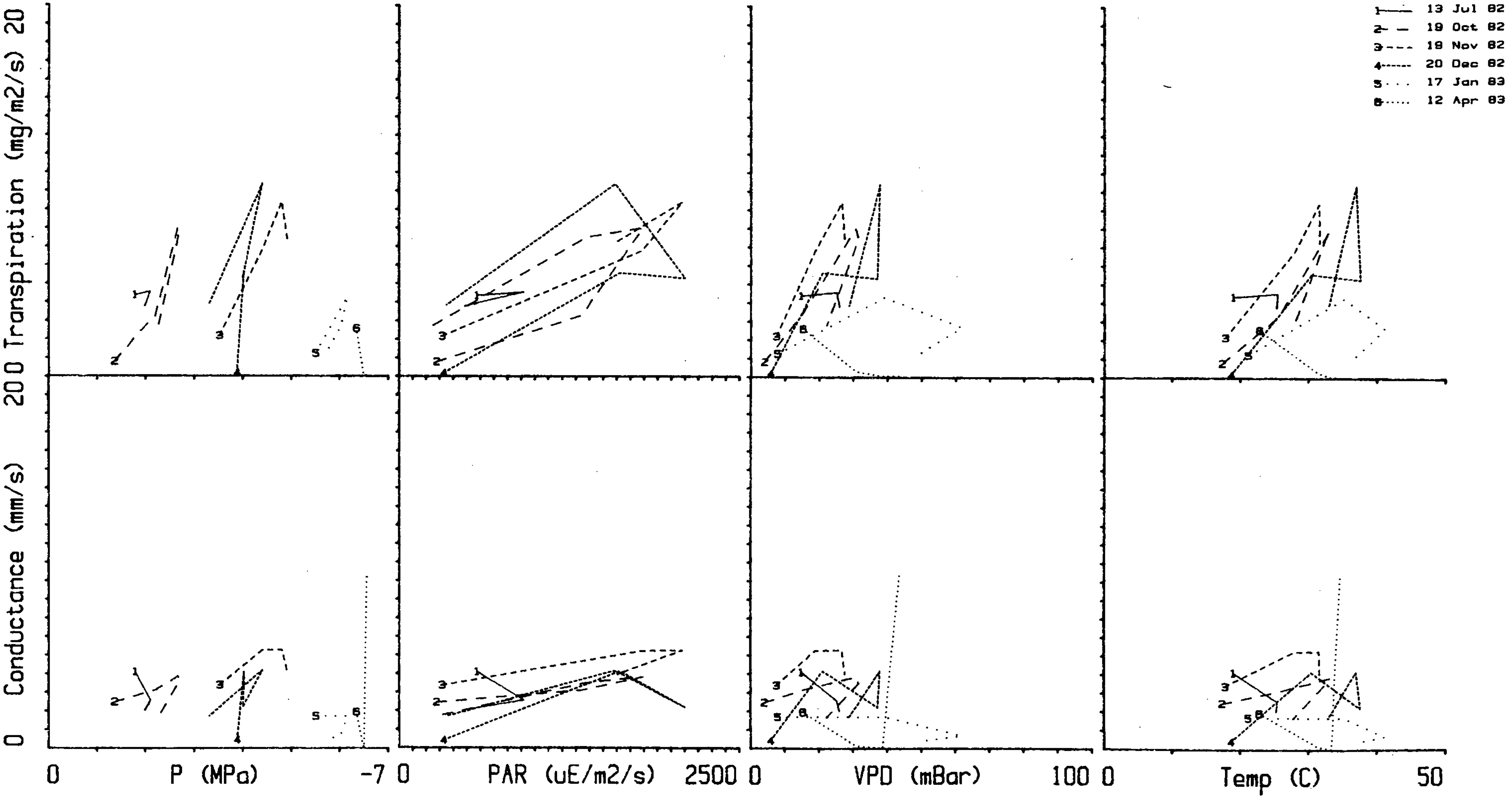


Figure A1.6 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for Nylandtia spinosa at site 3 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

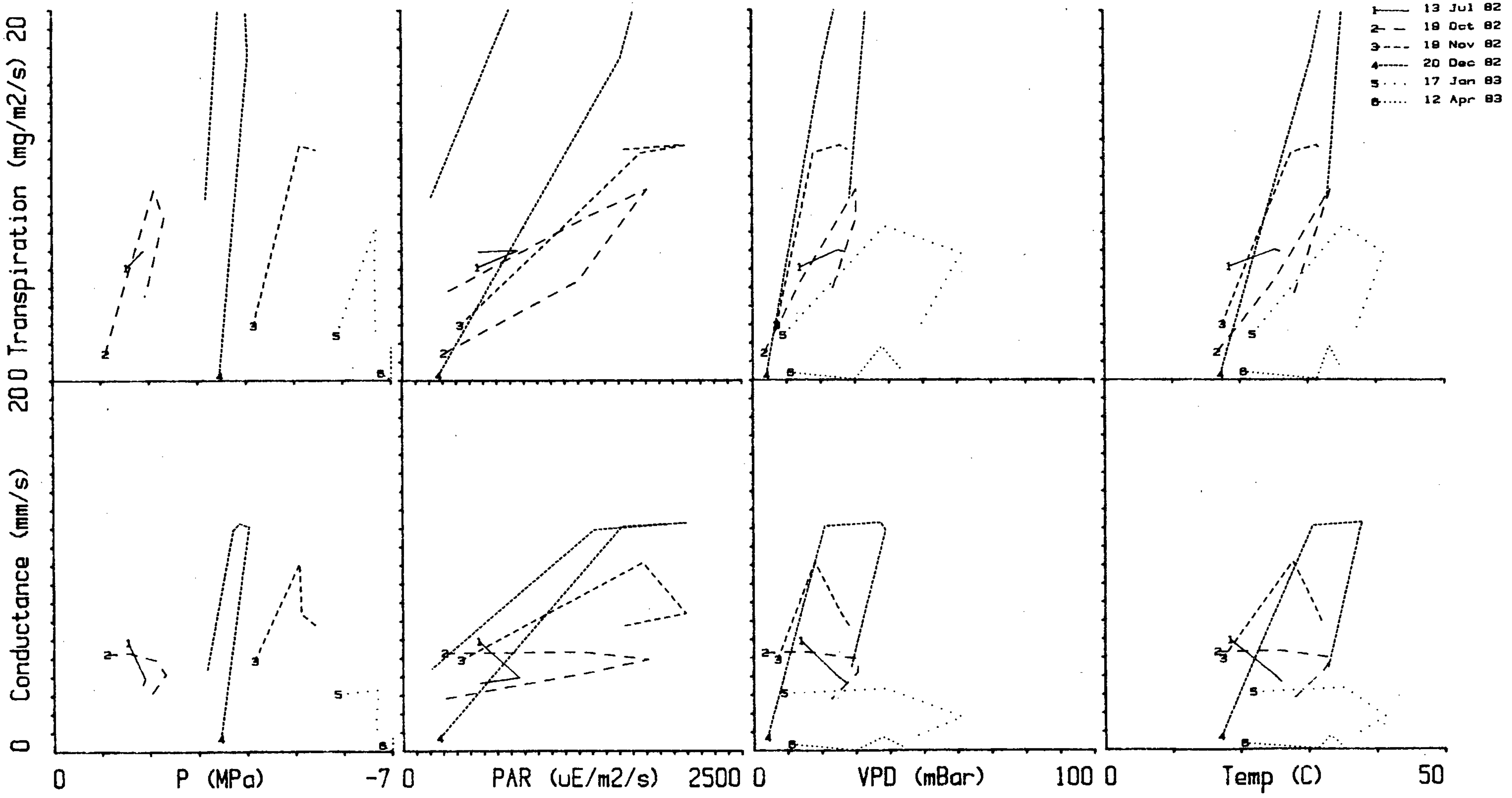


Figure A1.7 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for *Eriocephalus africanus* at site 3 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

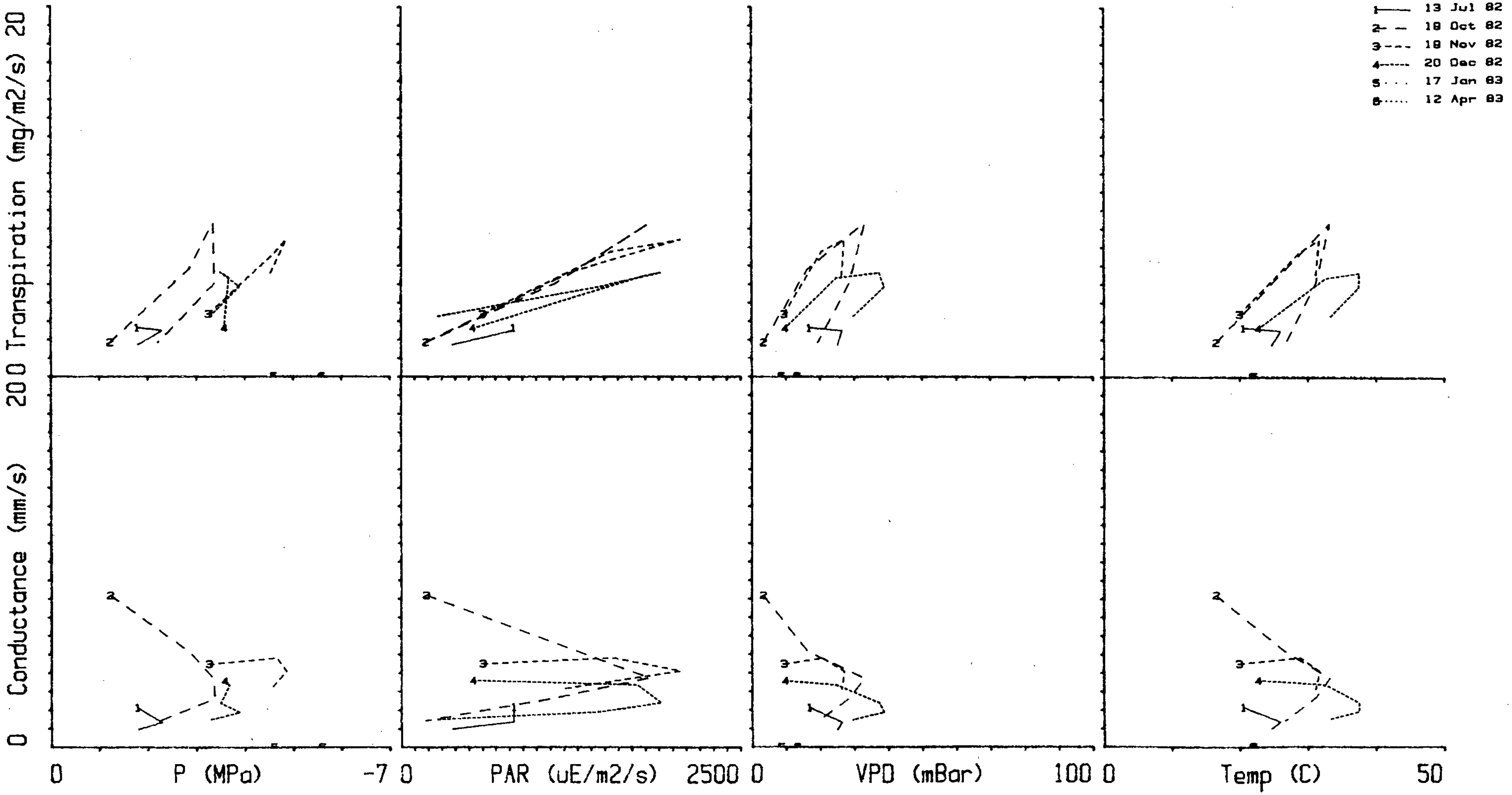


Figure A1.8 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for Rhus dissecta at site 3 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

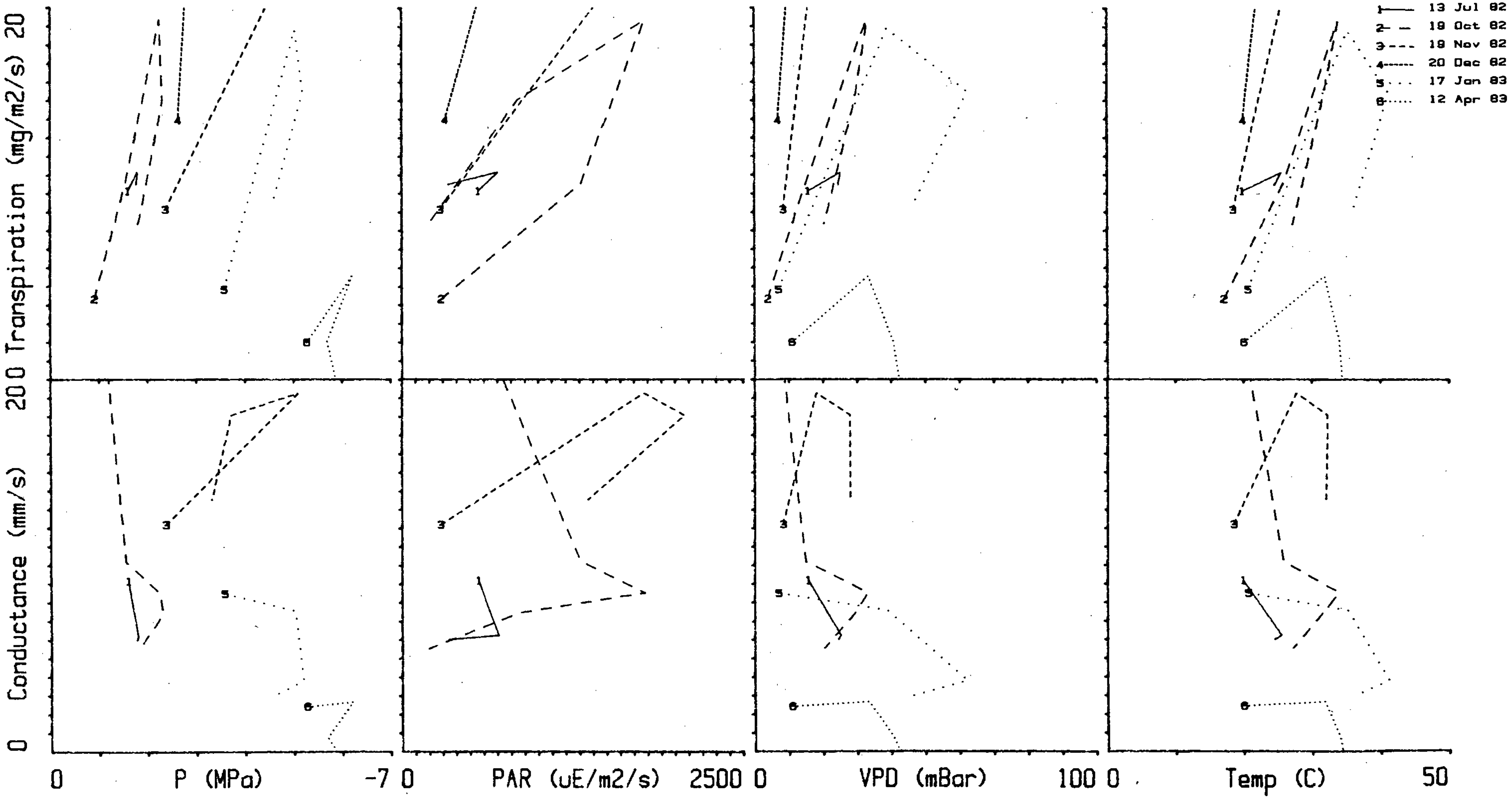


Figure A1.9 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for *Elytropappus gnaphaloides* at site 3 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

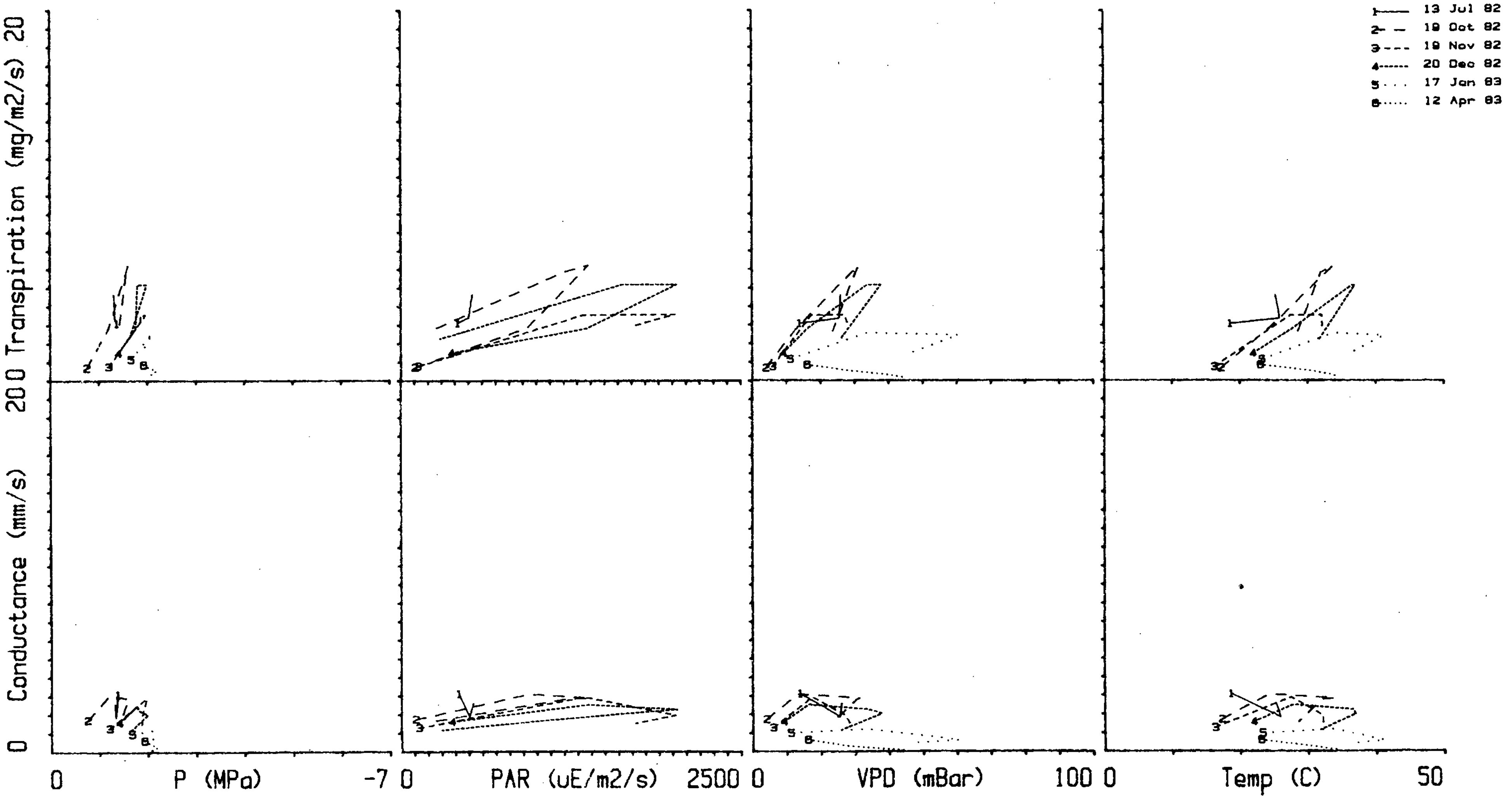


Figure A1.10 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for *Protea laurifolia* at site 3 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

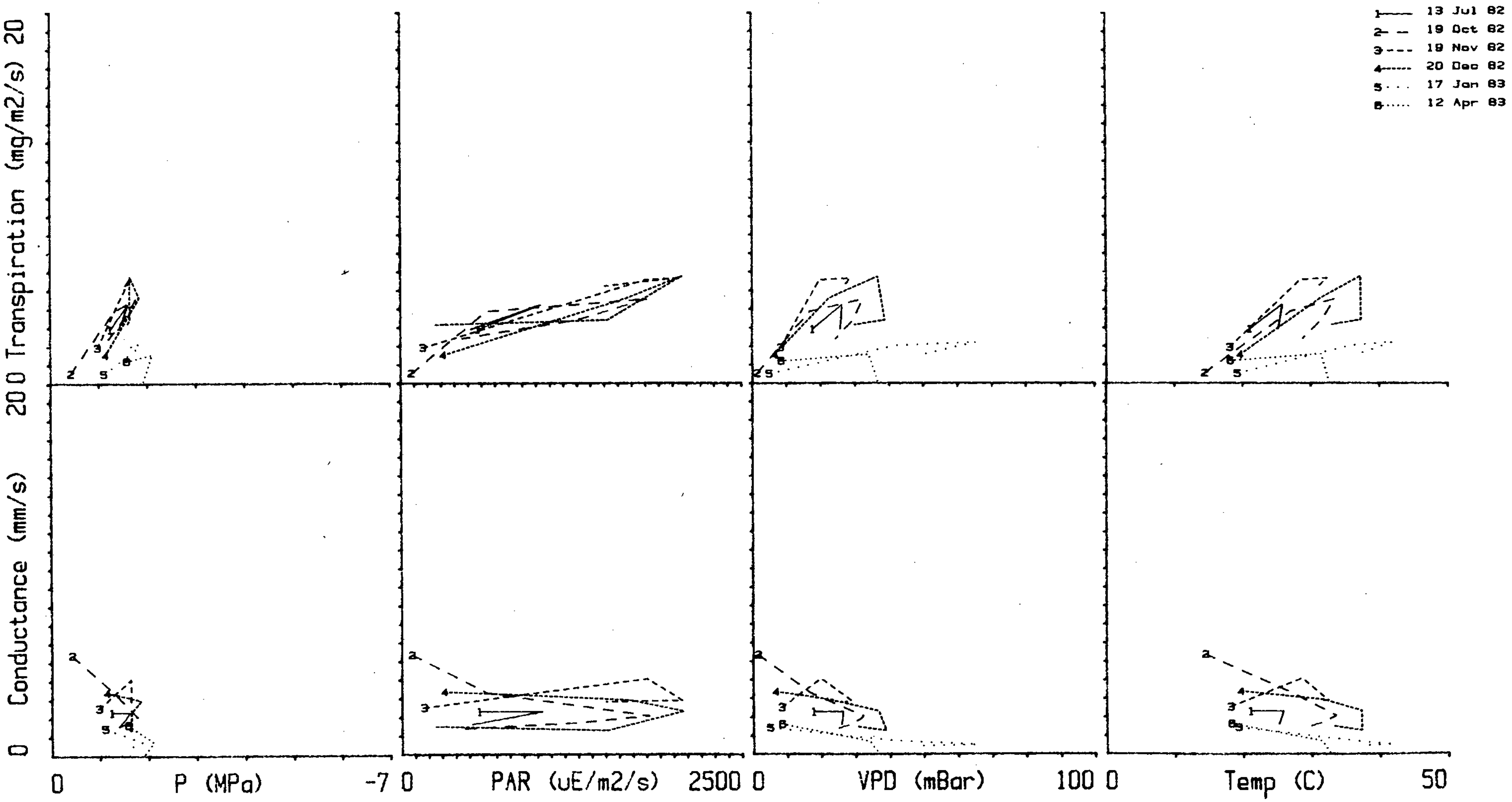


Figure A1.11 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for Protea glabra at site 3 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

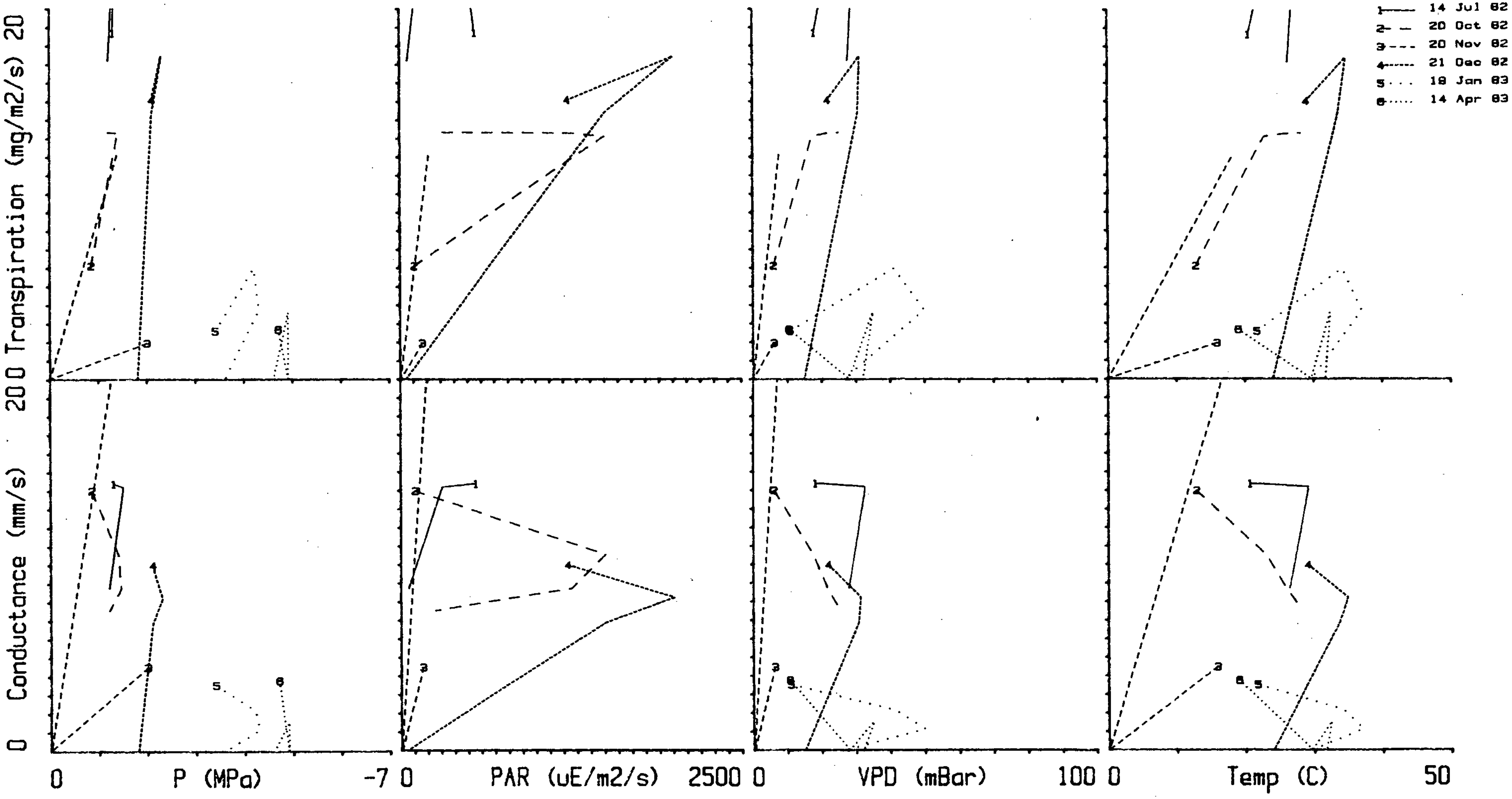


Figure A1.12 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for *Eriocephalus africanus* at site 5 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

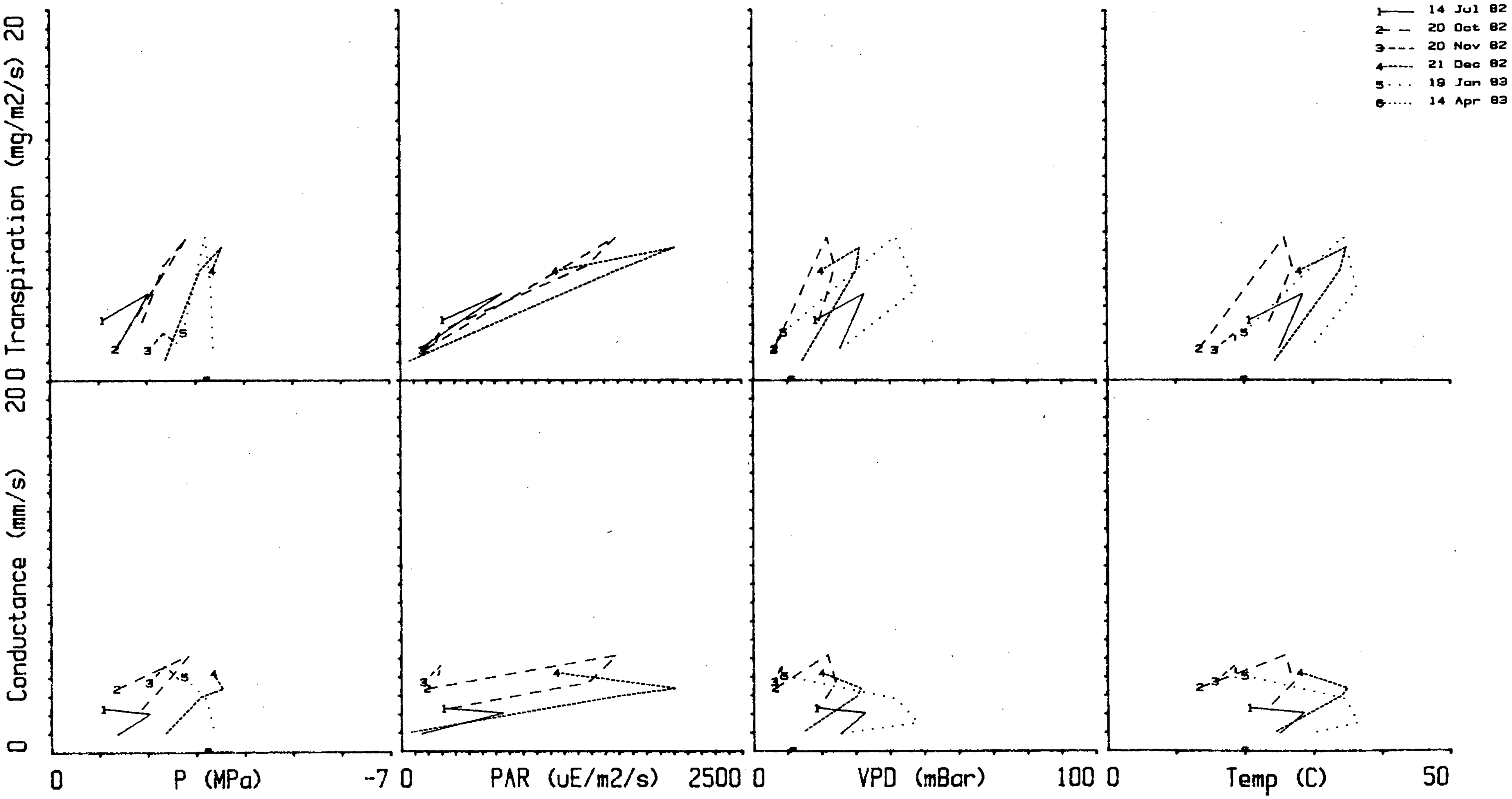


Figure A1.13 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for *Rhus dissecta* at site 5 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

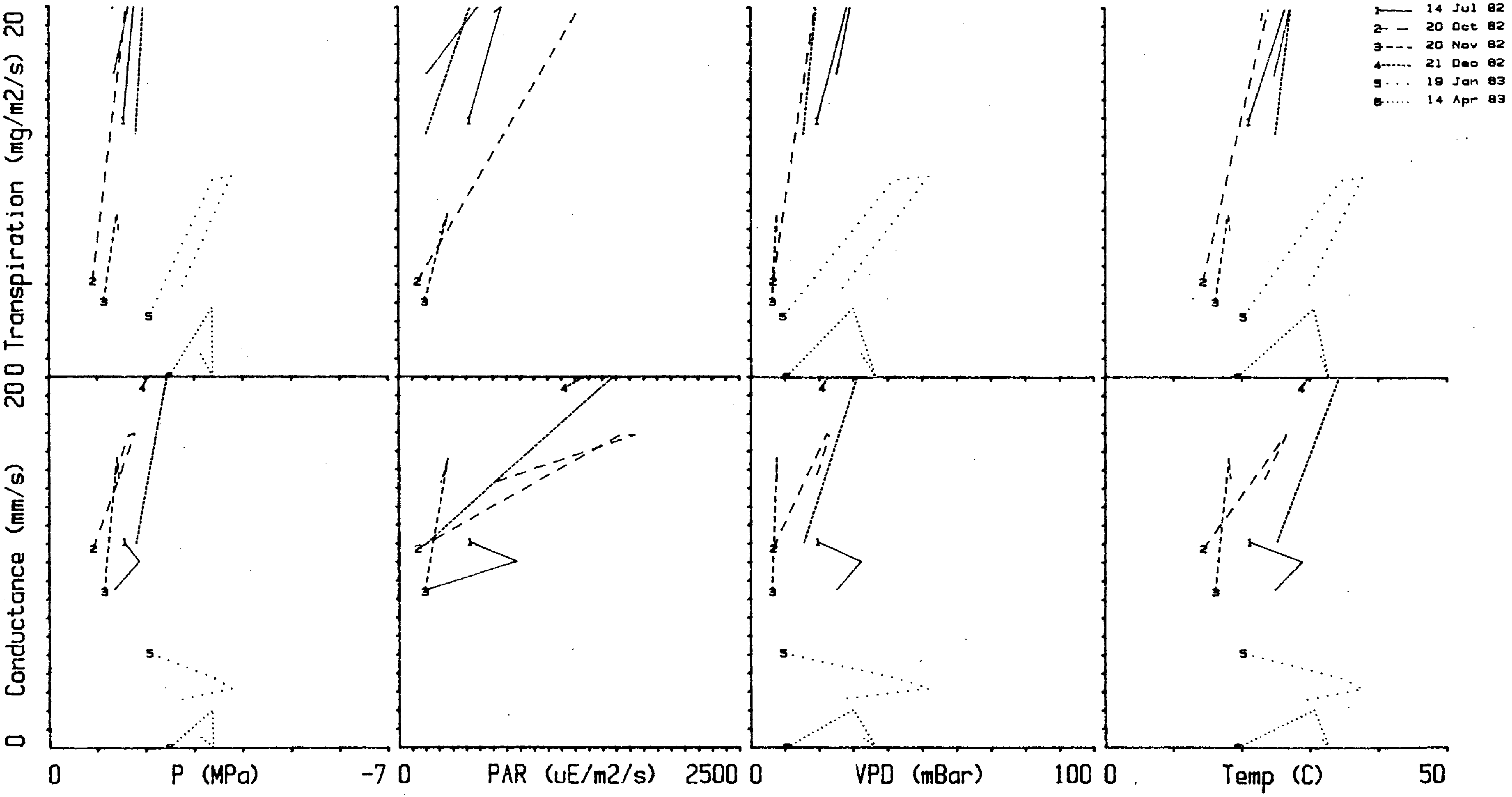


Figure A1.14 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for *Stoebe capitata* at site 5 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

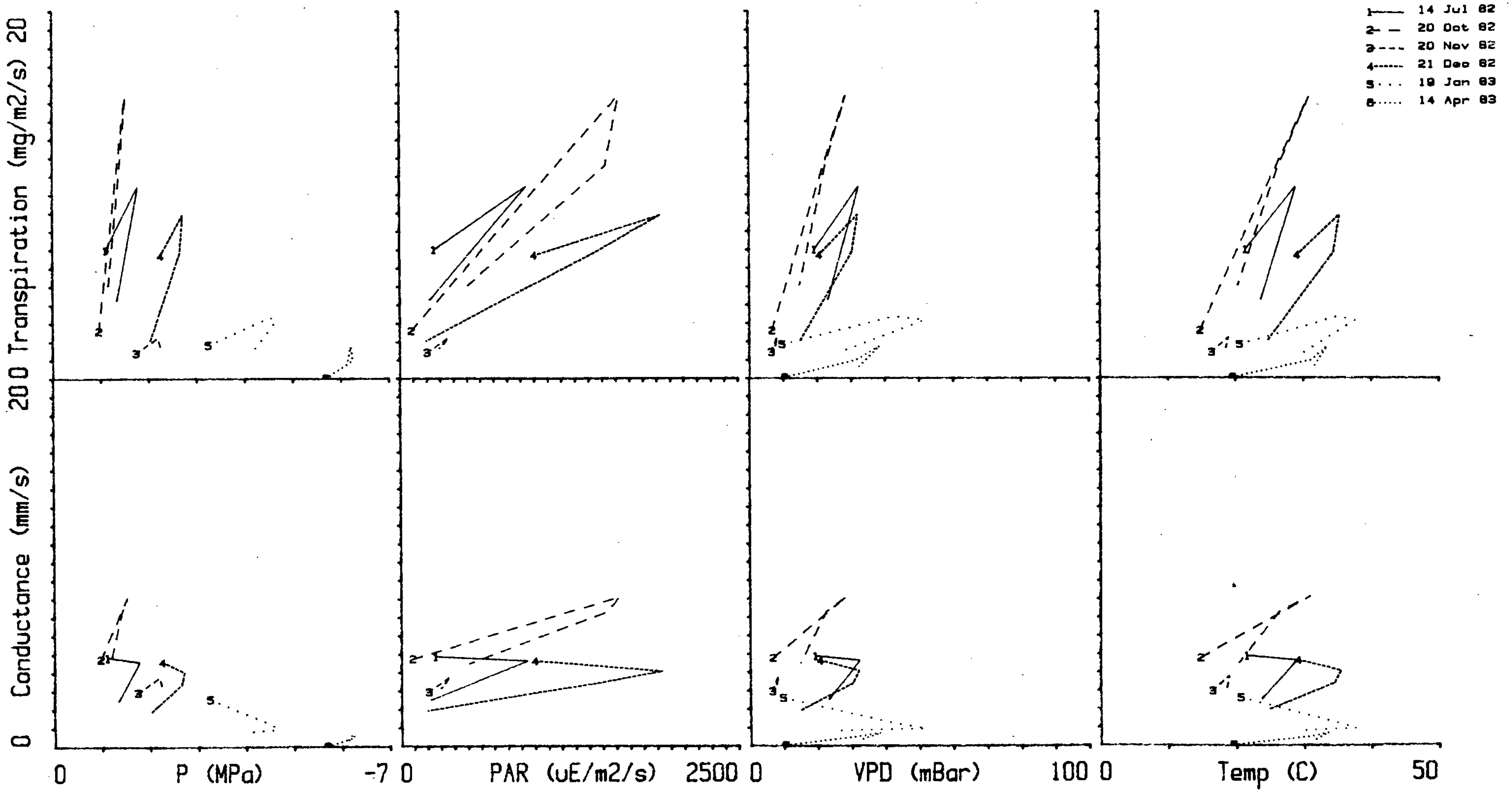


Figure A1.15 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for Agathosma giftbergensis at site 5 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

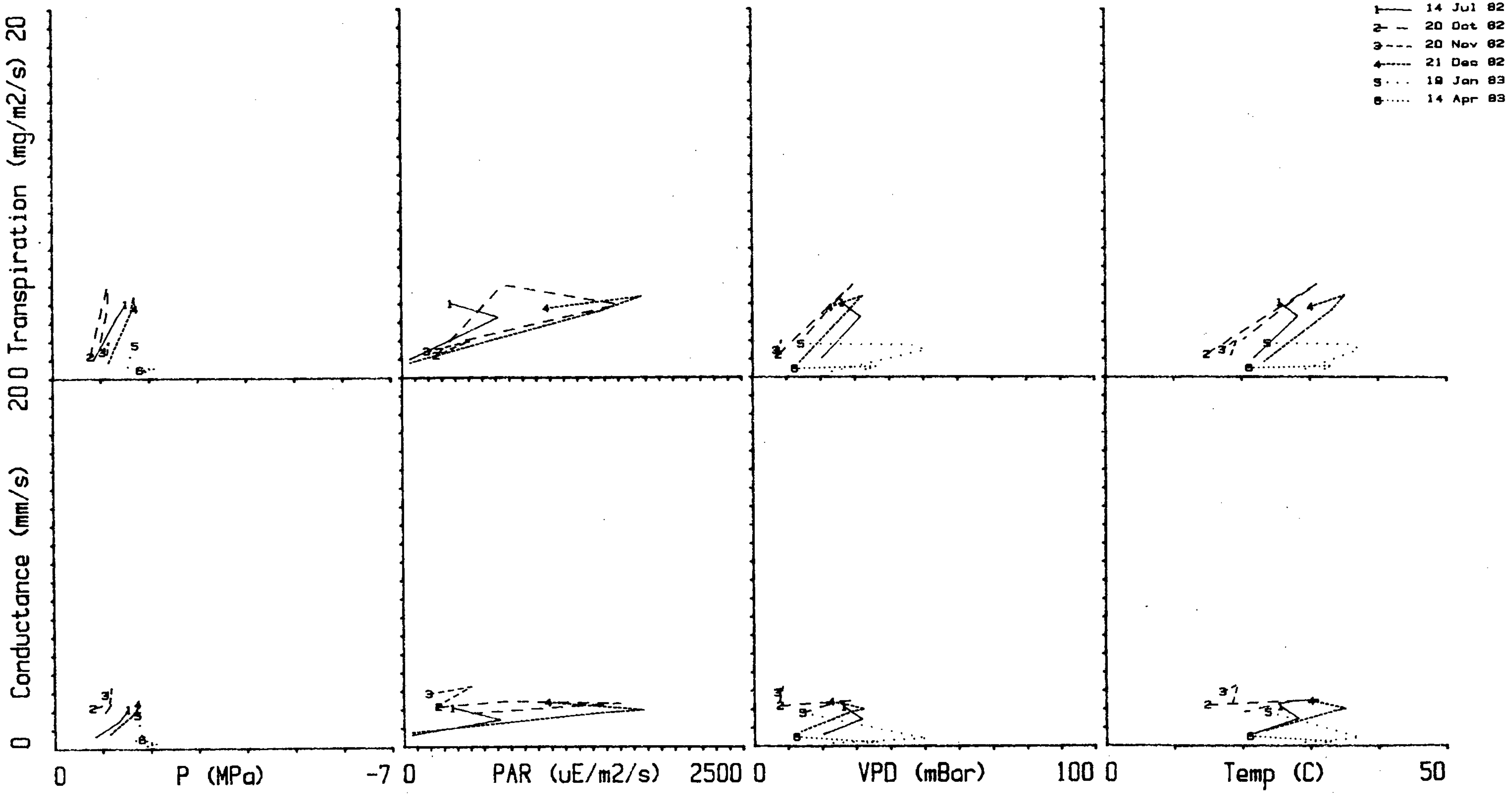


Figure A1.16 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for <u>Protea laurifolia</u> at site 5 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

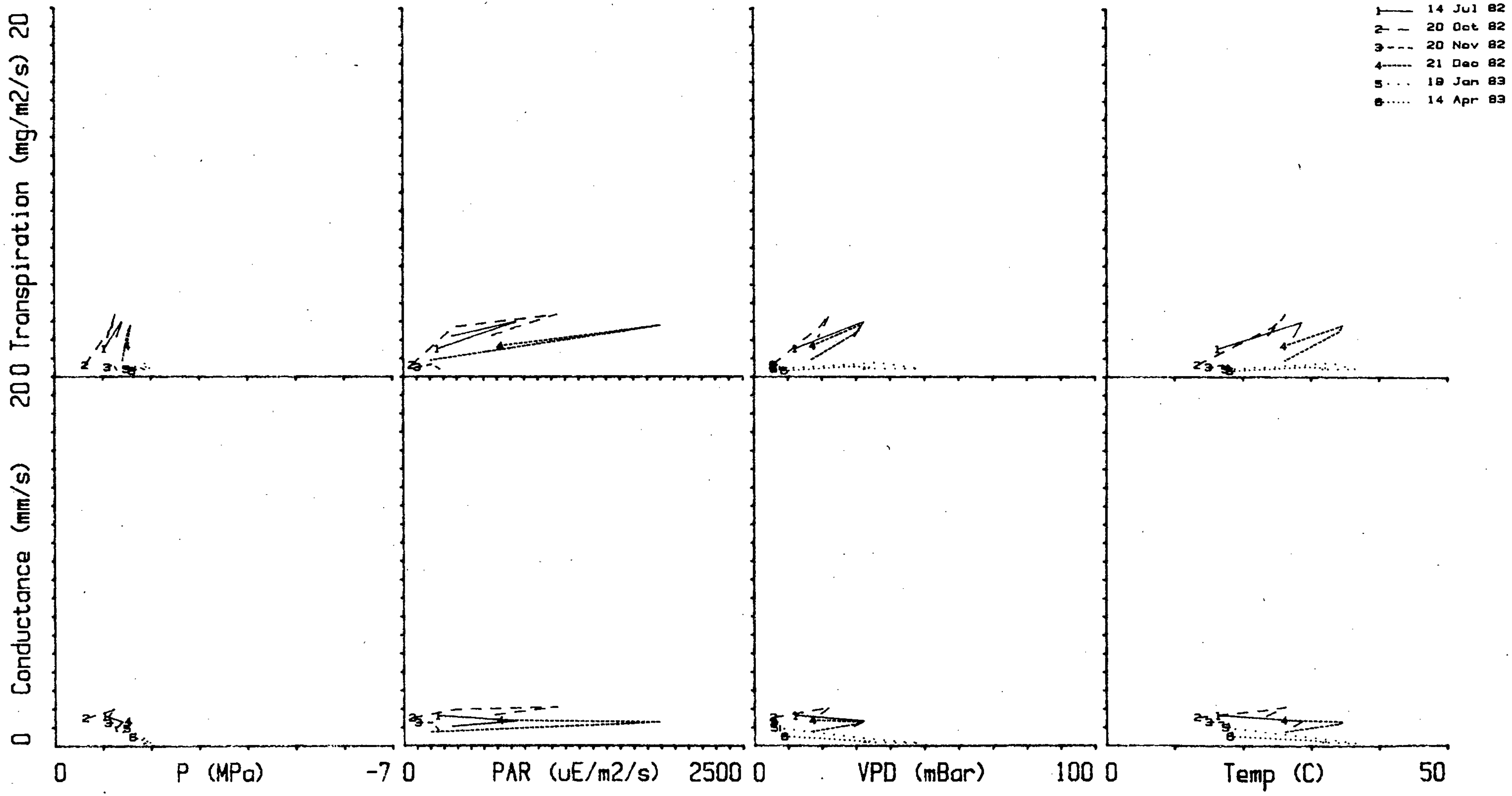


Figure A1.17 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for Paranomus bracteolaris at site 5 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

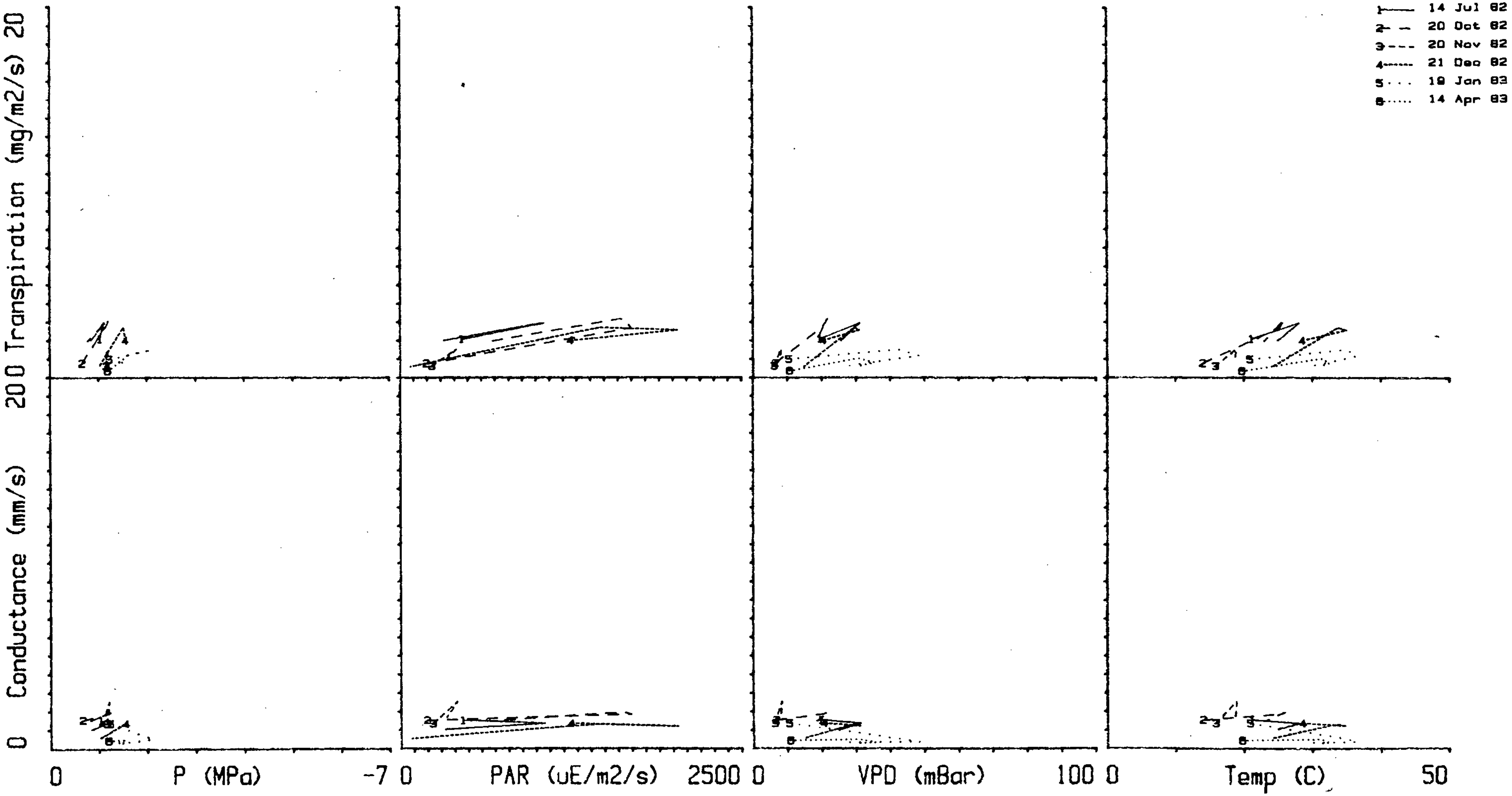


Figure A1.18 The diurnal response of leaf conductance to xylem pressure potential (P), photosynthetically active photon flux (PAR), vapor pressure deficit (VPD), and temperature (Temp) for *Leucadendron pubescens* at site 5 during the period July 1982 to April 1983. The numbers mark the beginning point for the day.

Appendix 2

The potential maximum response of leaf conductances of the 13 species to the controlling variables; xylem pressure potential, photosynthetically active photon flux, vapor pressure deficit, and air temperature.

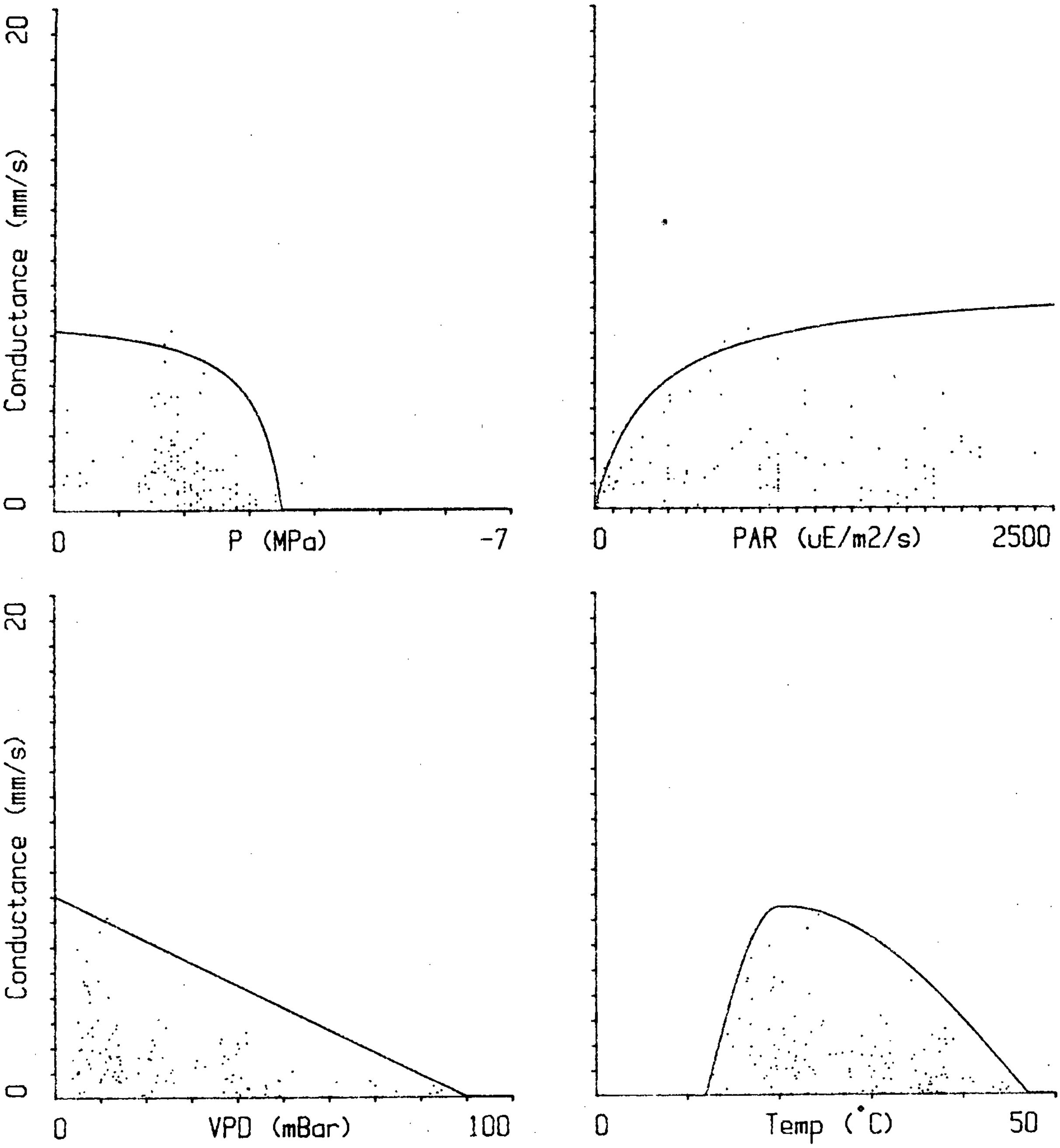


Figure A2.1 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for *Ruschia sp.* at site 1 .

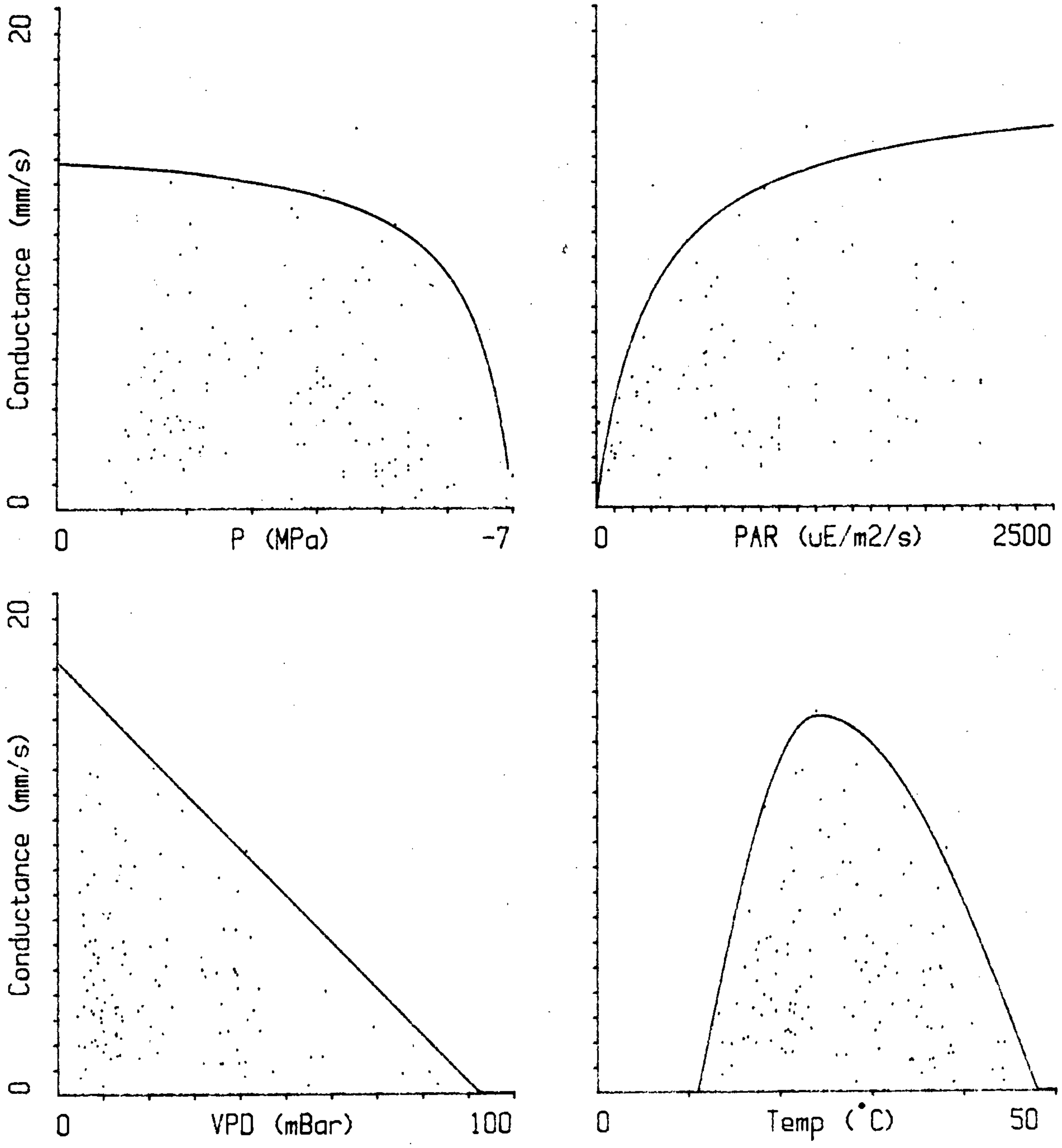


Figure A2.2 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for <u>Rhus incisa</u> at site 1 .

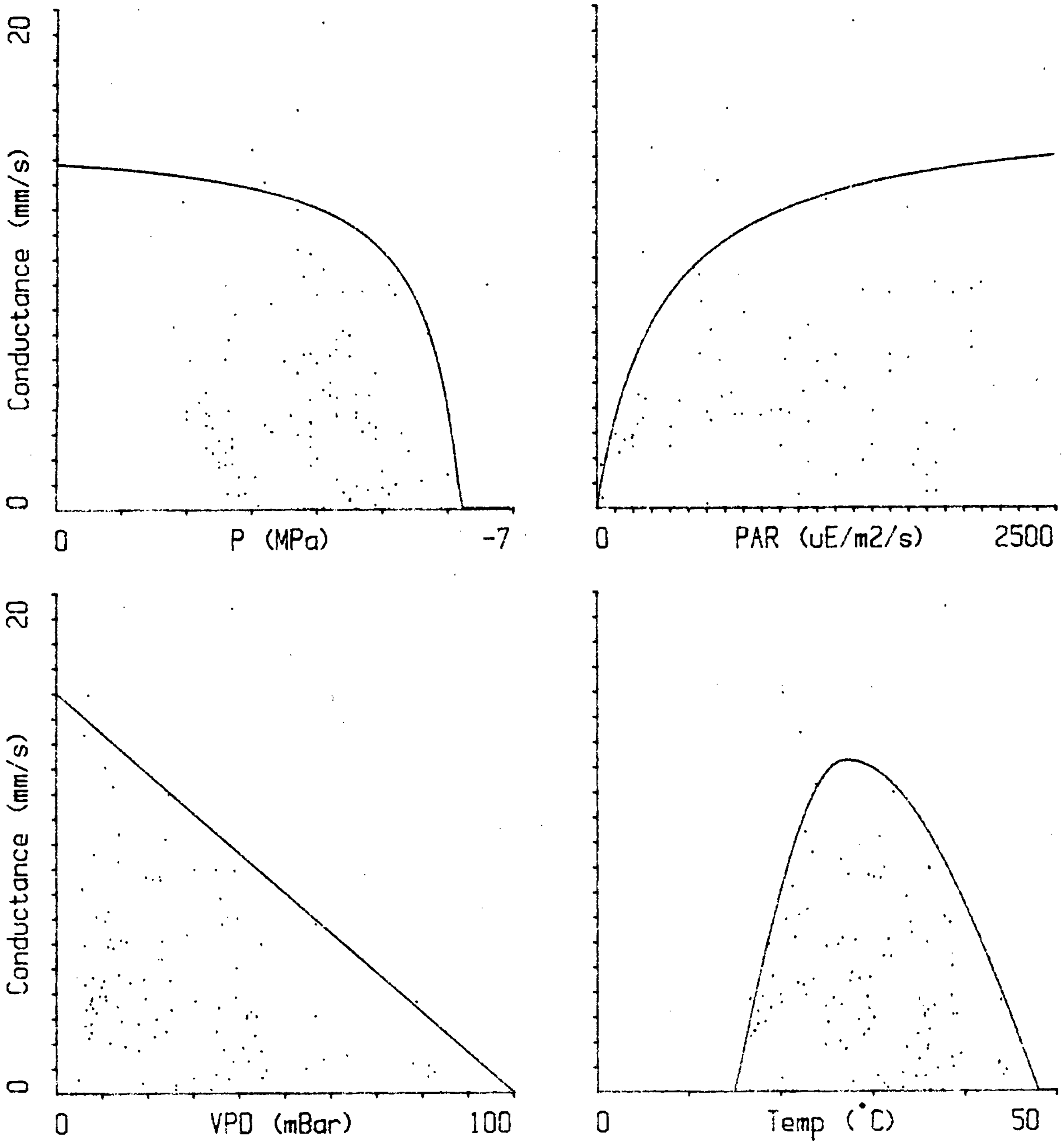


Figure A2.3 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for Galenia africana at site 1 .

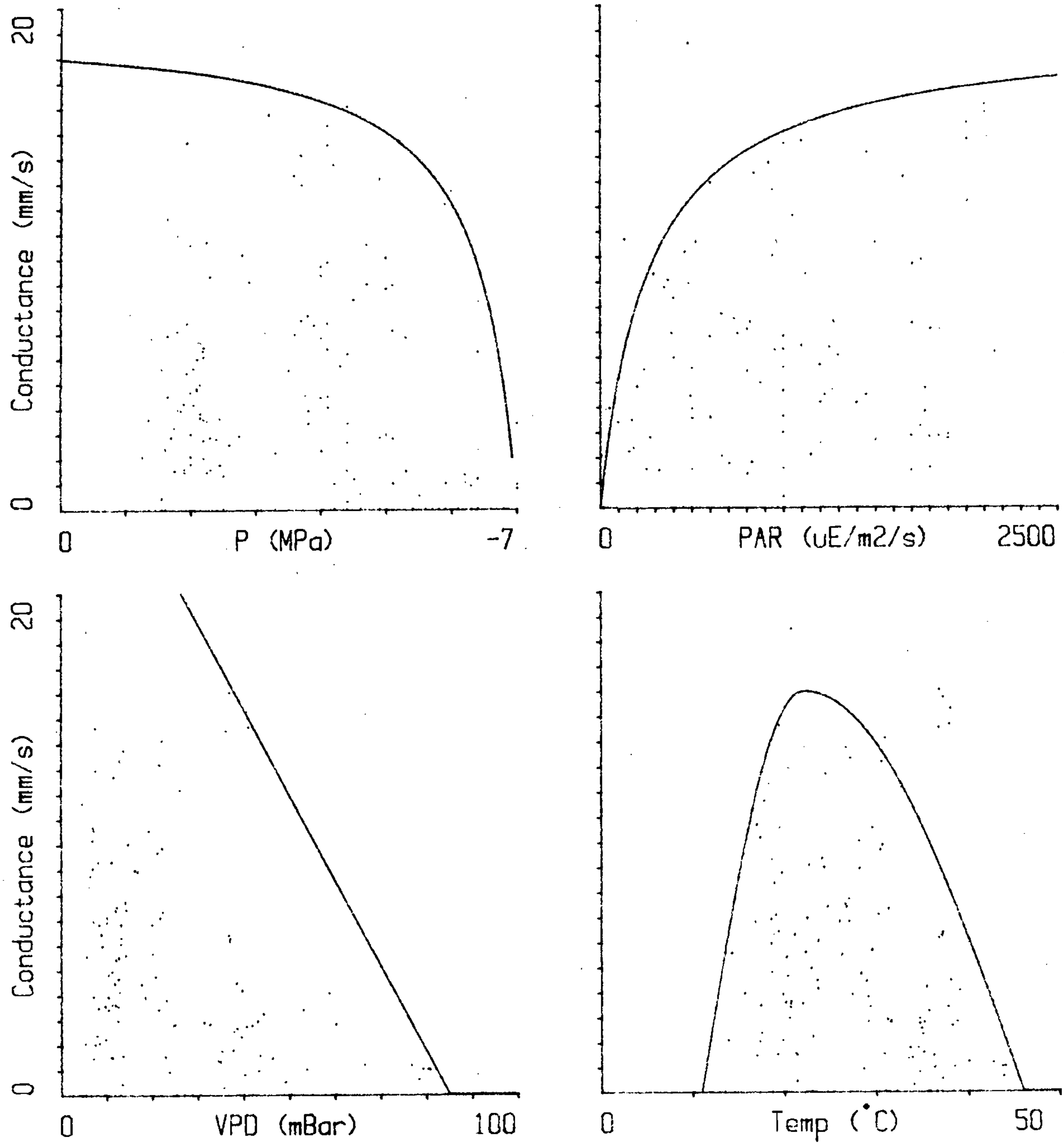


Figure A2.4 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for *Nylandtia spinosa* at site 1 .

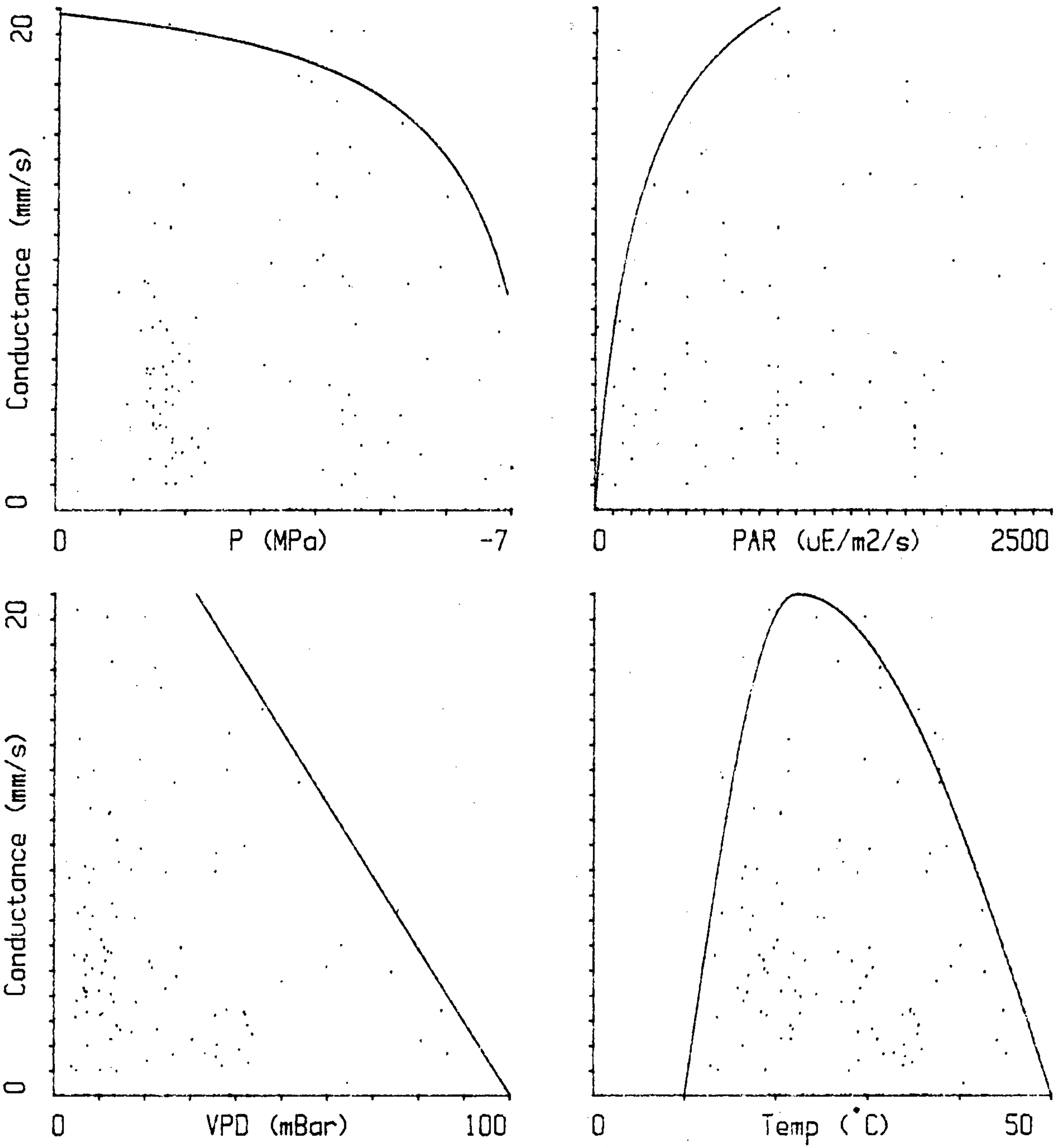


Figure A2.5 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for Eriocephalus africanus at site 1 .

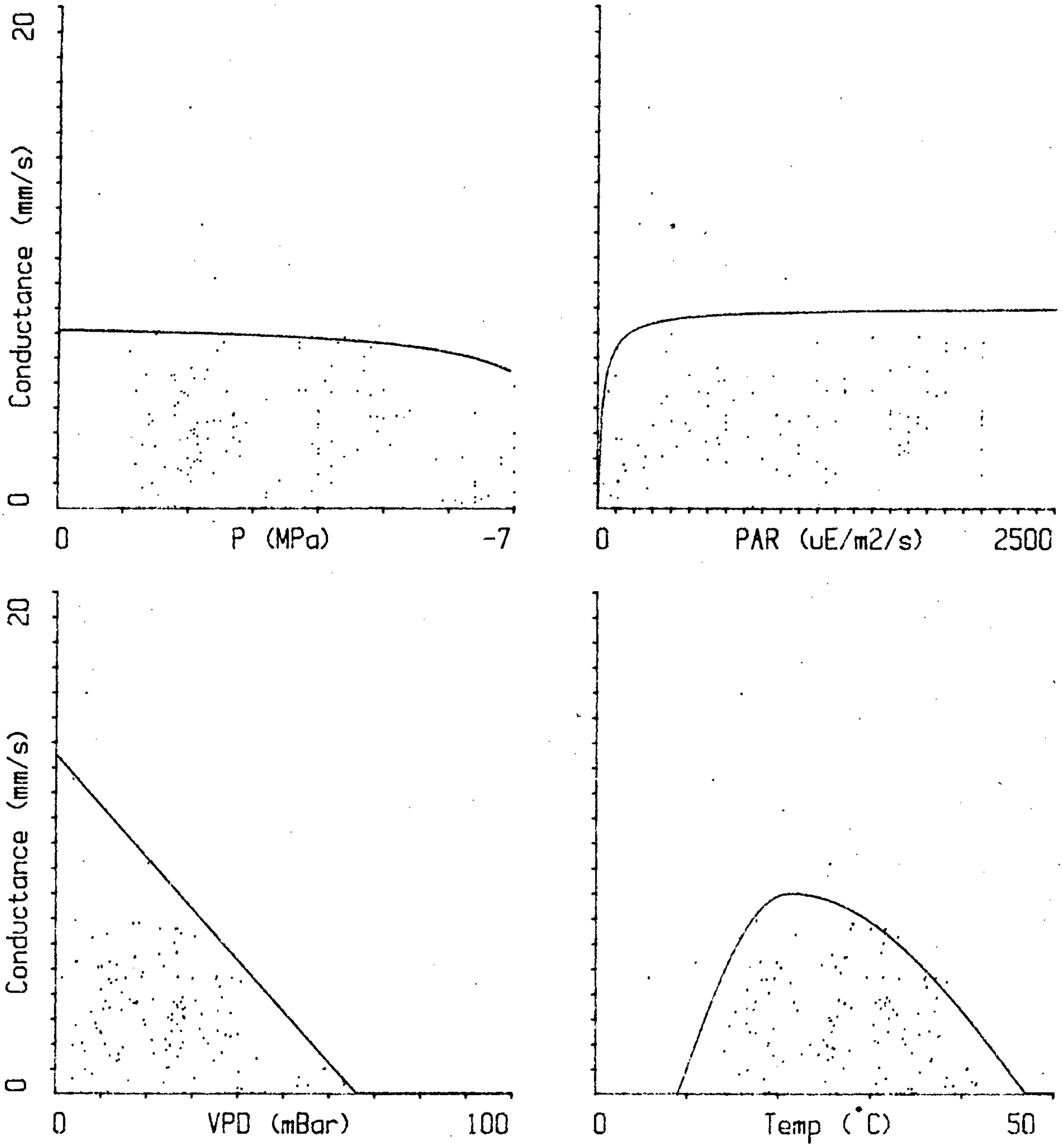


Figure A2.6 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for *Nylandtia spinosa* at site 3 .

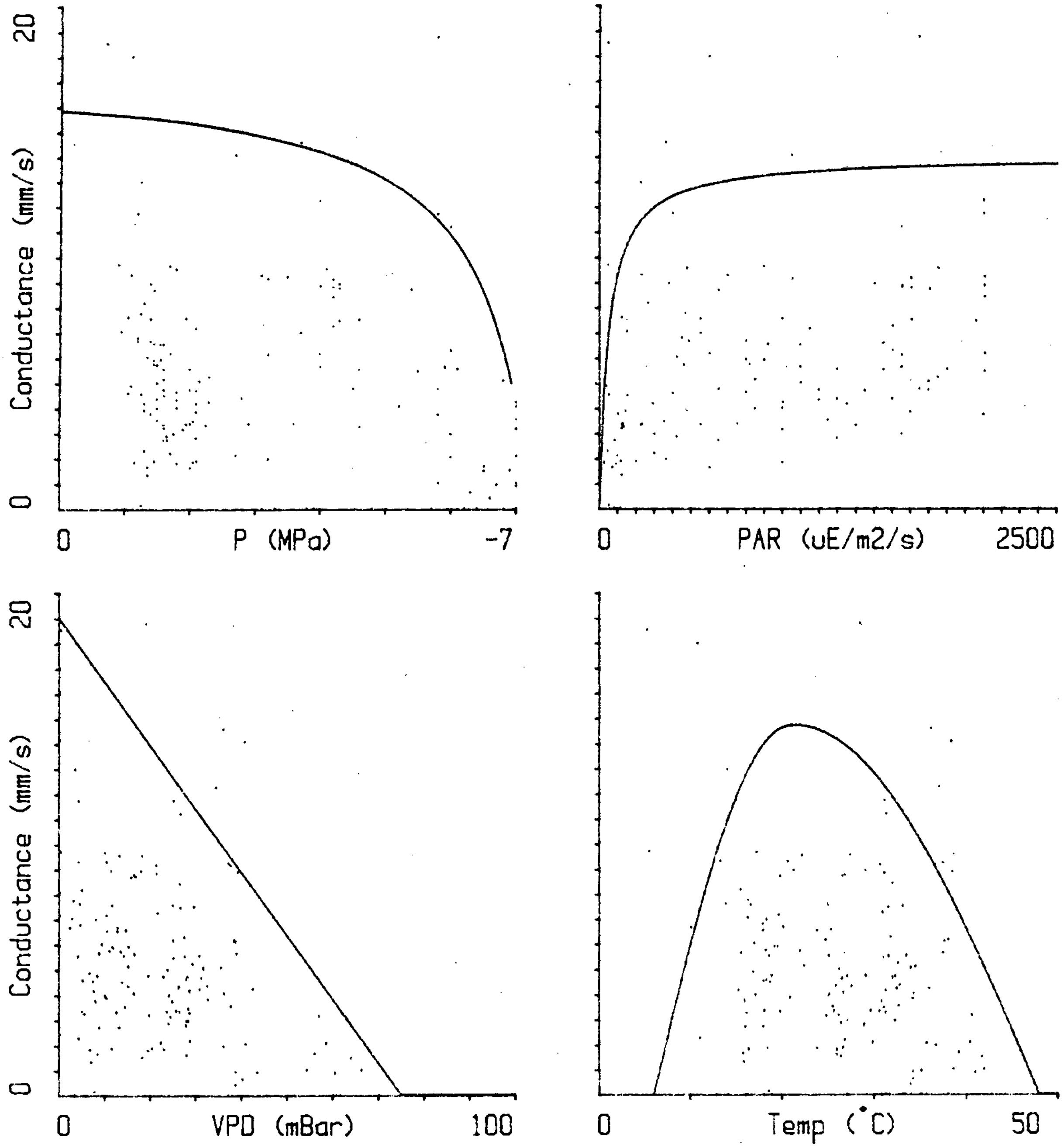


Figure A2.7 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for *Eriocephalus africanus* at site 3 .

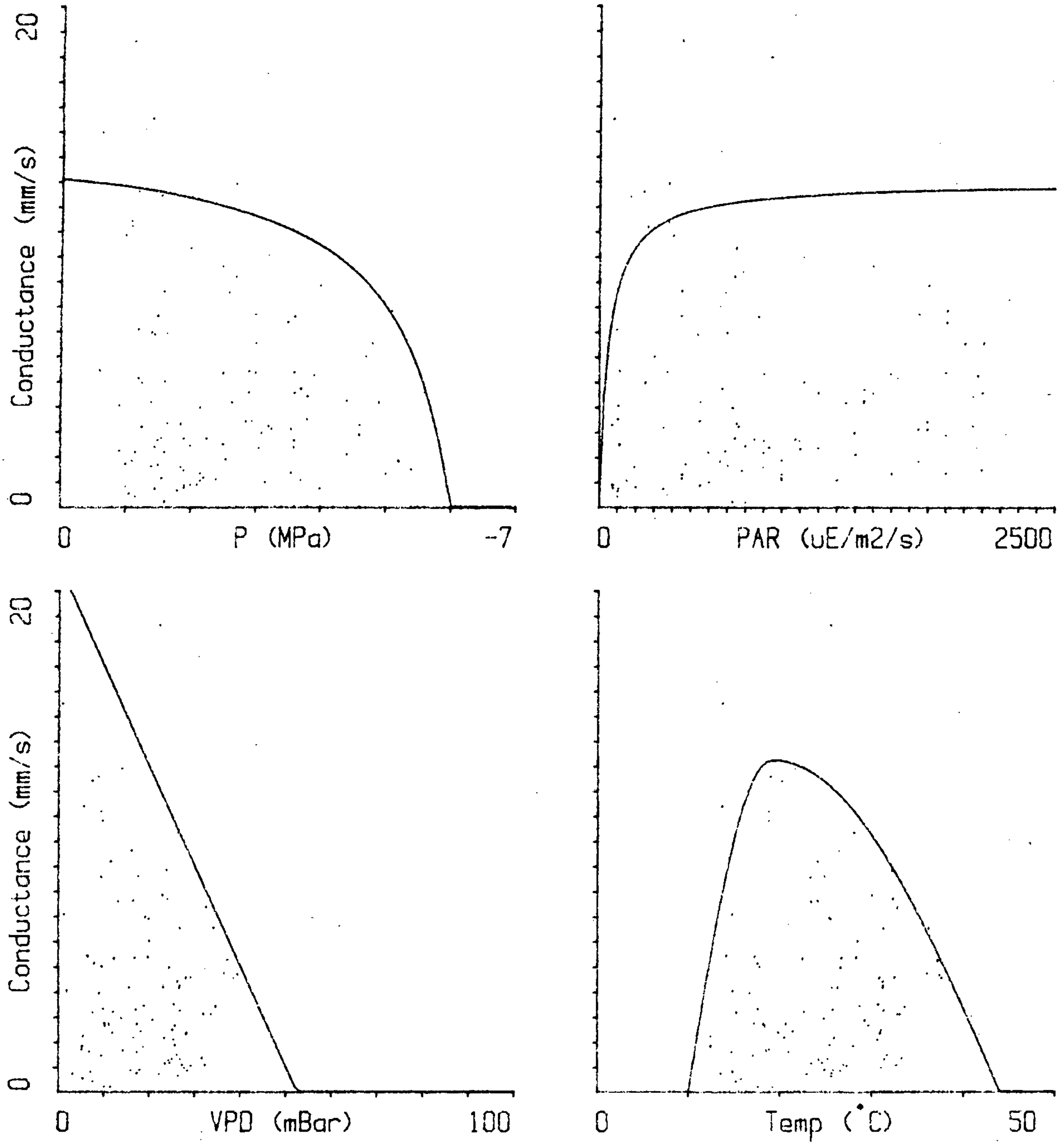


Figure A2.8 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for Rhus dissecta at site 3 .

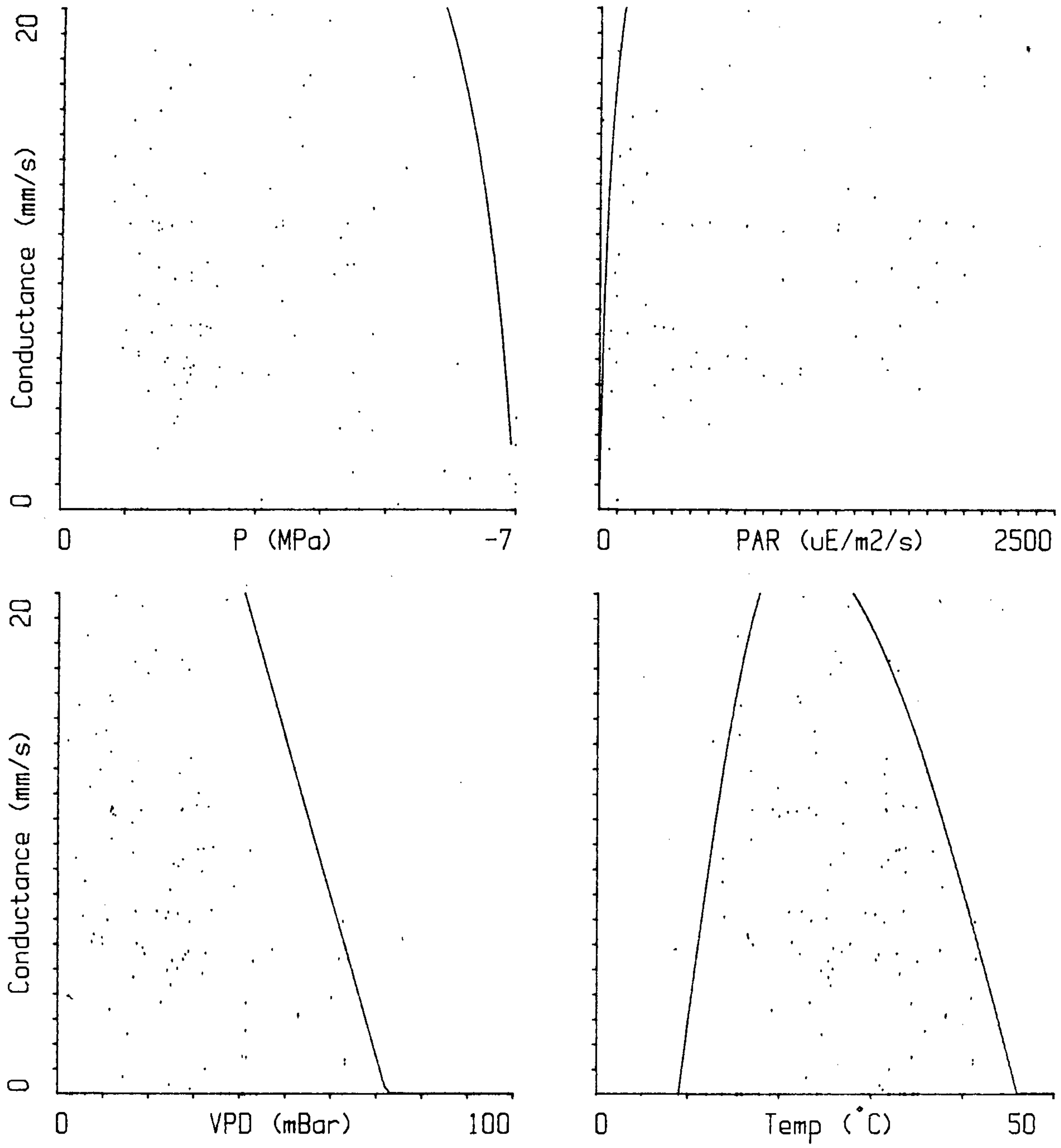


Figure A2.9 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for <u>Elytropappus gnaphaloides</u> at site 3 .

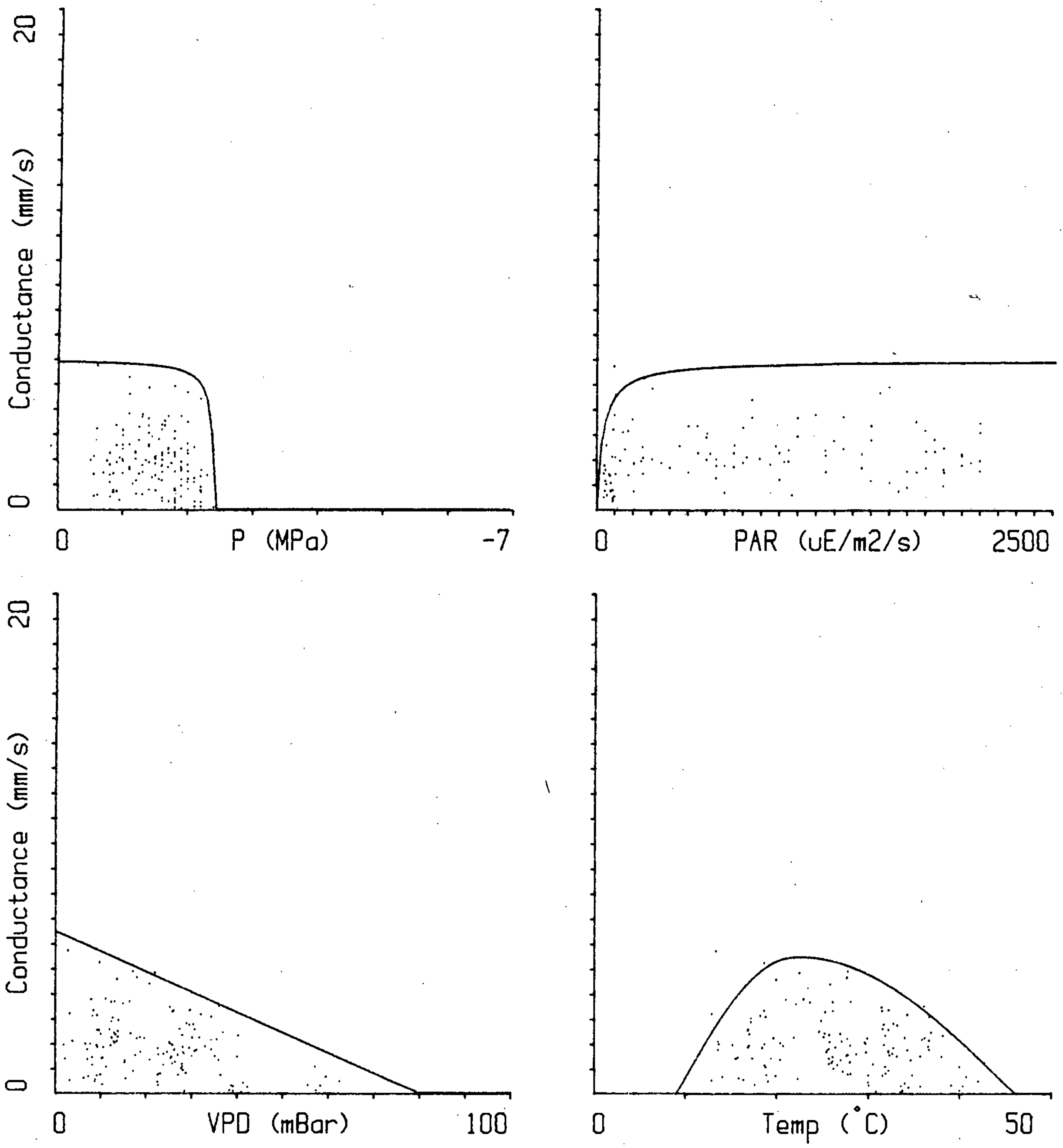


Figure A2.10 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for Protea laurifolia at site 3 .

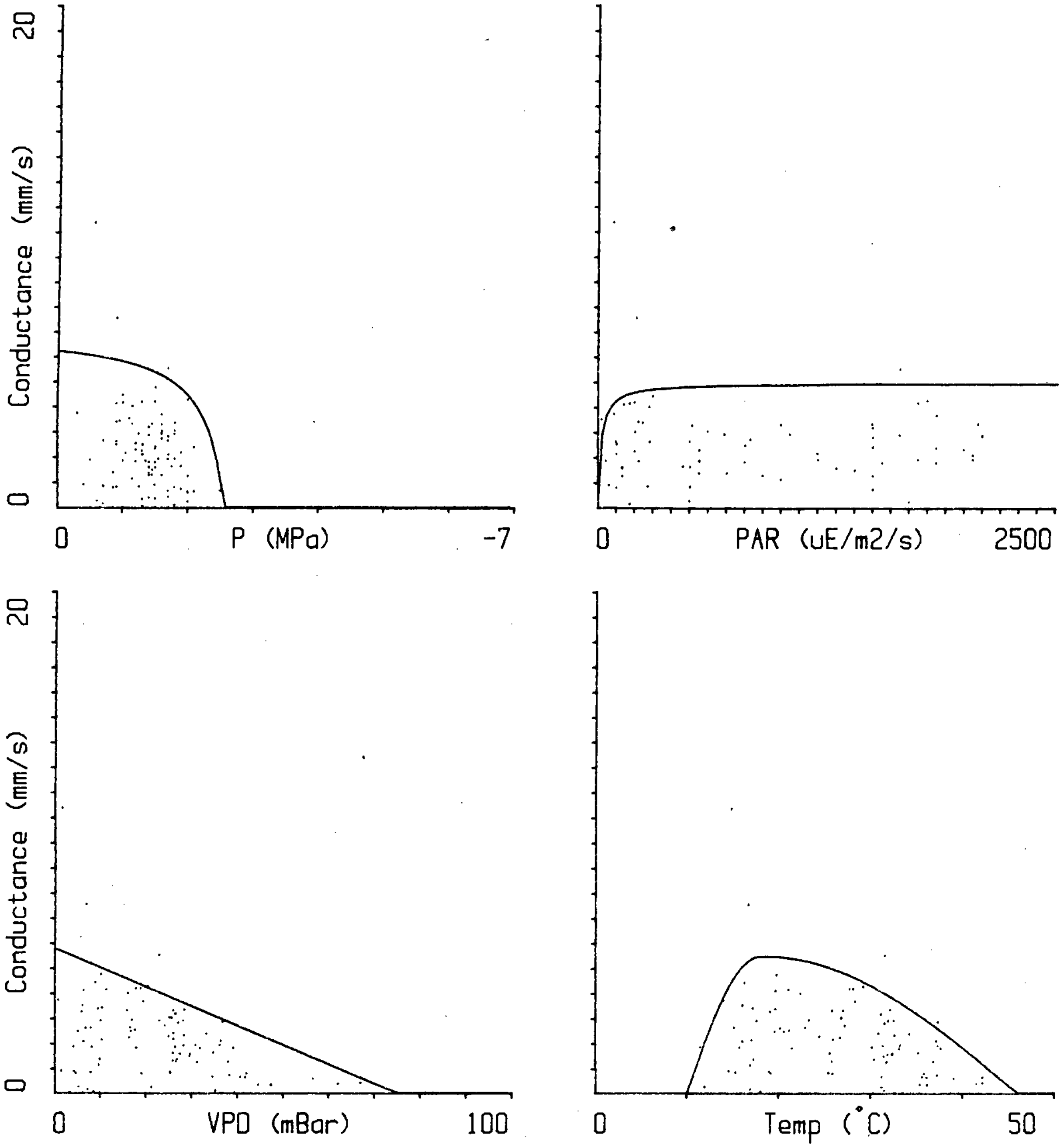


Figure A2.11 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for <u>Protea glabra</u> at site 3 .

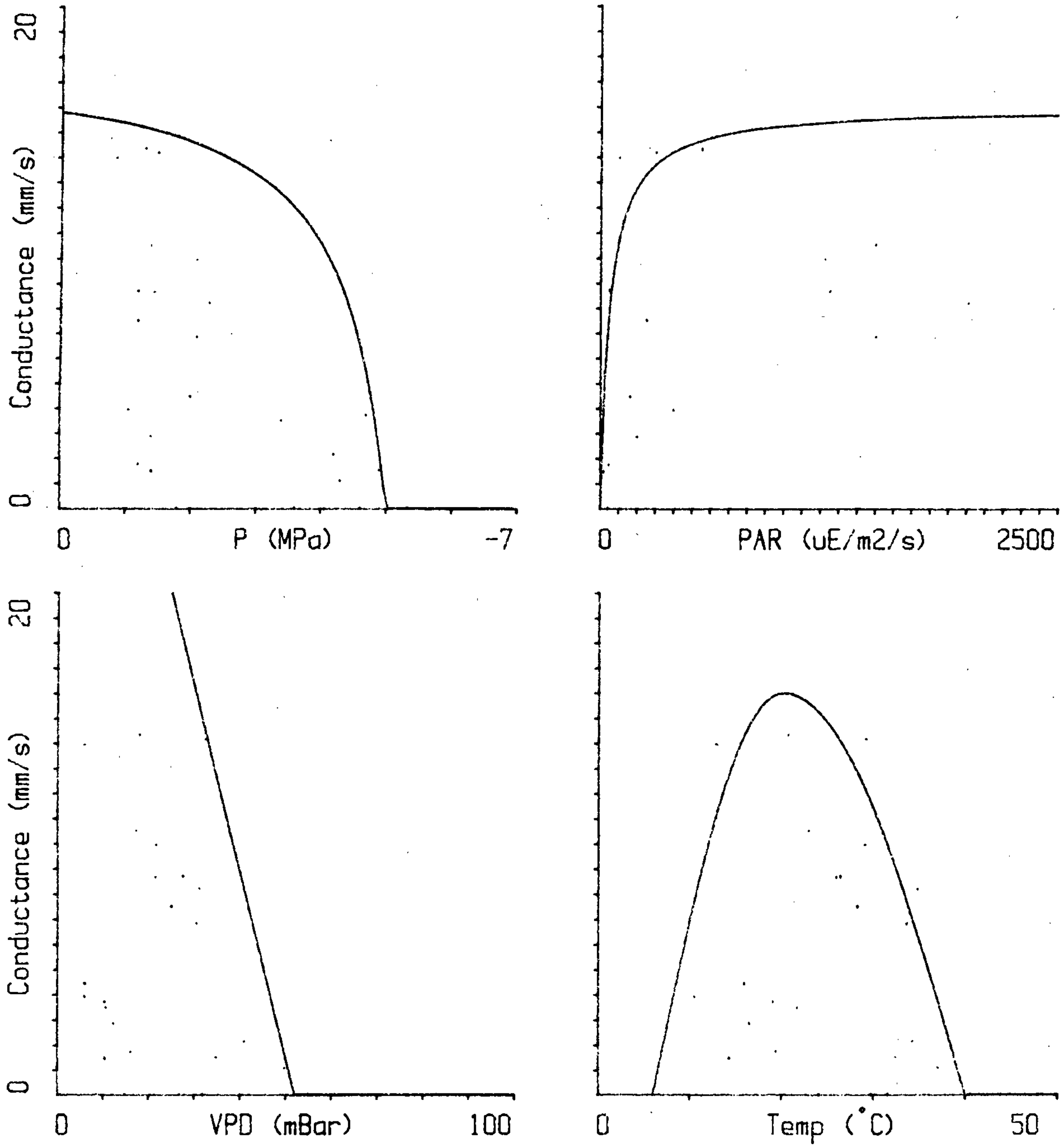


Figure A2.12 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for Eriocephalus africanus at site 5 .

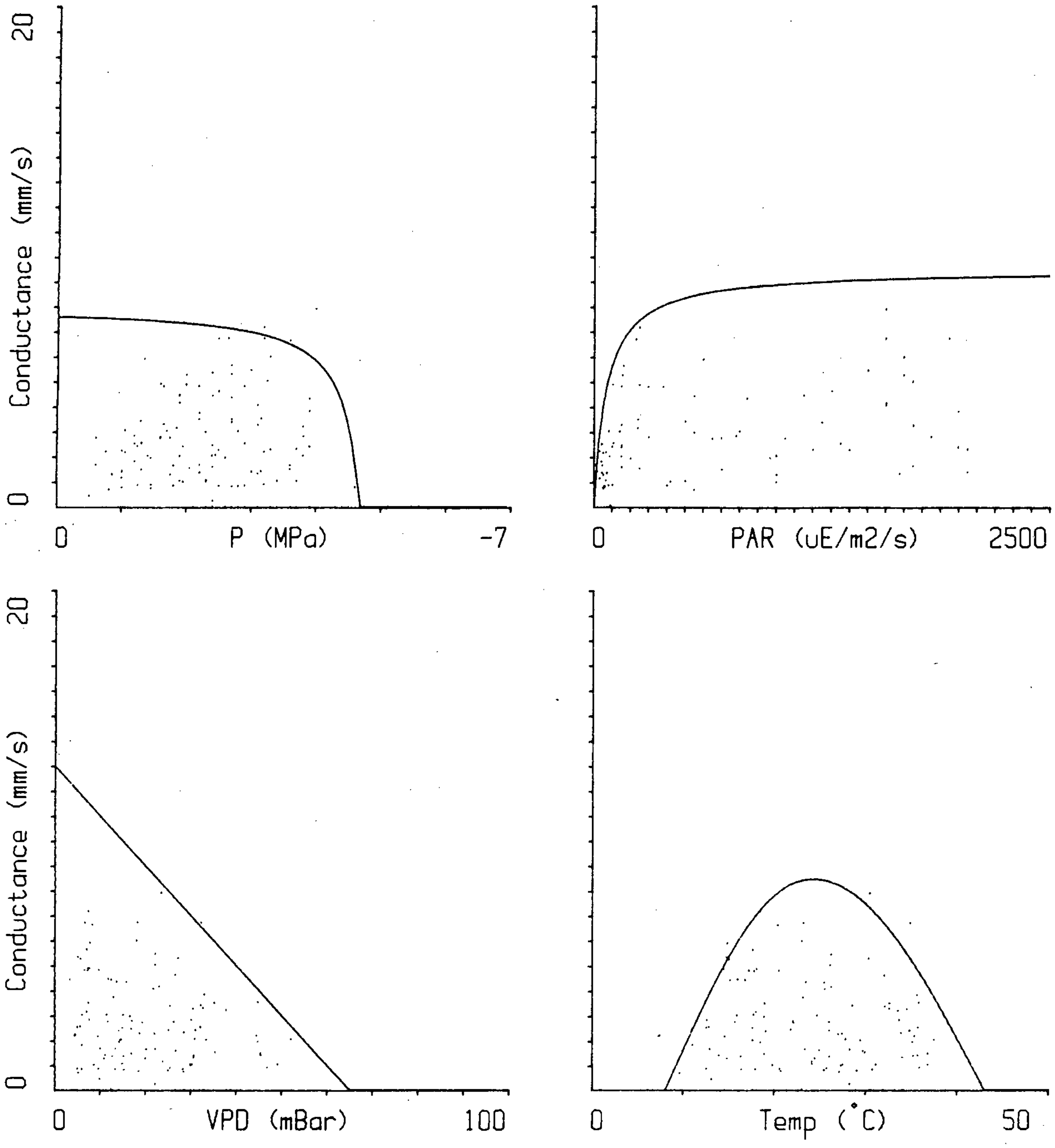


Figure A2.13 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for <u>Rhus dissecta</u> at site 5 .

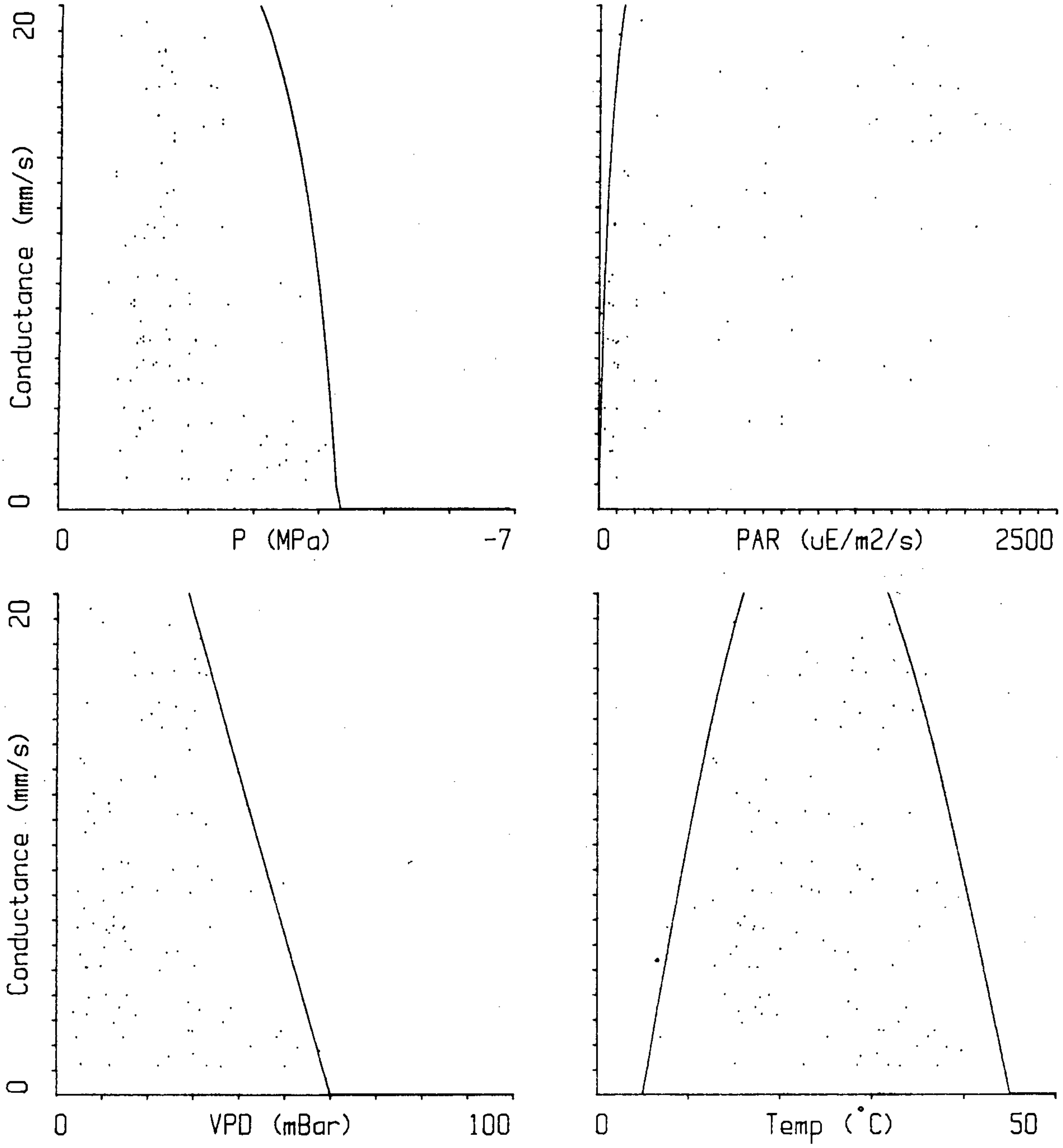


Figure A2.14 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for Stoebe capitata at site 5 .

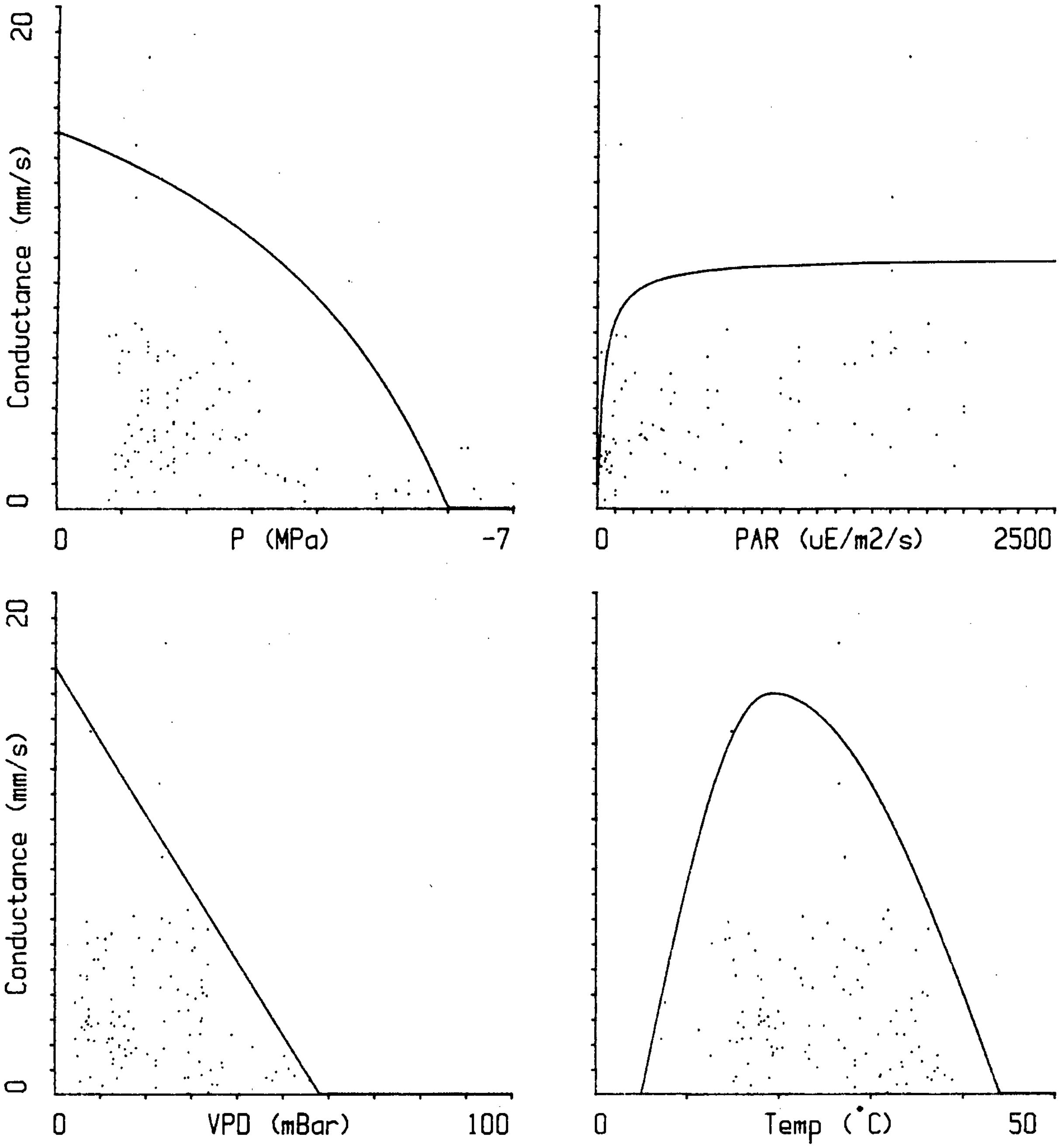


Figure A2.15 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for Agathosma giftbergensis at site 5 .

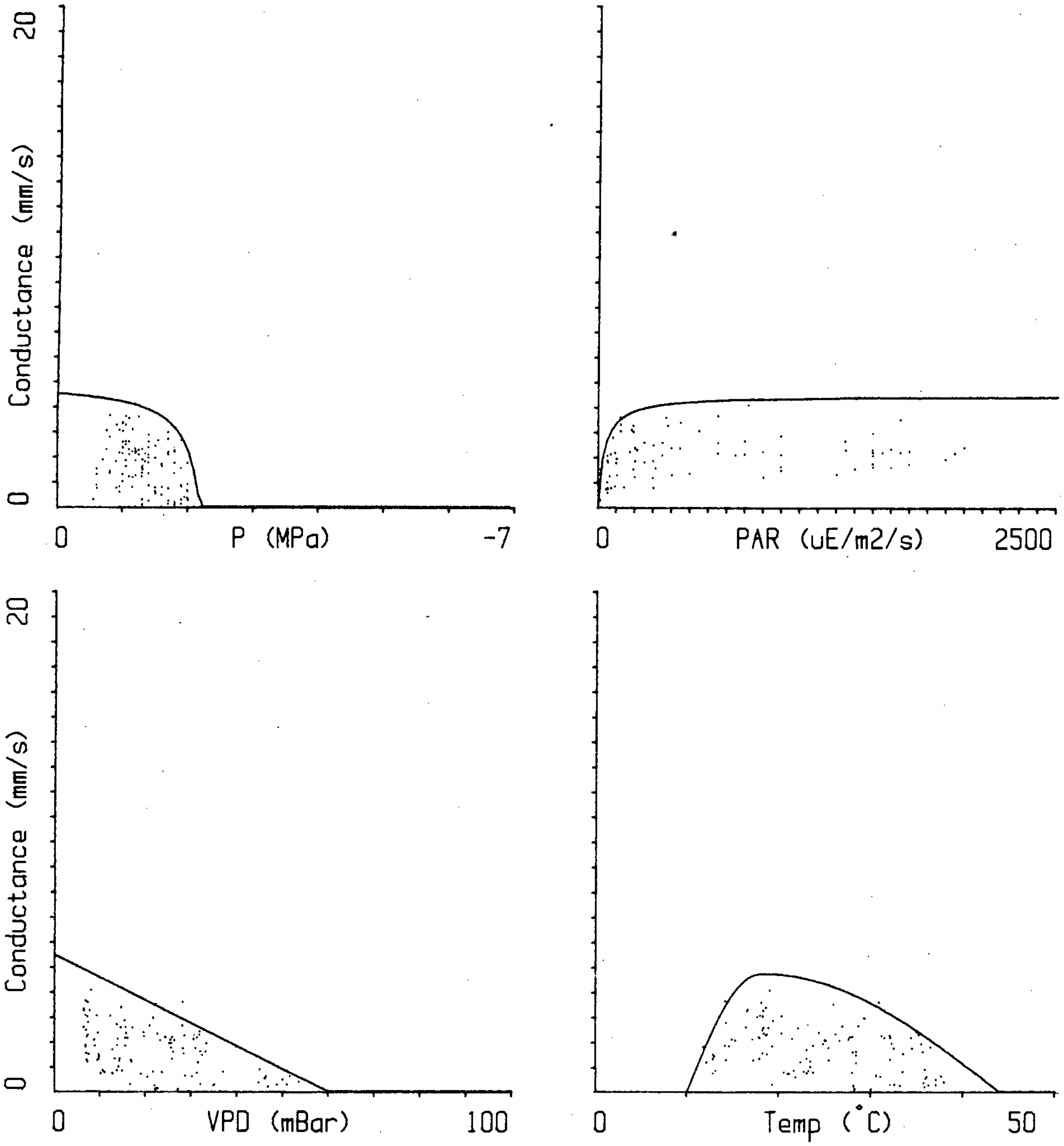


Figure A2.16 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for <u>Protea laurifolia</u> at site 5 .

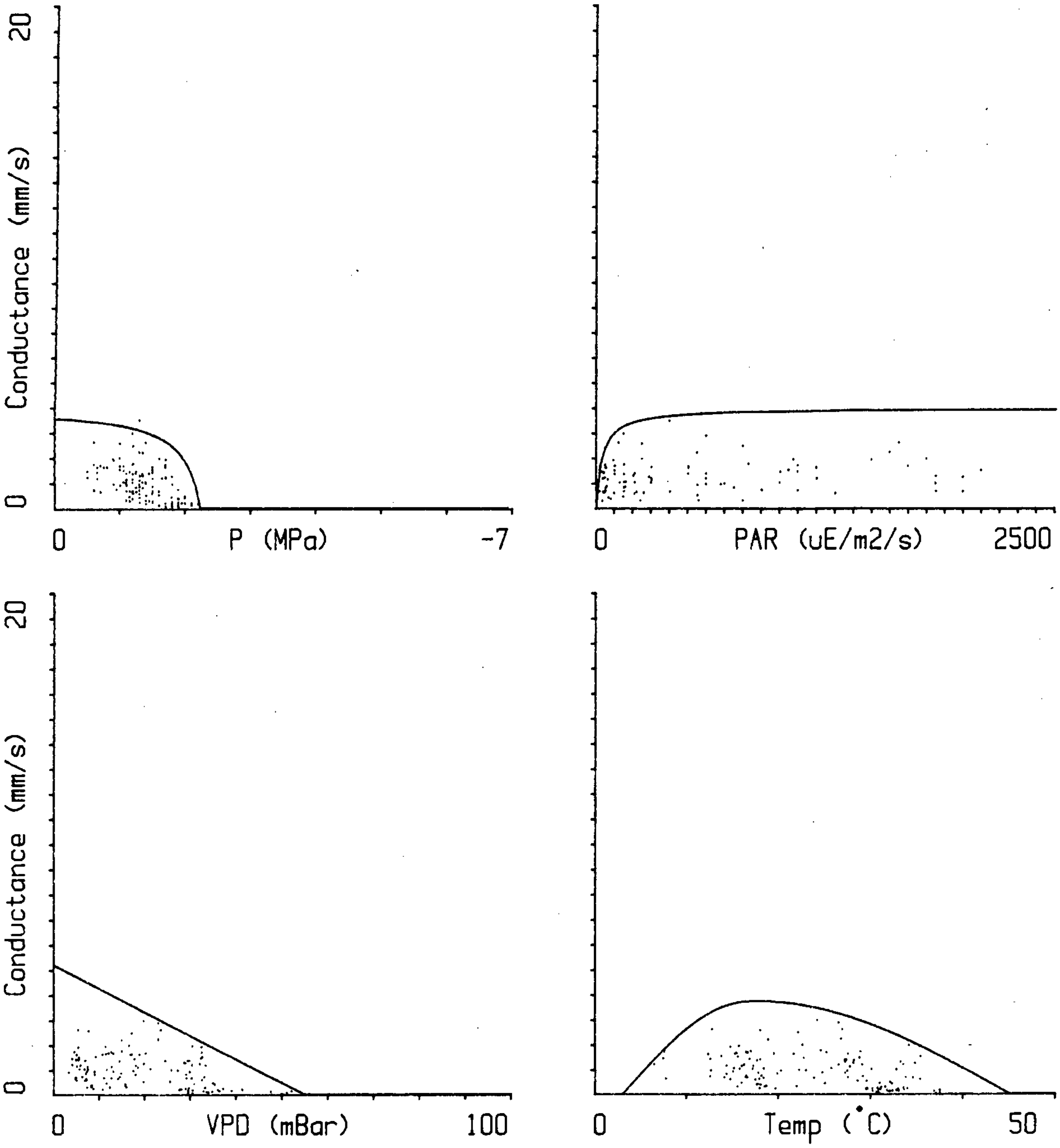


Figure A2.17 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for Paranomus bracteolaris at site 5 .

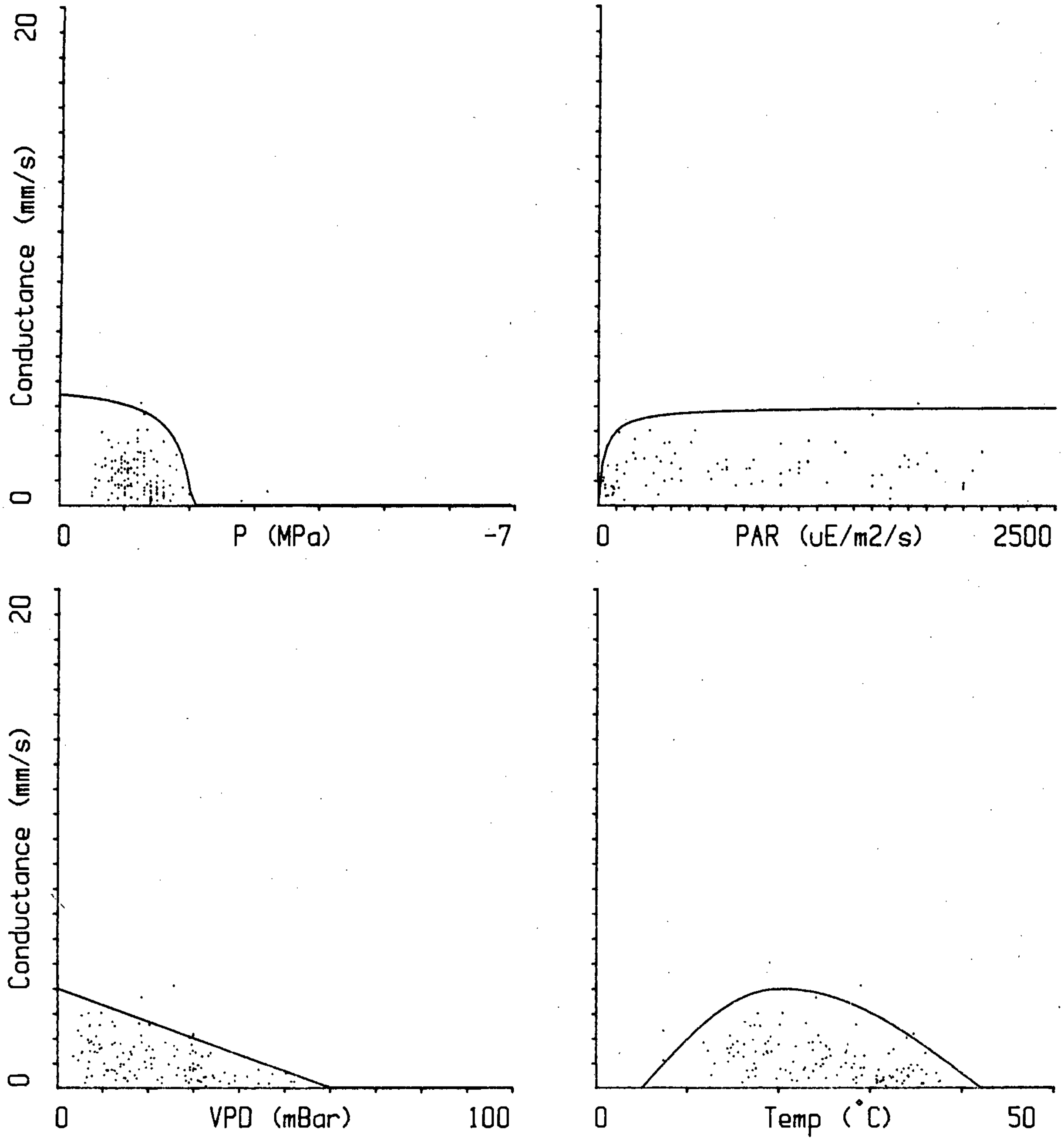


Figure A2.18 The actual and the potential maximum response of the leaf conductance to the xylem pressure potential (P), the photosynthetically active photon flux (PAR), the vapor pressure deficit (VPD), and the air temperature (Temp) for Leucadendron pubescens at site 5 .

The equations of the potential maximum leaf conductance (g) as a function of the xylem pressure potential (P) shown in Figures A2.1 to A2.18.

Species	Site	Equation
Ruschia sp.	1	$g = 8*(P+3.5)/(.42+(P+3.5))$
Rhus incisa	1	$g = 15*(P+7)/(.61+(P+7))$
Galenia africana	1	$g = 15*(P+6.2)/(.55+(P+6.2))$
Nylandtia spinosa	1	$g = 19.5*(P+7)/(.6+(P+7))$
Nylandtia spinosa	3	$g = 7.5*(P+8.167)/(.467+(P+8.167))$
Eriocephalus africanus	1	$g = 22*(P+7.467)/(.84+(P+7.467))$
Eriocephalus africanus	3	$g = 17.5*(P+7.23)/(.75+(P+7.23))$
Eriocephalus africanus	5	$g = 18*(P+5)/(.7+(P+5))$
Rhus dissecta	3	$g = 15*(P+6)/(.87+(P+6))$
Rhus dissecta	5	$g = 8*(P+4.67)/(.25+(P+4.67))$
Elytropappus gnaphaloides	3	$g = 37*(P+7)/(.933+(P+7))$
Stoebe capitata	5	$g = 33*(P+4.293)/(.8+(P+4.293))$
Agathosma giftbergensis	5	$g = 25*(P+6)/(4+(P+6))$
Protea laurifolia	3	$g = 6*(P+2.426)/(.046+(P+2.426))$
Protea laurifolia	5	$g = 5*(P+2.193)/(.233+(P+2.193))$
Protea glabra	3	$g = 7*(P+2.567)/(.327+(P+2.567))$
Paranomus bracteolaris	5	$g = 4*(P+2.24)/(.28+(P+2.24))$
Leucadendron pubescens	5	$g = 5*(P+2.053)/(.256+(P+2.053))$

The equations of the potential maximum leaf conductance (g) as a function of the photosynthetically active photon flux (PAR) shown in Figures A2.1 to A2.18.

Species	Site	Equation
Ruschia sp.	1	g = (9*PAR)/(300+PAR)
Rhus incisa	1	g = (17*PAR)/(300+PAR)
Galenia africana	1	g = (16*PAR)/(350+PAR)
Nylandtia spinosa	1	g = (19*PAR)/(267+PAR)
Nylandtia spinosa	3	g = (8*PAR)/(25+PAR)
Eriocephalus africanus	1	g = (25*PAR)/(250+PAR)
Eriocephalus africanus	3	g = (14*PAR)/(50+PAR)
Eriocephalus africanus	5	g = (16*PAR)/(50+PAR)
Rhus dissecta	3	g = (13*PAR)/(50+PAR)
Rhus dissecta	5	g = (9.5*PAR)/(67+PAR)
Elytropappus gnaphaloides	3	g = (30*PAR)/(67+PAR)
Stoebe capitata	5	g = (30*PAR)/(67+PAR)
Agathosma giftbergensis	5	g = (10*PAR)/(33+PAR)
Protea laurifolia	3	g = (6*PAR)/(33+PAR)
Protea laurifolia	5	g = (4.5*PAR)/(33+PAR)
Protea glabra	3	g = (5*PAR)/(17+PAR)
Paranomus bracteolaris	5	g = (4*PAR)/(33+PAR)
Leucadendron pubescens	5	g = (4*PAR)/(33+PAR)

The equations of the potential maximum leaf conductance (g) as a function of the vapor pressure deficit (VPD) shown in Figures A2.1 to A2.18.

Species	Site	Equation
Ruschia sp.	1	g = -.088888*VPD+8
Rhus incisa	1	g = -.186486*VPD+17.25
Galenia africana	1	g = -.16*VPD+16
Nylandtia spinosa	1	g = -.341*VPD+29
Nylandtia spinosa	3	g = -.20454*VPD+13.5
Eriocephalus africanus	1	g = -.29*VPD+29
Eriocephalus africanus	3	g = -.25333*VPD+19
Eriocephalus africanus	5	g = -.74038*VPD+38.5
Rhus dissecta	3	g = -.4*VPD+21
Rhus dissecta	5	g = -.2*VPD+13
Elytropappus gnaphaloides	3	g = -.635294*VPD+46
Stoebe capitata	5	g = -.64167*VPD+38.5
Agathosma giftbergensis	5	g = -.2931*VPD+17
Protea laurifolia	3	g = -.08125*VPD+6.5
Protea laurifolia	5	g = -.091667*VPD+5.5
Protea glabra	3	g = -.07733*VPD+5.8
Paranomus bracteolaris	5	g = -.094545*VPD+5.2
Leucadendron pubescens	5	g = -.066667*VPD+4

The parameters of the equations, and the equations of the potential maximum leaf conductance (g) as a function of the air temperature shown in Figures A2.1 to A2.18.

Species	Site	Parameters T[low]	T[max]	T[high]	CMAX
Ruschia sp.	1	12	20	47	7.5
Rhus incisa	1	11	24	48	15
Galenia africana	1	15	27	48	13.25
Nylandtia spinosa	1	11	22	46	16
Nylandtia spinosa	3	9	21	47	8
Eriocephalus africanus	1	10	22	50	20
Eriocephalus africanus	3	6	21	48	14.75
Eriocephalus africanus	5	6	20	40	16
Rhus dissecta	3	10	19	44	13.25
Rhus dissecta	5	8	24	43	8.5
Elytropappus gnaphaloides	3	9	21	46	22
Stoebe capitata	5	5	23	45	24.5
Agathosma giftbergensis	5	5	19	44	16
Protea laurifolia	3	9	22	46	5.5
Protea laurifolia	5	10	18	44	4.75
Protea glabra	3	10	18	46	5.5
Paranomus bracteolaris	5	3	17	45	3.75
Leucadendron pubescens	5	5	20	42	4

Equation for Temp >= T[low] and <= T[max] :

g = CMAX * SIN((3.14159/2)*((Temp-T[low])/(T[max]-T[low])))

Equation for Temp > T[max] And <=T[high] :

g = CMAX * SIN((3.14159/2)*((T[high]-Temp)/(T[high]-T[max])))

Appendix 3

Explanation of statistical procedures.

Analysis of variance

One- or two-way analyses of variances with replication were calculated for the pre-dawn, midday, and midday depressions in the xylem pressure potentials following Sokal and Rohlf (1969). There were a few cases were a species was not sampled at a site in July 1982. Where this occurred the values were extrapolated from the nearest site where that species was sampled during the same month. All the species at all of the sites had similar pre-dawn xylem pressure potentials in July 1982. Based on the patterns of the diurnal ranges that occurred in October 1982, the extrapolation of the midday values would also seem reasonable.

Student-Newman-Keuls test

The Student-Newman-Keuls test (Sokal and Rohlf 1969) of the significant differences between means was used to determine if the species groupings based on distribution and growth form could be extended to include physiological parameters. The yearly means of the pre-dawn xylem pressure potentials, the midday depressions in xylem pressure potential, and the daily average xylem pressure potentials of each species at each site were tested. This allowed groups to form either based on species, or based on site, or a combination of the two, and also allowed a test of the range of the mean values of a single species found at several sites.

Regression

During the period July 1982 to April 1983 the pre-dawn xylem pressure potentials of most of the species declined as a result of the seasonality of the rainfall and the occurrence of the summer drought. The relationship between the midday depression in the xylem pressure potentials, and the pre-dawn xylem pressure potentials were calculated for this period in order to exclude the next winter period when there were either new leaves or leaves that had hardened. Third order regression lines were found with the POLYFIT program (Spain 1984).

Curve fitting

The potential maximum responses of the various aspects of the water relations discussed in section 5 are lines which bound the upper limits of the data. The shapes of the curves include some hypothesized understanding of the theoretical responses.