Photosynthesis, Transpiration and Stomatal Morphology in
the Leafless, Desert Cucurbit, Acanthosicyos horrida.

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Summary: The !Nara plant (Acanthosicyos horrida Welw. ex.
Bentham & Hooker fil.) fulfils an important ecological
function in the Namib Desert by providing food and shelter
for a variety of desert vertebrates and invertebrates. It
is entirely leafless but its numerous thorns contain
chlorophyll and engage in photosynthesis. Water potential
within the xylem conduits is always positive as a result of
efficient water absorption by a deep tap root and very low
evaporative water losses from the surfaces of the plant.

Mean maximum rates of transpiration ($0.4-1.5$ mmol $m^{-2}S^{-1}$
and photosynthesis (2.9 umol $m^{-2}S^{-1}$) are low. The latter
value is among the lowest recorded and the low rates of
water loss are due to a cuticle with very low permeability
and deeply sunken stomata guarded by trichomes.

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Introduction

The 'Nara plant or <u>Acanthosicyos horrida</u> is a prominent feature of the Namib Desert flora. For millenia its fruit and particularly its seeds have been prized as food and confection by the palaeolithic nomads of this desert. It can survive for an indefinite number of years without rain. The age of many extant plants exceeds 100 years and J.D. Ward (pers. comm. 1987) has found fossil evidence suggesting that this species existed 40 million years ago.

The prominence of <u>A. horrida</u> within the floristic community of the Namib Desert is largely due to its very unusual growth form. It is entirely leafless but possesses many large, sharp thorns. These thorns are probably responsible for the specific name (<u>horrida</u>) of this species as they form intimidating thickets of thorns which protect its fruits as well as the small animals taking shelter within the thickets. The thorns do, however, contain chlorophyll and together with the stems are responsible for photosynthesis. The plant is dioecious and the fragile flowers, with a high moisture and low fibre content, provide food for several insect species. The sand beneath the plant becomes progressively more compacted and consolidated as the plant grows. This compacted sand hummock provides an ideal medium for nest and burrow construction by <u>Camponotus</u> ants and <u>Gerbillurus</u> rodent species.

Apart from the original botanical description of <u>A. horrida</u> and several anecdotal descriptions (Dinter 1912; Herre 1974/75; Dentlinger 1977; Budack, 1977, 1983; Pfeifer 1979)

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there is very little published information on this unusual plant. Nothing is, for example, known about its ecophysiology or micro-anatomy. For these reasons and the obvious ecological importance of the plant within the dune systems of both the northern and southern Namib, we have examined its morphology as well as its photosynthetic and transpiration rates. These studies were undertaken to gain a better understanding of how this plant survives in the desert environment and the opportunity to study photosynthesis in a leafless plant provided an additional incentive.

Methods and Materials

General field observations on the distribution, phenology and ecological role of A. horrida have been collected and recorded over the past 18 years during countless field excursions to both the southern and northern Namib Desert.

The transpiration and photosynthetic studies were all carried out within 2 km of the Namib Research Institute at Gobabeb, Namibia, some 56 km east of Sandwich Harbour. A first-order weather station at Gobabeb provided macro-meteorological data for these studies. Net photosynthetic rate was measured with a portable infra-red gas analyser (LCA2, Analytical Development Company) and a large cylindrical leaf chamber (PLC(C), Analytical Development Company). The leaf chamber was also provided with suitable sensors to allow measurement of photosynthetically active radiation (PAR), temperature and transpiration rate. The

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infra-red gas analysis system was calibrated by means of certified span gases and the humidity sensor by an accurate water vapour generator (ADC). Seventy six measurements of CO_2 assimilation and transpiration rates were made over a period of 10 days on eleven different plants. Measurements were evenly spaced between the hours of 05h00 and 18h00 to gain an impression of the effect of time on photosynthetic and transpiration rate. Outside this period, photosynthesis did not occur because of insufficient light. Results of the gas exchange measurements are expressed per unit of total surface area as this appears to be the conventional method for stems and for terete leaves (Nobel and Hartsock 1986). The methods and calculations employed were essentially those of Long and Hallgren (1985).

Transpiration ratios were calculated on the basis of the amount of water transpired (mg) per mg of CO_2 assimilated (Hellmuth 1971). The relative surface areas of the thorns and stems, theoretically exposed to incoming radiation, were measured on 50 samples (70 mm long) with vernier calipers. The surface micro-anatomy was examined using standard scanning electron microscopic techniques. The latter studies involved critical point drying, sputter coating and were directed mainly at observing the stomata which were not visible under the stereo dissecting microscope. The morphology of the root system was examined by excavating the root systems of two large plants on the banks of the dry Kuiseb River bed, some 8 km west of Gobabeb.

Results and Discussion

General field observations made over many years have led us
to the following conclusions. A. horrida is widely
distributed throughout the southern and northern Namib
Desert, extending well into southern Angola. Its
distribution is restricted to the banks of ephemeral desert
rivers or to the plinths of dunes where the water table is
high. Individual plants increase in size laterally to form
extensive thickets (Fig 1a,b). These thickets appear to be
dependent on the tap root of the original plant for water.
The plants naturally also reproduce by seed dispersion and
to this end they flower and fruit throughout the year,
although male flowers are far more abundant than female
flowers for most of the year.

Germinating plants are rarely seen in the field as they
require considerable rainfall before germinating and for
their subsequent survival. Small and Botha (1986) maintain
that the seeds of Acanthosicyos species remain dormant for
two years, long after fruit disintegration. Our experience
has shown, however, that under artificial cultivation the
seeds can be germinated readily within the first year.
Flowers are undoubtedly insect pollinated and meloid beetles
are the most likely vectors.

The delicate, fast-growing tips of the plant may droop and
burn on contact with hot sand and plants have been observed
to die back entirely and then regrow from the root stock.
Many animals are known to eat various parts of the plant.

For example, after the flowers fall to the ground they are eaten by the tenebrionid beetle _Onymacris plana_. While still in position the flowers are consumed by meloid beetles and nara crickets (_Acanthoproctus sp._). The growing tips are soft and juicy and are eaten by nara crickets, meloid beetles, ostriches and the lizard _Angolosaurus skoogi_. _Angolosaurus_ also feeds on the thorns and will twist its body through a complete revolution while attempting to break off a thorn. If sucessful, liquid plant sap (xylem exudate) will bead on the fractured surface of the plant and form a large droplet of liquid. The _Angolosaurus_ lizards drink these droplets and Mitchell et al. (1988) consider this source of water to be of critical importance in the water balance of this desert lizard.

The thorny thickets and consolidated sand hummock beneath the _A. horrida_ provide shelter for a large number of animals. For example, when one large plant (18,5 m x 13,5 m) was fenced in between 17 October and 14 December 1977, pit traps were placed within the fenced area to capture the epigaeic fauna living under the plant. The following animals were captured: 2221 tenebrionid beetles (_Onymacris plana_); 150 tenebrionids belonging to 9 other species; one side-winding adder (_Bitis peringueyi_); one legless lizard (_Typhlosaurus braini_); three lacertid lizards (_Meroles cuneirostris_); two solifuges (_Prosolpuga schultzei_); one scorpion (_Opistophthalmus flavescens_); one cricket (_Comicus sp._); one grasshopper; as well as uncountable numbers of _Campeonotus detritus_ ants and silverfish (lepismatids).

These observations, together with the well-known importance of this plant in the diet of palaeolithic nomads for millenia (eg. Sandelowsky 1977), underline its important ecological role in the Namib Desert.

The studies of rates of photosynthesis and transpiration were carried out over a period of 10 days when weather conditions were fairly typical of the central Namib Desert. The nights were cool with absolute screen minima ranging from 6.0 to 15.5 while maximum temperatures at midday ranged from 20.1 to 35.2. The relative humidity during this period was relatively high in the early mornings (20 - 100%) and low at midday (8 - 27%). The results of these studies have been summarised graphically in Fig. 2. From these data it is immediately apparent that $\underline{A.}$ $\underline{horrida}$ does not exhibit Crassulacean Acid Metabolism (CAM) as the CO_2 assimilation becomes zero as soon as sunlight disappears. This was confirmed by taking spot readings late at night (21h00 - 24h00). It is also evident from Fig. 2 that the rate of transpiration is, as expected, in close synchrony with the rate of photosynthesis. This pattern is similar to that obtained by Brix (1962) with pine seedlings. The net photosynthetic rate increased rapidly after 07h00, when the sun rose, to reach peak values at 10h00. These peak values were maintained with minor variations until 16h00, although a period of low activity was regularly discernable between 14h00 and 15h00. These reduced values were, however, not statistically different from the remaining peak values ($p > 0,90$), probably because of the high variation exhibited

by the data. After 16h00 photosynthetic rate declined
rapidly to reach zero at 18h00 when direct sunlight no
longer fell upon the plants. Although transpiration rate
oscillated in close synchrony with the net rate of
photosynthesis and, although its transpiration values were
very low at night, the latter process never ceased entirely.

The individual values obtained for net rate of
photosynthesis ranged from 0.14 μmol m^{-2} s^{-1} at sunset to a
peak of 3.13 μmol m^{-2} s^{-1} at 10h00. For comparative
purposes, however, the range of mean values obtained between
09h00 and 16h00 (Fig. 2), namely 2 - 2.9 μmol m^{-2} s^{-1} are
more suitable. Smith and Nobel (1986) have reviewed maximum
photosynthetic rates of various evergreen shrubs and trees
from the major deserts of the world and report a range of
1.5 - 26 μmol m^{-2} s^{-1}. The very low value of 1.5 μmol m^{-2}
s^{-1} was obtained for the Australian acacia, Acacia
craspedocarpa by Hellmuth (1971). Our results fall within
the very lowest range reported by Smith and Nobel (1986)
namely 1.5 - 4 μmol m^{-2} s^{-1} and are considerably lower than
the values obtained by von Willert et al. (1982) for the
Namib endemic Welwitschia mirabilis, namely 4.0 μmol m^{-2}
s^{-1}. Also, similar values (2 - 8 μmol m^{-2} s^{-1}) have been
recorded by Nobel and Hartsock (1985) in three subfamilies
of the Cactaceae. It should also be noted that respiration
rate in the growing tips of A. horrida was so high that the
production of CO_2 always exceeded the uptake of CO_2 and
consequently the growing tips were never used for measuring
net photosynthetic rate. If the transpiration rates of A.

horrida, recorded between 09h00 and 16h00, are examined
(Fig. 2), it is evident that maximum rates of transpiration
occurred simultaneously with the maximum rate of net
photosynthesis. This is naturally to be expected because
transpiration losses during this period are via both the
cuticle and the open stomata. The mean value during this
active period of photosynthesis (1.5 mmol m^{-2} s^{-1}) is low
when compared with the mean value of 2.7 mmol m^{-2} s^{-1}
obtained over a period of four months for the arid-adapted
mediterranean shrub Thamnocortus lucens (Van der Heyden
1988). It is considerably lower than the value of 6.51 mmol
m^{-2} s^{-1} obtained for Leucodendron salignum by the same
author. The minimum value recorded during the inactive
period of the present investigation (0.4 mmol m^{-2} s^{-1}) is
extraordinarily low and suggests that the cuticle of A.
horrida is very impermeable to water loss.

It has been suggested that the transpiration ratio, or the
amount of water vapour transpired per unit of CO_2
assimilated, is a useful index for evaluating the efficiency
with which arid-adapted plants utilise water (Hellmuth
1971). In the present study 50 concomitant measurements of
transpiration rate and net CO_2 uptake gave a transpiration
rate of 649. This value lies well within the broad range of
values (133 - 6171) reported by Hellmuth (1971) for
Australian arid species. In fact, our value is within the
range of 217 - 767 obtained by the same author for
Australian arid plants growing under optimal water
conditions. The transpiration ratio does not, however,

reflect the very low water loss rates recorded during the inactive phase of our study and therefore has only limited value.

We excavated two specimens of A. horrida to examine their tap roots and in both cases had to abandon the excavation at a depth of ca. 2 m because of sand collapsing into the excavation and other logistical problems. Both excavations, however, revealed a thick, robust tap root system, one of which is illustrated in Fig. 1c. Superficial branches are either connected to satellite plants or descend towards the water table. The tap root is covered by a dry, heavily keratinised layer of tissue which is clearly adapted for preventing water loss from within and not designed at this depth for water absorption. At a depth of 2 m the tap root is still thick (2.5 cm diameter), showing no attenuation or the appearance of root hairs. If the root is sectioned at this depth, plant sap immediately wells from the tissue and forms a large liquid bead on the cut surface. We concluded that the tap root must be in direct contact with the moist sand at or near the water table, which we know to be at a depth of c. 8 m, from measurements taken at a nearby well.

The 50 measurements of the relative surface areas of thorns and stems showed that the green thorns of A. horrida make up ca. 46% of the total surface area of the plant and must therefore contribute importantly to the total photosynthetic activity. This attribute of A. horrida is very unusual.

Examination of the stem surface under a dissecting

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microscope revealed a grooved surface with many hairs,
particularly surrounding the growing tips. The surface also
appeared waxy and when water droplets were placed on the
stem surface they did not appear to be rapidly absorbed. We
were, however, not able to find the stomata under the
dissecting microscope and for this purpose we split the stem
along one of the parallel grooves and examined it under the
scanning electron microscope. The results are depicted in
Fig. 3, in which the rows of sunken stomata within the
groove are clearly evident. Not only are the stomata hidden
within the groove but they are also sunken within the tissue
matrix on the interior surface of the groove. The outer
stomatal, ledge rim is very narrow and the guard cells are
not evident as they are probably obscured by peristomal rims
(sensu Wilkinson 1979). The stomata of A. horrida do not
fit easily into any of the many categories suggested by
Wilkinson (1979) in his excellent review on the plant
surface. Nevertheless, they are similar to Wilkinson's
(1979) description of those found on the xerophytic stems of
Bredemeyera colletioides (Polygalaceae) with the important
difference that the stomata of A. horrida are juxtapposed to
well developed hairs (Fig. 3). These hairs, or more
correctly trichomes, are of the uniseriate type (Esau 1960)
and when examined under the phase contrast microscope, most
of them were clearly alive with normal nuclei and cell
structure. Trichomes are very variable structures appended
to the epidermis of plants. They can be glandular or non
secretory but are usually prominent xeromorphic structures.
Parker (1968) has suggested the following possible functions

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for trichomes, scattering incoming radiation, preventing insect attack, helping to cool the leaf by increasing total radiating surface or finally for facilitating the absorption of water from surface droplets as has been found to be the case in _Crassula_. In the case of _A. horrida_, we do not know what the function of the trichomes is, but their regular and uniform positioning adjacent to the sunken stomata suggests that they are probably involved in reducing evaporative water loss by extending and protecting the boundary layer surrounding the stomata. The possibility that they may be involved in water absorption can, however, not be ruled out and, as the distribution of _A. horrida_ lies largely within the fog belt of the Namib Desert, this intriguing possibility should be followed up. This would not be a novel concept as another Namib Desert species occurring in the fog belt, _Trianthema hereroensis_, is capable of absorbing water through its leaves (Seely, de Vos and Louw 1977).

To conclude, _A. horrida_ fulfils an important ecological function in the Namib Desert by providing both food and shelter to a large variety of desert animals. The water potential in the xylem conduits is always positive and sectioning of any green portion of the plant always produces xylem exudate. This positive pressure is the result of efficient water absorption by a deep tap root and very low evaporative water losses from the surface of the plant. The latter is in part due to deeply sunken stomata, positioned within parallel grooves on the surface of the stem and

provided with adjacent trichomes. The function of the trichomes is not known. Rates of photosynthesis and transpiration are among the lowest reported to date and, although A. horrida is slow growing, it is very long lived. The survival of newly germinated and young plants without a deep taproot system has not yet been explained. It is not known if A. horrida can absorb condensed fog water through either the stems or thorns.

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FIGURES

Figure 1a, b. *Acanthosicyos horrida* growing near the Kuiseb
River in the central Namib.

Figure 1c. A partially excavated root system.

Figure 2. Mean (±SE) of PAR (o), leaf temperature (●), net
rate of photosynthesis (■) and transpiration (□) measured
between 12 and 18 May and 12 and 14 July 1987 for
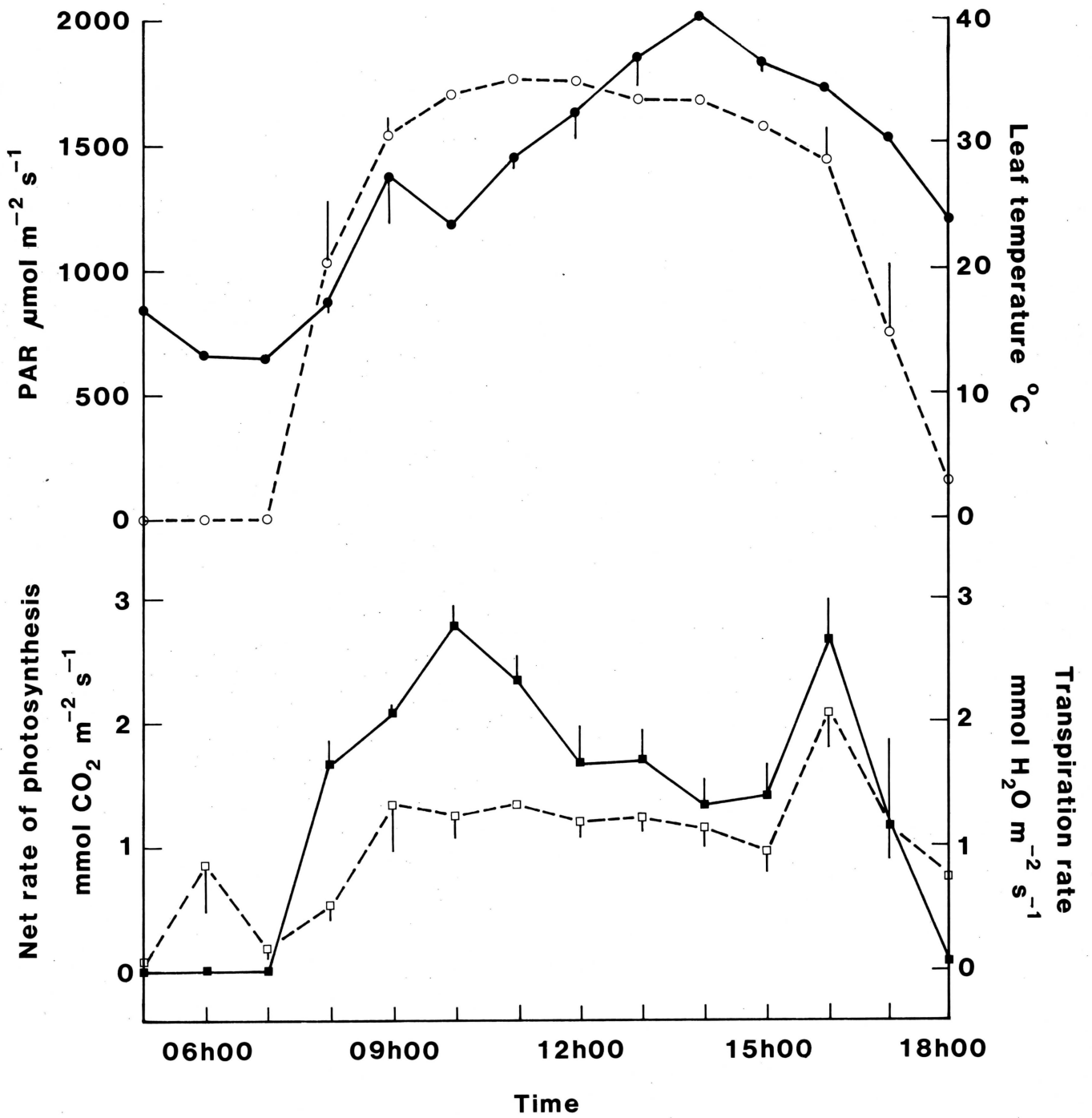*Acanthosicyos horrida* growing in the central Namib.

Figure 3. Scanning electron micrographs of *A. horrida* stems
and thorns:

Figure 3a. cross section of surface grooves with trichomes,
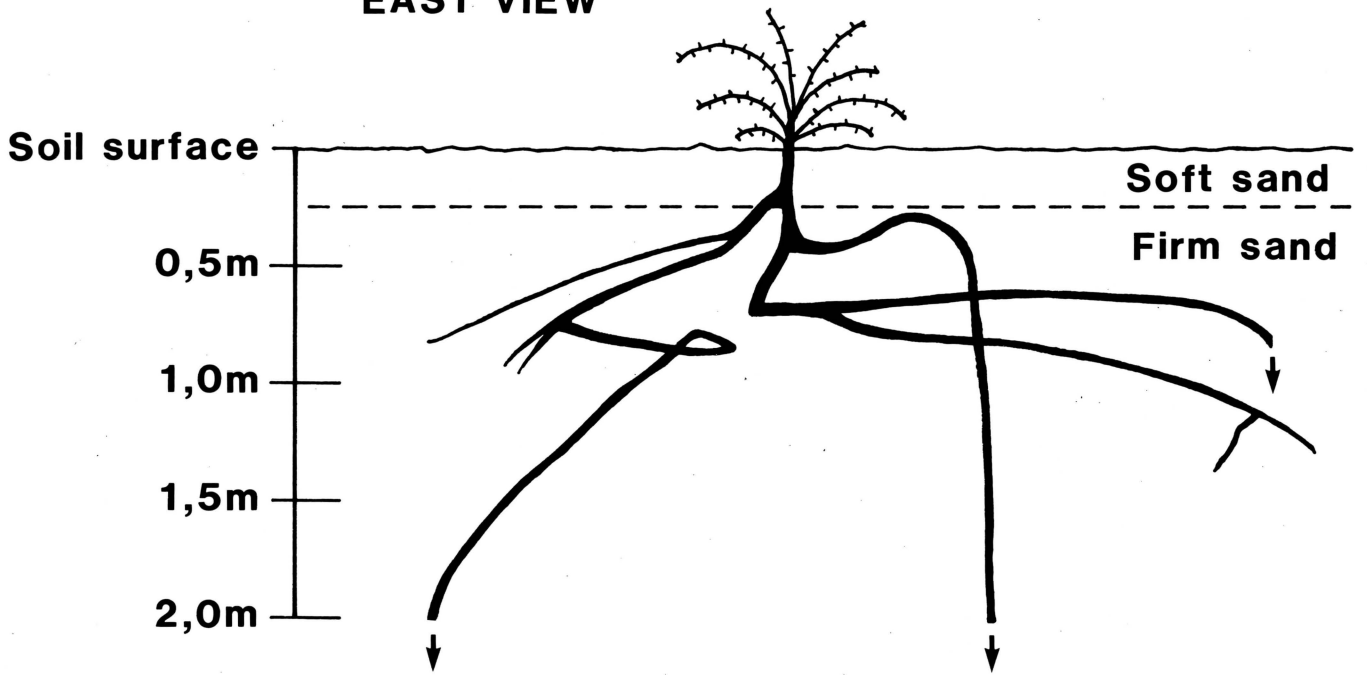light material around grooves is concentration of
chlorophyll,

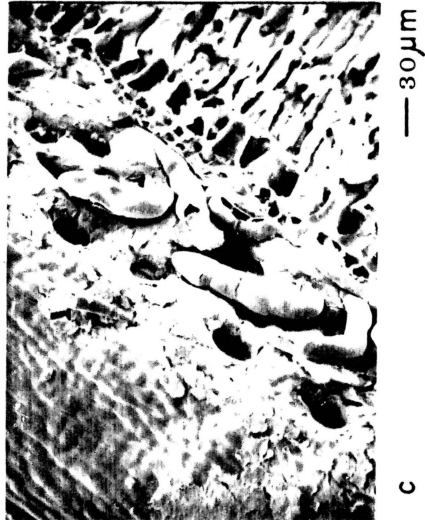Figure 3b. stomata and trichomes in surface groove,

Figure 3c. parallel trichomes and stomata in a groove,

Figure 3d. stomata.

EAST VIEW

Soil surface

Soft sand

Firm sand

0,5m

1,0m

1,5m

2,0m

30 μm

10 μm

b

d

300 μm

30 μm

a

c

EAST VIEW

Soil surface

Soft sand

0,5m

Firm sand

1,0m

1,5m

2,0m