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Comparative Studies of Two Flax (Linum usitatissimum) Cultivars for Stomatal Characteristics, Adaxial Stomatal Resistance, and Osmotic Potential

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COMPARATIVE STUDIES OF TWO SELECTED FLAX (*Linum usitatissimum*) CULTIVARS FOR STOMATAL CHARACTERISTICS, ADAXIAL STOMATAL RESISTANCE, AND OSMOTIC POTENTIAL

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This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable as meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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INTRODUCTION

Limitations on seed yield of flax (Linum usitatissimum L.) are a major concern of researchers trying to develop higher yielding oilseed cultivars (37, 71). Dybing (37) stated that comparative studies of physiological and biochemical factors could provide necessary insight into the cause of these limitations. Based on repeated observations and yield trials of lines from the world collection, CI 2522 ('Linott') and CI 1194 (Grant) were selected as an "appropriate" pair for such studies (37).

The basic criteria of selection of these two cultivars were a consistent difference in seed yield across environments tested and similarities in such categories as disease resistance, agronomic type, morphology, flowering habit, fruiting habit, and flowering date (37). During yield trials, Linott was consistently higher yielding than Grant. Although Grant expresses susceptibility to a North American race of rust (Melanpsora lini) and Linott does not, this factor was not responsible for the yield differences observed during the yield trials (37). Yield components data have indicated that the greater yield capacity of Linott stems from its ability to maintain more sinks, either as seeds per boll or bolls per area, than Grant (71). Comparison of Linott and Grant for total dry weight, period of main boll production (71), and net CO_2 exchange rate (37) failed to show any differences that would explain the different yield potentials.

Seed production in flax is very sensitive to environmental factors such as temperature and soil moisture level (42). Yet the crop is

grown in areas of medium to low rainfall. Therefore, it was decided that further comparative studies in Linott and Grant should include water relations. Stomatal characteristics, stomatal resistance, and osmotic potential were chosen as the areas that would be studied to determine if differences exist that could help to explain the difference in yield potential of Linott and Grant.

REVIEW OF LITERATURE

Function of stomata

Evolution of plants into higher terrestrial life forms was possible because of certain adaptive, morphological developments. One of these was an epidermal coating, cutin, which restricted the movement of water away from aerial structures. Though this effectively retarded water loss from the plant it also greatly constrained two essential plant functions, transpiration and gas exchange. Therefore, a necessary evolutionary development, accompanying the above mentioned modification, was a mechanism by which transpiration and gas exchange could be carried out at a level better suited to internal demand and which was regulated by the internal water status of the plant. This was provided by development of epidermal pores and associated, functionally specialized cells. These pores and associated cells are referred to as stomata (39). Control of both water loss and gas exchange is accomplished by internally controlled movements of the functionally specialized cells, guard cells, which border the pore. Stomata are, therefore, structural mediators between antagonistic drives of the plant. The balance stomata maintain between leaf turgor, which is an integral part of growth, and photosynthesis, which is the ultimate energy source in the plant system, has a major influence on growth (18).

Stomatal Characteristics

Genetic variation in leaf stomatal density is evident from

differences in frequencies between species (27, 111, 113) as well as within species (25, 36, 74, 86, 84, 123). Stomata are present on either or both leaf surfaces, depending on the species (39, 84). The general rule in agronomic crops is for amphistomatal leaves. Densities on the individual leaf surfaces are not necessarily related. In corn (27, 111), beans, pumpkin, tomato (27), cotton (89), sunflower (5), soybean (25), sorghum (36, 74), and panigrass (111) the abaxial surface has the greater stomatal frequency. The inverse is true in alfalfa (27, 111), Triticum aestivum, T. monococcum, T. turgidum, T. timopheevi (113), Bromus inermis (123), and creeping bentgrass (111). In barley (86) and Cassia auriculate L. (14) the stomata were reported to be equal in frequency on both leaf surfaces. The ratio of stomata on the adaxial surface to stomata on the abaxial surface is nearly three times greater in C_3 species than in C_4 species (30).

Guard cell length is negatively correlated with stomatal density (25, 74, 123, 128). Therefore, the leaf surface possessing the lower stomatal frequency can be expected to have the longer guard cells. An exception to this is found in Triticum spp. where no such relationship was observed (25). Guard cell length can be an indirect means of gauging the relative pore length of a stomata (86), because longer guard cells assumably surround longer pores.

Generally, a gradient exists for stomatal density and guard cell length across a leaf and along the entire plant (27, 111, 113). For an individual leaf, stomatal number decreases and guard cell length increases from leaf tip to leaf base and from leaf center to its

margins. An exception to this generalization has been reported in panicgrass (36) where stomatal density did not change along the leaf. In relation to leaf insertion, stomatal density increases and guard cell length decreases as one proceeds acropetally, but panicgrass (36) and Bromus inermis (123) are exceptions.

Stomata may be associated with morphologically distinct epidermal cells (84). These cells are referred to as subsidiary cells and are physically and metabolicly involved in the movement of guard cells (96). Subsidiary cells are part of the stomatal apparatus (84).

Though an organism's genes determine the maximum number of protoderm cells which differentiate into stomata, environmental factors can alter this potential. Among the environmental factors that influence stomatal density are irradiance (25, 66, 86), temperature (25), and water stress (25, 27, 80). An increase in irradiance produces a greater number of stomata on new leaves (25, 66). This occurs as a result of an increase in cell concentration per area (66, 84) and in the ratio of stoma mother cells to protoderm cells in developing leaf tissue (84). The change in stomatal density with temperature, at least in soybean, is not linear (25). The direction of change depends heavily on the variety. The effect of water stress on stomatal density, like that of light, is two fold. Through the inhibition of cell expansion, the superficial effect of water stress is to increase the number of stomata per square millimeter of tissue (25, 27, 70, 80). Zalenski was the first to associate this increase in cell concentration with a diminution of cell size (34). 'Zalenski's law' has been

indicated as the reason for the negative correlation between stomatal density and guard cell length (86, 123) and the gradient from the lower to the upper leaves of the canopy (36, 80). The latter results because the leaf environment includes a progressively greater level of water stress as one moves up the plant (65, 81, 121). The less obvious effect of water stress on stomatal frequency is the inhibition of stoma mother cell differentiation in the protoderm (25). This causes a decrease in the stomata-to-epidermal cell ratio of water stressed plants, in comparison to non-stressed plants.

Density variation, as illustrated, can be attributed either to smaller cells, i.e. the concentration of more cells into a given area, or to a greater stoma to epidermal cell ratio. Whether a density difference corresponds to one or the other situation can be determined by calculating "stomatal index", which is defined as follows (84):

$$\text{stomatal index} = \frac{\text{stomata per area}}{\text{stomata per area} + \text{epidermal cells per area}} \times 100$$

This value quantifies the percentage of protodern cells that successfully differentiate into stomata (113). Unlike a density value it will not vary greatly for an individual plant (84), if no significant inhibition of stoma mother cell differentiation takes place during the course of ontogeny.

For a time, stomatal density and pore area were considered as possible indirect selection criteria for photosynthetic rate (86, 113, 128). The central premise behind this position was that the

greater the number of stomata (86, 113, 128) and the greater the aperture area (113, 128) the less restricted would be the movement of CO_2 into the plant for photosynthesis.

The reality of a positive correlation between stomatal density and photosynthesis is doubtful considering the number of experiments which have failed to note a relationship (45, 65, 72, 87, 100) compared to those that have (87). In one particular study that failed to find a correlation, plants were compared with their colchicine doubled counterparts (100). In this study it was concluded that stomatal number and photosynthesis were not correlated because the lower ploidy member of the pair had the greater stomatal density but a lower rate of photosynthesis. Because this was a comparison of genetically similar individuals, except for ploidy level, the possibility of genetic variation in enzyme activity theoretically was eliminated. It, therefore, strongly suggests the lack of a relationship between stomatal frequency and photosynthetic rate and indicates that other factors maybe more important in limiting photosynthesis.

As was the case with stomatal density, neither guard cell length nor pore dimension have proved to be satisfactory indicators of photosynthetic capacity (45, 87, 100).

Diffusive Resistance

Though the stomatal density and full pore dimension define the maximum area across which diffusion can take place, rate of diffusion through a stomatal pore is dependent on the degree of pore opening (45, 56, 76, 87, 88, 121). Restriction of diffusion by the aperture

dimension is termed stomatal resistance, the units of which are s cm^{-1}. The degree and duration of stomata opening have been shown to be genetically variable (82).

Even though CO_2 and H_2O both are channeled through the stomata, a difference exists in the levels of resistance to their movement between a plant and its environment (17). This difference stems partially from their innate chemical differences and partially from the dissimilarities in their respective biochemical paths through the plant.

The total resistance to H_2O loss from a leaf surface, r_l, can be described as (17):

$$r_l = r_b + r_s^{-1} + r_c^{-1}$$

where r_b is the resistance to vapor diffusion away from the leaf surface, imposed by the boundary layer of air surrounding the leaf, and r_s and r_c define physical resistances to water loss which can be ascribed to the leaf. The parameter r_s, stomatal resistance, describes resistance to water vapor diffusion from the stomatal pore and varies with aperture area. Resistance to water loss through the cuticle layer of the epidermis is measured by r_c. The parameter r_c varies little between varieties and usually is of little importance, as r_s is much larger than r_c unless water stress is severe (12).

The diffusion of CO_2 into the plant encompasses the same resistance components defined for water vapor, but these resistance components of CO_2 differ from those of water vapor in magnitude. As a general approximation

$$r_b^{CO_2} + r_s^{CO_2\ -1} + r_c^{CO_2\ -1} = 1.7\ (r_b^{H_2O} + r_s^{H_2O\ -1} + r_c^{H_2O\ -1})(17).$$

This proportionality stems from the basic chemical difference between the two molecules, relative to their diffusivity into the air. Besides these common resistance components, CO_2 encounters additional points of resistance as it moves from the substomatal cavity to the cytoplasm of the mesophyll cell and finally to fixation. This intracellular resistance can be broken into the following subunits (48):

$$r_i = r_m + r_x + r_e$$

The intracellular resistance, r_i, is the sum total of resistances along the route of CO_2 to fixation. Resistance to the movement of carbon dioxide through the mesophyll walls lining the substomatal cavity and finally to the site of fixation is represented by r_m. The term r_x comprises resistance to CO_2 movement posed by the rate of carboxylation. The excitation resistance, r_e, relates to resistance exerted because of the limits of energy availability for carboxylation and is not important if light is saturating (48).

Intracellular resistance, r_i, and non-intracellular resistance, $r_l - r_i$, contrast in their relative importance in CO_2 regulation. Intracellular resistance is far more important when CO_2 is not limiting (48, 87, 93). When CO_2 is limiting, then $r_l - r_i$ is more consequential. With C_4 species, $r_l - r_i$ is of greater importance to the level of net photosynthesis, whereas in C_3 species, r_i is the limiting resistance (93).

A detailed scenario of stomatal movement has yet to be developed (51, 73, 96). The mechanism of active guard cell movement centers around alteration of osmotic potential in the guard cell vacuole (73).

Shifts in osmotic potential of the vacuole cause guard cell turgor pressure to change with the osmosis of water (73). A decrease in the osmotic potential of the guard cell vacuole causes endomosis of water from the adjacent epidermal cells, which results in an increase in turgor pressure of the guard cell. Guard cells separate, to open the pore, when their turor pressure exceeds that of the surrounding epidermal cells, which allows the dorsal walls of the guard cells to deform (84). Pore closure occurs when a rise in osmotic potential of the vacuoles causes exomosis of water from the guard cells. This results in a loss of turgor pressure and the guard cells being pushed together by the expansion of the more turgid, surrounding, epidermal cells.

Certain fundamental features of events during opening have been documented (51, 73, 96). These are "(a) uptake of K^+ into the vacuoles, (b) excretion of H^+ from guard cells, (c) production of organic acids, particularly malic acid, (d) disappearance of starch" (96). In his 1975 review of stoma physiology, Raschke (96) tentatively outlined the following probable sequence for these occurrences. Upon receiving the signal to open, H^+ is excreted from the guard cell. This raises cytoplasmic pH and stimulates malate production at the expense of starch reserves stored in the guard cells. Malate then serves as a donor for additional protons and as an osmoticum for lowering osmotic potential in the vacuole. Electroneutrality of the cell is re-established by an influx of potassium ions into the guard cell and their transport to the vacuole to counterbalance the charge of the

malate cations. This K ion migration further drops osmotic potential in the vacuole.

The system by which osmotic potential of the guard cell vacuole increases to produce closure is as obscure as the system responsible for opening. Essentially, two main events take place. Malate is transported out of the guard cell (122) and K^+ is returned to storage sites (96).

The mechanism of control is not exact (84, 96). Overshooting of the optimum aperture generally occurs. A decrescendoing vacillation between extremes follows until the optimum level of CO_2 intake is achieved (29).

The transport of K^+ during guard cell movement is energy requiring (51). It appears that both photosynthesis and respiration provide energy for the K^+ pump (51).

The maintenance of stomatal opening is also energy requiring (84); but, because the energy demands for maintenance are less then for opening, it can be assumed that separate mechanisms are involved in guard cell movement and the maintenance of a particular aperture dimension (84).

The identity of the signaling agent (or agents) that initiates stomatal movement has not been unequivocally shown. Raschke (96) proposed that intracellular CO_2 and ABA are the signaling agents in stomatal movement. He contended that intracellular CO_2 is the key signaling agent in periods of low water stress whereas ABA dominates the control system when a plant is undergoing high water

stress. Cowan (28) did not limit the control of stomatal movement to just those factors indicated by Raschke. Instead he supported an integration of signaling factors which interact to produce the optimum stomatal aperture for a particular combination of internal and external environments.

Since stomata commonly demonstrate an acute sensitivity to intracellular CO_2 concentration (126), CO_2 is a prime candidate for the signaling agent of stomatal movement. The intracellular CO_2 monitoring system lies in the guard cells (96). High intracellular carbon dioxide levels may instigate closure by providing sufficient substrate concentrations so that the synthesis of malate becomes self limiting (96). Inhibition results from increased pH as malate production outstrips the cell's ability to deacidify malate or move it to the vacuole (96). As the malate level is reduced by deacidification and transport to the vacuole, osmotic potential increases and the cell turgor drops (96). Reduction in stomatal aperture restricts diffusion of additional CO_2 into the plant. If the new intracellular concentration is no longer saturating photosynthesis, leaf photosynthesis diminishes the intracellular CO_2 supply until malate synthesis is no longer self restricting. Malate production then rises, which causes the stomata to open.

The involvement of abscisic acid in the regulation of guard cell movement during water stress is widely documented (57, 83, 84, 96, 107, 127). Its importance in the non-stress control of stomatal movement is demonstrated by a tomato mutant with a one-locus lesion,

which causes it to be deficient in ABA (53). This wilty mutant lacks the capability to rapidly close its stomata with the onset of mild diurnal water deficits (110, 125).

In plants under non-stress conditions, ABA is concentrated in the chloroplast fraction of the leaf; whereas in stressed plants a greater percentage of the total leaf ABA is found in the non-chloroplast fraction (78, 129). The reason for the latter increase is that during stress ABA is transported from the chloroplast, where it is produced (70), to metabolic sinks (129), such as the stomata (46), stem tip, roots (125), and fruits, in larger quantities than normal. The level of ABA in leaf tissue needs only to double for stomatal closure to occur (70, 79). This is an over estimation of the concentration necessary for stomatal closure, as much of the ABA in a total leaf extract is uninvolved in stomatal closure (79). Genetic variation in rate of ABA biosynthesis and metabolism has been reported (43).

Only the positive enantiomer of ABA is capable of causing stomatal closure (70, 96). This specificity may relate to conformational demands at the possible site of activity, the stomatal plasma membrane (46). Two binding sites were found on this structure. The site with the greater affinity for ABA involves a "membrane-bound, Mg^{2+} dependent, K^{+} stimulated, ATPase and glucan synthetase" (46).

The means by which ABA regulates stomatal movement is yet undetermined. ABA is not directly involved in movement but instead interferes in the metabolic processes of stomatal movement. Its activity may be related to movement of malate from the guard cell to

adjacent cells (55, 99, 122). This hypothesis is supported by the observation that ABA is ineffective on the stomata of leaf discs floating on solutions containing a high concentration of C_1^-, as influx of C_1^- into guard cells ionically compensates for loss of malate and prevents closure (99).

The effectiveness of ABA is amplified by the presence of water deficits at the time of application of exogenous sources of ABA and by previous periods of water stress (32). It is probable that other changes within the plant, associated with water stress, interact with ABA to cause closure. The necessity of these other factors is exemplified by plant response to waterlogging. In this situation, there is an increase in the level of ABA greater than that in water stressed plants, but there is no significant increase in stomatal resistance (107).

Other hormones and growth regulators influence stomatal movement. These are auxin (110), kinetin, and cytokinin (1, 13, 15, 54, 67, 96, 110). Like ABA, auxin increases stomatal resistance. In contrast to ABA and auxin, both kinetin and cytokinin promote stomatal opening. The various hormones may possibly constitute a system of regulation where the balance between the various hormones is the key rather than an individual molecule (53, 59, 75). This type of a system is supported by Tal's (110) work with the previously mentioned wilty tomato mutant.

The influence of the signaling agent is not restricted to the leaf on which a stimilus is applied. Stomata have been observed to respond to stimuli applied on other parts of the plant (84).

In the course of stomatal movement the subsidiary cells play an important role. By their physical presence they provide the epidermal counterforce which is partially responsible for the characteristic movement of the guard cells (96). Also, they ostensibly serve as storage sites for ions involved in guard cell movement (51, 96) or at least as channels for ion movement (96).

A number of environmental factors influence r_s. Among these are humidity (77, 84, 96), leaf surface positioning (5, 22, 31, 89, 118), light (61, 67, 73, 84, 96, 117, 118, 126), temperature (84), ambient CO_2 concentration (2, 48), leaf water deficits (60, 116, 117), and source-slink manipulation (3, 34, 44, 68, 69, 79, 114). Only the latter two will be discussed in this thesis.

The effect of water stress on r_s has long been known. The connection between internal water deficits and stomatal behavior is an indirect one (4, 21, 116, 117). Guard cell turgor is independent of that of the surrounding tissue. This is demonstrated by the Iwanoff surge (5, 21, 84), which refers to the gradual increase in transpiration over a period of several minutes after petiole excision (84). The Iwanoff surge is a passive response of stomata resulting from dehydration of the mesophyll, which literally pulls the still turgid guard cells apart. The Iwanoff response is preceded by an insignificant jump in resistance (84). This jump is also a passive response, which occurs within the initial minute after excision, due to the momentary increase in water available to the epidermal tissue. This water increases turgor in the epidermal cells and, therefore,

increases their resistance to guard cell expansion. Eventually, as subsidiary cells lose water, a rise in stomatal resistance is noted after the Iwanoff surge. Extent of this response is dependent on leaf water potential in that when leaf water potential is low a less marked response is observed (84). If bulk leaf water potential is sufficiently low, no increase in transpiration accompanies petiole excision (84).

Early experiments on plant response to water stress showed the existence of a threshold water potential for stomatal closure (60, 116, 117). Supposedly, stomata resisted closure during development of water deficits until a certain threshold was reached. This postulated critical water stress level varied with species (116, 117), age, previous stress history, and leaf position (117). A recent study has challenged the idea that a threshold for closure is real (58). This study indicates that the rate at which stress is imposed is the dominant factor in determining the pattern of stomatal closure with stress and that threshold closure previals only when drought stress is imposed rapidly. The position held by challengers to the threshold hypothesis is that closure takes place gradually over a wide water potential range in the field (58).

Source-sink manipulation studies have shown that changes in r_s occur as a result of such treatments. Sink removal is characterized by an increase in r_s (3, 44, 68, 79, 114). Source removal is followed by a decrease in r_s of the remaining leaf or leaves (3, 34, 44, 54). Shading of all but one leaf also results in a decrease in

r_s of the lighted leaf (114). Changes in intracellular CO_2 level, which is a plant response associated with these stimuli, is thought to be the cause of the corresponding changes in r_s (126).

Changes in a plant's internal environment during the season, in response to external environmental variation or as the result of plant senescence, stimulate changes in r_s. Principally, changes in r_s follow the pattern of fluctuation in photosynthesis. In the case of perennials, photosynthetic rate varies seasonally with sink demand (11). In annuals, variation occurs not only with sink demand during the season (3, 114) but also stems from a gradual deterioration of the photosynthetic mechanism as the plant senescences (3, 34, 59).

Although changes in photosynthetic activity are associated with eventual changes in r_s, the inverse is not necessarily true (94, 113). For instance, when CO_2 is not limiting, increases in r_s will not cause a corresponding reduction in the rate of photosynthesis, as long as closure does not reduce CO_2 to limiting levels. A low r_s is not necessarily associated with high photosynthetic rates. Plants in the C_4 group have a high rate of photosynthesis but also a high r_s compared to C_3 species (30). This is possible because the morphology of C_4 species allows them to maintain high internal CO_2 levels. Evidence that a deceleration of photosynthesis precedes stomatal closure (3, 10) contradicts the belief of some authors that stomatal movement is the central regulating force between these two systems. As it appears now, stomata respond to the rise in intracellular CO_2 concentrations, which follow the initial reduction

in photosynthetic rate. Movement of CO_2 into the plant in then curtailed, and this further diminishes photosynthetic rate. The only exception to this generalization is in the case of stomatal response to humidity deficits where stomatal closure occurs first (77).

Besides intracellular CO_2 levels, an additional mechanism binds the r_s and photosynthetic rate together. This one revolves around ABA. As was discussed earlier, ABA has a marked influence over stomatal behavior. Recent studies have indicated that an early metabolite of ABA, phaseic acid (69, 79), possesses the capacity to interfere in electron transport processes of photosynthesis (20, 79). In the case of water stress (96) and possibly sink removal (96) an ABA-PA regulation system may dominate the CO_2 regulation mechanism (69).

Osmotic Potential

A widely accepted expression of water stress describes the chemical activity of cell water compared to that of "pure free" water under the same conditions of pressure and temperature (109). The critical assumption behind this postulated measure of water stress is that the chemical activity and the physiological activity of water are strongly related. It should be noted that a positive relationship between water potential and physiological activity is, so far, only theoretical (50, 109). How they relate in reality is uncertain.

The symbol ψ_w is used to signify the sum total of the component potentials of chemical activity in the symplastic system (16):

$$\psi_w = \psi_\pi + \psi_p + \psi_m + \psi_g$$

Gravitational potential, ψ_g, is of little importance when leaf water potential is determined on excised tissue. Matrix potential, ψ_m, which includes the reduction in free energy of the water in the cell due to absorbed solutes, binding of water by the solid phase, and matrix surface tension between the cell water and the cell wall, commonly is considered to be insignificant unless stress is extreme (16, 90). However, Boyer (16) cautioned that this assumption may not be universally true. The general contention, therefore, is that ψ_π and ψ_p are the primary component potentials of the overall leaf water potential. Osmotic potential, ψ_π, measures the contribution of cell solutes to the decrease in free enthalpy of the cell water. Effect of the hydrostatic tension within the cell, turgor, on the free energy of the water in the cell is expressed by ψ_p. Unlike ψ_π and ψ_w, ψ_p is positive.

Because ψ_π varies curilinearly with ψ_w (85, 91, 124), it is considered an indicator of water stress, though a less sensitive one then ψ_w (9). In initial stages of a slowly applied stress, ψ_π of the tissue decreases only slightly with decreases in ψ_w (51). After ψ_p becomes negible, changes in ψ_w depend solely on decreases in ψ_π (51).

Osmotic potential of a plant varies diurnally (58, 98, 119, 124). Across the season a gradual decline in the ψ_π may (63, 98) or may not occur (119). Osmotic potential follows the same gradient in the plant canopy as ψ_w (81). Upper leaves possess a more negative ψ_π than lower leaves in the canopy, and this gradient provides part of the driving force for water movement up the plant (112).

A decline in ψ_π may correspond to a decrease in water (9, 23, 98, 124) or the accumulation of solutes (1, 9, 23, 98, 102), such as soluble

carbohydrates (63, 119) and amino acids (63).

A correlation between photosynthetic activity and osmotic potential has been projected (9), as maintenance of leaf turgor by osmotic adjustment in the cell was thought important in sustaining the rate of photosynthesis during stress (9). However, research by Jones (58) into the effect of the rate of stress on plant response has shown in sorghum that the osmotic adjustment of a plant does not closely relate to photosynthetic rate. Therefore, osmotic adjustment of a plant may not actually relate to the maintenance of the rate of this physiological system.

Relation of stomatal characteristics, stomatal resistance, and osmotic potential to yield.

A positive correlation between stomatal frequency and yield of guard cell length and yield was not indicated in the literature reviewed, when yield was defined as weight of grain produced (65, 74, 114). However, when yield was defined as total biomass, one study reported a positive correlation between yield and stomatal density (128).

Between stomatal resistance and yield, a relationship has not been consistantly observed. Peet (94) concluded that in soybean there existed a correspondence between low r_s at pod set, and seed yield through in his study the variety 'Pinto' was among the high yielding varieties in the study but had a r_s level during pod set in the intermediate range of the varieties studied. Comparisons of C_3 and C_4 species have shown that though C_4 species have a higher rate of biomass production (90) they do not have lower r_s (30).

Osmotic adjustment was associated by early researchers with a plant's drought tolerance, i.e. its ability to yield satisfactorily under water stress conditions (64). In many water stress studies though the relationship between osmotic potential and yield has been variable (64). Keim (64) found the association between osmotic potential with yield not to be statistically significant in all cases and, therefore, indicated that the relationship was not an absolute.

MATERIALS AND METHODS

General Information

Linott, a widely grown cultivar in South Dakota, and Grant, a line from the collection of supplementary differentials compiled by Flor (41), were used in this study. For simplicity, the term cultivar has been redefined in this thesis to include both.

These cultivars were part of a nursery planted in 1977 and 1978 on Lismore silty clay loam at Brookings, South Dakota. Planting dates in 1977 and 1978 were April 29 and May 2 respectively. Plots were arranged in a randomized, complete block design with four replications in 1977 and three replications in 1978. In both years, seed was drilled in rows 0.36 meters apart at a seedling rate of 207 viable seeds/meter of row. The plots consisted of four rows 5.49 meters in length in 1977 and twelve rows 3.05 meters long in 1978.

Data were collected from the center rows of the plots and sampling from row ends was avoided. In 1978 the twelve rows of each plot were not totally available for sampling throughout the season. Although early in the season samples were collected from any location in the plot, application of spray treatments for a concurrent experiment starting on July 7 restricted sampling to the untreated portion of the plot. Because border rows were not used in sampling, the area for sampling was limited for the remainder of the year to two rows which were 1.52 meters long.

Fertilizer was broadcast over the plots at a rate of 23-11-0 actual kg per ha. Weed control measures in the plots involved

1.82 kg a.i./ha of propaclor applied pre-emergence and 0.11 kg a.i./ha of MCPA applied when plants were at a height of approximately 10 cm.

Seed yield was based on the quantity of seed produced in 1.73 m^2 area in 1977 and a 0.3 m^2 area in 1978. In 1978, yield components, harvest index, and daily flower counts were determined on plants in 7.5 cm sections of row in each plot.

Experiment 1: Stomatal Characteristics

In 1977, ten plants of each cultivar were pulled at random from each plot 60 days after planting. This corresponded to 17 days after the first flowers were noted in Linott and approximately 11 days after the first flowers were noted in Grant. Plants were transported from the field to the laboratory in plastic bags containing moistened paper towels and refrigerated until they could be processed that same day.

In the laboratory, replicas of leaf surfaces were made by coating the surface with liquefied plastic prepared by dissolving 9 g of polystyrene in 50 milliliters of a 50:50 (v/v) mixture of benzene and toluene (95). Four leaves were taken from each of five locations on a plant. Two of these were used to make replicas of the adaxial surface, and the other two were used to make replicas of the abaxial surface. Areas on the plant sampled were: base segment of stem, middle segment of stem, stem segment just below the panicle, and within the panicle (bracts and sepals). No special procedure was followed in storage of the replicas prior to their examination.

For clarification, various ambiguous terms will be defined for the purposes of this thesis as follows:

stomata -- epidermal pore and its associated guard cells.

subsidiary cells -- two morphologically distinct cells in the epidermis which surround guard cells.

stomatal apparatus -- stomatal pore, guard cells, and adjacent subsidiary cells.

epidermal cell -- non-stomatal apparatus cell of the epidermis.

combined guard cell width -- width across the two guard cells.

After removal of leaf debris, replicas were mounted in water and examined with a light microscope. Counts of stomata per microscope field (0.05 mm^2) were made at the tip, middle, and base of each leaf. The only deviation from this pattern was for the abaxial surface of the sepal which contains no stomata on the lower half; in this case readings were made only at the apex. Microscope fields were set in the general sampling regions on the leaf without the use of the eyepieces. Field adjustment was made afterwards so that only whole stomata were included in the sampling field. Also, at these positions, length and width were measured on a typical stomatal apparatus. Stomatal apparatus width was measured from the outside wall of one of the subsidiary cells to the outside wall of the other at the broadest point (Figure 1). Stomatal apparatus length was determined along a line perpendicular to the width measurement (Figure 1). To accommodate extreme differences in the contour of individual subsidiary cell, which sometimes occurred, an average maximum length was estimated.

In 1978, this experiment was repeated with only minor modification. Plants were pulled 57 days after planting (10 days after flowers were

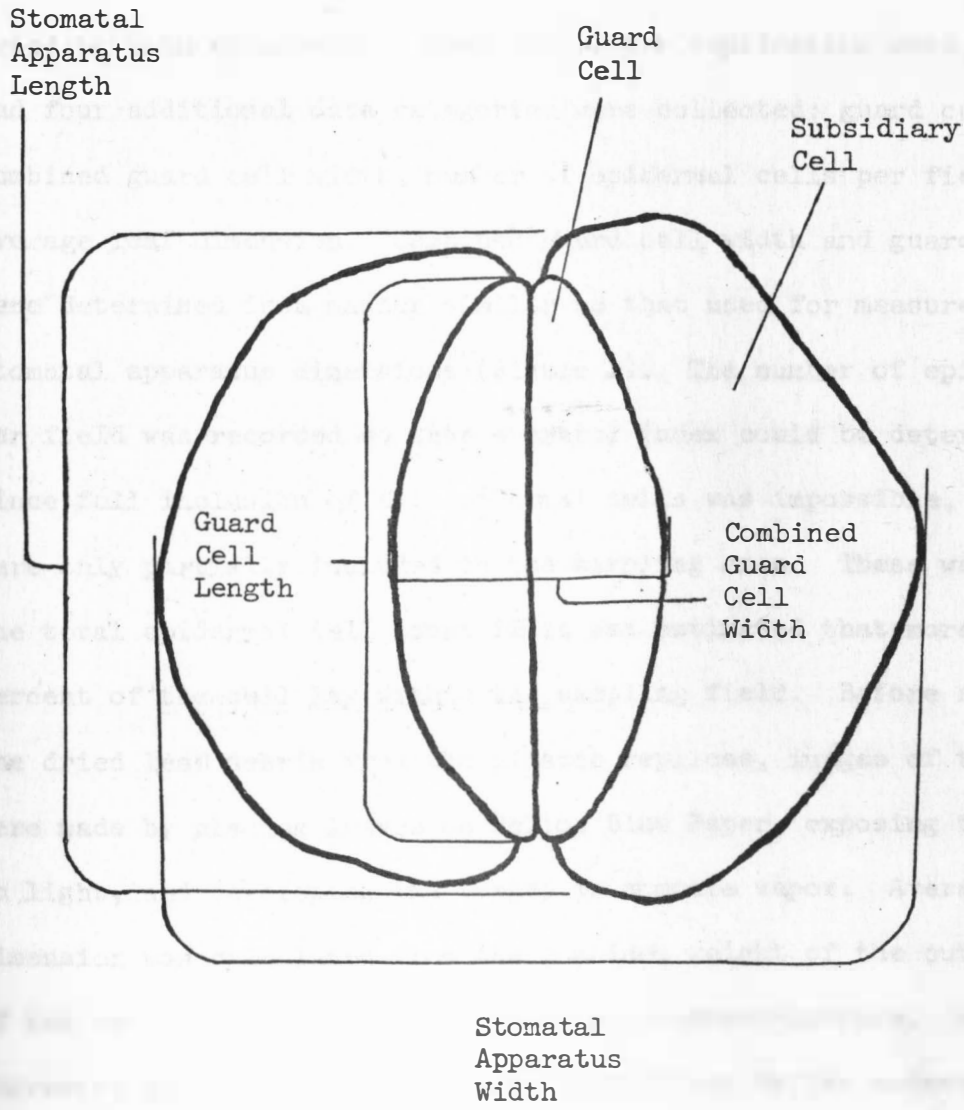


Figure 1. Diagram showing the manner in which stomatal apparatus and guard cell dimension measurements were made.

noted in both cultivars). Five plants per replication were processed, and four additional data categories were collected: guard cell length, combined guard cell width, number of epidermal cells per field, and average leaf dimension. Combined guard cell width and guard cell length were determined in a manner similar to that used for measurement of stomatal apparatus dimensions (Figure 1). The number of epidermal cells per field was recorded so that stomatal index could be determined. Since full inclusion of all epidermal cells was impossible, some cells were only partially included in the sampling area. These were added to the total epidermal cell count if it was estimated that more than 75 percent of the cell lay within the sampling field. Before removal of the dried leaf debris from the plastic replicas, images of the leaves were made by placing leaves on Helios Blue Paper, exposing the paper to light, and developing the images in ammonia vapor. Average leaf dimension was calculated from the combined weight of the cut-out images of the two leaves sampled per plant per location-surface. Weights were converted to average leaf areas by multiplying by the conversion factor 7.255×10^{-3} g cm^{-2} and then dividing by two.

Stomatal index was obtained from the following formula:

$$\text{Stomatal index} = \frac{\text{\# of stomata per area}}{\text{\# of stomata per area} + \text{\# of epidermal cells per area}} \times 100$$

Data were analyzed by location-surface as a factorial design with subsampling (105). There were no missing data so analysis of variance was used to calculate the sums of square values (7).

Experiment 2: Stomatal Resistance

In 1978 field measurements of stomatal resistance were made using a Li-Cor Model Li 65 Autoporometer. Sensor modifications were necessary for adaptation to the small size of flax leaves. First of all, the aperture in the pad on the under surface of the sensor cup was reduced from 20 mm x 10 mm to 4 mm x 10 mm, without altering the aperture resistance plate. This smaller aperture was positioned over the aperture resistance plate so that calibration could still be carried out using the Model 201S Calibration Plate. In all calibration positions, the ratio of the cross-sectional area of the calibration holes to the new aperture area was greater than the minimal value of 1/30 suggested (62). The other modification was to substitute a plexiglass plate for the foam pad of the sensor acrylic base plate. This allowed visual positioning of the leaf over the aperture in the foam so that total aperture coverage was accomplished with each sample. This exchange appeared not to cause tissue damage. The tighter seal produced by this substitution, however, meant that the sensor needed to be held open during drying of the chamber in order to extend the life of the pump batteries.

Calibration was carried out according to the manual instructions (7) with the following exceptions. To assure adequate water reserves during calibration of the sensor, blotter paper was used for the water reservoir and chromatography paper was utilized for the water wicks and to cover the coarser blotter paper. Also, before the equilibration period prior to calibration, the knurled knobs on the

calibration plate were tightened until water from the blotter paper reservoir rose up in the calibration holes. The knobs were then losened just enough to lower the water level to the paper surface. Slope, intercept, and summary statistics of the calibration curve used are listed in Appendix I (105). Calculation of resistances was based on the equation of Kanemasu et al. (62).

Leaves were detached from the stem for insertion into the sensor cup. This departure from the common procedure of sampling attached leaves was followed because of the difficulty in positioning the flax leaf over the sensor aperture. Leaf angle from the stem was not used as a criterion for sampling, though the manual (7) indicated that it introduced additional variability into readings in other species.

It was not possible with this modified sensor to collect both stomatal resistance readings and temperature readings without repositioning the leaf, because of the small leaf size and the comparatively large distance between the aperture and the thermistor. Repositioning of the leaf under the thermistor of the sensor was, therefore, carried out after each diffusive resistance reading.

Diffusive resistance values were determined for the adaxial surface of detached leaves from the first four nodes at the top of the stem. Initially, only plants from which leaves had not previously been taken were used for sampling. This policy was abandoned later in the season because of insufficient plants in the area available for sampling. Both the sensor and sampled leaf were shaded during data collection.

Data collection started June 19, (48 days after planting). Plants had just begun flowering. Readings were made on Monday, Wednesday, and Friday of each week until July 26. Data collection was terminated (87 days after planting) because of the spread of an unidentified leaf disease. Five leaves were sampled per replication per cultivar during each sampling period. Readings were made at 0700, 1000, 1300, 1600, and 1900 hours, except when rain or dew prohibited sampling. Sampling was carried out in the order of the replications, but varieties were sampled at random within each replication. Most readings for a single time period were collected in an hour.

Data were evaluated as a factorial design with subsampling (105). A balanced data set was constructed by dropping all 0700 readings and all days in which data for all four remaining periods were unbalanced. The sums of squares were calculated for the reduced data using analysis of variance (7).

Experiment 3: Osmotic Potential

Samples for osmotic potential (ψ_π) analysis were collected in 1978. For each sample, five leaves were randomly detached from within the canopy for pooling. The locations for sampling were the nodes on the bottom one-third of the stem and the first four nodes at the top of the stem. As far as possible all foreign matter, such as moisture or dirt, was removed from the leaves before they were inserted into a 7.62 cm length of tygon tubing (interior diameter 0.635 cm). The tube containing tissue then stoppered at both ends and immediately placed in a container with dry ice. Later the tubes were transferred to a freezer

for storage. Two such samples were taken per location per plot at 0700, 1200, and 1700. Order of sampling was the same as that used for stomatal resistance. Collection of samples for a single time period required less than an hour.

The first samples were taken June 16 (45 days after planting). At this time a few plants had produced flowers. Subsequent samples were collected on Tuesday of each sampling week. After the July 11 sampling date no further samples were taken from the stem base since leaf abscission had removed most of the leaves from this area. Sampling at the top of the stem continued until July 27 (84 days after planting). By this time an unidentified leaf disease had caused necrotic areas on the leaves.

Processing of the samples was carried out in the laboratory using a psychrometeric technique (52). After removal from storage, samples were allowed to warm to room temperature before sap was expressed from the leaf tissue in the tube by placing the tube in a vise. Sap was absorbed on a 0.6 cm disc punched from Schleicher and Schuell #1 filter paper and then placed in a Wesor Inc. Model C-51 Sampling Chamber. After the sample chamber was sealed, a one minute equilibration period was allowed before application of a 1.35 volt, 3.8 milliamperes cooling current. The resulting current flow produced by the cooling period was read on a microvolt meter connected to the sample chamber. Sample holders were left in the slide during cleaning to avoid handling between samples. Two readings per sample tube were recorded and later averaged. Samples were randomly processed in a single day for a

specific sampling date and time, although instrument problems prevented this in some cases.

Calibration was based on readings obtained from known solutions of KCl ranging from 0.1 to 0.5 molality. The calibration curve was revised whenever stock solutions were changed. Intercepts, slopes, and summary statistics for the calibration curves used are presented in Appendix II (105).

Since there were no missing data the sums of squares were calculated using analysis of variance (7). The experiment was analyzed as a factorial design (105).

RESULTS

General

Weather data from April 15 to July 30 for 1977 and 1978 are presented in Appendix III and IV respectively. For this period the total precipitation for 1977 was 30.96 cm; of this, 12.14 cm fell on June 16. For the same period in 1978, 33.05 cm of rain fell. Daily precipitation totals for that period in 1978 did not exceed 5 cm. Generally, in 1978 temperatures were lower than in 1977.

Wilting, presumably from moisture stress, was observed in 1977 but not in 1978. On July 12, 1978 (71 days after planting (DAP)), it was noted that a leaf disease, possibly pasmo (Septoria linicola (Speg.) Gar.), had begun to attack both cultivars. Disease severity increased towards the end of the season. No major disease outbreak was observed in 1977. By July 24, 1978 (83 DAP), Linott was becoming chlorotic whereas Grant still remained green. Harvesting in 1978 was carred out when plants in the individual replications reached agronomic maturity. Therefore, replications two and three of Grant were harvested on August 14 (104 DAP), replication one of Grant and two and three of Linott were harvested on August 24 (114 DAP), and replication one of Linott was harvested August 31 (121 DAP).

In 1977, the seed yield of Grant was higher than that for Linott, but the inverse was true in 1978 (Appendix V). In 1978, Linott produced more bolls per area and more seeds per boll than Grant (Appendix V). In addition, Linott had a higher harvest index (Appendix V). The 1978 season totals for flower counts (Appendix VI) shows that

more flowers were observed in subplots of Linott than in those of Grant. Daily flower count totals show that flowering in the cultivars began approximately at the same time and that the number of flowers observed per day was similar for the two cultivars until the middle of the flowering period (55 to 59 DAP), during which time Linott produced more flowers. The number of blossoms per day again became quite similar during the latter part of the flowering period.

Experiment 1: Stomatal Characteristics

In 1977 and 1978 stomatal density (Table 1) increased in an acropetal direction on both leaf surfaces. A gradient of increasing stomatal number was also present from leaf base to the tip (Table 1). In both years stomatal frequency was greater on the adaxial surface than the abaxial surface, except for sepals in 1978 where the inverse was true. Stomatal apparatus width (SAW) (Table 2) and stomatal apparatus length (SAL) (Table 3) tended to decrease, in both years, from the sampling location at the base of the stem to the sepals, for both leaf surfaces. No such gradient was apparent from the base of the leaf to the leaf apex for SAW (Table 2) or SAL (Table 3). However, a stomatal apparatus on the leaf tip was most often shorter than one in either of the other leaf regions (Table 3). A stomatal apparatus on the abaxial surface was wider and longer than one on the adaxial surface, except for the sepals (Table 2 and 3). On the sepals, adaxial stomatal apparatus averaged wider and shorter than those of the adaxial surface.

Table 1. Stomatal Frequency. Means ($\bar{x}$), standard deviation (S), and F-test results of cultivar comparisons of stoma counts per 0.05 mm^2 at three regions on the leaf and both leaf surfaces for leaves taken from five locations on the plant. Information is presented on two flax cultivars, Linott and Grant, grown at Brookings, South D kota in 1977 and 1978.

Number of stomata	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[6]	Linott		Grant		F-test[6]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 1[4]										
1977[1]										
Leaf Region[5]										
Tip	5	1.1	5	1.2	N.S.	4	1.1	4	1.4	N.S.
Middle	4	0.9	4	1.0	N.S.	4	1.1	4	1.1	N.S.
Base	4	1.2	3	1.0	N.S.	3	1.3	3	0.9	N.S.
Average[3]	4	--	4	--	--	4	--	4	--	--
1978[2]										
Leaf Region										
Tip	4	1.3	5	1.3	N.S.	3	1.2	3	1.0	N.S.
Middle	4	0.9	4	0.9	N.S.	3	1.0	3	1.0	N.S.
Base	3	1.1	3	1.1	N.S.	2	1.4	2	0.7	N.S.
Average	4	--	4	--	--	3	--	3	--	--
Location 2[4]										
1977[1]										
Leaf Region[5]										
Tip	6	1.2	6	1.3	N.S.	5	1.2	5	1.3	N.S.
Middle	5	1.4	5	1.1	N.S.	4	1.1	4	1.2	N.S.
Base	5	1.7	4	1.1	N.S.	4	1.1	4	1.2	N.S.
Average[3]	5	--	5	--	--	4	--	4	--	--

Table 1. Continued.

Number of stomata	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[6]	Linott		Grant		F-test[6]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
1978[2]										
Leaf Region										
Tip	6	1.5	7	1.5	N.S.	5	1.3	5	1.0	N.S.
Middle	5	1.1	5	1.3	N.S.	4	0.7	4	1.1	N.S.
Base	4	1.1	4	1.3	N.S.	4	0.7	3	0.9	N.S.
Average	5	--	5	--	--	4	--	4	--	--
Location 3[4]										
1977[1]										
Leaf Region[5]										
Tip	7	1.2	6	1.2	*	6	1.3	6	1.3	N.S.
Middle	6	1.2	6	1.2	N.S.	5	1.1	5	1.2	N.S.
Base	5	1.3	4	1.1	N.S.	4	1.3	4	1.1	N.S.
Average[3]	6	--	5	--	--	5	--	5	--	--
1978[2]										
Leaf Region										
Tip	7	1.5	8	1.7	*	6	1.7	7	1.2	N.S.
Middle	6	1.1	6	1.5	N.S.	5	1.2	5	1.3	N.S.
Base	5	1.2	4	1.4	*	3	1.1	4	1.1	N.S.
Average	6	--	6	--	--	4	--	5	--	--
Location 4[4]										
1977[1]										
Leaf Region[5]										
Tip	10	4.5	10	4.2	N.S.	7	3.0	9	4.5	N.S.
Middle	6	1.3	6	1.4	N.S.	5	1.2	5	1.5	N.S.
Base	6	1.3	5	1.1	N.S.	4	1.2	4	1.3	N.S.
Average[3]	7	--	7	--	--	5	--	6	--	--

Table 1. Continued.

Number of stomata	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[6]	Linott		Grant		F-test[6]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
1978[2]										
Leaf Region										
Tip	8	1.4	8	2.3	N.S.	7	1.6	6	1.7	N.S.
Middle	7	1.3	6	1.3	N.S.	5	1.3	5	1.0	N.S.
Base	5	1.6	5	1.6	N.S.	4	1.4	4	1.0	N.S.
Average	7	--	6	--	--	5	--	5	--	--
Location 5[4]										
1977[1]										
Leaf Region[5]										
Tip	9	1.5	9	1.6	N.S.	9	1.3	9	1.2	N.S.
Middle	7	1.2	6	1.3	N.S.	-	--	-	--	--
Base	4	1.9	3	1.7	N.S.	-	--	-	--	--
Average[3]	7	--	6	--	--	-	--	-	--	--
1978[2]										
Leaf Region										
Tip	8	1.1	8	1.5	N.S.	10	1.8	9	1.5	N.S.
Middle	6	1.3	5	1.4	N.S.	--	--	-	--	--
Base	3	1.9	3	1.8	N.S.	--	--	-	--	--
Average	6	--	5	--	--	--	--	-	--	--

[1] 80 observations per cultivar.

[2] 30 observations per cultivar.

[3] Average = (Tip + Middle + Base)/3.

Table 1. Continued.

4/ Location 1 = leaves from lower 1/3 of stem; Location 2 - leaves from middle 1/3 of stem; Location 3 = leaves from upper 1/3 of stem; Location 4 = bracts; Location 5 = sepals.

5/ Tip = upper 1/3 of leaf; Middle = middle 1/3 of leaf; Base = lower 1/3 of leaf.

6/ * - significant at 5% level, ** - significant at 1% level, N.S. - not significant at 5% or 1% level.

Table 2. Stomatal apparatus width. Means ($\bar{x}$), standard deviations (S), and F-test results for cultivar comparisons of stomatal apparatus width at three regions on the leaf and both leaf surfaces for leaves taken from five locations on the plant. Information is presented on two flax cultivars, Linott and Grant, grown at Brookings, South Dakota in 1977 and 1978.

Stomatal apparatus width[6]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[7]	Linott		Grant		F-test[7]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 1[4]										
1977[1]										
Leaf Region[5]										
Tip	47	5.0	48	5.4	N.S.	49	5.6	50	5.6	N.S.
Middle	47	5.9	49	5.7	N.S.	49	5.8	49	4.9	N.S.
Base	48	5.8	52	6.2	N.S.	50	5.9	51	5.5	N.S.
Average[3]	47	--	50	--	--	49	--	50	--	--
1978[2]										
Leaf Region										
Tip	47	4.8	49	5.3	N.S.	49	5.3	51	5.6	N.S.
Middle	47	4.3	49	6.1	N.S.	50	5.2	52	5.8	N.S.
Base	47	5.2	49	5.6	N.S.	49	6.9	50	5.6	N.S.
Average	47	--	49	--	--	49	--	51	--	--
Location 2[4]										
1977[1]										
Leaf Region[5]										
Tip	43	5.4	46	5.2	N.S.	43	3.5	47	4.6	N.S.
Middle	43	3.9	46	4.9	*	45	4.5	48	4.7	N.S.
Base	45	5.1	50	6.2	*	45	5.1	47	4.6	N.S.
Average[3]	43	--	47	--	--	44	--	47	--	--

Table 2. Continued.

Stomatal apparatus width[6]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[7]	Linott		Grant		F-test[7]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
1978[2]										
Leaf Region										
Tip	42	3.2	43	3.6	N.S.	44	3.7	46	4.0	N.S.
Middle	42	3.4	45	4.3	N.S.	45	3.0	47	5.8	N.S.
Base	45	4.6	47	4.4	N.S.	45	3.6	46	4.6	N.S.
Average	43	--	45	--	--	45	--	46	--	--
Location 3[4]										
1977[1]										
Leaf Region										
Tip	42	3.6	44	3.9	N.S.	44	4.3	46	3.9	N.S.
Middle	41	3.7	44	3.3	*	44	4.3	46	4.0	*
Base	45	4.1	47	3.7	N.S.	43	4.1	47	4.0	*
Average[3]	43	--	45	--	--	44	--	46	--	--
1978[2]										
Leaf Region										
Tip	41	3.4	41	3.5	N.S.	43	3.1	42	3.4	N.S.
Middle	40	2.8	41	4.1	N.S.	43	3.2	45	3.9	*
Base	43	4.5	44	4.4	N.S.	42	3.9	42	4.0	N.S.
Average	41	--	42	--	--	43	--	43	--	--
Location 4[4]										
1977[1]										
Leaf Region[5]										
Tip	40	3.6	41	4.4	N.S.	43	4.9	44	5.1	N.S.
Middle	41	4.1	43	4.0	*	43	4.2	44	3.7	N.S.
Base	42	4.1	44	4.4	N.S	44	4.9	45	4.3	N.S.
Average[3]	41	--	43	--	--	43	--	44	--	--

Table 2. Continued.

Stomatal apparatus width[6]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[7]	Linott		Grant		F-test[7]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
1978[2]										
Leaf Region										
Tip	39	3.0	39	3.7	N.S.	39	3.6	40	3.3	N.S.
Middle	38	2.4	40	3.6	N.S.	41	2.5	42	4.2	N.S.
Base	38	3.5	40	3.4	N.S.	42	3.6	41	4.4	N.S.
Average	38	--	40	--	--	41	--	41	--	--
Location 5[4]										
1977[1]										
Leaf Region[5]										
Tip	40	3.7	40	5.0	N.S.	40	2.8	38	2.9	*
Middle	41	4.8	42	4.7	N.S.	--	--	--	--	--
Base	39	4.8	37	3.6	N.S	--	--	--	--	--
Average[3]	40	--	40	--	--	--	--	--	--	--
1978[2]										
Leaf Region										
Tip	38	3.6	40	3.3	N.S.	36	2.7	38	3.5	N.S.
Middle	39	2.7	40	3.3	N.S.	--	--	--	--	--
Base	38	3.7	39	3.6	N.S.	--	--	--	--	--
Average	38	--	40	--	--	--	--	--	--	--

[1] 80 observations per cultivar.

[2] 30 observations per cultivar.

[3] Average = (Tip + Middle + Base)/3.

[4] Location 1 = leaves from lower 1/3 of stem; Location 2 = leaves from middle 1/3 of stem; Location 3 = leaves from upper 1/3 of stem; Location 4 = bracts; Location 5 = sepals.

Table 2. Continued.

5/ Tip = upper 1/3 of leaf; Middle = middle 1/3 of leaf; Base = lower 1/3 of leaf.

6/ Units μ

7/ * - significant at 5% level, ** - significant at 1% level, N.S. - not significant at 5% or 1% level.

Table 3. Stomatal apparatus length. Means ($\bar{x}$), standard deviations (S), and F-test results for cultivar comparisons of stomatal apparatus length at three regions on the leaf and both leaf surfaces for leaves taken from five locations on a plant. Information is presented on two flax cultivars, Linott and Grant, grown at Brookings, South Dakota in 1977 and 1978.

Stomatal apparatus length[6]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[7]	Linott		Grant		F-test[7]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 1[4]										
1977[1]										
Leaf Region[5]										
Tip	34	3.0	36	3.2	N.S.	37	3.3	40	3.5	*
Middle	36	3.0	39	3.4	*	38	3.0	42	3.7	N.S.
Base	35	3.5	38	2.8	N.S.	37	3.6	42	4.1	N.S.
Average[3]	35	--	38	--	--	37	--	41	--	--
1978[2]										
Leaf Region										
Tip	38	3.7	41	4.2	N.S.	42	4.6	43	4.7	N.S.
Middle	41	3.2	43	4.6	N.S.	44	3.8	47	4.3	N.S.
Base	40	3.6	42	5.7	N.S.	42	4.6	46	4.0	N.S.
Average[3]	40	--	42	--	--	43	--	45	--	N.S.
Location 2[4]										
1977[1]										
Leaf Region[5]										
Tip	34	2.5	36	2.5	N.S.	37	3.5	39	3.3	N.S.
Middle	35	3.1	37	2.8	N.S.	37	2.9	40	3.1	**
Base	35	3.2	38	3.0	N.S.	36	3.4	40	3.5	**
Average[3]	35	--	37	--	--	37	--	40	--	--

Table 3. Continued.

Stomatal apparatus length[6]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[7]	Linott		Grant		F-test[7]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
1978[2]										
Leaf Region										
Tip	37	3.6	37	3.1	N.S.	39	2.5	40	2.7	N.S.
Middle	39	2.8	40	4.2	N.S.	42	3.0	44	3.5	N.S.
Base	38	3.7	40	3.9	N.S.	38	3.8	40	3.8	N.S.
Average	38	--	39	--	--	40	--	41	--	--
Location 3[4]										
1977[1]										
Leaf Region										
Tip	34	2.5	36	2.5	N.S.	37	3.5	39	3.3	N.S.
Middle	35	3.1	37	2.8	*	37	2.9	40	3.1	*
Base	36	3.2	38	3.0	N.S.	36	3.4	40	3.5	N.S.
Average[3]	35	--	37	--	--	37	--	40	--	--
1978[2]										
Leaf Region										
Tip	36	2.8	34	2.9	N.S.	37	2.9	37	2.8	N.S.
Middle	36	2.4	38	3.7	*	38	2.6	39	3.3	N.S.
Base	36	3.2	36	3.4	N.S.	36	2.2	38	3.1	N.S.
Average[3]	36	--	36	--	--	37	--	38	--	--

Table 3. Continued.

Stomatal apparatus length[6]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[7]	Linott		Grant		F-test[7]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 4[4]										
1977[1]										
Leaf Region[5]										
Tip	34	3.1	35	3.0	*	36	3.8	38	3.2	N.S.
Middle	35	3.5	37	3.2	*	37	3.8	38	3.8	N.S.
Base	35	3.5	38	3.1	*	37	3.8	39	3.4	**
Average[3]	35	--	37	--	--	37	--	38	--	--
1978[2]										
Leaf Region										
Tip	33	2.8	34	2.5	N.S.	36	3.1	36	3.2	N.S.
Middle	33	2.4	35	3.0	N.S.	36	2.7	36	2.6	N.S.
Base	33	3.7	34	2.4	N.S.	34	3.0	36	2.8	N.S.
Average	33	--	34	--	--	35	--	36	--	--
Location 5[4]										
1977[1]										
Leaf Region[5]										
Tip	33	3.0	33	3.0	N.S.	38	3.0	38	2.7	N.S.
Middle	34	3.7	34	3.7	N.S.	--	--	--	--	--
Base	36	4.4	36	3.9	N.S.	--	--	--	--	--
Average[3]	34	--	34	--	--	--	--	--	--	--

Table 3. Continued.

Stomatal apparatus length[6]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[7]	Linott		Grant		F-test[7]
	$\bar{x}$	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
1978[2]										
Leaf Region										
Tip	31	2.4	33	2.4	N.S.	37	3.0	37	3.3	N.S.
Middle	32	2.4	34	3.8	N.S.	--	--	--	--	--
Base	35	2.9	37	3.9	N.S.	--	--	--	--	--
Average	33	--	35	--	--	--	--	--	--	--

[1] 80 observations per cultivar.

[2] 30 observations per cultivar.

[3] Average = (Tip + Middle + Base)/3.

[4] Location 1 = leaves from lower 1/3 of stem; Location 2 = leaves from middle 1/3 of stem; Location 3 = leaves from upper 1/3 of stem; Location 4 = bracts; Location 5 = sepals.

[5] Tip = upper 1/3 of leaf; Middle = middle 1/3 of leaf; Base = lower 1/3 of leaf.

[6] Units μ

[7] * - significant at 5% level, ** - significant at 1% level, N.S. - not significant at 5% or 1% level.

stomatal apparatus dimensions. All location-surface combinations for SAW were wider in 1977 than in 1978 (Table 2). Averages for SAL (Table 3) were greater in 1978 then 1977 for leaves collected from the first two locations on the plant, but at leaf insertions higher on the plant the opposite was true. From a closer examination of the individual leaf regions means in Table 1 through 3, it appears that an overall change in the categories measured for all leaf regions, rather than a drastic change in one particular region, is responsible for the difference between years.

In 1978 combined guard cell width (CGW) decreased from the leaf apex to the leaf base, was greater on the adaxial surface than on the abaxial surface, but did not change greatly from the base of the plant to the top (Table 4). Guard cell length (GCL) followed no pattern from leaf tip to leaf base (Table 5) but did decrease from stem base to the stem top.

Average leaf dimensions increased from the base of the stem to the top of the stem (Table 6). For sampling sites above the stem, average leaf area decreased as one moved to the bracts and then to the sepals (Table 6). Stomatal index (Table 7) showed a decreasing gradient from the leaf tip to leaf base and plant base to plant top. In addition, stomatal indices of the adaxial surface appeared greater than those of the abaxial surface, except on the sepals where the inverse was true.

In both years, differences between cultivars for stomatal density were significant ($\alpha = 0.05$) for the top of the adaxial surface of

Table 4. Combined guard cell width. Means ($\bar{x}$), standard deviations (S) and F-test results for cultivar comparisons of combined guard cell width at three regions on the leaf and both leaf surfaces for leaves taken from five locations on the plant. Information is presented on two flax cultivars, Linott and Grant, grown at Brookings, South Dakota in 1978.

Combined guard cell width[1]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[6]	Linott		Grant		F-test[6]
	$\bar{x}$[2]	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 1[4]										
Leaf Region[5]										
Tip	21	1.8	21	2.3	N.S.	20	2.0	19	2.2	N.S.
Middle	20	2.5	20	1.6	N.S.	20	2.2	19	1.9	N.S.
Base	18	3.1	20	3.1	N.S.	17	1.8	17	2.1	N.S.
Average[3]	20	--	20	--	--	19	--	18	--	--
Location 2[4]										
Leaf Region[5]										
Tip	20	1.7	19	1.8	N.S.	19	1.8	17	1.5	N.S.
Middle	20	2.2	20	1.6	N.S.	18	1.5	17	1.5	*
Base	18	2.9	18	2.8	N.S.	15	2.1	15	2.0	N.S.
Average[3]	19	--	19	--	--	17	--	16	--	--
Location 3[4]										
Leaf Region[5]										
Tip	20	2.6	19	1.8	N.S.	18	1.6	16	1.9	N.S.
Middle	18	1.6	18	2.0	N.S.	17	1.6	16	1.7	*
Base	18	2.7	17	1.9	N.S.	14	2.2	15	2.1	N.S.
Average[3]	19	--	18	--	--	16	--	16	--	--

Table 4. Continued.

Combined guard cell width[1]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[6]	Linott		Grant		F-test[6]
	$\bar{x}$[2]	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 4[4]										
Leaf Region[5]										
Tip	20	1.6	18	2.1	N.S.	19	1.7	16	1.8	**
Middle	18	1.6	18	2.0	N.S.	16	1.6	16	1.1	N.S.
Base	17	1.7	16	1.6	N.S.	15	1.9	15	2.4	N.S.
Average[3]	18	--	17	--	--	17	--	16	--	--
Location 5[4]										
Leaf Region[5]										
Tip	20	2.5	20	2.3	N.S.	17	2.4	17	2.3	N.S.
Middle	19	2.0	18	2.1	N.S.	--	--	--	--	--
Base	18	2.7	18	2.6	N.S.	--	--	--	--	--
Average[3]	19	--	19	--	--	--	--	--	--	--

[1] Units μ

[2] 30 observations per cultivar.

[3] Average = (Tip + Middle + Base)/3

[4] Location 1 = leaves from lower 1/3 of stem; Location 2 = leaves from middle 1/3 of stem; Location 3 - leaves from upper 1/3 of stem; Location 4 - bracts; Location 5 = sepals.

[5] Tip = upper 1/3 of leaf; Middle = middle 1/3 of leaf; Base = lower 1/3 of leaf.

[6] * - significant at 5% level, ** - significant at 1% level, N.S. - not significant at 5% or 1% level.

Table 5. Guard cell length. Means ($\bar{x}$), standard deviations (S), and F-test results for cultivar comparisons of guard cell length at three regions on the leaf and both leaf surfaces for leaves taken from five locations on the plant. Information is presented on two flax cultivars, Linott and Grant, grown at Brookings, South Dakota in 1978.

Guard cell length[1]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[6]	Linott		Grant		F-test[6]
	$\bar{x}$[2]	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 1[4]										
Leaf Region[5]										
Tip	36	3.4	38	3.2	N.S.	38	3.4	38	3.5	N.S.
Middle	38	2.9	40	3.7	N.S.	39	2.5	42	3.1	*
Base	38	3.1	42	5.5	N.S.	38	4.0	41	3.0	N.S.
Average[3]	37	--	40	--	--	38	--	40	--	--
Location 2[4]										
Leaf Region[5]										
Tip	34	3.0	34	2.5	N.S.	35	1.9	35	2.8	N.S.
Middle	36	2.4	36	4.4	N.S.	36	2.5	37	1.8	N.S.
Base	36	3.6	37	3.6	N.S.	34	3.8	36	2.5	N.S.
Average[3]	35	--	36	--	--	35	--	36	--	--
Location 3[4]										
Leaf Region[5]										
Tip	33	3.3	32	2.6	N.S.	33	2.3	34	2.8	N.S.
Middle	34	1.9	35	3.5	N.S.	34	2.3	36	2.4	N.S.
Base	34	2.7	35	2.9	N.S.	33	1.8	34	2.5	*
Average[3]	34	--	34	--	--	33	--	35	--	--

Table 5. Continued.

Guard cell length[1]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[6]	Linott		Grant		F-test[6]
	$\bar{x}$[2]	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 4[4]										
Leaf Region[5]										
Tip	31	2.3	32	2.3	N.S.	33	3.1	33	2.5	N.S.
Middle	31	1.8	33	2.4	*	32	2.9	33	1.8	N.S.
Base	31	3.0	32	2.1	N.S.	30	2.6	33	2.4	**
Average[3]	31	--	32	--	--	32	--	33	--	--
Location 5[4]										
Leaf Region[5]										
Tip	30	3.3	31	2.6	N.S.	35	3.2	34	3.9	N.S.
Middle	30	3.9	33	3.9	*	--	--	--	--	--
Base	33	3.9	36	4.3	N.S.	--	--	--	--	--
Average[3]	31	--	33	--	--	--	--	--	--	--

[1] Units μ

[2] 30 observations per cultivar.

[3] Average = (Tip + Middle + Base)/3

[4] Location 1 = leaves from lower 1/3 of stem; Location 2 = leaves from middle 1/3 of stem; Location 3 = leaves from upper 1/3 of stem; Location 4 = bracts; Location 5 = sepals.

[5] Tip = upper 1/3 of leaf; Middle = middle 1/3 of leaf; Base = lower 1/3 of leaf.

[6] * - significant at 5% level, ** - significant at 1% level, N.S. - not significant at 5% or 1% level.

Table 6. Average leaf dimension. Means ($\bar{x}$), standard deviations (S), and F-test results for cultivar comparisons of the average leaf dimension of leaves used in collection of stomatal characteristics data. Information is presented on a location basis for two flax cultivars, Linott and Grant, grown at Brookings, South Dakota in 1978.

Average leaf dimension[1]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[4]	Linott		Grant		F-test[4]
	$\bar{x}$[2]	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 1[3]	0.4360	0.1250	0.4519	0.1197	N.S.	0.4597	0.0920	0.4590	0.1281	N.S.
Location 2[3]	1.1882	0.1463	1.1031	0.2069	N.S.	1.1865	0.1034	1.2058	0.2347	N.S.
Location 3[3]	1.2029	0.1602	1.1540	0.2689	N.S.	1.2638	0.1779	1.2122	0.2882	N.S.
Location 4[3]	0.6693	0.1526	0.6444	0.1098	N.S.	0.7552	0.1199	0.7407	0.2162	N.S.
Location 5[3]	0.17069	0.0281	0.1633	.0215	N.S.	0.1915	0.0257	0.1949	0.0338	N.S.

[1] units cm^2

[2] 30 observations per cultivar.

[3] Location 1 = leaves from lower 1/3 of stem; Location 2 = leaves from middle 1/3 of stem; Location 3 = leaves from upper 1/3 of stem; Location 4 = bracts; Location 5 = sepals.

[4] * - significance at 5% level, ** - significance at 1% level, N.S. - not significant at 5% or 1% level.

Table 7. Stomatal index. Means ($\bar{x}$), standard deviations (S), and F-test results for cultivar comparisons of stomatal index at three regions on the leaf and both leaf surfaces for leaves taken from five locations on a plant. Information is presented on two cultivars, Linott and Grant, grown at Brookings, South Dakota in 1978.

Stomatal[1] Index	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[6]	Linott		Grant		F-test[6]
	$\bar{x}$[2]	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 1[4]										
Leaf Region[5]										
Tip	26	6.5	28	5.5	N.S.	24	7.1	23	6.9	N.S.
Middle	25	6.2	28	5.0	N.S.	22	6.6	23	7.1	N.S.
Base	21	6.6	23	6.2	N.S.	18	7.2	18	5.9	N.S.
Average[3]	24	--	26	--	--	21	--	21	--	--
Location 2[4]										
Leaf Region[5]										
Tip	30	5.3	29	6.7	N.S.	24	5.0	22	3.9	N.S.
Middle	27	4.5	26	5.8	N.S.	21	4.7	23	5.5	N.S.
Base	19	5.5	22	5.7	N.S.	16	3.7	17	4.3	N.S.
Average[3]	25	--	26	--	--	20	--	21	--	--
Location 3[4]										
Leaf Region[5]										
Tip	26	3.8	26	4.7	N.S.	24	4.8	22	4.2	N.S.
Middle	24	4.3	27	5.1	N.S.	20	5.3	20	5.3	N.S.
Base	22	5.1	20	5.4	**	14	4.5	18	4.5	N.S.
Average[3]	24	--	24	--	--	19	--	20	--	--

Table 7. Continued.

Stomatal Index[1]	Adaxial surface					Abaxial surface				
	Linott		Grant		F-test[6]	Linott		Grant		F-test[6]
	$\bar{x}$[2]	S	$\bar{x}$	S		$\bar{x}$	S	$\bar{x}$	S	
Location 4[4]										
Leaf Region[5]										
Tip	25	4.0	25	5.3	N.S.	22	4.5	20	4.0	N.S.
Middle	25	4.0	22	3.6	N.S.	19	4.6	18	4.0	N.S.
Base	20	4.4	21	4.5	N.S.	15	4.8	16	4.3	N.S.
Average[3]	23	--	23	--	--	19	--	18	--	--
Location 5[4]										
Leaf Region[5]										
Tip	16	1.8	17	3.4	N.S.	22	3.1	20	2.4	N.S.
Middle	15	3.4	15	3.8	N.S.	--	--	--	--	--
Base	9	5.1	9	4.4	N.S.	--	--	--	--	--
Average[3]	13	--	14	--	--	--	--	--	--	--

[1] {No. stomata/(No. stomata + No. cell epidermal)} x 100.

[2] 30 observations per cultivar

[3] Average = (Tip + Middle + Base)/3

[4] Location 1 = leaves from lower 1/3 of stem; Location 2 = leaves from middle 1/3 of stem; Location 3 = leaves from upper 1/3 of stem; Location 4 = bracts; Location 5 = sepals.

[5] Tip = upper 1/3 of leaf; Middle = middle 1/3 of leaf; Base = lower 1/3 of leaf.

[6] * - significant at 5% level, ** - significant at 1% level, N.S. - not significant at 5% or 1% level.

leaves sampled from the upper third of the stem (Table 1). However, while Linott showed the greater density at this location in 1977, Grant had the greater density in 1978. For GCL, CGL, SAL, and SAW, Grant averaged slightly higher, but in only a few instances did this prove to be statistically important (Table 2 through 5). No consistent, statistically significant differences were present between cultivars for average leaf area or stomatal index (Table 6 and 7).

Experiment 2: Stomatal Resistance

During the day, adaxial stomatal resistance (r_{ad}) basically followed a parabolic pattern of change, with the lowest values occurring around midday (Table 8 and Figure 2). Differences between the overall means for the sampling periods were highly significant ($\alpha = 0.01$) (Appendix VIII). Daily average r_{ad} for both cultivars declined sharply after the fourth sampling date and remained relatively low for about 15 days after which there was a rise in r_{ad}. Differences between sampling dates and the Day (D) x Time (T) interaction were highly significant (Appendix VIII).

Linott and Grant were not significantly different for r_{ad} (Appendix VII). However, the interactions of T x Cultivar (C) and DC were highly significant. Figure 2, which shows overall means for daily time periods, indicates that Grant and Linott had similar r_{ad} readings early in the day, but that as the day progressed a difference between cultivars developed and increased in magnitude. Daily r_{ad} for the cultivars were very similar during the first half of the season, but by post-bloom Grant generally showed a greater daily mean r_{ad} than

Table 8. Adaxial stomatal resistance. Means ($\bar{x}$) and standard deviations (S) of adaxial stomatal resistance readings of flax leaves detached from the top of the stem. Sampling took place five times per day at two day intervals starting in early bloom and continuing for approximately five weeks.

r_{ad} Sample[1]	Days after planting: 48 $\bar{x}$	48 S	50 $\bar{x}$	50 S	52 $\bar{x}$	52 S	55 $\bar{x}$	55 S	57 $\bar{x}$	57 S	59 $\bar{x}$	59 S
0700 hrs[2]			2.42	--	2.17	--					2.05	--
Linott			2.42	0.475	2.17	0.215					2.16	0.512
Grant			2.42	0.335	2.17	0.333					1.94	0.217
1000 hrs[3]	2.92	--	1.78	--	1.11	--	1.36	--			1.48	--
Linott	2.95	0.672	1.79	0.280	1.16	0.289	1.38	0.363			1.58	0.418
Grant	2.89	0.510	1.77	0.448	1.06	0.194	1.34	0.496			1.37	0.351
1300 hrs[2]	2.01	--	2.14	--	1.33	--	1.94	--	1.25	--	1.16	--
Linott	2.02	0.397	2.17	0.752	1.41	0.362	2.08	0.436	1.19	0.294	1.24	0.264
Grant	2.00	0.414	2.10	0.375	1.25	0.389	1.80	0.374	1.31	0.405	1.09	0.184
1600 hrs[2]	1.53	--	2.12	--	1.68	--	2.50	--	1.03		1.08	
Linott	1.59	0.277	2.13	0.789	1.58	0.253	2.38	0.728	1.08	0.269	1.02	0.201
Grant	1.47	0.265	2.10	2.102	1.79	0.281	2.63	0.446	0.98	0.136	1.14	0.205
1900 hrs[2]	1.81	--	2.16	--	1.94	--	3.33	--	1.44	--	2.04	--
Linott	1.72	0.521	2.27	0.274	1.95	0.332	3.06	0.641	1.45	0.251	2.05	0.363
Grant	1.89	0.266	2.04	0.276	1.93	0.279	3.61	0.804	1.44	0.304	2.03	0.207
Daily $\bar{x}$												
Combined	2.07	--	2.12	--	1.65	--	2.28	--	1.24	--	1.56	--
Linott	2.07	--	2.16	--	1.65	--	2.22	--	1.24	--	1.61	--
Grant	2.06	--	2.09	--	1.64	--	2.35	--	1.24	--	1.51	--

[1] Units s cm^{-1}. Sampling took place on the first four nodes on the top of the stem.

[2] 15 observations per cultivar.

[3] 12 observations per cultivar on date 52. All other dates had 15 observations per cultivar at this time period.

Table 8. Continued.

r_{ad} Sample[1]	Days after planting: 62 $\bar{x}$	62 S	64 $\bar{x}$	64 S	66 $\bar{x}$	66 S	69 $\bar{x}$	69 S	71 $\bar{x}$	71 S	73 $\bar{x}$	73 S
0700 hrs[2]									2.16	--	2.16	--
Linott									2.26	0.267	2.23	0.405
Grant									2.07	0.161	2.08	0.462
1000 hrs[2]	1.17	--	1.80	--			0.84	--	1.22	--	0.95	--
Linott	1.20	0.261	1.86	0.263			0.77	0.170	1.16	0.210	0.83	0.320
Grant	1.14	0.232	1.74	0.282			0.91	0.284	1.29	0.299	1.07	0.261
1300 hrs[2]	1.32	--	1.57	--	1.62	--	1.18	--	1.04	--	1.56	--
Linott	1.33	0.315	1.52	0.206	1.50	0.318	1.09	0.396	0.95	0.237	1.55	0.318
Grant	1.32	0.584	1.62	0.118	1.74	0.819	1.27	0.433	1.13	2.058	1.58	0.499
1600 hrs[2]	1.50	--			1.07	--	1.28	--	1.17	--	1.70	--
Linott	1.51	0.191			1.01	0.287	1.16	0.220	1.24	0.196	1.87	0.694
Grant	1.48	0.309			1.12	0.337	1.39	0.327	1.10	0.141	1.53	0.401
1900 hrs[2]	2.32	--			1.86	--	2.56	--	1.95	--	2.74	--
Linott	2.21	0.310			1.68	0.410	2.28	0.411	1.91	0.354	2.32	0.553
Grant	2.43	0.523			2.05	0.476	2.84	0.800	2.00	0.644	3.16	1.256
Daily $\bar{x}$												
Combined	1.58	--	1.68	--	1.52	--	1.47	--	1.51	--	1.82	--
Linott	1.56	--	1.68	--	1.40	--	1.33	--	1.50	--	1.76	--
Grant	1.59	--	1.68	--	1.64	--	1.60	--	1.52	--	1.88	--

[1] Units s cm^{-1}. Sampling took place on the first four nodes on the top of the stem.
[2] 15 observations per cultivar.

Table 8. Continued.

r_{ad} Sample[1]	Days after planting: 76 $\bar{x}$	76 S	78 $\bar{x}$	78 S	80 $\bar{x}$	80 S	83 $\bar{x}$	83 S	85 $\bar{x}$	85 S	$\bar{x}$ across all days
0700 hrs[2]	2.30	--					2.48	--			2.25
Linott	2.18	0.321					2.44	0.237			2.27
Grant	2.42	0.390					2.51	0.317			2.23
1000 hrs[2]	1.55	--	1.94	--			1.72	--	1.78	—	1.54
Linott	1.46	0.305	1.60	0.371			1.73	0.655	1.69	0.579	1.51
Grant	1.63	0.557	2.28	0.935			1.71	0.[illegible]1	1.87	0.432	1.57
1300 hrs[2]	2.47	--	2.40	--	1.99	—	2.05	--	2.24	—	1.72
Linott	2.16	0.468	2.39	0.668	2.01	0.335	2.07	0.548	2.24	0.383	1.70
Grant	2.78	1.608	2.41	0.567	1.98	0.293	2.03	0.286	2.24	0.551	1.74
1600 hrs[2]	2.35	--	2.40	--	2.13	--	1.36	--	2.31	--	1.70
Linott	2.11	0.479	1.87	0.575	2.06	0.541	1.24	0.599	2.38	0.794	1.64
Grant	2.60	0.416	2.94	1.160	2.19	0.313	1.49	0.377	2.25	0.697	1.76
1900 hrs[2]	3.11	--	4.34	--	2.59	--	2.90	--	3.47	--	2.54
Linott	2.91	0.742	2.78	0.778	2.44	0.568	2.91	0.468	3.30	0.651	2.33
Grant	3.30	0.950	5.90	3.867	2.75	0.424	2.90	0.632	3.64	0.833	2.74
Daily $\bar{x}$											
Combined	2.35	--	2.77	--	2.24	--	2.10	--	2.45	--	1.95
Linott	2.16	--	2.16	--	2.17	--	2.08	--	2.40	--	1.89
Grant	2.55	--	3.38	--	2.31	—	2.13	--	2.50	—	2.01

[1] Units s cm^{-1}. Sampling took place on the first four nodes on the top of the stem.

[2] 15 observations per cultivar.

Figure 2. Adaxial stomatal resistance (r_{ad}). Overall cultivar means of r_{ad} for five sampling periods (0700, 1000, 1300, 1600, 1900). Adaxial stomatal resistance was determined during 1978 at Brookings, S.D. for leaves from the first four nodes of the stem.

(▲•••▲ Linott, ■——■ Grant)

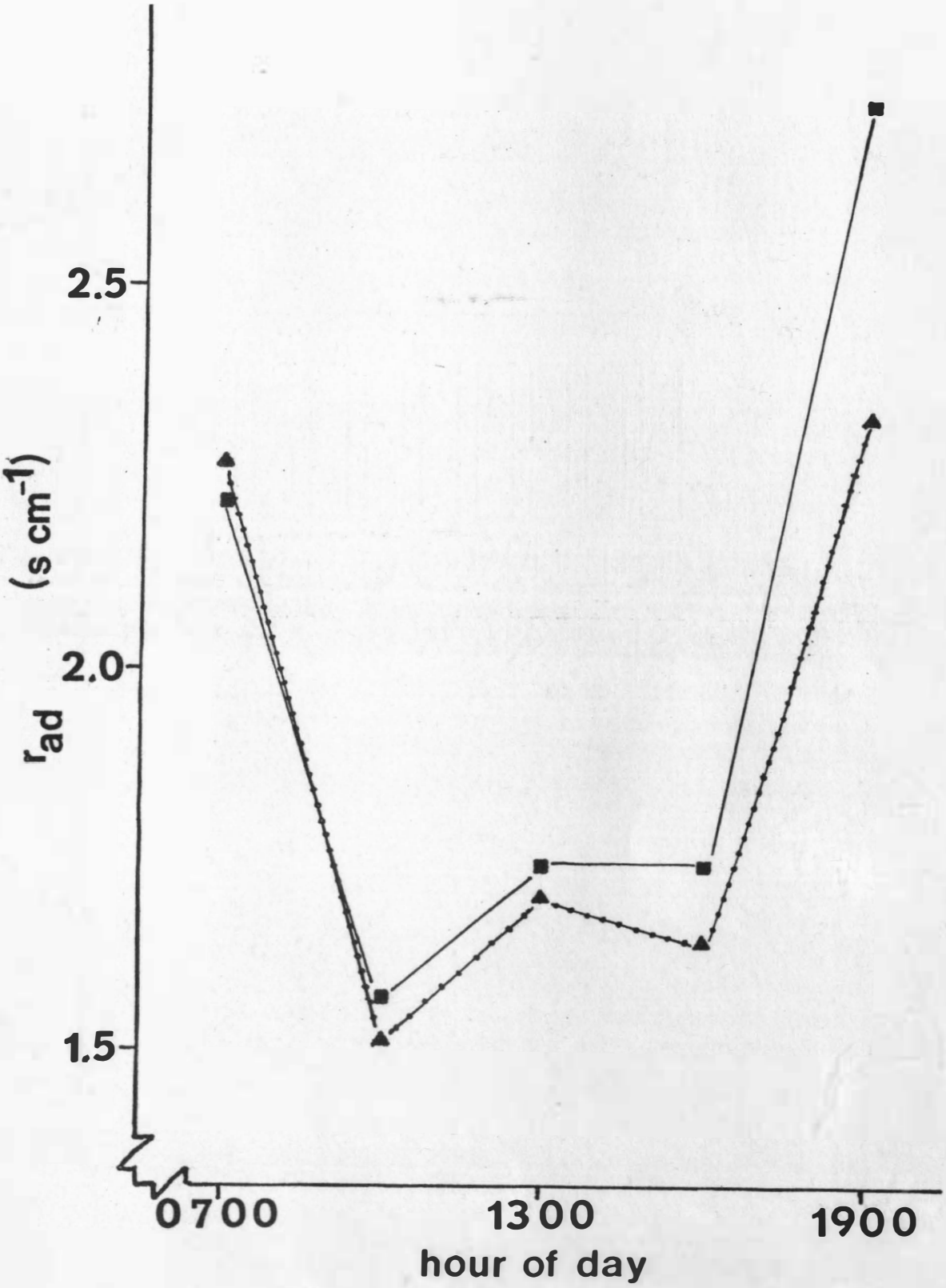

2.5
2.0
1.5
r_{ad} (s cm^{-1})
0700
1300
1900
hour of day

Figure 3. Adaxial stomatal resistance (r_{ad}). Daily cultivar means of r_{ad} across all sampling dates and precipitation data from 48 through 85 days after planting. Osmotic potential samples were collected in 1978 at Brookings, S.D. from the lower third of the stem and the first four nodes of the stem.

(▲•••▲ Linott, ■——■ Grant; DAP - days after planting)

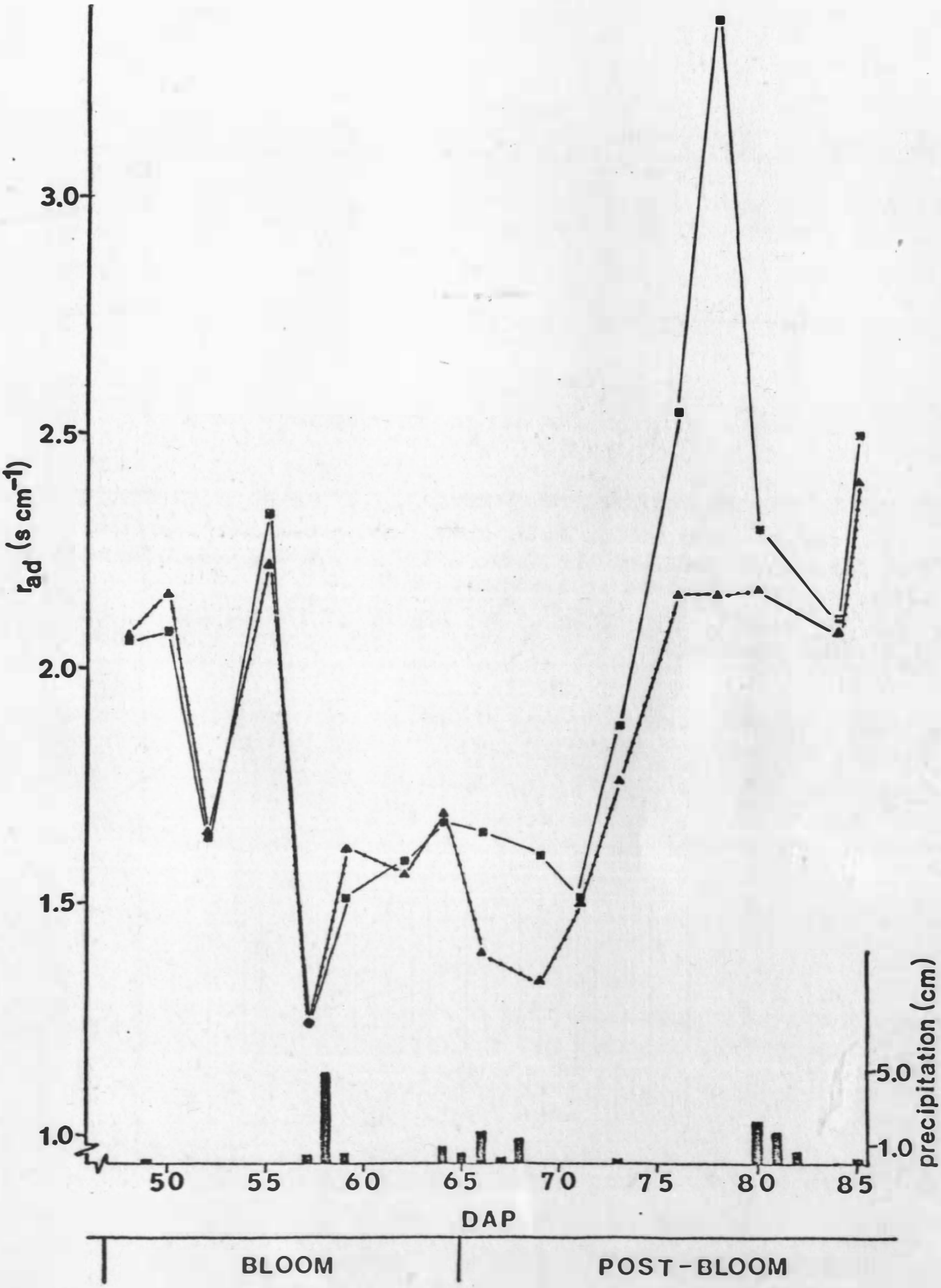
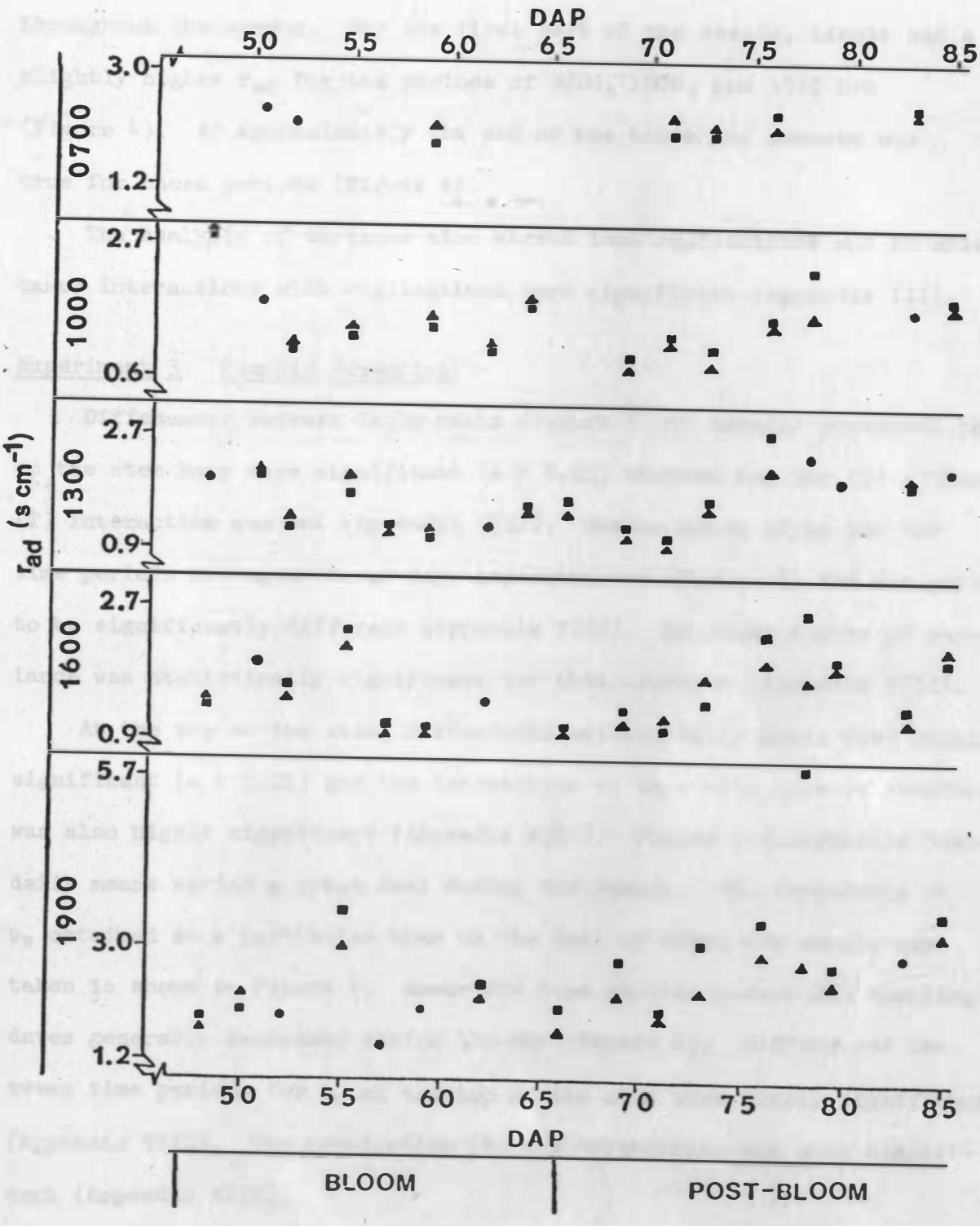

3.0
2.5
2.0
1.5
1.0
r_{ad} (s cm^{-1})
5.0
1.0
precipitation (cm)
50
55
60
65
70
75
80
85
DAP
BLOOM
POST-BLOOM

Figure 4. Adaxial stomatal resistance (r_{ad}). Means of cultivars for r_{ad} by day and hour (0700, 1000, 1300, 1600, 1900) for readings from the first four nodes of the stem. Adaxial stomatal resistance readings were made in 1978 at Brookings, S.D.

(▲ Linott, ■ Grant, ● Linott and Grant; DAP - days after planting)


DAP
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
3.0
1.2
0700
2.7
0.6
1000
2.7
0.9
1300
2.7
0.9
1600
5.7
3.0
1.2
1900
r_{ad} (s cm^{-1})
50
55
60
65
70
75
80
85
DAP
BLOOM
POST-BLOOM

Linott (Figure 3). The DTC interaction also proved highly significant. Linott repeatedly showed a lower r_{ad} at 1600 and 1900 hrs than Grant throughout the season. For the first part of the season, Linott had a slightly higher r_{ad} for the periods of 0700, 1000, and 1300 hrs (Figure 4). At approximately the end of the bloom the inverse was true for these periods (Figure 4).

The analysis of variance also showed that replications and in most cases interactions with replications were significant (Appendix III).

Experiment 3: Osmotic Potential

Differences between daily means (Figure 5) of osmotic potential (ψ_π) at the stem base were significant ($\alpha = 0.05$) whereas the Day (D) x Time (T) interaction was not (Appendix VIII). Season means of ψ_π for the time periods averaged across days and cultivars (Figure 6) did not prove to be significantly different (Appendix VIII). No other source of variance was statistically significant for this location (Appendix VIII).

At the top of the stem, differences between daily means were highly significant ($\alpha = 0.01$) and the interaction of days with time of sampling was also highly significant (Appendix VIII). Figure 5 illustrates that daily means varied a great deal during the season. The dependency of ψ_π obtained at a particular time on the date on which the sample was taken is shown in Figure 7. Means for time periods across all sampling dates generally decreased during the day (Figure 6). Differences between time periods for ψ_π at the top of the stem were highly significant. (Appendix VIII). The replication (R) x D interaction was also significant (Appendix VIII).

Table 9. Osmotic potential. Means ($\bar{x}$) and standard deviations (S) of osmotic potential readings from leaves sampled for the base and the top of the stem. Sampling took place three times per day on a weekly basis starting just before bloom and continuing for approximately six weeks.

ψ_π Sample[1]	Days after planting: 45 $\bar{x}$	45 S	49 $\bar{x}$	49 S	56 $\bar{x}$	56 S	63 $\bar{x}$	63 S	70 $\bar{x}$	70 S	77 $\bar{x}$	77 S	84 $\bar{x}$	84 S	$\bar{x}$ accross all days
Stem Top[3]															
0700 hrs	- 8.9	--	-10.7	--	- 8.9	--	-11.8	--	- 7.8	--	-14.1	--	-13.8	--	-10.9
Linott	- 8.4	1.51	-11.3	2.25	- 8.5	1.15	-13.3	4.12	- 6.3	3.92	-13.5	2.78	-12.4	0.78	-10.5
Grant	- 9.4	1.10	-10.1	1.73	- 9.3	1.58	-10.3	2.77	- 9.2	2.43	-14.7	2.19	-15.2	1.59	-11.2
1200 hrs	-11.0	--	-13.8	--	-10.7	--	-11.7	--	- 8.1	--	-11.5	--	-14.9	--	-11.7
Linott	-11.1	0.88	-13.0	2.12	-11.2	4.70	-10.3	1.39	- 6.8	1.24	-10.4	1.57	-14.0	2.35	-11.0
Grant	-10.9	1.17	-14.5	2.03	-10.2	4.27	-13.1	3.34	- 9.4	2.49	-12.5	3.98	-15.7	2.82	-12.3
1700 hrs	-13.0	--	-17.9	--	-12.3	--	-12.4	--	- 9.3	--	-14.6	--	-14.3	--	-13.4
Linott	-12.7	1.93	-18.0	1.38	-13.1	4.58	-12.4	2.78	- 9.4	1.56	-14.2	2.20	-11.8	2.20	-13.0
Grant	-13.2	1.25	-17.8	4.34	-11.5	2.71	-12.4	2.97	- 9.3	1.63	-14.9	2.63	-16.9	2.63	-13.7
Daily $\bar{x}$															
Combined	-11.0	--	-14.2	--	-10.7	--	-12.0	--	- 8.4	--	-13.4	--	-14.4	--	-12.0
Linott	-11.2	--	-14.0	--	-10.9	--	-12.0	--	- 7.5	--	-12.8	--	-12.7	--	-11.5
Grant	-10.7	--	-14.2	--	-10.4	--	-11.9	--	- 9.3	--	-14.0	--	-16.0	--	-12.4
Stem Base[4]															
700 hrs	- 8.5	--	-10.8	--	-11.9	--	-12.6	--	- 8.0	--					-10.3
Linott	- 8.2	1.01	-10.9	1.94	-12.3	2.68	-12.9	1.72	- 7.6	3.42					-10.4
Grant	- 8.8	1.03	-10.7	2.65	-11.5	2.52	-12.3	2.25	- 8.4	1.96					-10.2

Table 9. Continued.

ψ_π Sample[1]	Days after planting: 45 $\bar{x}$	45 S	49 $\bar{x}$	49 S	56 $\bar{x}$	56 S	63 $\bar{x}$	63 S	70 $\bar{x}$	70 S	77 $\bar{x}$	77 S	84 $\bar{x}$	84 S	$\bar{x}$ across all days
1200 hrs	- 8.2	--	-11.6	--	-11.2	--	-13.8	--	- 7.6	--					-10.1
Linott	- 7.9	1.03	-11.2	2.82	-12.1	2.92	-12.2	4.59	- 7.5	2.46					- 9.6
Grant	- 8.5	1.19	-12.0	1.85	-10.2	3.63	-15.3	7.03	- 7.6	1.85					-10.5
1700 hrs	- 8.7	--	-13.4	--	-11.1	--	-15.2	--	- 9.3	--					-11.5
Linott	- 8.7	0.80	-11.5	2.53	-11.1	2.10	-16.2	2.63	- 9.7	1.80					-11.4
Grant	- 8.7	2.25	-15.3	1.40	-11.1	3.28	-14.2	3.67	- 8.8	3.73					-11.6
Daily $\bar{x}$															
Combined	- 8.5	--	-12.0	--	-11.4	--	-13.9	--	- 8.3	--					-10.7
Linott	- 8.7	--	-11.2	--	-11.8	--	-13.8	--	- 8.3	--					-10.5
Grant	- 8.3	--	-12.7	--	-10.9	--	-13.9	--	- 8.3	--					-10.8

[1] Units bars

[2] 6 observations per cultivar.

[3] Sampling took place on the first four nodes on the top of the stem.

[4] Sampling took place on the lower third of the stem.

Figure 5. Osmotic potential (ψ_π). Daily cultivar means of ψ_π across all sampling dates and precipitation data from 48 through 85 days after planting. Osmotic potential samples were collected in 1978 at Brookings, S.D. from the lower third of the stem and the first four nodes of the stem.

(Top of stem •••▲••• Linott, ——■—— Grant;
Base of stem —··▲··— Linott, --■--- Grant;
DAP - days after planting)

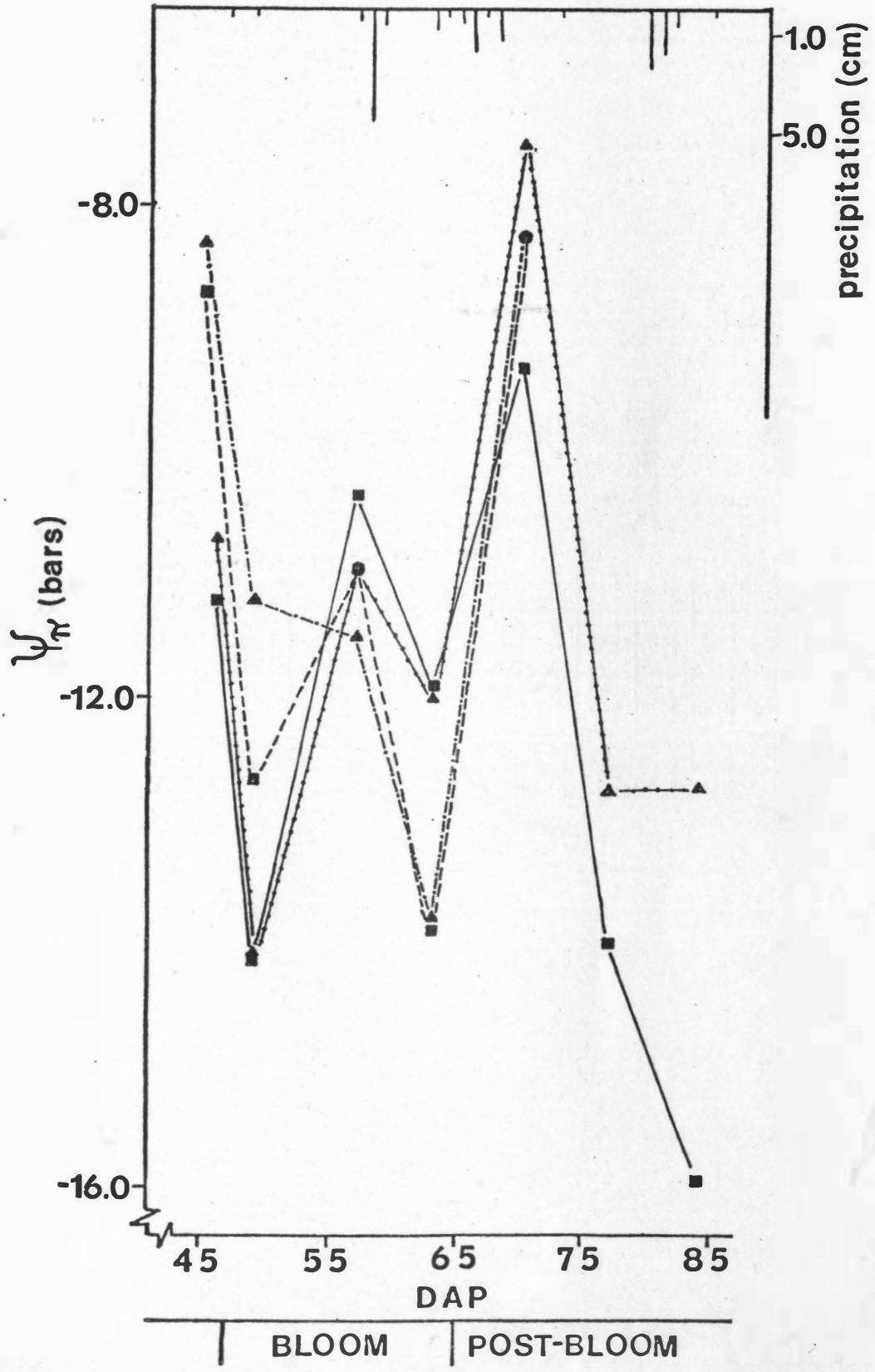

1.0
5.0
precipitation (cm)
-8.0
-12.0
-16.0
ψ_π (bars)
45
55
65
75
85
DAP
BLOOM
POST-BLOOM

Figure 6. Osmotic potential (ψ_π). Overall means of ψ_π of three sampling periods (0700, 1200, 1500). Osmotic potential samples were collected in 1978 at Brookings, S.D. from the lower third of the stem and the first four nodes of the stem. Note the means for the sampling location at the top of the stem includes data from two additional sampling dates.

(Top of stem -•-▲-•- Linott, —■— Grant;
Base of stem -·-▲-·- Linott, – –■– – – Grant)

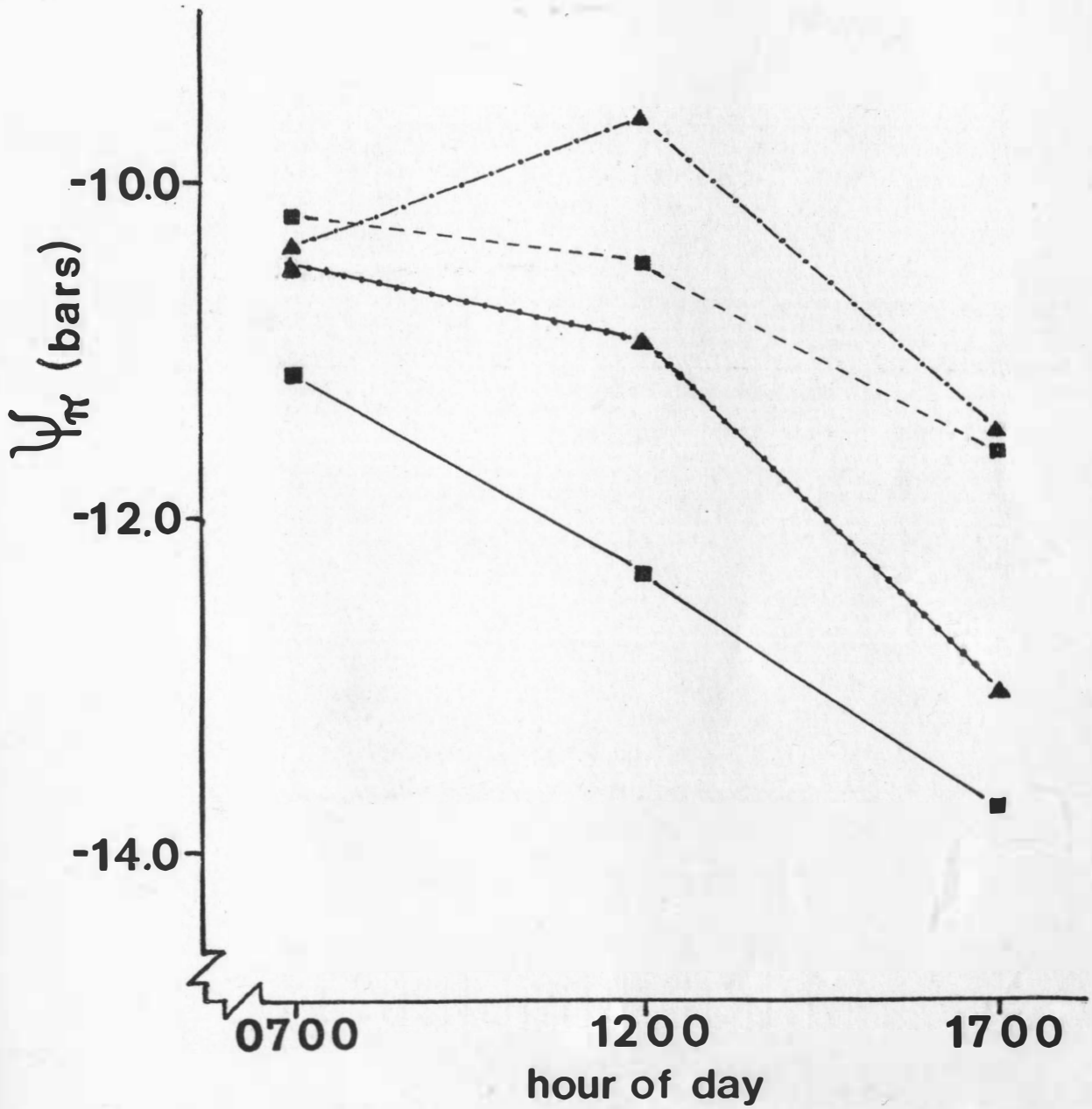
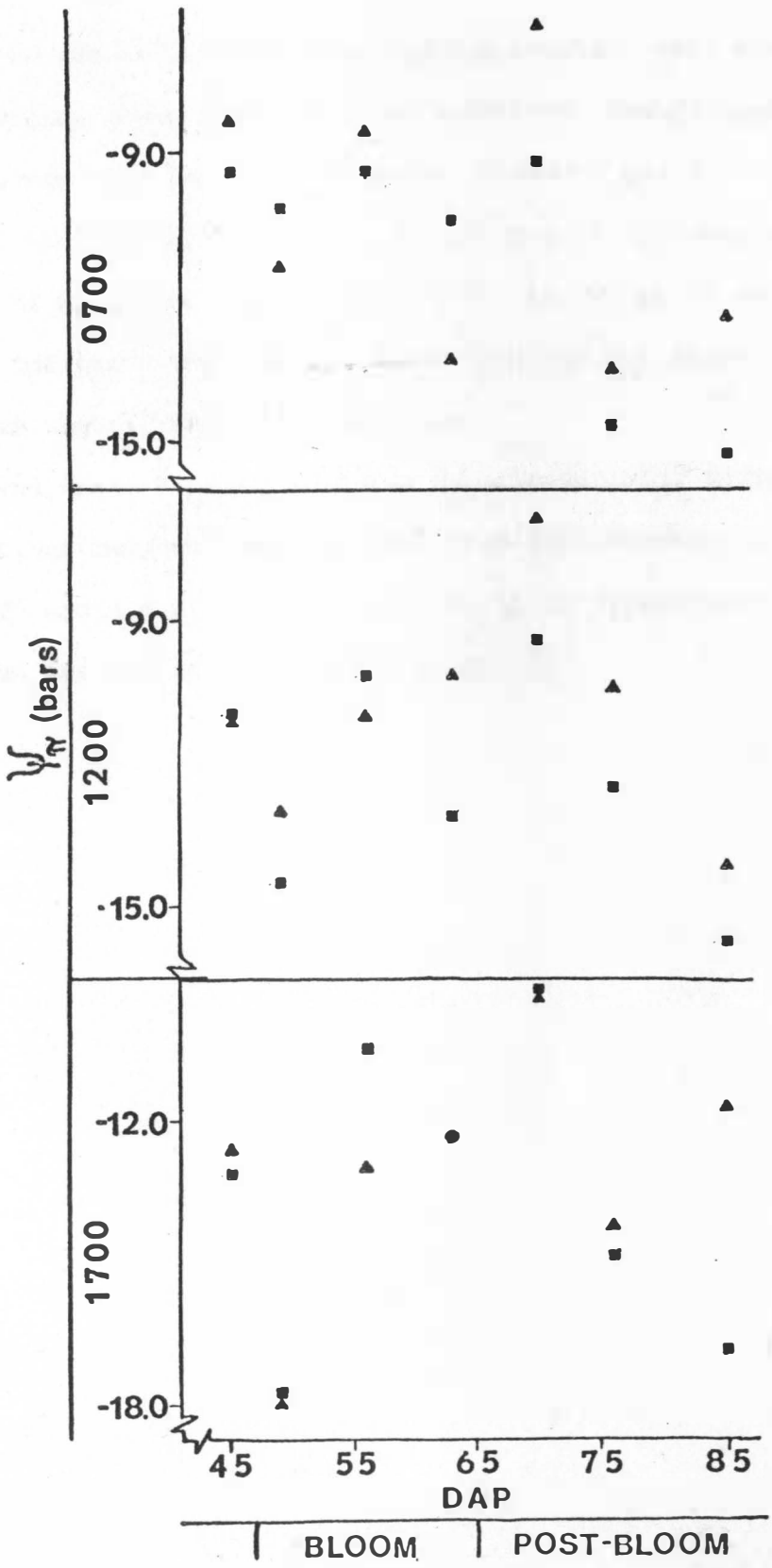

-10.0
-12.0
-14.0
ψ_π (bars)
0700
1200
1700
hour of day

Figure 7. Osmotic potential (ψ_π). Means of cultivars for ψ_π by day and hour (0700, 1200, 1500) for samples from the first four nodes of the stem. Osmotic potential samples were collected in 1978 at Brookings, S.D.

(▲ Linott, ■ Grant, ● Linott and Grant;
DAP - days after planting)


0700
1200
1700
-9.0
-15.0
-9.0
-15.0
-12.0
-18.0
ψ_{π} (bars)
45
55
65
75
85
DAP
BLOOM
POST-BLOOM

DISCUSSION

The 1977 yield results (Appendix V) contradict the yield results reported by Dybing (37) and Lay et al. (71). During seven location years of field trials and four years of greenhouse testing prior to 1977, Linott had always out yielded Grant. It is possible that an interaction of genotypes with environment was the cause of the discrepancy observed in 1977. The cultivars were observed to be in different physiological stages at the time when plants for leaf replica were collected. At this point, Linott had been in the reproductive stage six days longer than Grant. Under these circumstances, it is possible that Linott experienced some environmental stress at a critical point in boll or seed production whereas, when Grant reached this critical stage, conditions had improved. In 1978, when the flowering periods of the cultivars more closely coincided (Appendix VII), Linott out yielded Grant (Appendix V).

Results of harvest index and yield components studies in 1978 (Appendix V) agree with those reported by Lay et al. (71). From the yield components study, it can be concluded that the greater seed yield in 1978 of Linott resulted from its ability to produce more bolls per area and more seeds per boll than Grant. The harvest index study showed that Linott also partitioned a greater percentage of its total dry matter production to seed production.

Daily flower counts (Appendix VI) indicated that the periods of main boll production were similar in 1978 for the two cultivars, which agrees with Lay's conclusion based on 1976 data (71). They also

indicate that some factor or factors limit Grant's potential for flower bud production, because flowering in Grant peaked at a much lower level than it did in Linott.

In both 1977 and 1978, the cultivar with the higher yield also showed a statistically lower stomatal frequency at the apex of leaves collected from the top of the stem (Table 1). This relationship may be a chance occurrence and requires further verification before anything conclusive can be stated. If it is a causal association, it contradicts the concept that a greater stomatal frequency allows for high yield by providing of a greater area for CO_2 intake. A possible reason for the association is that factors that effected stomatal frequency during the ontogeny of leaves in this location also influenced yield potential. However, 1978 stomata counts at the base of leaves from the top of the stem showed Grant to have statistically fewer stomata then Linott. Because this is the opposite of the results at the leaf tip of that location, it is more likely that the association of frequency and yield observed is of little real importance. If this association was due to environmental factors, a more uniform change in stomatal frequency across the leaf would have been expected.

Otherwise, there was an absence of consistent and statistically significant differences between the cultivars for stomatal frequency (Table 1), stomatal apparatus width (Table 2) and length (Table 3), combined guard cell width (Table 4), guard cell length (Table 5), average leaf dimension (Table 6), and stomatal index (Table 7). This indicates that Linott and Grant possess the same potential area for

gas or water diffusion. Therefore, in the case of these two cultivars the difference in the yield potential could not be attributed to a difference between the cultivars in the potential area for gas and water vapor exchange. This conclusion agrees with those of similar studies in winter wheat (65, 72), barley (87), and alfalfa (100).

The sharp drop in stomatal indices on the adaxial surface, which occurred between the bracts and the sepals (Table 7), may in part be an artifact of the replica technique used. Replicas were of poor quality for that location-surface because the natural concave shape of that sepal surface allowed the liquid plastic to accumulate on the surface replica and form a thicker than normal coating. As a result of the greater replica thickness, the outline of the epidermal cell was distorted. Stomata in a field could still be distinquished and length and width measurements made; however, the count of epidermal cells may have been inflated.

The term stomatal index as calculated in this thesis has the same meaning as Salisbury's (84) because in flax the guard cells and subsidiary cells arise from the same meristoid (92).

In comparison to the literature, the values obtained for adaxial stomatal resistance (r_{ad}) in this study (Table 8) do not seem to be unusual for low stress environments. Turner (116) reported that leaf resistance (defined as (abaxial resistance)$^{-1}$ + (adaxial resistance)$^{-1}$) for tobacco ranged from 3 s cm^{-1} at 1200 hrs to 20 s cm^{-1} at 2000 hrs. Whereas in sorghum it ranged from 2 s cm^{-1} at 1300 hrs to 11 s cm^{-1} at 2100 hrs, and in maize it ranged from 3 x cm^{-1} at 1200 to 15 s cm^{-1} at

1900. Sojka (104) reported r_{ad} values around 5 to 20 s cm^{-1} for wheat. Peet (94) reported r_s of 1.58 s cm^{-1} to 3.62 s cm^{-1} during first flowering and 1.00 s cm^{-1} to 2.31 s cm^{-1} during early pod development. It was not possible to determine if this represented leaf or surface resistance. Early in this study on flax cultivars (Figure 3) (49 through 56 DAP (days after planting)), r_{ad} averaged 1.85 s cm^{-1} at 1300 and 2.31 s cm^{-1} at 1900. During the period of relatively low daily r_{ad} values (57 through 71 DAP), r_{ad} averaged 1.13 s cm^{-1} at 1300 hrs and 2.13 s cm^{-1} at 1900 hrs. For the remaining portion of the sampling period (73 through 85 DAP), r_{ad} averaged 2.15 s cm^{-1} at 1300 hrs and 3.19 s cm^{-1} at 1900 hrs.

The parabolic change in r_{ad} observed during the day (Figure 2) agrees with that observed by Turner (117) for leaf resistance (r_l) but differs from the pattern of change in r_{ad} seen by Sojka for wheat (104). In the latter stomatal resistance rose slightly during the day in the nonstress control.

Davis (34) concluded from greenhouse studies of soybean that there was a drop in r_l throughout the season whereas Peet (94) reported that r_s dropped for some soybean varieties around early pod fill and that a rise in r_s occurred for these varieties during late pod fill. The change in r_{ad} during the season in the flax cultivars observed resembles that reported by Peet (94) for r_s with a general drop in r_{ad} occurring around mid-bloom and then a general rise in r_{ad} at mid post-bloom (Figure 3).

Detachment of the leaf for stomatal resistance measurements should

not have invalidated the resistance data presented. Admittedly, detachment would have resulted in an initial jump in adaxial stomatal resistance due to the Iwanoff surge after excision (84). The extent of this deviation should not be large because the initial decline in transpiration is short lived after excision (84) and the Iwanoff surge requires a time period of approximately five minutes to reach its peak (84). In all cases in this study readings were completed in less than a minute. Higher order interactions proved to be significant indicating that this method of sampling would allow differences to be distinguished.

The alternate method of sampling for stomatal resistance values required the use of attached leaves. Because the length of time needed to position leaves in the porometer sensor was variable, the use of attached leaves while sampling in flax could have resulted in a large experimental error.

Replications and most interactions with replications proved statistically important in the analysis of variance for stomatal resistance (Appendix VII). A probable reason for this is that sampling in replication was separated in time. Therefore, a change in r_{ad} with time occurred with the change in replication because r_{ad} is in a state of flux. Another possible reason for the significance of replications is that individual replications may have had different soil moisture levels, which would have affected maturity rates. This would be supported by the staggered maturity within the different replications of the same cultivar.

Overall, osmotic potential (ψ_π) at the stem top of these flax

cultivars averaged -11.6 bars at 1200 hrs and -13.4 bars at 1700 hrs (Table 9). Sojka (104) determined that at 1200 and 1600 hrs flag leaves of wheat under minimal stress showed ψ_π of -15 and -19 bars respectively. Turner (116) found that ψ_π at the top of the canopy for maize was -15 bars at 1200 hrs and -16 bars at 1400 hrs, for sorghum was -10 bars at 1300 hrs and -13 bars at 1700 hrs, and for tobacco was -8 bars at 1200 hrs and -15 bars at 1500 hrs, under low water stress conditions.

At the base of the stem the flax cultivars averaged -10.1 at 1200 hrs and -11.5 bars at 1700 hrs (Table 9). Tucker (116) found that ψ_π at the base for maize was -8 bars at 1200 hrs and -9 bars at 1400 hrs, for sorghum was -10 bars at 1300 hrs. and -13 bars at 1700 hrs and for tobacco was -6 bars at 1200 hrs and -7 bars at 1500 hrs.

Under high soil moisture levels, Turner found a diurnal decline in ψ_π at the top of the canopy for maize (116, 177) and tobacco (116) and a parabolic pattern of change in ψ_π for sorghum (116). For the flax cultivars observed, both patterns of change were present within the season (Table 9). However, cultivars were not necessarily coordinated in their response during a particular day as they generally were for r_{ad}. The overall means of the time periods do show a general tendency for ψ_π to decrease with time (Figure 6).

Turner (116) did not observe ψ_π at the base of the plant to change during the day with the same magnitude as that for the top portion of plants of maize, tobacco, or sorghum. This parallels the results in this study as the overall means of time periods were not significantly

different at the base whereas they were at the stem top (Appendix VIII). Turner (116) also found differences between the ψ_π of the base and at the top of the canopy that were much larger than those observed in flax. In the cultivars observed, ψ_π at the base and the stem were not statistically different.

During the processing of samples unexplained shifts in ψ_π of standards did occur. This equipment problem should not have biased the results of this experiment because samples were randomly processed within a particular combination of sampling date, time period, and sampling position on the plant. However, instrument problems may have reduced the sensitivity of the analysis by increasing the experimental error and causing standard deviations of the ψ_π for cultivars for the individual sampling periods to vary more than standard deviations in the other experiments (Table 9).

Analyzing the ψ_π data as a split-split plot with subsampling would have provided extra sensitivity, but the ratio of interaction terms that were to be respectively pooled deviated from unity to such a degree that pooling to obtain terms would not have provided valid estimates of the true error variances.

The method utilized in this thesis to determine ψ_π has of late come under criticism (23). Values obtained by this procedure are supposed to represent the ψ_π of the cytoplasm. However, some authors insist that the values include components of matric and apoplastic water. These criticisms need to be considered if the technique is to be used in the future because the fraction of apoplastic

water in a plant is genetically variable (23).

The change in daily mean r_{ad} and ψ_π at the top of the stem does seem to correspond. The decline in r_{ad} was accompanied by a rise in ψ_π just after the end of the pre-bloom period (Figure 3 and 5). During the period when r_{ad} was at its lowest level during the season ψ_π was at its highest (less negative). The sharp decrease in ψ_π during the latter half of post-bloom occurred at the same time that r_{ad} increased greatly. In all these situations r_{ad} and ψ_π coordinate in their theoretical description of the physiological condition of the plant in terms of water status.

It is uncertain as to what extent these coordinated responses of ψ_π and r_{ad} are caused by environmental factors affecting the physiological status of the plant or to what extent they reflect physiological changes that took place during ontogeny. No pattern in the data for pan evaporation, temperature range, or daily total solar radiation appeared to correspond to the changes in daily mean r_{ad} and ψ_π across the dates sampled (Appendix II). Rain cannot be discounted as having influenced the values obtained for r_{ad} and ψ_π because the period during which r_{ad} and ψ_π were at optimum levels (57 to 71 DAP) corresponded to a period when rain occurred nearly every day (Figure 3 and 5). However, soil moisture content was not the sole controlling factor in the change in daily mean r_{ad} and ψ_π through the sampling period. Rain that took place during the latter part of the sampling season did not return daily mean r_{ad} or ψ_π to mid-season levels. It, therefore, can be concluded that seasonal changes in r_{ad} and ψ_π, though they are modified by environmental conditions at a particular time, as a whole represent

underlying physiological changes in the plant that influence r_{ad} and ψ_π.

The divergence of cultivars in daily mean r_{ad} and ψ_π started at late boll fill. Grant showed a greater increase in r_{ad} and decrease in ψ_π than Linott, though this was not statistically significant in the latter. Assumably, this has no relationship to yield potential differences between the two cultivars as the yield components that differentiate the two cultivars are determined during bloom. The greater rise in r_{ad} and decrease in ψ_π that was seen for Grant may relate to a more rapid rate of senescence as the result of a greater level of pasmo infection.

Though it appeared that r_{ad} and ψ_π were affected by the same physiological changes in the plant, the osmotic potential experiment was not as sensitive to these changes because it failed to show a Cultivar x Time or Cultivar x Day interaction whereas the stomatal resistance experiment did. Though this means that osmotic potential was not sensitive enough to differentiate cultivars, it does not eliminate the possibility of cultivar differences in leaf water potential or turgor.

Seeds per unit area in flax is determined during flowering because at this time maximum bolls per area and seeds per boll are established. Grant and Linott most often differ in bolls per area and seeds per boll (71). Seed weight could still be modified later in the season, but in the case of these two cultivars this is not a consistently

differentiating trait. Therefore, it is during the bloom period that the difference between cultivars would be most critical, as photosynthesis during this period, rather than stored assimilates, provides the basic material for sink production (38). In flax, greater photosynthetic activity at this time is implied from the observation that increasing ambient CO_2 level early in bloom increases flower bud formation (49). However, no large cultivar differences were observed at bloom for r_{ad} or ψ_π and so cultivar differences in photosynthetic activity during bloom were not indicated by these parameters. The failure to observe such a difference for r_{ad} differs from results with soybeans in which strong varietial difference were observed in r_s at early pod fill which could later be related to yield difference (94).

Throughout the season, though, Grant closed its stomata earlier in the day than Linott. It will require further testing to determine if this association between the rate of daily stomata closer and yield is as consistent as the yield difference.

The earlier closure of stomata in Grant, itself, should not be the cause for the yield potential difference. In C_3 plants, stomatal resistance does not limit the rate of CO_2 intake for photosynthesis unless internal CO_2 concentrations are limiting. Rather, internal resistance to CO_2 movement does, and this is regulated by the rate of photosynthesis (93). However, because stomatal movement occurs in response to internal and external environmental changes (84 and 96), the earlier closure of Grant does imply that it is undergoing metabolic changes that Linott is not or is undergoing at a slower rate.

As changes in stomatal resistance were not associated with changes in pan evaporation, the reason for stomatal change must involve the CO_2 or abscisic acid mechanism of control.

It may still be valid to consider water potential as a possible area of difference between cultivars. It is possible that the cultivars have morphologically different root systems. Work on soybean by Sullivan (106), in which the above ground portion of a particular cultivar was grafted onto phenotypically different root types, showed that yield, photosynthetic rate, and stomatal resistance were affected by the roots; capacity to absorb sufficient water to meet demands. Assuming that the cultivars in this study do have differences in their root systems, then Grant would possess the root system which cannot prevent a lag from developing between transpiration and absorption. Stomatal resistance would rise diurnally because of increased ABA production due to the widening gap between transpiration and absorption as the day progressed. The differences between cultivar in the rate of closure, therefore, may relate to yield as both the production of sinks and the rate of photosynthesis are sensitive to water stress (18).

An alternative explanation of the relationship of the change in r_{ad} and yield relates to the assimilate feedback system that has been supported by some researchers (3, 44, 68, 70, 114). If Grant lacks the ability to move assimilates out of the site of production to sinks at as fast a rate as Linott then the shut down of photosynthesis eventually would result. With the shut down of photosynthesis a rise in intracellular CO_2 levels would cause Grant's stomata to close before Linott's. This

means that Grant is not capable of supporting as many sinks as Linott because of a limited ability to keep assimilate level from becoming inhibitory to photosynthesis.

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APPENDIX

Appendix I. Diffusive resistance calibration. Slope, intercept, coefficient of determination, standard error of estimate, standard deviation of the slope, and standard deviation of the intercept pertaining to the calibration curve used to convert 1978 field readings to values of resistance.

Slope = b_1 = 246.67 seconds/seconds centimeter^{-1}

Intercept = b_0 = 669.35 seconds

r^2 = 0.98

$s_{y \cdot x}$ = 288.58 seconds

s_{b1} = 9.49 seconds/seconds centimeter^{-1}

s_{b0} = 152.40 seconds

Appendix II. Osmotic potential calibration. Slopes, intercepts, coefficients of determination, standard errors of estimate, standard deviation of the slopes, and standard deviation of the intercepts pertaining to the calibration curves used to convert 1978 psychrometer readings to bar equivalence.

Curve I: Slope = b_1 = -0.41 millivolts/bar

Intercept = b_0 = 2.65 millivolts

r^2 = 0.96

$s_{y \cdot x}$ = 0.64 millivolts

s_{b1} = 0.01 millivolts/bar

s_{b0} = 0.16 millivolts

Curve II: b_1 = -0.48 millivolts/bar

b_0 = 4.28 millivolts

r^2 = 0.95

$s_{y \cdot x}$ = 0.02 millivolts

s_{b1} = 0.29 millivolts/bar

s_{b0} = 0.82 millivolts

Curve III: b_1 = -0.49 millivolts/bar

b_0 = 4.28 millivolts

r^2 = 0.97

$s_{y \cdot x}$ = 0.69 millivolts/bar

s_{b1} = 0.02 millivolts/bar

s_{b0} = 0.25 millivolts

Appendix III. 1977 weather data. Total solar radiation, precipitation, pan evaporation, and daily temperature range from April 15 to July 31 for Brookings, South Dakota. Solar radiation data were collected approximately six kilometers from the nursery site. The remaining information was collected less than two kilometers from the nursery site.

Days after planting	Calendar date	Solar radiation ($cal/cm^2/min$)	Precip. (cm)	Pan evaporation (cm)	Temperature (°C) High	Low
	April 15	329.5	0.18	--	19	10
	16	408.4		0.43	24	12
	17	447.6	0.08	0.25	24	12
	18	140.0	0.03	0.66	22	12
	19	206.9		0.30	13	6
	20	60.8	0.25	0.25	14	4
	21	522.7	1.91	0.28	6	1
	22	438.4		0.46	16	-1
	23	423.1		0.53	20	4
	24	448.6		0.89	18	0
	25	541.1		0.36	14	0
	26	514.7		1.22	18	2
	27	458.6		0.61	24	5
	28	518.5	0.05	1.40	30	4
	29	496.4		0.64	19	6
1	30	555.1		0.58	22	3
2	May 1	554.8		1.19	24	11
3	2	454.2		0.53	17	2
4	3	465.4	0.03	0.84	21	9
5	4	185.4	0.03	0.46	18	12
6	5	284.3	0.08	0.58	23	8
7	6	551.0		0.56	23	--
8	7	536.2		1.42	24	7
9	8	532.4		0.74	23	--
10	9	470.8		0.56	26	6
11	10	555.2		1.17	25	8
12	11	530.3		0.21	24	8
13	12	500.5		0.91	26	11
14	13	497.7		1.24	28	12
15	14	449.0		1.12	30	13
16	15	508.6		0.94	30	13
17	16	471.7		1.19	27	8
18	17	537.6	0.10	1.02	31	12
19	18	451.0		0.99	29	15
20	19	340.8		0.84	31	17
21	20	28.4	1.37	0.91	27	13

Appendix III. Continued.

Days after planting	Calendar date		Solar radiation (cal/cm^2/min)	Precip. (cm)	Pan evaporation (cm)	Temperature (°C) High	Low
22	May	21	139.1		0.61	23	12
23		22	348.4	1.91	0.20	21	13
24		23	538.0	0.38	0.30	18	10
25		24	511.2		0.97	26	10
26		25	538.7		0.91	29	17
27		26	298.2		1.04	28	18
28		27	266.3	0.58	0.43	27	16
29		28	484.4	0.79	0.64	23	13
30		29	567.9		0.41	26	13
31		30	181.2		0.58	27	12
32		31	587.0	0.23	0.58	22	11
33	June	1	579.2		1.09	24	9
34		2	601.5		0.97	25	6
35		3	535.4		0.33	26	10
36		4	503.4		1.30	31	17
37		5	537.6		1.17	33	16
38		6	609.3		1.42	34	10
39		7	565.5		0.99	23	9
40		8	594.8	0.15	1.42	31	11
41		9	208.4		1.12	27	9
42		10	429.4	0.03	0.43	22	11
43		11	410.5	0.05	1.17	32	14
44		12	360.5		0.64	27	10
45		13	498.2		0.91	24	13
46		14	482.8		0.48	26	10
47		15	325.0	2.31	1.68	29	11
48		16	498.1	12.14	--	26	15
49		17	406.0	0.86	--	27	16
50		18	568.1		--	25	12
51		19	560.4		0.79	24	11
52		20	562.4		0.56	27	9
53		21	120.1		0.94	21	10
54		22	225.5	0.48	0.20	19	13
55		23	565.6	0.53	0.30	21	12
56		24	556.6		0.69	30	13
57		25	560.4		1.02	28	11
58		26	474.4		1.19	29	19
59		27	452.5		0.64	32	18
60		28	520.3	0.03	0.89	29	14
61		29	430.3		0.89	24	8
62		30	548.3	1.98	1.02	28	10

Appendix III. Continued.

Days after planting	Calendar date	Solar radiation (cal/cm^2/min)	Precip. (cm)	Pan evaporation (cm)	Temperature (°C) High	Low
63	July 1	590.2	1.98	0.94	21	11
64	2	507.0		0.84	26	12
65	3	570.3		0.76	28	19
66	4	542.5		0.84	33	22
67	5	533.6		1.24	36	23
68	6	214.7	0.28	1.07	35	22
69	7	485.5		0.13	27	16
70	8	486.6		0.76	31	13
71	9	159.9		0.94	24	10
72	10	416.8		0.28	19	14
73	11	533.0	0.64	0.61	27	16
74	12	584.0		1.04	28	13
75	13	498.6		1.07	26	14
76	14	367.4		1.02	35	18
77	15	519.9		0.69	27	13
78	16	408.6		0.84	28	14
79	17	420.6	0.18	0.66	33	21
80	18	466.2		0.71	32	21
81	19	505.7		1.27	37	22
82	20	160.6		1.12	37	21
83	21	562.1	1.07	0.53	25	13
84	22	536.4		0.86	27	11
85	23	438.1		0.97	28	12
86	24	424.6	1.96	0.84	32	18
87	25	526.1		0.86	31	13
88	26	474.7		0.71	24	12
89	27	452.0		0.61	23	12
90	28	496.5	0.25	0.79	31	14
91	29	468.8		0.56	28	13
92	30	480.2	0.05	0.79	31	14
93	31	479.3		1.19	29	14

Appendix IV. 1978 weather data. Total solarradiation, precipitation, pan evaporation, and daily temperature range from April 15 to July 31 for Brookings, South Dakota. Solar radiation data were collected approximately six kilometers from the nursery site. The remaining information was collected less than a two kilometers from the nursery site.

Days after planting	Calendar date	Solar radiation (cal/cm^2/min)	Precip. (cm)	Pan evaporation (cm)	Temperature (°C) High	Low
	April 15	247.4		0.69	11	0
	16	288.6		0.28	11	1
	17	32.0		0.13	14	2
	18	65.1	2.36	0.53	4	0
	19	103.2	0.64	--	2	-1
	20	363.5		--	1	-4
	21	535.8		--	4	-3
	22	110.0		1.04	13	2
	23	96.1	0.66	0.15	9	4
	24	46.1	1.17	--	7	3
	25	458.5	0.05	--	6	3
	26	453.3		0.53	16	2
	27	467.9		0.10	17	2
	28	174.2		0.91	19	7
	29	186.9		0.20	14	9
	30	439.0		0.30	16	4
	May 1	573.5		.13	16	-1
	2	549.4		--	12	-3
1	3	544.5		1.27	16	-1
2	4	322.3		0.30	18	2
3	5	346.8		0.48	16	-1
4	6	457.0		0.61	16	-1
5	7	118.6	0.30	0.36	16	--
6	8	147.2	3.00	--	8	4
7	9	576.5	0.46	--	8	5
8	10	508.5		2.11	17	6
9	11	595.1		0.89	27	8
10	12	75.6		0.91	22	10
11	13	548.4	.53	1.78	15	3
12	14	556.8		0.64	17	2
13	15	588.1		0.28	20	3
14	16	566.1		0.76	22	7
15	17	566.4		0.36	21	6
16	18	423.4		0.89	21	6
17	19	538.6	.51	0.69	25	9
18	20	541.5		1.02	23	7
19	21	554.6		0.53	19	2

Appendix IV. Continued.

Days after planting	Calendar Date		Solar radiation (cal/cm^2/min)	Precip. (cm)	Pan evaporation (cm)	Temperature (^{o}C) High	Low
20	May	22	503.9		0.79	24	8
21		23	298.0		0.71	22	11
22		24	326.0		0.28	23	13
23		25	526.7	1.32	0.91	27	14
24		26	293.0		0.81	29	18
25		27	312.0	3.30	--	27	16
26		28	236.0	0.08	1.57	23	16
27		29	163.6	0.76	0.38	24	14
28		30	466.6	0.10	0.33	19	10
29		31	238.6	0.23	0.53	23	8
30	June	1	214.6	0.20	0.20	14	7
31		2	368.4	0.13	0.18	12	5
32		3	353.9		0.71	20	7
33		4	378.8		0.64	21	11
34		5	602.2		0.74	22	7
35		6	610.1		0.79	25	9
36		7	434.1		0.71	--	10
37		8	581.6		.91	17	2
38		9	548.4		--	23	8
39		10	560.6		1.88	28	13
40		11	554.4	0.38	0.66	32	13
41		12	566.3	0.08	0.58	24	9
42		13	450.2		0.69	22	9
43		14	413.9	0.25	0.89	27	12
44		15	408.5	0.08	0.69	26	17
45		16	336.7		0.71	29	16
46		17	428.4		0.64	28	14
47		18	436.6	0.38	0.58	23	8
48		19	328.7		0.99	25	11
49		20	526.7	0.23	1.55	27	7
50		21	507.2		0.76	19	4
51		22	255.8		0.61	24	10
52		23	446.4		0.46	23	15
53		24	227.8		0.81	29	17
54		25	468.6	0.05	0.28	28	19
55		26	581.4		0.84	30	14
56		27	596.1		0.81	27	12
57		28	426.4	0.43	1.30	28	14
58		29	514.5	4.57	1.17	31	18
59		30	547.2	0.56	1.43	32	19
60	July	1	272.9		0.86	33	19

Appendix IV. Continued.

Days after planting	Calendar Date	Solar radiation (cal/cm^2/min)	Precip. (cm)	Pan evaporation (cm)	Temperature (°C) High	Low
61	July 2	563.1		0.41	27	18
62	3	493.2		0.79	29	17
63	4	463.9	0.89	0.89	31	18
64	5	118.7	0.25	1.55	31	21
65	6	379.5	0.53	0.25	26	16
66	7	435.6	1.70	1.27	27	16
67	8	139.9	0.25	0.71	24	12
68	9	505.5	1.24	0.33	21	13
69	10	557.0		0.71	21	7
70	11	563.4		0.38	27	11
71	12	476.6		1.09	24	14
72	13	588.3		0.76	31	12
73	14	562.7	0.25	0.86	26	14
74	15	565.3		0.81	29	14
75	16	549.5		0.86	33	15
76	17	500.0		0.84	32	19
77	18	456.8	0.10	0.71	33	18
78	19	517.9		--	28	14
79	20	328.3		0.64	27	14
80	21	326.8	2.44	--	22	15
81	22	345.4	1.78	--	20	14
82	23	378.4	0.58	--	21	7
83	24	536.1		1.17	26	10
84	25	348.2		0.51	27	16
85	26	564.1	0.20	0.66	33	16
86	27	579.0		1.35	29	12
87	28	486.4		0.74	24	12
88	29	147.0		0.76	32	16
89	30	524.4		0.23	18	14
90	31	412.8		0.66	25	13

Appendix V. Seed yield of Linott and Grant for the plots grown in 1977 and 1978. Harvest index and yield components data taken in 1978 for these same cultivars. Data collected at Brookings, S.D.

	Year		
	1971-76[1/]	1977	1978
Seed Yield (kg/ha)			
Linott	883	1470	1960
Grant	628	1678	1580
Harvest Index (%)			
Linott			29.61
Grant			25.59
Yield Components			
Bolls/Area (0.0271 m^2)			
Linott			163.7
Grant			127.3
Seeds/Boll			
Linott			7.8
Grant			7.46
mg/thousand seeds			
Linott			5556
Grant			5374

[1/] Average of yield under field conditions reported by Dybing (37) and Lay (71).

Appendix VI. Replication totals for daily flower counts made in 7.5 cm subplots of Linott and Grant during 1978 at Brookings, S.D.

Days after planting	Total number of flowers per 267 cm^2	
	Linott	Grant
45	0	0
46	--	--
47	0	1
48	4	2
49	6	11
50	21	17
51	13	12
52	29	27
53	29	27
54	56	54
55	71	41
56	114	50
57	--	--
58	48	8
59	38	9
60	17	15
61	6	13
62	4	3
63	4	8
64	1	1
65	2	5
TOTAL	463	304

Appendix VII. Adaxial stomatal resistance. Degrees of freedom, mean squares, and F-test results for reduced adaxial stomatal resistance data. Analysis was carried out on a balanced set of data created by dropping all 0700 readings and time period readings for days in which all four remaining time periods were not represented or data set was unbalanced.

Source	d.f.	m.s.	F-test[1/]
Replication (R)	2	5.8266	**
Day (D)	11	61.7766	**
Time (T)	3	188.0788	**
Cultivar (C)	1	2.7345	N.S.
RD	22	1.1132	N.S.
RT	6	1.2101	N.S.
RC	2	11.7908	**
DT	33	6.9933	**
DC	11	2.7422	**
TC	3	16.1059	**
DTC	33	2.0452	**
RDT	66	2.0887	**
RDC	22	3.7840	**
RTC	6	0.5174	N.S.
RDTC	66	1.6754	**
Subsampling	1152	0.3697	**

[1/] ** - significant at 1% level; N.S. - not significant.

Appendix VIII. Osmotic potential. Degrees of freedom, mean squares, and F-test results for osmotic potential data from leaves sampled from the base and the top of the stem. The design was balanced and only replications were considered fixed.

Source	Base of stem			Top of stem		
	d.f.	m.s.	F-test[1/]	d.f.	m.s.	F-test[1/]
Replication (R)	2	5.1120	N.S.	2	6.1718	N.S.
Date (D)	4	196.4053	**	6	167.0075	**
Time (T)	2	21.8190	N.S.	2	43.0582	**
Cultivar (C)	1	0.8980	N.S.	1	49.2480	N.S.
DT	8	7.6696	N.S.	12	24.3363	**
DC	4	7.0899	N.S.	6	15.8246	N.S.
TC	2	2.4222	N.S.	2	3.7011	N.S.
DTC	8	8.8539	N.S.	12	8.6080	N.S.
RD	8	12.6389	N.S.	12	10.7894	*
RT	4	10.3745	N.S.	4	1.7225	N.S.
RC	2	3.3583	N.S.	2	7.9923	N.S.
RDT	16	8.3233	N.S.	24	7.8487	N.S.
RDC	8	5.9672	N.S.	12	10.9209	*
RTC	4	4.7831	N.S.	4	3.3995	N.S.
RDTC	16	7.7122	N.S.	24	10.5669	*
Subsampling	90	7.2100	--	126	5.6213	--

[1/] * - significant at 5% level; ** - significant at 1% level; N.S. - not significant.