

Figure 4.11 SEM of the surface of the surface of a leaf of IS-2123 (G line), showing a smooth wax layer and a trichome (1500X).

In the nonglossy lines, very little smooth wax is visible on the leaf surface. Uniform needleshaped wax crystals are observed under high magnification (Fig. 4.12). Silica bodies are also generally covered by the crystal layer. The small areas on glossy lines are visible with small numbers of large, irregular crystals which is in sharp contrast to the almost complete covering of crystals in nonglossy lines. Some cultivars (IS-4292, IS-4621, IS-914 and IS-4405) have clear characteristics of the nonglossy and glossy lines.

Electron microscopy

Electron micrographs show that the photosynthetic cells are in bundle sheath and the membrane organization within chloroplast and mitochondria can be distinguished (Figs. 4.13-4.15). A crosssection of C4 sorghum leaf shows mesophyll and bundle sheath chloroplasts. The chloroplasts show an outer double-membraned envelope and lamellar membrane in the stroma. Osmophilic granules are profuse. Bundle sheath chloroplast with distinct arrangement of thylakoids and starch granules are clearly observed (Maiti *et al.* 1983b).

Leaf anatomy in crosssection (Maiti *et al.* 1983b)

Lamina: Transverse sections of young leaf lamina show the following structure (Fig. 4.16-4.17):

Epidermis: Epidermis consists of roundish to flattened cells with thin cuticle on both surface of the leaf. Stomata are embedded in a suboptimal cavity with guard cells. Bulliform cells are present on the upper epidermis.

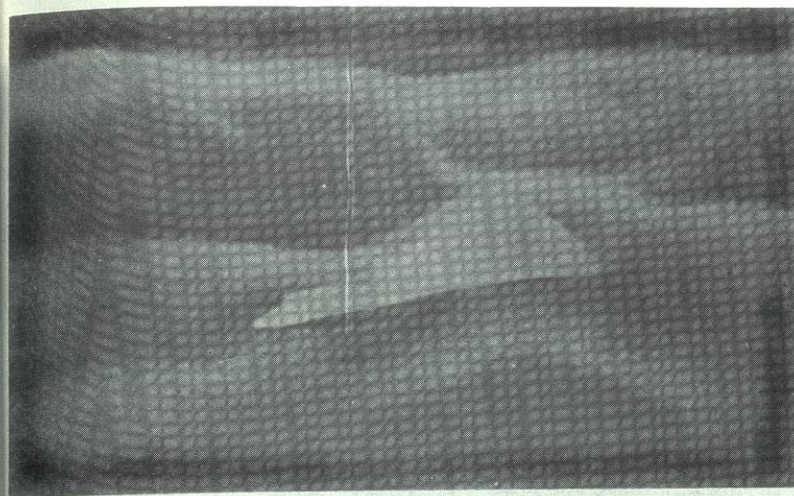


Figure 4.12 SEM of the surface of a leaf of E-202 (Non-glossy line), showing an uneven surface, the underlying needleshaped crystals and a trichome (1500X).

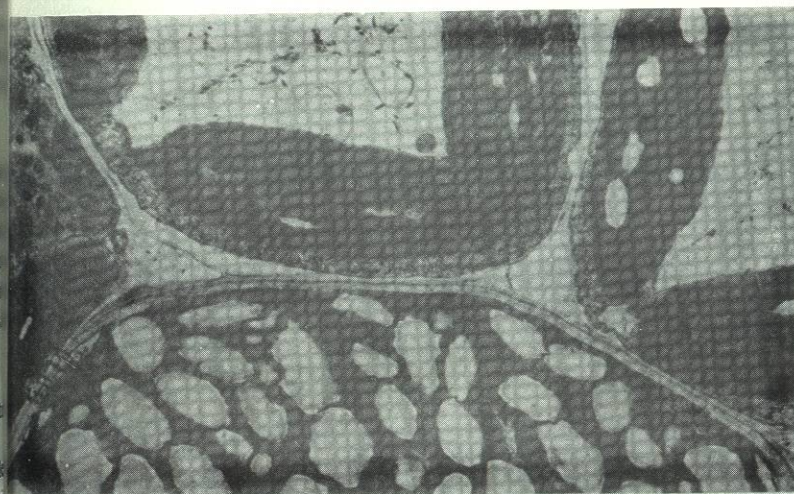


Figure 4.13 Electron micrograph of a sorghum leaf, showing a mesophyll chloroplast (top) and a bundle sheath (bottom, with large starch granules).

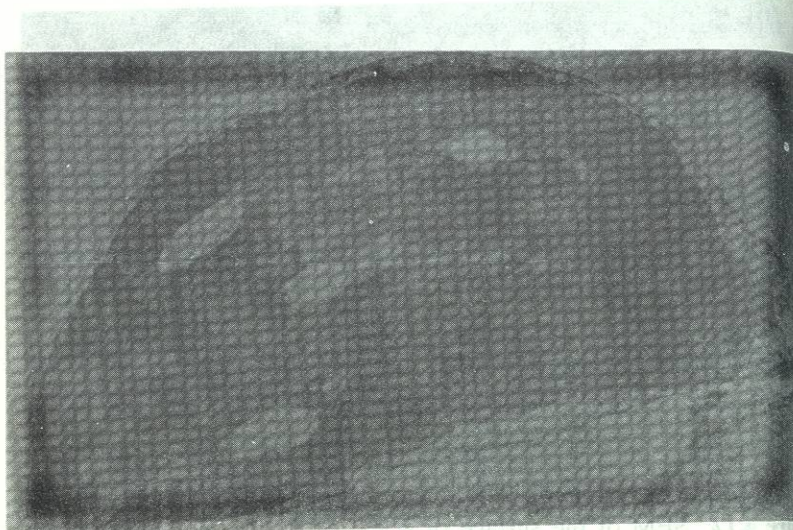


Figure 4.14 Electron micrograph of a mesophyll chloroplast.



Figure 4.15 Electron micrograph of a section of a leaf, showing differences between a transverse and a longitudinal cut.

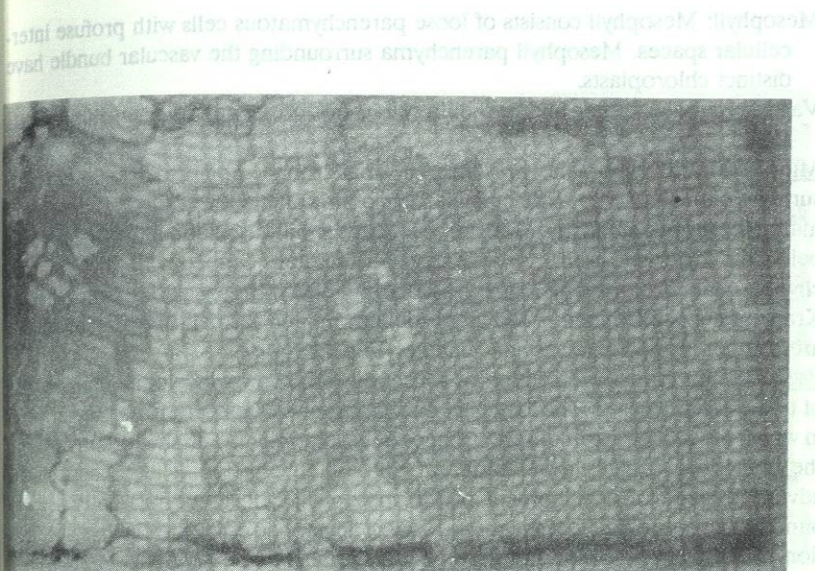


Figure 4.16 Transverse section of a young leaf, showing upper and lower epidermis, sunken stomata (substomatal cavity), mesophyll cells and Kranz tissue.

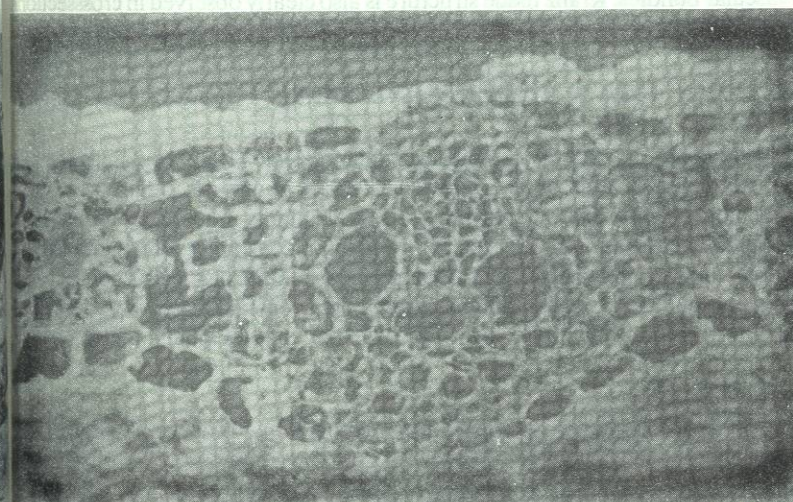


Figure 4.17 Scanning electron micrograph (SEM) of a crosssection of leaf, showing 'Kranz' anatomy.

Mesophyll: Mesophyll consists of loose parenchymatous cells with profuse intercellular spaces. Mesophyll parenchyma surrounding the vascular bundle has distinct chloroplasts.

Vascular bundle: Young bundle sheath cells show presence of distinct chloroplasts (Kranz tissue).

Midrib: Midrib shows the presence of small round, epidermal cells on both surfaces of the leaf with more cuticular thickening on the lower surface. Parenchymatous cells are compactly arranged. Large and small vascular bundles are present below the lower epidermis. A large vascular bundle is capped with thick sclerenchyma sheath, followed by 3 small vascular bundles with no-sclerenchyma sheath. Kranz tissue is prominent. Two large metaxylem and 2 small protoxylem vessels are distinct in the large vascular bundle (Fig. 4.18-4.19).

Pseudostem: Transverse section of a pseudostem shows developmental pattern of tissue in leaf sheath. The center of the culm shows cross-section of younger stem in which the tissues are at different stages of development. The sheath surrounding the stem is the youngest developing leaf. Subsequent enveloping leaf sheath shows advanced stage of development of the mesophyll cell, epidermis and vascular bundle. The outermost leaf sheath shows well developed epidermal cells, sclerification of the bundle sheath and developed vascular bundle (Fig. 4.20-4.21).

Glossy lines do not show distinct differences from nonglossy in anatomical characteristics, but glossy lines show more cuticular thickness compared to nonglossy ones. Chloroplast containing mesophyll are organized in relation to vascular tissue. Typical Kranz anatomy, characteristic of C₄ (dicarboxylic acid pathway of photosynthesis) plants is observed, and consists of an inner cylinder of bundle sheath cells around the vascular bundle and adjacent layer of mesophyll cells. Two to three rows of mesophyll cells are arranged in concentric circles about the vascular bundles. Kranz tissue structure is also clearly observed in cross-section of midrib.

FACTORS THAT DETERMINE LEAF DEVELOPMENT

Growth of leaf is controlled by different factors. Dale (1982) explained the effect of environmental factors on leaf growth which are summarized here:

Light: chlorophylls a and b control the growth of plants in the presence/absence of light. The duration of light period remaining constant, there is an increase in leaf area with intensity of light. A curvilinear relationship exists between leaf area and photoperiod, light intensity remaining constant. The response of leaf area to the total quantity of light per day is a complex phenomenon.

Temperature: temperature has a marked effect on the initiation of the primordia and number of leaves.

Water: growth of cells in leaves is largely dependent on water content which maintains the turgor pressure. Leaf expansion is highly dependent on water uptake. The water content of the leaf is brought about by maintaining a gradient of water potential between the cells and the water source.

Mineral nutrition - Nitrogen, phosphorus, potassium and magnesium are important for leaf growth. Pests affect leaf growth considerably.

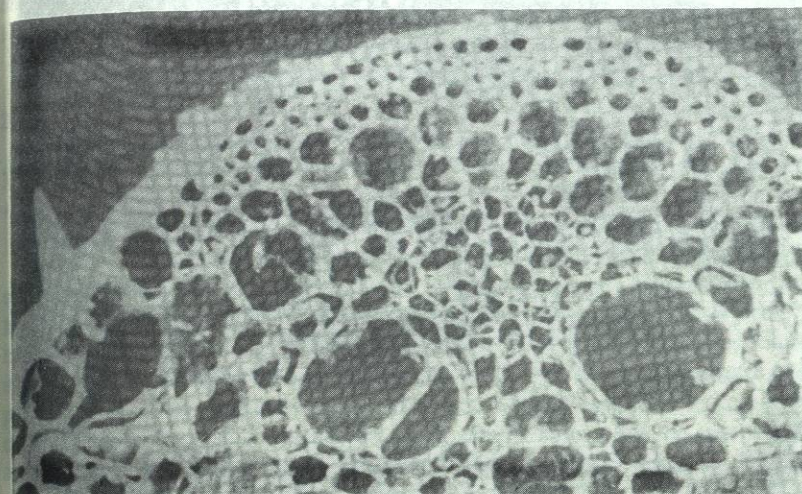


Figure 4.18 SEM of the midrib showing thick walled epidermis (E), trichome (T) sclerenchyma sheath (Scl.) and 'Kranz' anatomy.

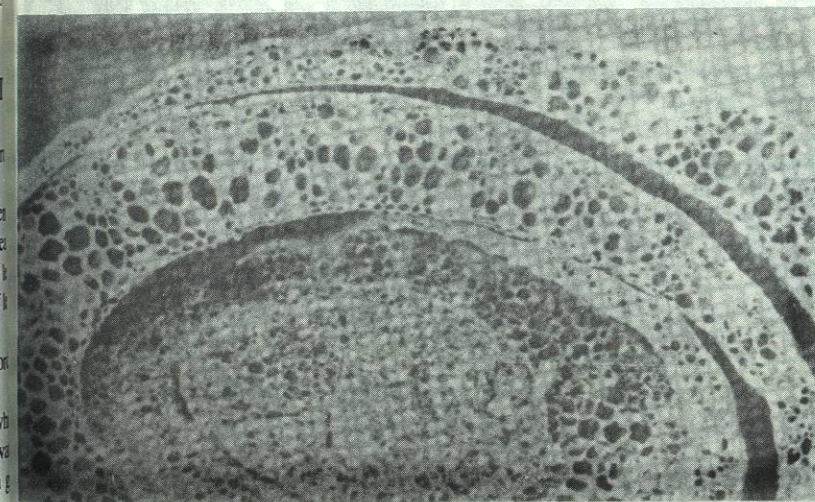


Figure 4.19 Transverse section of a midrib, showing the orientation of the vascular bundle and the internal tissues.

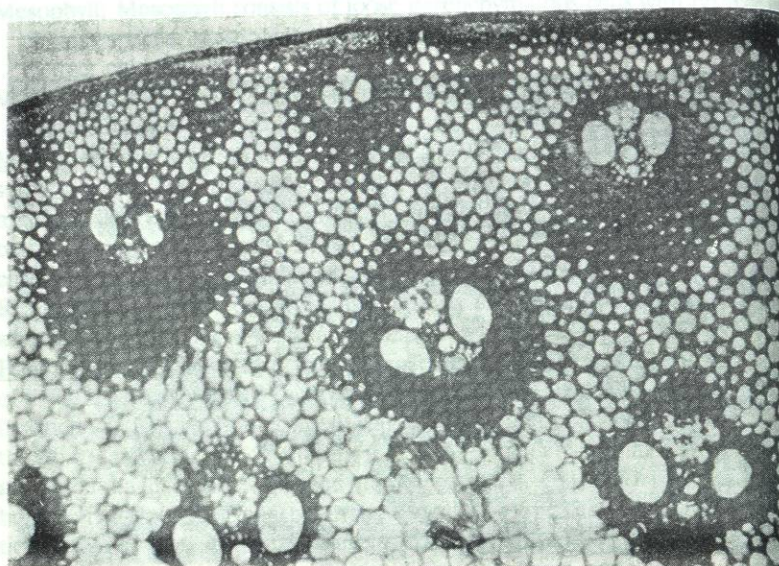


Figure 4.20 SEM through transverse section of a culm, giving orientation development of the tissue of the leaf sheaths encircling the stem.

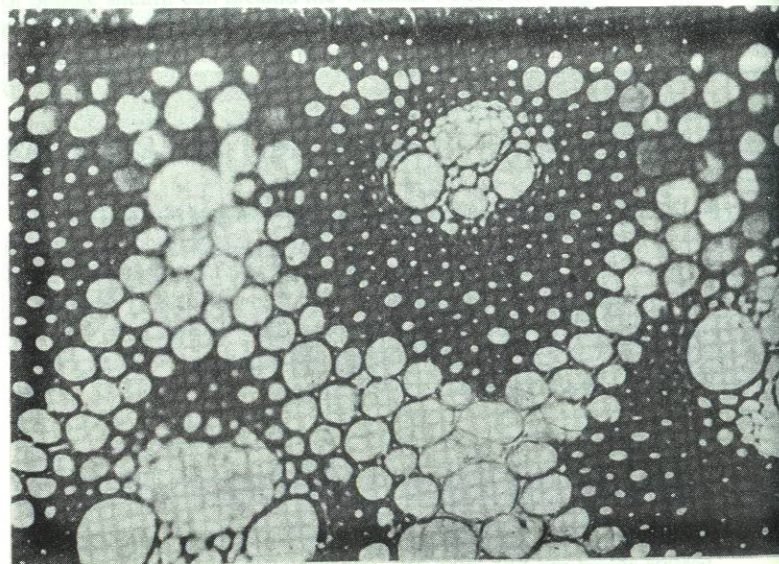


Figure 4.21 Transverse section of a pseudostem, depicting little mechanical tissue and small and large vascular bundles in the peripheral region.

Temperature is by far the major deciding factor in determining the length of each developmental phase and the heat unit requirement for each phase differs in different phenological stages of the plant (Seetharama, 1980).

1. A leaf is said to be visible when the tip of the leaf blade is seen in the whorl.
- A leaf is considered as expanded (maximum leaf area) when the collar is visible.
2. Leaves need to be counted from the bottom following the development of the plant. The first leaf is usually less rectangular and has a round tip.
3. Culm means the stem along with the leaf sheath around it.
4. In sorghum 4 - 5 leaf primordia are found in the embryo (inside the kernel itself). The remaining leaf primordia are produced from the apex of the shoot.

In cereals, cell division and leaf expansion stop first at the tip when leaf lamina emerge from the encircling leaf sheath that has already stopped growing. Therefore, the growth of the whole leaf lamina is complete with the emergence of ligule but leaf sheath continues to expand (Milthorpe and Moorby, 1972). The leaf meristem is present at the base of the leaf enclosed in the whorl of the centre of pseudostem and the leaf cells are produced by cell division. The leaves are expanded by cell elongation at the base of the leaf. This helps in the extension and final expansion of the leaves. Each leaf passes through 3 stages of development: initiation, expansion and senescence. The leaf growth and canopy development of the crops are of great interest to crop physiologists as these factors contribute to the photosynthesis and yield of crop. Large differences are found to exist in leaf growth and canopy development in different sorghum cultivars.

Leaves grow through 3 main phases of development: emergence, expansion and leaf area development.

Leaf emergence

Clark (1970) studied from both longitudinal and transverse sections, the number of embryonic leaves of some cultivars of sorghum, sudangrass (*Sorghum sudanense*), Johnsongrass (*S. halepense*) and shattercane. He reported 4 embryonic leaves in *S. bicolor* and shattercane but 3 embryonic leaves in Johnsongrass and sweet sudangrass.

In general, 6 or 7 embryonic leaves emerge at approximately 0.5 leaf per day; the rate of emergence of the subsequent leaves is slower. The rate of emergence and the final number of leaves vary in different cultivars, with early maturing cultivars generally having fewer leaves and a faster rate of emergence. The rate of development of the total leaf area per plant is a product of the rate of leaf expansion, size and the longevity of individual leaves.

The rate of leaf development is obtained by counting all the leaves at constant intervals on the stem from base to the top of the plant. The rate based on leaves emerging from enclosing leaf sheath is usually lower than that based on the portion of leaf primordia at the base of the culm. At panicle initiation, all the leaf primordia are developed by the shoot meristem and enclose the reproductive apex, but only 7 to 9 leaves would have expanded by that time. The rate of leaf emergence increases with a rise in temperature (Wade *et al.* 1982; Peacock, 1982). Leaves elongate quickly after emergence and start functioning. The life span of individual leaves differs widely among cultivars.

A study during rainy season with a number of cultivars in 1981 at ICRISAT the author showed that it took about 5 days after seedling emergence for the first leaf to emerge and 10-12 days for the fifth leaf. It took about 25-30 days for the expansion of 6 to 7 leaves by which time the vegetative shoot apex was converted into a reproductive meristem. By this time all, the leaf initials were laid down. Subsequent leaves expanded slowly with elongation of stem internodes. It took 35-50 days for the final leaf to emerge (flag leaf) depending on cultivars (unpublished).

Leaf extension

Wade *et al.* (1980) laid emphasis on techniques to study the effect of temperature on leaf extension rate, since it is a direct function of the total leaf expansion process and is also the most sensitive of all components of leaf development.

Leaf extension rate is equal to the change in leaf length divided by the time interval between the leaf length measurements. Leaf length is measured with a ruler as the distance from the soil surface to the tip of the expanding leaf. However, during the growth stage when panicle development culminates in anthesis, the increase in leaf length will consist of stem extension plus leaf extension. Leaf extension rate is equal to the change in ligule height divided by the time interval between ligule height measurements. The true leaf extension rate is then determined by subtracting the stem extension rate from the original leaf extension rate. Ligule height is measured with a ruler as the distance from the soil surface to the ligule of the youngest fully expanded leaf. These measurements are normally made twice in a day, at 9:00 and 16:00 hours, throughout the expansion of the leaf. The leaf extension rate (LER) could be calculated in the following way:

$$\text{Leaf extension rate (LER)} = \frac{(LD2 - LD1)/(D2 - D1) \text{ [mm/hour, cm/day]}}{= (\text{Total change in leaf length}) / (\text{Time})}$$

where: LD1 = leaf length at day 1 (D1), LD2 = leaf length at day 2 (D2)

Temperature can be measured with thermistors connected to a recorder, and appropriate temperature for each leaf being that measured at the height of the growing point. Leaf extension rate is then plotted against temperature and a regression of leaf extension rate on temperature is calculated. In comparing genotypes, treatments, slope (responsiveness), maximum rate and critical temperature at which leaf extension reaches its limit are important in interpretation of data (Wade *et al.*, 1982). However, since the leaf extension rate (LER) is just a component of leaf area development, it is essential to simultaneously study components affecting the process, viz. lifecycle duration, the timing of panicle initiation and its influence on leaf number, the rates of leaf appearance, leaf expansion and leaf senescence, duration of leaf expansion, and finally, the combined effects of these factors on leaf size, leaf area index and leaf area duration.

Leaf elongation of sorghum is slowest at night, presumably because of low temperature, but reaches a peak in daytime, when leaf water potential (Ψ) is high. Solute potential also decreased during daytime which maintained the turgor pressure necessary for cell expansion (Acevedo *et al.*, 1979). Peacock (1979) reported a correlation between temperature, leaf extension and expansion in sorghum.

The effect of fertility level (N) and water on leaf extensions of cultivars was

studied by Seetharama *et al.* (1982) during 1981 post-rainy season, in vertisols at ICRISAT. The authors observed that LER was a direct function of temperature in the range of 10 to 30°C. LER is known to have a curvilinear response to temperature (Fig. 4.22). This study also points out that LER was affected more by nitrogen stress than by water stress. The duration of extension was unchanged under water stress but time of emergence, full expansion and longevity of leaves under different irrigation treatments were affected; at the same time, individual leaves of zero N plants took 13 (leaf 4) to 20 (leaf 14) more days to emerge than those under 80 kg N/ha.

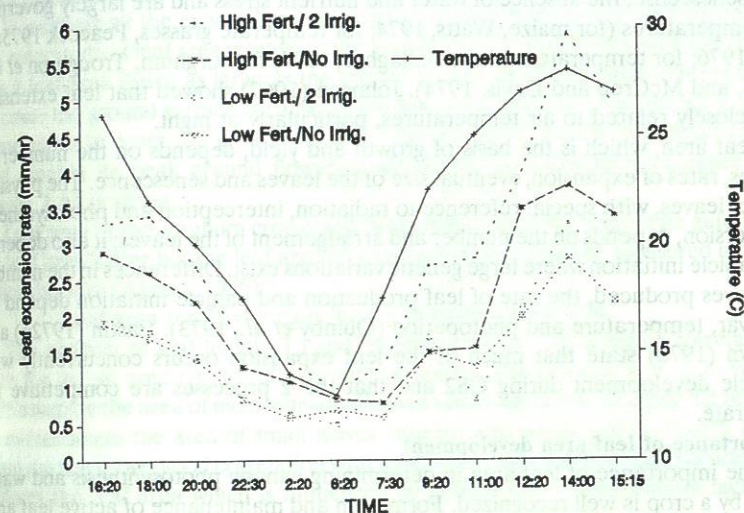


Figure 4.22 Diurnal variation in leaf expansion rates in sorghum under different watering (2x) and fertilization (80 kg N/ha) treatments.

Wade (1980) stated that the maximum area of each leaf is a product of duration of leaf expansion, LER and leaf width. He also stated that the combined effect of area per leaf and number of green leaves determines maximum leaf area, which was reduced drastically under nitrogen stress but less so under water stress from 40 days after sowing.

There are few reports about the effect of low temperature on leaves. McWilliam (1983) stated that high temperature accelerates leaf growth and low temperature intensifies injury in chilling sensitive tissue. Slack *et al.* (1974) observed chlorotic bands on sorghum leaves exposed to temperatures close to 0°C. McWilliam *et al.* (1979) concluded from electron micrograph studies that the failure to develop chloroplasts under low temperature is associated with the arrested development of thylakoid membrane system of the developing plastids.

Downes (1968) showed that leaf appearance in sorghum increased linearly with air temperature from 13 to 23°C. Genetic variation in leaf growth in relation to