SELECTION PROCEDURES FOR THE GENOTYPIC IMPROVEMENT
OF MAIZE IN HOT AND DRY CLIMATES

by

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B.S., Kansas State University, 1985

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A MASTER'S THESIS

Submitted in partial fulfillment of the
requirements for the degree

MASTERS OF SCIENCE

Department of Agronomy

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1988

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ACKNOWLEDGMENTS

I wish to express my appreciation to my major professor, Dr. C.E. Wassom, for his guidance and assistance in the preparation of this thesis. I am grateful to him for the suggestions and expertise he shared in the collection of field data. He has given me insights towards various aspects of plant breeding. His dedication to science was a helpful influence.

My thanks to Dr. Raja Nassar for his assistance in analysis and interpretation of much of the data. I would like to thank Drs. J.A. Guikema, G.M. Paulsen and M.B. Kirkham for their guidance and assistance concerning plant physiology. Dr. Kirkham provided helpful information concerning plant water relations and generously allowed the use of an infrared thermometer for this research and Dr. Paulsen generously allowed the use of a fluorometer. Dr. Guikema shared his expertise in photosynthesis and gave me an inspiring education in plant physiology.

I am thankful to Clemence Mushi, Scott Harding, and John Moffatt, fellow graduate students, for their assistance and friendship throughout my graduate study. I would like to thank Larry Klocke, Agriculture Technician, who aided data collection and provided constructive suggestions.

My special thanks goes to my wife, Julie, for her understanding, dedication and encouragement.

INTRODUCTION

The performance of hybrid maize is an expression of genotypic and environmental effects. Characterizations of genotypic effects in maize varietal trials requires careful measurement of plant responses. Plant physiological responses may be a useful means to identify productive maize cultivars by revealing important aspects of plant metabolism for which there is genetic variation. To be effectively utilized in cultivar development, physiological measurements must be accurate, rapidly obtained and sensitive to detection of genetic differences which are pertinent to the objectives of breeding programs.

An important goal of maize breeding research is the development of cultivars able to withstand adverse environmental conditions of hot and dry climates. Drought, high temperatures and intense solar radiation associated with these climates limit maize yields in several areas of the world. These environmental stress factors often occur simultaneously and act upon interrelated processes of plant metabolism, growth and development to produce complex and synergistic effects of crop injury.

The current study was undertaken to research the possible use of chlorophyll fluorescence and canopy leaf temperature differentials as a means to quantify environmental stress tolerance among experimental lines of

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maize. The magnitudes of the fluorescence induction and temperature differential data were expected to quantify plant capabilities of photosynthesis and transpiration, respectively. Experiments were conducted under conditions of environmental stress in the field. Experimental objectives were to estimate heritability for the physiological traits and measure their correlations with each other and with yield. The ultimate experimental purposes were to determine the feasibility of using these physiological measurements as selection criteria, improvement of the identification and utilization of genetic variation and to gain insights into mechanisms of plant environmental stress tolerance.

LITERATURE REVIEW

Yield Improvement in Maize

Duvick (22), Castelberry et al. (15) and Russell (56) evaluated elite maize cultivars released from 1930 to the present in order to assess genetic improvements achieved over several years in maize breeding. These studies found that about 65% of the improvement in maize yields could be attributed to genetic gain.

Castelberry et al. (15) considered that crop improvement from maize breeding efforts have resulted in the development of hybrids capable of utilizing favorable environments created by improved cultural practices. His assessments of genetic improvements in maize were conducted at several locations with poor yield potentials to separate progress due to plant breeding from its interaction with advances in farming systems technology. He manipulated soil fertility and water regimes at several experimental sites to separate genetic gain under these more specific environmental constraints. Castelberry et al. found that breeders have made significant genetic improvement in the productivity of maize, independent of improvements which have resulted from farming systems research. He showed recently released hybrids could adjust to conditions of low soil moisture and fertility levels, remaining more

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productive than the more recent cultivars.

Genotypic selection has increased plant tolerance to unfavorable environments by utilizing yield as the major selection criteria. Boyer (12) concluded that physiological information and experimental techniques suitable for use in breeding programs were generally lacking.

Drought Stress in Maize

Available water has a substantial role in the growth, development and yield of maize. Robins and Domingo (55), and Claasen and Shaw (16), have shown that drought reduces maize yields. Claasen and Shaw attributed reduction in grain yield to drought stress at flowering due to lack of silk and ear shoot development. Beadle et al. (3) reported that transpiration and photosynthesis were less drought sensitive in sorghum than in maize. Aparicio and Boyer (2), reported that water stressed maize had reduced transpiration and substantially increased rates of leaf senescence.

Canopy Leaf Temperatures

Crop scientists utilize infrared (IR) thermometry to measure leaf temperatures of environmentally stressed crops. Thermal radiation from the sun is absorbed by crop canopies and is normally dissipated by evaporation of water through the stomata under conditions of adequate soil

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moisture (28,36,40,64,70). Crops not experiencing water stress have open stomata and transpiration normally keeps the leaf surfaces below ambient air temperatures. As plant water deficits increase, the stomata close and leaf surfaces then emit an increased proportion of absorbed solar energy back into the atmosphere as thermal radiation.

The infrared (IR) region of the thermal spectrum is utilized in remote sensing of crop canopy temperatures (28,36,40,64,70). Leaves are near perfect absorbers of this thermal energy frequency. Crop canopies such as maize absorb about 95-99% of the solar IR flux which interacts with leaves. This energy is either utilized to drive transpiration or emitted back into the atmosphere when water is unavailable for transpiration and/or the stomata are closed (28,64). The infrared (IR) flux from crop canopies depends almost entirely on plant processes of evaporative cooling provided by transpiration. Variations of IR fluxes from crop canopies due to differential leaf absorptivity, reflectivity or transmissibility are negligible because leaves are near perfect absorbers of solar IR radiation. Temperature estimates of crop canopy surfaces which are obtained through applications of thermal radiation science are highly accurate.

The infrared sensor of IR thermometers is located inside of the instrument, protected by a spectral filter. Infrared emittance which is in the field of view of the

thermometer reach the sensor. Thermometer field of view is controlled by the distance and angle at which the thermometer is held in relationship to the crop canopy measured (49). Field of view also depends on the lens size of the instrument. The lens is a concave mirror which initially receives thermal radiance from canopy surfaces and reflects it to the sensor. Temperature responses are rapidly obtained with IR thermometers and these instruments sample relatively large areas of canopy leaf surfaces in comparison to such devices as leaf thermocouples.

A thermocouple mounted on IR thermometers measures ambient air temperatures and automatically calculates temperature differentials. Temperature differential, (T_D), is the difference between the canopy temperature and air temperature. T_D measurements account for environmental variation in plant responses which are due to changes in ambient air temperatures. T_D measurements are important plant responses used to characterize drought stress in plant water relations research.

Field Measurements of Environmental Stress

Canopy leaf temperatures, or temperature differential, are extremely dynamic plant responses influenced by environmental factors such as wind, solar radiation, and relative humidity (10,48,64,69). Genotypic effects for leaf temperature responses may be difficult to detect because

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these environmental factors have profound effects on trans-
piration rates. O'Tool, et al.(48), studied the effects of
wind speed on crop transpiration and IR canopy temperature
measurements. They found that wind speed influenced trans-
piration rates, and thus, canopy leaf temperatures. Blad
and Rosenberg (10), compared leaf temperature responses
measured with thermocouples with those measured by an IR
thermometer in alfalfa and maize. They reported $1^{\circ}C$ - $2^{\circ}C$
discrepancies between measurement techniques. They conclud-
ed that thermal emissions from soil surfaces affected can-
opy temperature estimates. Hot, dry soils tended to over-
estimate, where as, cool, wet soils tended to underestimate
canopy temperature estimates measured by IR thermometry.
Their experiments were conducted when crop canopies maxim-
ally covered soil surfaces.

IR Thermometry and Crop Drought Modeling

Clawson and Blad (17) assessed the use of IR
thermometry to determine irrigation schedules of maize.
The design of their experiments used sampling techniques
that farmers would have at their disposal for use with IR
thermometers. Experimentally scheduled treatments were
watered when the maximum range among a series of IR
temperature measurements exceeded $.7^{\circ}$ C within the plot.
Experimentally scheduled plots required 150 mm less water
during the season and grain yields were 95% of those

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obtained on plots which were watered by conventional techniques. Maize plots irrigated on canopy temperature schedules did not require irrigation when atmospheric vapor pressure deficits and crop water demands were low.

Relationships between canopy leaf temperatures and hybrid maize yields have been studied. Heerman and Duke (34) reported that elevated canopy temperatures reflected significant reductions in yield when differences of 1.5° C were measured between irrigated and water stressed treatments. Gardener and Blad (27) measured canopy temperatures of hybrid maize under varying conditions of water stress. Average canopy temperature responses calculated from measurements taken from pollen shed through the grain filling phases of development predicted grain yields within 10%.

Sharratt et al. (64) measured canopy leaf temperatures, leaf water potential and transpiration rates in irrigated versus non-irrigated alfalfa during a diurnal cycle. Plant responses showed maximum differences between stressed and non-stressed treatments during the afternoon heat. Canopy temperature measurements between stressed and irrigated treatments showed the least sensitivity but were the easiest and most rapid measurements to obtain.

Hashimoto et al. (31) photographed infrared temperature images over leaf surfaces of sunflower. Plants were hydroponically grown with either intact or pruned root systems. Dark pretreated plants at equal leaf water potent-

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ials and steady-state transpiration were transferred into the light. Infrared images were taken during stomatal opening and activation of transpiration. Hashimoto et al. showed that reduced root size limited evaporative cooling provided by transpiration. Root pruned plants averaged approximately three degrees warmer and had 50 % lower CO_2 fixation rates under steady-state conditions in the light. Patterns of IR images taken over the leaf surfaces of root pruned plants were distinctly altered and indicative of water stress and reduced transpiration.

IR Thermometry and Genotypic Selections of Maize

Assessments of crop water stress using IR thermometry is a difficult task for plant breeders because detection of subtle differences among genotypes may be difficult to reproduce under field conditions. Experiments which have shown genotypic differences in maize have emphasized the need for numerous and repeated measurements throughout the season to account for temperature variations caused by environmental factors (69). Mtui et al. (46) Kirkham et al. (40) and Spanogle (69) studied several drought tolerant and drought sensitive genotypes of maize.

Mtui et al. (46) measured the canopy temperatures of hybrids classified as drought tolerant and drought susceptible. Measurements from these cultivars were compared to those of the Kansas White Synthetic (KWS) and to their

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inbred parental lines. The drought tolerant hybrid had much cooler leaf temperatures and higher yields than the KWS. Yield and canopy temperature differences between the drought susceptible hybrid and KWS were less distinct. Hybrid combinations had cooler canopy temperatures than their parental sources. Inbred lines which produced the cooler drought tolerant hybrid had warmer leaf temperatures than parental lines which produced the drought susceptible hybrid.

Kirkham et al. (40) studied canopy temperatures of another set of inbred lines and their hybrid combinations and reported similar results. Inbred lines classified as drought tolerant had warmer leaf temperatures than the drought sensitive parental lines. Drought tolerant parental lines produced relatively cooler and higher yielding hybrids than those produced from inbred lines classified as drought susceptible. The researchers theorized that inbred lines with warmer canopy temperatures required lower transpiration rates and were drought tolerant types because they used available water efficiently.

More recent work by Spanogle (69) using hundreds of experimental genotypes of maize over a three year study found that lines with cooler IR canopy temperatures were taller, earlier to flower and yielded higher than genotypes with warmer leaf temperatures. Spanogle found that canopy temperature responses in maize were heritable and that

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genetic gains for drought tolerance could be achieved by plant selection using IR thermometry. Spanogle used experimental lines selected from within the KWS population, with relatively low levels of inbreeding throughout his study.

The Kinetics of Chlorophyll Fluorescence

Chlorophyll fluorescence induction is a fluorometric technique of plant physiology which uses chlorophyll from dark adapted leaves as a sensitive physiological probe of photosynthesis (43,50,65,63). Chlorophyll pigments from dark adapted chloroplasts of intact leaves emit transient patterns of fluorescence which vary in intensity over the time of photosynthetic induction by light. The status of photosynthetic reactions are measured from emissions of chlorophyll fluorescence during photosynthetic activation. Dark adapted leaves typically emit "Kautsky Effect" induction curves of fluorescence during photosynthetic activation. Fluorescence variables obtained from the curve are F_o, F_i, F_d, F_p, F_s, F_m, and F_t. Each variable marks transient physiological changes which occur as dark adapted plant chloroplasts pass through their light activation phases.

Energy absorption causes conversions of ground state chlorophylls to more unstable excited state chlorophylls (43,50,60). Absorbed energy from excited state chlorophylls can follow several different paths of liberation. Accessory pigments in the light harvesting chlorophyll

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protein (LHCP) primarily transfers absorbed energy to other accessory pigments and bulk chlorophylls whose energy absorption spectra overlaps those of the excited pigments. Exiton transfers among LHCP pigments function in gathering energy for electron transport reactions associated with photosynthesis. The LHCP is primarily associated with PSII antennae pigments during the early phases of photosynthetic induction (1,35,43,50). Energy received by PSII antennae chlorophyll migrates to Chl_a678 pigments which function to transfer exitons to PSII reaction centers (64). Chl_a678 are highly fluorescent pigments, exhibiting their maximum emission spectra at 685nm (43,44,50). Other photosynthetic pigments are fluorescent in solution; however, in vivo, they primarily either transfer their absorbed energy to other chlorophylls, emit energy as thermal radiation, or function to couple absorbed energy to photochemical reactions associated with electron transport. Chlorophylls other than Chl_a678 are weakly fluorescent and contribute to the fluorescence emission from chloroplasts at room temperatures. Weak fluorescence emanates from PSI at 735nm and is resolved from PSII reaction centers at 693nm.

Fluorescence represents a pathway for energy liberation from excited state chlorophyll whereby energy is emitted from the photosynthetic system in the form of light. Alternatively, absorbed energy which drives photosynthetic electron transport is chemically conserved. Examples of

reactions coupled to photosynthetic electron transport are steps in the Calvin Cycle which require ATP, NADPH or enzyme activation, NO_2 reduction catalyzed by nitrite reductase, and O_2 reduction defined as the Mehler reaction.

F_O Fluorescence

F_O fluorescence emanates from excited state antennae chlorophyll, measured while constituents of photosynthetic electron transport systems of dark adapted chloroplasts are oxidized (43,50,63,65). The LHCP is capable of exiton transfer to either PSII or PSI antennae pigments due to its mobility in the thylakoid membrane. The intensity of F_O fluorescence depends on the degree of association between the LHCP and PSII antennae. Strong association distributes exitons to the highly fluorescent PSII antennae at the expense of energy transferred to the less fluorescent PSI. Exiton energy predominantly transfers from the LHCP to PSII antennae chlorophyll during initial photosynthetic activation in response to the low energy state of dark adapted chloroplasts (43,50). Phosphorylation of the LHCP and/or stromal Mg^{+2} ions can decrease F_O fluorescence by increasing the association of the LHCP with PSI (1,35,43,50). These chemical treatments simulate specific changes which occur in chloroplasts as photosynthesis becomes light activated.

Additionally, the intensity of F_O fluorescence depends

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on the status of the structural organization between anten-
nae systems and reaction centers of PSII which affect exit-
on transfer efficiency (43,61,62). Proper organization of
the photosynthetic apparatus promotes exiton transfer bet-
ween thylakoid components. In healthy chloroplasts, energy
is efficiently transferred within pigment systems and
hence, F_O fluorescence is relatively low. Thylakoid memb-
rane damage which effects the association between PSII
reaction centers and antennae pigments decreases the effic-
iency of exiton transfer. This increases F_O fluorescence.
F_O fluorescence emitted as a result of ineffective exiton
transfer constantly occurs, but are distinguished at F_O,
before photochemistry affects the fluorescence induction
emissions.

Fluorescence Responses from Photochemistry

Exitons transferred to PSII reaction centers, derived
from the associated LHCP, are absorbed by P680 chlorophyll
and utilized in an endergonic redox reaction defined as
charge separation (39,43,50,60). Pheophytins, (Phe), which
are intermediary electron acceptors associated within PSII
reaction centers, become reduced by excited state P680
chlorophyll when the reaction center, (P680)(Phe), converts
to the charge separated, $(P680^+)(Phe^-)$, state. Energy
absorbed by the reaction center may either be emitted as
fluorescence (693nm) or heat, returned to the antennae

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chlorophylls and emitted as fluorescence or heat, trans-
ferred to another reaction center, or utilized in electron
transport whereby electrons from (Phe⁻) are transferred to
quinnone-type electron transport acceptors designated as Q.
Photosynthetic reduction of Q acceptors are the favored path
of energy utilization when acceptors are in an oxidized
state at the time of charge separation. Under oxidized
circumstances, electron donation to Q occurs in less than
400 picoseconds (39). However, Q acceptors can not accept
electrons when in the reduced (Q⁻) state.

The reduction state of Q is a primary factor which
influences the intensity of fluorescence emitted after
photochemistry has activated (39,43,63,65). Experiments
presented by Kimov and Krasnovskii (39) show that molecular
changes which characterize (P680⁺)(Phe⁻) photochemical
formation continue to occur when further electron transport
reactions were blocked by maintaining Q acceptors completely
reduced. Kimov and Krasnovskii reported that when electron
transport from (Phe⁻) to Q was blocked, PSII reaction
centers could remain poised in their charge separated,
(P680⁺)(Phe⁻), state for approximately 4 nanoseconds, after
which, electrons from (Phe⁻) recombine with P680⁺ in a back
reaction of charge separation. Reaction centers then return
to the more stable (P680)(Phe) conformation. Energy liber-
ated in response to the back reaction of charge separation
are primarily absorbed by antennae pigments and emitted as

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fluorescence. Fluorescence emission becomes an increasingly favored path for energy liberation as PSII reaction centers unsuccessfully transport high energy electrons to Q acceptors (43,50). Fluorescence generally increases from F_o to F_p as primary photochemistry at PSII causes excessive reduction of the Q acceptors. F_i and F_d responses occur within this fluorescence rise. F_i to F_d fluorescence marks a shoulder or delay within the fluorescence rise. This occurs response to a brief period when the rate of Q oxidation by subsequent electron transport carriers increases relative to the rate of Q reduction by PSII reaction centers. Processes such as these, which decrease fluorescence, are known as quenching. Induction of other physiological processes by light substantially quenches fluorescence after F_p has been reached.

The occurrence of F_p fluorescence in response to excessive reduction of Q acceptors is transient and occurs primarily because subsequent electron transport carriers after Q and photosynthetic CO_2 fixation are activated more slowly by light. In addition, the LHCP is almost exclusively associated with PSII and ionic gradients across the thylakoid membrane have not yet established. The F_p fluorescence rise coincides with a transient decrease in photosynthetic O_2 evolution. As Q acceptors become excessively reduced, electrons are no longer capable of leaving PSII reaction centers, which causes the photolysis of water to

decline.

F_p fluorescence may reach emissions that are five times greater than those measured at F_o in healthy chloroplasts (50). Intact thylakoid systems such as these have high concentrations of photochemically active PSII reaction centers which rapidly and efficiently utilize energy to reduce Q acceptors prior to onset of CO_2 fixation. Fluorescence at F_p primarily emanates from the antennae chlorophylls of PSII (43,44,50). Exitons utilized in charge separation at photochemically active reaction centers are primarily transferred back to antennae chlorophyll and liberated as fluorescence in response to excessive Q reduction. Environmental stress which results in thylakoid damage usually lowers F_p by decreasing the concentration of photochemically active reaction centers.

Fluorescence Quenching

After chloroplasts have reached F_p, substantial fluorescence quenching occurs in response to several factors (1,20,35,42,43,50,63,65). Fluorescence emission declines to F_s, followed by a transitory rise to F_m. Fluorescence may oscillate through several F_s to F_m cycles before reaching steady state fluorescence levels at F_t.

Crowther et al. (20) studied the effects of photosynthetic carbon metabolism on fluorescence quenching in isolated chloroplasts from maize. Calvin Cycle intermedi-

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ates were added to determine the effects of ATP and NADPH utilization on fluorescence quenching. Substrates which quenched fluorescence utilized NADPH as a reductant. ATP utilization was not effective in fluorescence quenching. Measurements of cyclic and linear photosynthetic electron transport revealed that increased ATP utilization stimulated cyclical electron transport while increased NADPH utilization stimulated linear transport. Crowther et al. concluded that NADPH turnover quenched fluorescence by abstracting electrons from reduced Q by stimulating linear electron transport. Fluorescence quenching due to activation of photosynthetic carbon metabolism which causes NADPH turnover is known as photochemical quenching. Photochemical quenching rates are generally high when CO_2 fixation is not impaired.

The fluorescence decline from F_p to F_t is not exclusively determined by photochemical mechanisms associated with CO_2 fixation (1,35,42,43,50,65). Investigations have shown that factors such as protonation of the thylakoid channel, increased concentrations of Mg^+ in the stroma and phosphorylation of the LHCP contribute to fluorescence quenching. These processes impose mechanisms of control on energy transducing pigment systems in chloroplasts (43,50). Collectively, they are referred to as non-photochemical quenching mechanisms.

The initial ATP synthesized by the light reactions is

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capable of phosphorylating LHCP subunits (1,35). The LHCP increases its association with the PSI in response to phosphorylation. Absorbed energy then becomes preferentially transferred to PSI at the expense transferred to PSII. Fluorescence emission from PSI is relatively low. Allen and Bannent (1) found that PSII specific fluorescence (685nm) decreased while PSI fluorescence (735nm) increased in response to LHCP phosphorylation. Allen and Bannent concluded that a specific kinase phosphorylates LHCP subunits in response to excessive pastiquinnone reduction. Horton and Black (35) noted similar results in their experiments. Removal of Mg^+ or ATP from isolated chloroplasts decreased LHCP phosphorylation and fluorescence quenching. Horton and Black concluded Mg^+ and ATP were required as cofactors for LHCP phosphorylation catalyzed by a specific kinase.

Acidification of the thylakoid channel is a primary factor which quenches fluorescence from F_p, influences F_s to F_m fluorescence oscillations and contributes to fluorescence quenching at F_t (42,43,45,50,65). Prior to the onset of photosynthetic CO_2 fixation, the pool of ADP in the stroma is depleted by the initial synthesis of ATP and lack of ATP turnover. ATP synthesis cannot occur under conditions of limiting ADP substrate. As a result, protons build up in the thylakoid channel. Krause (41,42) found that acidification of thylakoid channels modifies thylakoid membranes in a manner which promotes photosynthetic reduct-

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ion of electron acceptors such as O_2. Photochemical O_2 reduction, known as the Mehler reaction, abstracts electrons from surfaces of energized electron transport carriers and pigments thereby oxidizing Q and quenching fluorescence (23,51,59).

Proton gradients across the thylakoid are a primary factor which quenches fluorescence from F_p to F_s (41,42,43,50). Following F_s, fluorescence usually rises to F_m as Calvin Cycle activation causes the turnover of ATP. This dissipates the pH gradients built up across thylakoid membranes. Several F_s to F_m can occur until ATP turnover, ultimately influenced by Calvin Cycle activity, reaches steady-state conditions. At F_t fluorescence levels are constant because photosynthetic mechanisms which affect fluorescence reach steady-state conditions.

Fluorescence Indicators of Environmental Stress

Effects of Heat Stress on F_o and F_p

Heat stress often changes fluorescence induction because photochemical reactions of PSII are extremely heat sensitive (7,8,9,43,61,62,66,67). Santarius (57) studied the effects of heat stress on photosynthesis in isolated spinach chloroplasts. He used artificial PSII and PSI electron donors and acceptors to measure specific rates of electron transport in stressed and non-stressed chloro-

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plasts. He found that PSII electron transport rates were extremely heat sensitive. In a later study, Santarius (58) found that changes in membrane phospholipids accompanied heat stress damage. He postulated that these changes may inhibit PSII reactions. Volger and Santarius (72) found that inactivation of PSII electron transport correlated with the release of specific thylakoid proteins.

Schrieber and Armond (62) studied heat induced fluorescence induction changes in L. divariacata, a desert shrub. Chloroplasts were isolated and subjected to heat treatments. Changes in fluorescence induction characteristics were monitored as a function of increasing thermal stress. Increases of F_o and declines of F_p occurred as a function of the heat stress severity. These stress induced changes in fluorescence correlated with fluorescence changes measured by low temperature spectroscopy. Schrieber and Armond concluded that increases of F_o were caused by separation and disorganization of antennae pigment subunits from PSII reaction centers. They reported the decline in F_p as being caused by a decreased capacity of PSII reaction centers to utilize energy and mediate primary photochemical reactions.

Smillie and Gibbons (67) ranked barley, pea, bean, tomato, maize and papaya in order of increasing heat tolerance using chlorophyll induction fluorescence techniques. Fluorescence variables used in their heat tolerance determ-

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inations were the stress temperatures at which F_o sharply rose, the maximum F_o value attained by stress treatments, the stress induced decline of the slope coefficient produced by the fluorescence rise from F_o to F_p and declines in F_p minus F_o. The slope parameter was termed as F_v. F_p minus F_o relates to F_v but does not account for variations in time at which F_p fluorescence levels are reached. Changes in each of the fluorescence parameters were analyzed as a function of heat stress severity. F_v gave the most meaningful and sensitive species separations according to heat stress in their analyses. This variable accounts for both increased levels of F_o and decreased levels of F_p, both of which are indicative of heat stress damage. Smillie and Hetherington (66) ranked pea, snow pea, pigeon pea, wheat, peanut, millet and papaya in order of heat sensitivity using similar techniques.

Smillie and Gibbons (67) studied heat acclimation of barley and the reversibility of heat stress damage in peas. Barley plants were acclimated to heat at super-optimal temperatures of either 40/28 or 37/29 C^o day/night temperatures. Fluorescence changes, indicative of heat damage, shifted to temperatures 6-9 C^o higher in the acclimated plants. These results indicated that heat acclimation had occurred. Reversibility of heat stress in peas used heat stressed pea plants followed by 6, 36, or 1400 minute recovery periods. Fluorescence measurements were taken before

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and after allowing the respective recovery times. The heat induced rise in F_o was reversible while F_p and F_v components remained inhibited throughout all of the recovery times.

Bilger and Schreiber (8) compared the variable Tl_{50}, the temperature treatment required to induce leaf scald symptoms on 50% of the leaf area, with stress temperatures at which F_o sharply rose during heat stress. A low intensity actinic light was used to maintain the F_o signal indefinitely while simultaneously increasing the temperature of the thermal stress. They reported very good correlations between the stress ranking procedures over 26 species tested.

Fluorescence Induction and Photoinhibition

Photosynthetic injuries as the direct result of exposure to high light intensities are defined by Powels (51) as photoinhibition. PSII electron transport reactions are thylakoid processes most sensitive to photoinhibition. P680 reaction centers and/or the 32 Kd protein on the electron accepting side of PSII reaction centers are believed to become irreversibly damaged.

Photooxidation are secondary inhibitory reactions related to photoinhibtion (23,30,51,59). The rate of oxygen reduction by the Mehler reaction increases under high light intensity in response to limited NADP availability in the

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stroma. Superoxide produced from the Mehler reaction give rise peroxides (23,30). These reaction products are very hazardous and reactive towards membrane lipids, pigments, enzymes and DNA. The Mehler reaction has been proposed as a protective mechanism against photoinhibition because chloroplasts contain metabolites which discharge superoxides. The Mehler reaction may dissipate energy from the thylakoid similar to the functions of the photorespiratory pathway.

Powels and Bjorkman (54) found that fluorescence techniques could be used to indicate photoinhibition. Nerium orleander plants were exposed to photoinhibitory treatments followed by simultaneous measurements of PSII and PSI specific fluorescence at 692 nm and 734 nm, respectively. The research reports showed that a 3 hour high light treatment decreased PSII fluorescence responses by 50%. PSI fluorescence changed very little. An increased association of the LHCP with PSI, its dissociation from either photosystem, or increased rates of energy transfer from PSII to PSI could have decreased PSII fluorescence (692 nm) observed. These causes were ruled out because various relationships between PSI and PSII fluorescence characteristics did not correspond to these theories. The researchers then concluded that inhibition of PSII photochemistry was revealed by fluorescence.

Fluorescence experiments by Critchley (18) reached similar conclusions on the effects of photoinhibition.

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These experiments used room temperature chlorophyll fluorescence induction on intact cucumber leaves. Declines of F_p fluorescence with photoinhibition stress were obtained. These results were substantiated by the use of appropriate electron acceptors which distinguished the rates of PSII, PSI, and whole chain electron transport. Critchley concluded that photochemical reactions at PSII were sensitive to photoinhibitory stress and therefore revealed by declines in F_p.

Critchley and Smillie (19) used fluorescence induction techniques to study the effects of photoinhibition on cucumber. They found that photoinhibition lowered F_p fluorescence in cucumber. Additionally, they reported photoinhibition caused both reversible and irreversible effects on F_p fluorescence levels. The extent of reversibility depended on plant exposure time to light stress and subsequent recovery period allowed prior to fluorescence measurements. Smillie and Hetherington (66) also observed decreases of F_p in apple subjected to photoinhibition stress.

Water Stress and Fluorescence Measurements

Berkowitz and Gibbs (4) Keck and Boyer (38) and Fry (24) found that reduced osmotic potential causes inhibition of photosynthetic electron transport. Berkowitz and Gibbs showed that electron transport inhibition in isolated spin-

ach chloroplasts were not substantial until extremely low water potentials were reached. Keck and Boyer, using sunflower, and Fry, using chloroplasts from cotton, found that electron transport reactions were extremely sensitive to water stress. Differential sensitivities of thylakoid reactions to low water potentials may reflect variations among species and/or among experimental techniques.

Berkowitz and Gibbs (5) and Boag and Portis (11) studied inhibition of Calvin Cycle enzymes at low water potentials. Results from both studies found that bisphosphatase enzymes of the Calvin Cycle were inhibited by low osmotic potentials. Berkowitz and Gibbs theorized that inhibition of the bisphosphatase enzymes inhibited the cyclical functions of the Calvin Cycle, thus limiting the supply of available CO_2 acceptor molecules. Low concentrations of ribulose bisphosphate and substantial imbalances in other Calvin Cycle intermediates were measured in water stressed chloroplasts. Berkowitz and Gibbs found that exogenously added ribulose-5-phosphate restored CO_2 fixation activity. Later reports by Berkowitz and Gibbs (6) found that inhibition of Calvin Cycle enzymes by water stress was caused by stromal acidification.

Ogren and Onquist (47) studied fluorescence induction changes of willow trees subjected to increasing water stress. Water stress altered fluorescence quenching. F_s to F_m fluorescence oscillations diminished with increasing

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water stress. Ireland et al. (37) and Leegood and Furbank (45) reported the same phenomenon in maize when CO_2 fixation was limited. Leegood and Furbank used cool temperatures and low ambient CO_2 concentrations to induce CO_2 fixation inhibition. Ireland used young leaf tissue which had not yet established high Calvin Cycle activity. Sivak and Walker (65) Ireland et al. (37), Leegood and Furbank (45) and Ogren and Onquist (49) discuss inhibition of ATP utilization in chloroplasts which causes a disappearance of F_s to F_m fluorescence transients. Ogren and Onquist (49) found that F_t conditions in water stressed willow plants were immediately reached following F_p fluorescence. Ogren and Onquist also showed that F_t levels were higher under stressed conditions. They concluded that decreased NADPH utilization caused decreased fluorescence quenching in response to limited Calvin Cycle activity.

Interaction between Drought and Photoinhibition

Photoinhibitory effects may be produced by interactions between light absorption and factors such as water stress which inhibit CO_2 fixation (21,49). Powels (51),Powels et al. (52), and Powels et al. (53) discussed that dissipation of photosynthetically absorbed energy by NADPH utilization and ATP are necessary for protecting the light reactions from photoinhibition. Powels et al. (52) studied effects of

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high light intensity on photosynthetic electron transport inhibition in maize and other C_4 species under varying O_2 and CO_2 levels. Maximum photoinhibition occurred at low CO_2 and O_2 levels. From a similar experiment, Powels et al. (53) showed that electron transport inhibition in C_3 species decreased substantially when ambient O_2 levels were raised. Powels established that photorespiration in C_3 species protects the photosynthetic apparatus from photo-inhibition. Photorespiration provided an additional sink for dissipation of absorbed energy from thylakoid reactions when CO_2 fixation was inhibited.

Powels et al. (52) found that maximum stress treatments in maize caused a 50-60% decline in electron transport and resulted in severe bleaching of leaf pigments. Unlike the O_2 responses of C_3 plants, photoinhibition in maize was only minimized by increasing ambient CO_2 (52,53). They concluded that the rates of photorespiration and/or Mehler reaction were apparently insufficient to protect maize from photoinhibition when CO_2 fixation rates were limited.

Downton (21) studied interactions between drought stress and photoinhibition in grapevine. Water stressed plants had substantially lower F_p values than unstressed plants. These results indicated that drought stress had direct effects on thylakoid reactions. Simultaneous photo-inhibition and drought stress caused a further decline in

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F_p fluorescence. Downton then studied the effects of plant acclimation to water stress on fluorescence changes caused by simultaneous drought and photoinhibition. Plants were either rapidly desiccated or acclimated to low water potentials by slow desiccation. Comparisons of F_p minus F_o were made as a function of declining water potential in plants subjected to photoinhibitory light treatments. Fluorescence values in rapidly desiccated plants declined rapidly with decreasing water potentials when accompanied by light stress. Fluorescence values were relatively stable in slowly desiccated plants until extremely low water potentials were reached. Downton concluded that osmotic adjustment protected grapevine against photoinhibition under water stress.

Fluorescence Changes in Drought Stressed Maize

Havaux and Lannoye (33) studied fluorescence induction changes from intact leaves of maize subjected to drought stress. F_p/F_o ratios declined as relative water contents (RWC) of leaves decreased during the first 8 days in which water was withheld. They concluded that drought stress in maize directly inhibited photochemical processes. During these stress phases, F_t emissions also increased and F_s to F_m transients decreased. These changes indicated of Calvin Cycle inhibition. Fluorescence characteristics prior to the onset of water stress were nearly reached after three days

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of recovery in plants which were rewatered after eight days of water stress. F_p/F_o ratios drastically declined in plants which were not rewatered until after 15 days of stress. Havaux and Lannoye showed that chlorophyll fluorescence could be used as a rapid and accurate water stress indicator in maize. They also showed that chlorophyll fluorescence could be used as a rapid and accurate water stress indicator in maize.

MATERIALS AND METHODS

Field trials were conducted during the 1985 and 1986 maize growing seasons. The 1985 tests were planted at an irrigated site at the Kansas State University Ashland Agronomy Farm, Manhattan, Kansas ($39^O11'N$ latitude, elevation 310 m). The 1986 replicated tests were conducted at the Ashland Agronomy Farm under irrigated and non-irrigated conditions. A third test was planted in 1986 at the Kansas River Valley Experiment Station, Rossville, Kansas ($39^O7'N$ latitude), 95 km to the east of Manhattan.

Soil type at the Manhattan sites was a Haynie fine sandy loam (Mollic Udifluvent coarse silty mixed mesic). Nitrogen (210 Kg/ha) fertilizer was applied at this site in both seasons. At Rossville the soil was a Sarpie sandy loam (typic Udipsamments mixed mesic). Fertilizer application at Rossville was 230, 43 and 27 Kg/ha of N, P, and K, respectively.

Daily temperatures and rainfall amounts for each year at each of the sites are presented in Figs. 1, 2 and 3. The Manhattan site was irrigated weekly during all of June and part of July in 1985. The 1986 irrigation schedules are shown in Table 1. The 1985 season was relatively hot and dry in comparison to 1986; however, some intermittent periods of hot weather with little or no rainfall occurred in 1986.

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Fig. 1   1985   Temperature and Rainfall data from Manhattan.

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1986 MANHATTAN TEMPERATURE—RAINFALL
MAY—SEPTEMBER

Fig. 2   1986 Temperature and Rainfall data from Manhattan.
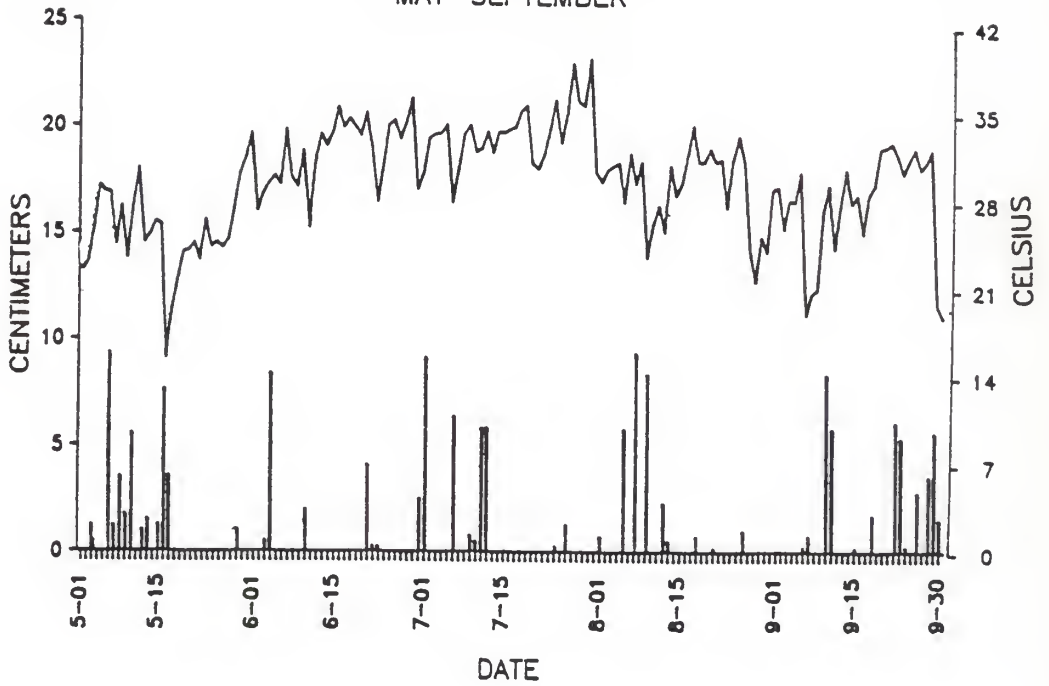
Fig. 3   1986 Temperature and Rainfall data from Rossville.

Table 1. Irrigation and Rainfall, May to September 1986.

Location	Irrigation	Rainfall	Total
	cm	cm	cm
Ross-Irr	37.8	62.4	100.2
Ash-Irr	20.0	72.4	92.4
Ash-Dry	0.0	72.4	72.4

Plant Materials

S_o seeds from two experimental populations, designated as hot and cool, were planted on May 24, 1985. Classifications of the populations were based on temperature differential (T_D) responses of the parental lines which were previously selected and recombined by Spanogle (69). T_D responses are measurements of canopy temperatures taken relative to ambient air temperatures. T_D is defined as the canopy temperature of a given plant or crop minus the ambient air temperature, expressed in degrees celsius as follows:

$$T_D \ (^oC) = T \ (^oC)_{canopy} - T \ (^oC)_{air}$$

In 1985, the hot and cool populations were planted at seeding rate of 57406 plant ha^{-1}, in rows spaced 76 cm apart and 4.5 m long. There were 35 rows of the cool population and 16 rows of the hot population. Individual plants from each population were self pollinated and evaluated in the nursery. 140 plants from the cool population and 68 plants from the hot population were

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evaluated and S_1 seed produced. Canopy leaf temperatures, canopy temperature differentials (T_D) and root measurements were obtained from each parental plant. Selections were based on T_D responses and root morphology. S_1 seed from selected lines were sent to a winter nursery to produce seed for further testing.

1985 Plant Selection Procedures

T_D responses in 1985 were obtained using a model #42 infrared (IR) thermometer from Everest Interscience Corporation, accurate to within $0.5^{\circ}C$. This thermometer is fitted with a thermocouple which continuously senses ambient air temperatures during its operation and automatically calculates T_D measurements. The thermometer was interfaced with a model #516 Omnidata Polycorder for data collection. Temperature data were automatically entered into the polycorder memory for later transfer to floppy disks via a microcomputer.

T_D responses were obtained from each plant which had been selfed in the nursery. Measurements were taken during clear sunny afternoons between 12:00 and 15:00 hours (Central Standard Time) on eight separate occasions from flowering through the grain filling stages of the plants (40,46,69). Each plant was measured four times on each occasion, two with the instrument facing south and two facing north. Measurements were taken consecutively, in

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order of row number, from the beginning to end of the nursery. Reverse order through the nursery was used alternately to compensate for time and temperature changes during the measurement period.

The thermometer was held in such a manner as to measure the uppermost leaves of each plant (49). The instrument was held approximately 30 cm above each plant, directed downward at about a 30° angle. These techniques were similar to those used by Spanogle (69) Kirkham (40) and Mtiu (46). Distances between the thermometer and plant leaves were modified because measurements were taken on an individual plant basis rather than on a whole plot basis (49). T_D measurements taken over the entire season were averaged and used as T_D responses for each of the individual S_o plants.

After harvesting the S_1 seeds in the nursery, approximately 30 cm of the uppermost root system from each of the parental plants were mechanically extracted from the soil using a Massey-Ferguson potato digger. Plants which appeared to have their uppermost secondary and fibrous root branches relatively intact were removed from the field and washed. These partial root systems were visually ranked according to their volume and extent of branching. Ratings were on a scale of 1 to 9 for overall root size and extent of fibrous roots. Large scores indicate greater volume and more fibrous roots.

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T_D averages were used as the primary selection criteria. Among plants measured from the cool population, those which had the coolest T_D responses and high root scores were designated as drought tolerant. Plants with relatively warm T_D averages and low root scores were selected from the hot population and designated as drought susceptible. Entry numbers above 689 represent lines from the hot population. S_1 seeds from 19 tolerant and 6 susceptible plants were used for progeny testing in 1986. S_2 seed and a series of hybrid combinations were produced from these lines in a winter nursery. Equal portions of seed from three or more identical pollinations were bulked in order to represent each S_2 line and hybrid combination in the 1986 tests.

1986 Replicated Field Trials

Lines were planted at the two Ashland sites on May 15 and at Rossville on May 19 in 1986. The 25 S_1 lines, their S_2 progenies and hybrid combinations were planted at seeding rates of 57406 plants ha^{-1}. Lines were seeded in single row plots 4.5 m long with 76 cm between rows. A randomized complete block design with two replications at each location was used. S_1 and S_2 lines were randomly distributed within replications. The hybrids were planted in separate replications, adjacent to the parental lines at each location.

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Canopy Temperature Measurements

Temperature differential (T_D) measurements were taken in 1986 using the same model infrared thermometer as used in 1985. The thermometer was held at a $30°$ angle above several guarded plants in each plot, directed towards the upper most leaves of each canopy. Measurements were taken on hot and sunny afternoons between 12:00 and 15:00 hours (Central Standard Time). Measurements were taken during approximately the late pollen shed through grain filling stages of the plants. These growth stages occurred during the months of July and August. T_D responses were obtained from S_1 and S_2 lines at all locations and from the hybrid combinations at Rossville. Two measurements were taken facing north and two facing south on each occasion. Data were obtained on five separate occasions at the Ashland sites and three at Rossville.

Fluorescence Measurements

Chlorophyll fluorescence measurements were taken using a Plant Productivity Fluorometer, model SF-20, manufactured by Richard Brancker Research Ltd. Measurements were taken in the field, at night, over the same S_1, S_2 and hybrid plant materials as the T_D responses. Data were obtained on three occasions at the Ashland sites and twice at Rossville. Measurements were taken during the same period of the season as the IR readings. Fluorescence data were

taken from seven plants within each plot on each occasion. Data were also collected over two replications at Ashland when plants were in their fourth leaf stage of development. Seedlings were measured on the underside of the third leaf, one-third the distance from the leaf tip (67).

Fluorescence readings commenced at least one half-hour after total darkness. F_o and F_p data were obtained from the third leaf from the tassel. Upper leaves were measured because they were same as those primarily measured by the IR thermometer. The probe of the fluorometer was placed on the underside of these leaves, about one-third the distance from the leaf tips, avoiding the central vein (67). F_o and F_p fluorescence responses were measured directly from the instrument's LED read-outs, expressed in units relative to the calibration of the fluorometer. The data obtained were keyed into the polycorder. F_v responses were calculated from the difference between F_p and F_o responses collected from each leaf in the field:

$$F_v \text{ (relative)} = F_p \text{ (relative)} - F_o \text{ (relative)}$$

Grain Harvest

Plots were hand harvested when the moisture of the grain had reached approximately 20 percent in the field. Ears were harvested from ten guarded plants within each

plot. Shelled grain weights and percent moisture were recorded. Grain yields of the individual plots were adjusted for moisture and expressed as grams per plant.

Analyses of the Physiological Measurements

Fluorescence, temperature differential and yield data from the 1986 tests were utilized in analyses of variance procedures. The fluorescence and canopy temperature data obtained from each plot during the entire season were averaged and used as response variables for the entries. Differences for F_V, T_D and yield among locations and among entries were determined at the .05 significance level.

Regression analyses were utilized to determine relationships among F_V, T_D and yield. Data from each entry were averaged within each location separately to produce dependent and independent regression variables. These analyses determined relationships among F_V, T_D and yield for each location separately. Data from each of the entries were also averaged over locations and utilized in similar regression analyses in order to summarize the relationships among T_D, F_V and yield.

Regression analyses were also utilized to determine relationships between hybrid grain yield and fluorescence and temperature differential responses from their parental lines. These analyses utilized midparent values calculated from T_D and F_V as independent regression variables and

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hybrid yield data as the dependent variable. Midparent values for T_D and F_v were calculated from S_1 lines, S_2 lines or their averages. The yield and physiological data from each of the separate locations were utililized in single factor and two factor regression analyses. These analyses provide evidence of genetic relationships among the traits measured and determined the feasibility of measuring F_v and T_D responses from inbred lines for hybrid yield improvement. Only 46 of the 52 hybrids were used in these regression analyses because sufficient seeds were not available from some parental lines.

Heritability Analyses

Parent-offspring and midparent-offspring regression procedures described by Hallauer and Miranda (29) were used to estimate heritability (h^2) for F_v, T_D, and yield. Estimates of heritability were calculated from the regression coefficients ($B_1 \pm$ 95% confidence interval) of these regression models. Both procedures utilized separate location averages from each entry for T_D, F_v and yield data as response variables. Estimates of heritability for F_v, T_D and yield were calculated by using data obtained from each location in separate analyses.

Estimates of heritability from parent-offspring and midparent-offspring analyses were refined by methods described by Vogel (71) and Casler (14) for situations when

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both parent and offspring are evaluated during the same season. Parent and offspring data obtained from different locations were utilized as regression variables in these analyses. Parent-offspring regression analyses utilized data obtained from S_1 and S_2 lines grown at the Ashland Dryland and Rossville Sites because these environments were the most dissimilar. Midparent-offspring regression utilized data from S_1 and S_2 lines grown at the Ashland Dryland Site as midparent responses and data obtained from hybrids grown at Rossville. These modifications account for an upward bias in heritability due to environmental covariances between parents and their progenies when evaluations are conducted during the same season.

Regression coefficients of parent-offspring analyses were adjusted with modifications developed by Smith and Kinman (68). These procedures account an upward bias of heritability due to the fixation of dominant alleles and were necessary in this study because S_1 parental lines were used. Smith and Kinman derived the factor r_{xy} from the probability of dominance fixation from inbreeding. Smith and Kinman indicated that estimates of heritability calculated by parent-offspring regression equal three-fourths of the regression coefficient when S_1 parental lines are used.

RESULTS AND DISCUSSION

Population Responses for 1985

Variation due to the effects of the hot and cool populations were statistically significant in the analyses of variance for T_D responses and method of rating root systems of individual plants, as shown in Tables 2 and 3. Population effects for T_D responses indicate that previous plant selections by Spanogle (69) effectively separated parental lines based on genetic effects. The number of degrees of freedom for error was less in the root rating analysis of variance because fewer root systems were evaluated.

Table 2. 1985 Analysis of variance for T_D responses of the hot and cool populations.

Source	D.F.	M. S.	F-value	P. Level
Population	1	13.467	78.2	.0001
Error	206	.1723		

Table 3. 1985 Analysis of variance for visual ratings of root sizes for the hot and cool populations

Source	D.F.	M. S.	F-value	P. Level
Population	1	190.50	38.3	.0001
Error	132	4.97		

Average T_D and root rating values from the hot and cool populations are presented in Table 4. T_D responses and

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root evaluation values differed significantly among plants measured from the hot and cool populations.

Plants from the cool population had cooler T_D responses and higher root scores. Average seasonal T_D values among the plants in each population are shown in Fig. 4. None of the T_D averages of plants measured from the cool population exceeded ambient air temperatures.

Table 4. 1985 T_D (^{O}C) and root score (visual) means of the hot and cool populations

Population	T_D Mean	Root Score Mean
	C	Score
Hot	-.058a	2.56a
Cool	-1.13b	5.20b

Means followed by the same letter in each of the respective columns do not differ statistically at the .05 level.

Plants from the hot population had relatively low root scores and warm T_D responses. This indicated that small root systems limited water uptake and transpiration. Methods used to evaluate root systems may not have been very accurate for comparisons of individual plants because the entire root system was not rated. However, root score values between the two populations differed significantly. Root data supplemented the temperature differential measurements for classification of drought tolerant and susceptible plants. Lines selected for further progeny tests, their root scores and average T_D responses are presented in Table 5.
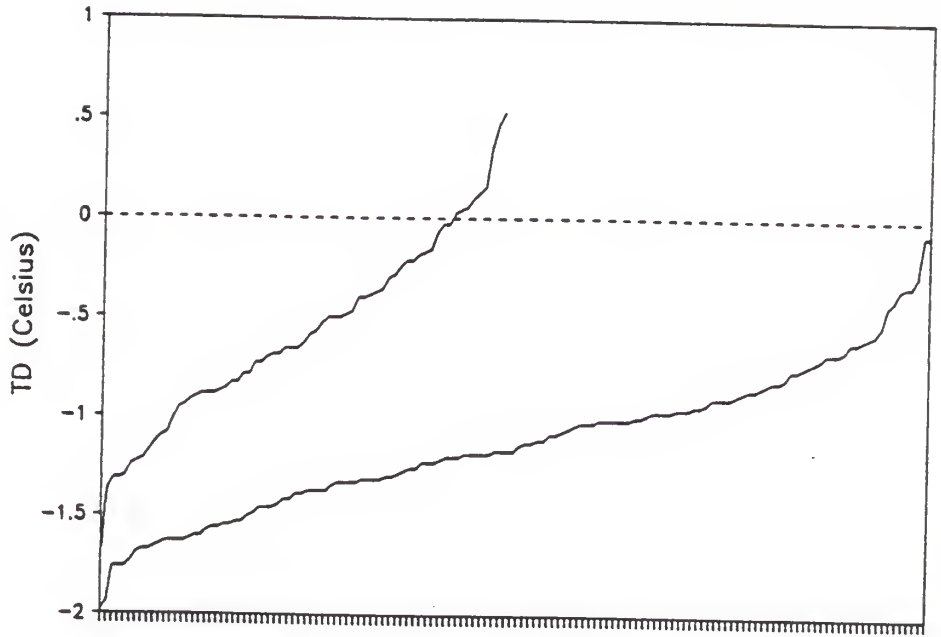
Fig. 4   1985 T_D responses of plants within the hot and cool populations.

Table 5. 1985 Root scores (visual) and T_D responses (°C) of lines selected for further progeny tests.

Source	Line	Root	T_D(°C)	Source	Line	Root	T_D(°C)
cool	655-4	5	-1.67	cool	676-2	8	-1.09
cool	656-3	5	-1.00	cool	677-1	9	-.94
cool	657-1	8	-1.17	cool	677-3	1	-1.67
cool	658-4	8	-1.33	cool	683-3	-	-1.63
cool	660-2	9	-1.19	cool	685-4	8	-1.34
cool	662-3	5	-1.94	cool	686-1	8	-1.20
cool	665-1	8	-1.63	hot	692-2	1	.16
cool	665-2	9	-1.46	hot	697-1	-	-.90
cool	668-2	2	-.53	hot	697-4	-	-.66
cool	672-1	7	-1.31	hot	698-2	1	-.50
cool	674-1	8	-1.19	hot	701-2	-	-.86
				hot	706-1	1	-.23

1986 Analyses of S_1 and S_2 Lines

Yield

Variation of yield due to entry and location effects were significant for both S_1 and S_2 lines as shown in Tables 6 and 7. Genotype by environment interactions and effects due to the replications were not statistically significant. Genotype by environment interactions also were not significant in similar analyses of temperature differential (T_D) and chlorophyll fluorescence (F_v) measurements.

Yield, F_v and T_D responses from the entries were averaged over locations and utilized as response variables in several regression analyses. Average yields from each entry were utilized as dependent variables, and

Table 6.   1986 Analysis of variance for yield of S_1 lines.

SOURCE	D.F.	M.S.	F value	P. Level
Location	2	8023.65	12.79	.0001
Entries	24	4418.68	7.04	.0001
Reps	3	689.65	1.10	.36
Ent x Loc	48	783.59	1.25	.19
Error	76	627.28		

Table 7.   1986 Analysis of variance for yield of S_2 lines.

SOURCE	D.F.	M.S.	F value	S. Level
Location	2	8577.92	18.78	.0001
Entries	24	2798.59	6.14	.0001
Reps	3	785.94	1.73	.17
Ent*loc	48	393.72	.86	.70
Error	76	455.59		

physiological measurement as independent variables. Responses averaged in these manners did not significantly alter the relative order of the entries in respect to one another because no statistically significant genotype by environment interactions were found.   These analyses, presented in the following discussions, provide useful information as to the overall effectiveness of each of the physiological measurements for identifying superiority among genotypes in regards to yield and yield stability over environments.

Average yields of S_1 and S_2 lines among locations are given in Table 8. Environmental stress associated with limited water apparently resulted in significantly lower yields at the Ashland dryland site. S_1 lines at Rossville

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irrigation conditions. S_2 lines did not benefit from the superior environment of the Rossville site, possibly due to the effects of inbreeding depression and increased competition from S_1 lines which were randomized within the same blocks.

Table 8. 1986 Location means for yield (g/plant) among S_1 and S_2 lines.

Location	S_1 Yield	S_2 Yield
	g/plant	g/plant
Rossville Irrigated	94.59a	76.10a
Ashland Irrigated	85.23a	77.80a
Ashland Dryland	59.65b	54.30b

Means followed by the same letter in each of the respective columns do not differ statistically at the .05 level.

T_D Responses

The analyses of variance for T_D responses among entries at each of the experimental sites are presented in Tables 9 and 10. Genotypic effects were not significant but variation among replications and locations were significant. Replication differences most likely resulted from environmental influences which affected measurements over the field and/or data collection period. Daytime variation in factors such as heat, light intensity and humidity made detection of genotypic differences difficult. Variation in soil moisture may have also contributed to the masking of genotypic effects.

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S_1 and S_2 lines grouped according to their original hot and cool classifications expressed similar patterns of differences as those observed in 1985. T_D responses of genotypes derived from the hot population averaged significantly warmer than those from the cool population, as

Table 9. 1986 Analysis of variance for T_D responses among S_1 lines.

Source	D.F.	M.S.	F value	P. Level
Location	2	3.35	1.27	.0001
Entries	24	.35	18.96	.22
Reps	3	2.44	11.09	.0001
Ent x Loc	48	.09	.39	.99
Error	76	.22		

Table 10. 1986 Analysis of variance for T_D responses among S_2 lines.

Source	D.F.	M.S.	F. value	P. Level
Location	2	3.66	14.20	.0001
Entries	24	.21	.84	.68
Reps	3	3.56	13.82	.0001
Ent x Loc	48	.16	.62	.96
Error	76	.26		

shown in the Appendix.   This suggests that responses were dependent on genetic factors.

Average T_D values among S_1 and S_2 lines for each location are given in Table 11.   Differences among locations indicate that T_D responses detected shortages of soil moisture. Temperature measurements were warmest at the Ashland dryland site for both S_1 and S_2 lines. Among S_2

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lines, T_D responses from Rossville indicated environmental
stress. As was the case with yield, this may have been due
interactions among S_1 and S_2 lines. S_1 lines may have
effectively competed with S_2 lines in the utilization of
factors provided by the superior environment. Also, S_2 lines
may not have been able to utilize the more favorable
growing conditions provided by the Rossville environment
due to inbreeding depression.

Table 11. 1986 Location means for T_D responses among
S_1 and S_2 lines.

Location	S_1 T_D mean	S_2 T_D mean
Rossville irrigated	-.818a	-.439a
Ashland irrigated	-.859a	-.856b
Ashland dryland	-.340b	-.348a

Means followed by the same letter in each of the respective
columns do not differ statistically at the .05 level.

Relationships between T_D and Yield

Regression analyses of T_D responses versus grain
yields are presented in Table 12. Relationships between T_D
and yield were significant and lines with cooler T_D
responses tended to yield higher, as shown by the negative
regression coefficients presented. Relationships between T_D
and yield were most evident at the dryland site, probably
due to increased water stress.

A graphic presentation of the relationship between T_D
responses and yield for S_1 and S_2 entries averaged among
locations is shown in Fig. 5. The correlation coefficient

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Table 12. 1986 Regression analyses of T_D (°C) responses versus yield (g/plant) among parental lines.

Location	$B_1 \pm$ 95% C.I.	P. LEVEL	R^2
Rossville irrigated	-70.8 ± 43.4	.002	.18
Ashland irrigated	-57.6 ± 37.4	.003	.17
Ashland dryland	-31.2 ± 15.0	.01	.27
Sites averaged	-71.2 ± 27.6	.0001	.36

was higher in this analysis than in the analyses which utilized data from each of the locations separately. Entries with relatively cool canopies and high yields can be distinguished from Fig 5. Genotypic effects were significant in the analysis of variance for T_D presented in the Appendix. Therefore, relationships presented for T_D versus yield were due to genetic factors, at least in part.

F_v Responses

Analyses of variance for chlorophyll fluorescence measurements among S_1 and S_2 lines indicated that F_v responses measured plant factors which were highly dependent on genetic effects. Genotypic effects were highly significant as shown in Tables 13 and 14. Chlorophyll fluorescence measured photosynthetic processes which were highly dependent upon genetic factors.

Location effects for F_v were not significant in the analysis which involved S_2 lines. Location effects among S_1 lines were less significant than location effects for

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Fig. 5   1986 Relationship between T_D and yield among inbred lines averaged over locations.

Table 13. 1986 Analysis of variance for F_v responses among S_1 lines.

Source	D.F.	M.S.	F. value	P. Level
Location	2	120.96	5.89	.0084
Entries	24	306.47	12.90	.0001
Reps	3	8.46	.36	.79
Ent x Loc	48	20.25	.85	.72
Error	76	23.75		

either T_D or yield by more than a factor of ten. Diminutive location effects amplify genetic effects. Less variation of fluorescence values due to location effects meant that less environmental variations were available to interact with genotypic effects.

Table 14. 1986 Analysis of variance for F_v responses among S_2 lines.

Source	D.F.	M.S.	F value	P. Level
Location	2	35.23	70.45	.24
Entries	24	238.63	9.65	.0001
Reps	3	25.37	1.03	.39
Ent x Loc	48	35.82	1.45	.076
Error	72	24.72		

Replication effects and genotype by environment interactions were not statistically significant for F_v. This indicated that F_v responses across replications and environments ranked the genotypes relatively similarly. These are important advantages in plant breeding research where variation due to genetic factors are important for selection. Daytime fluctuations of factors such as heat, wind, solar radiation or humidity did not influence

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fluorescence because these measurements were taken during the night.

Average values of F_v among S_1 and S_2 lines for each location are given in Table 15. F_v responses from S_1 lines at Rossville were significantly higher than responses at Ashland. This difference corresponded to the differences observed for grain yields. F_v responses from S_2 lines showed

Table 15. 1986 Location means of F_v (relative) responses among S_1 and S_2 lines.

Location	F_v means expressed in relative units	
	S_1 lines	S_2 lines
Rossville irrigated	45.01a	42.01a
Ashland irrigated	42.29b	41.67a
Ashland dryland	42.38b	40.42a

Means followed by the same letter in each of the respective columns do not differ statistically at the .05 level.

trends of higher F_v values at both irrigated locations. Differences with respect to the dryland site were not statistically significant.

Relationships Between F_v and Yield

Results from the regression analyses of F_v responses versus grain yields are shown in Table 16. Regression coefficients were highly significant among analyses. F_v responses varied directly with grain yield at all locations. Lines which had high F_v values tended to yield higher.

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Table 16. 1986 Regression analyses of F_v responses versus
          yield among parental lines.

Location	B1 ± 95 % C.I.	P. LEVEL	R^2
Ashland irrigated	2.31 ± 1.10	.0001	.27
Rossville irrigated	1.71 ± .79	.0001	.27
Ashland dryland	1.82 ± 1.13	.002	.18
Sites averaged	2.32 ± .86	.0001	.38

Regression coefficients were not significantly different among locations, which indicates that F_v responses accounted for similar plant limitations across locations. Lower R^2 values at the dryland site were probably due to fluctuating environmental stress which affected fluorescence responses and yield values more independently. Relationships between F_v and yield from data averaged among locations is shown in Fig. 6.

F_v and T_D Relationships

Results of the regression analyses of F_v responses versus T_D responses are shown in Table 17. Lines which had high F_v values tended to have cool T_D values. Inverse relationships between F_v and yield were significant for all locations except Ashland not significant possibly because environmental stress factors were more severe, complex and tend to interact. There also were greater climatic differences between night and day conditions at this site. Relationships between F_v and T_D data averaged over locations
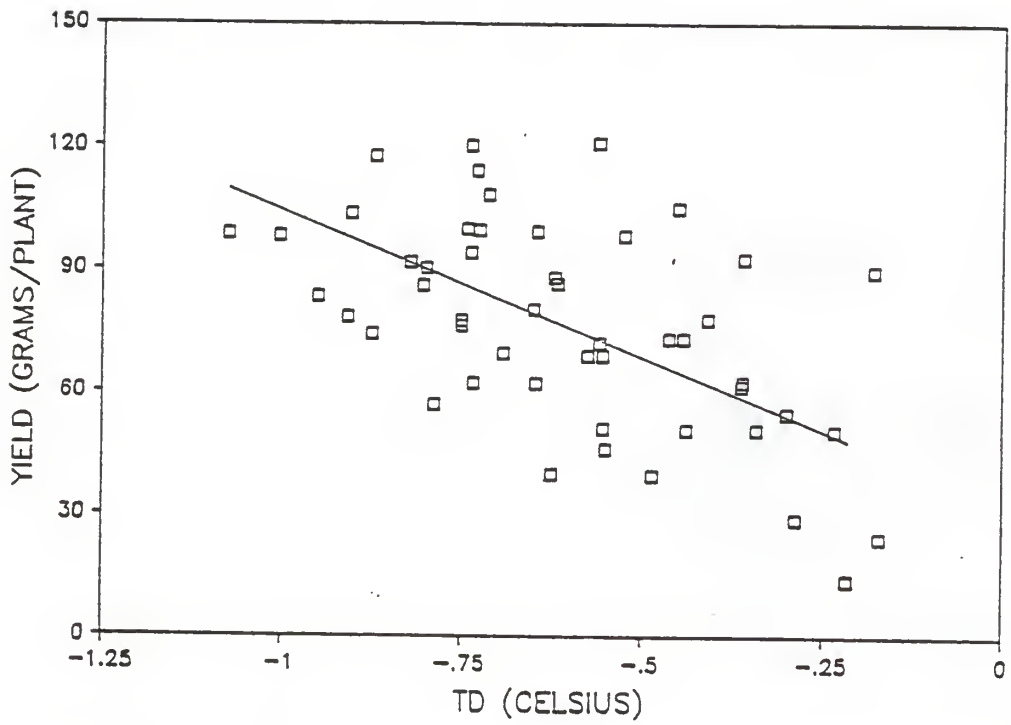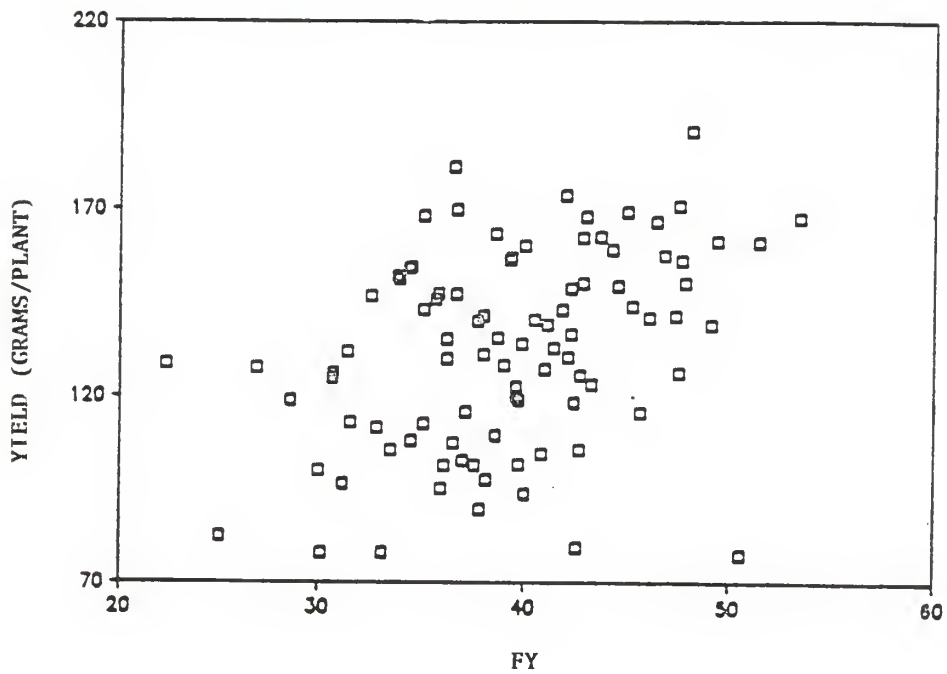
Fig. 6 1986 Relationship between F_y and yield among inbred lines averaged over locations.

Table 17. 1986 Regression analyses of FV responses versus TD responses among parental lines.

Location	$B_1 \pm$ 95 % C.I.	P. LEVEL	R^2
Ashland Irrigated	$-.007 \pm .007$	.05	.08
Ashland dryland	$-.136 \pm .01$	.25	.03
Rossville Irrigated	$-.022 \pm .01$	.002	.18
Sites averaged	$-.013 \pm .008$	.004	.16

are shown in Fig. 7.

Regression coefficients from Table 17 indicate general relationships for F_V and T_D. However, measurements were assumed as independent due to low R^2 values. Each of the physiological responses measured relatively independent plant factors related to yields.

Two Factor Regression Analyses

Two factor regression analyses which simultaneously used F_V and T_D to compare the relationship of physiological responses with grain yield among S_1 and S_2 lines are presented in Table 18. Results indicated that both physiological parameters accounted for yield variations among genotypes. Regression coefficients for F_V and T_D were significant among all of the two factor analyses.

Significance levels for T_D among the two factor analyses were highest under dryland conditions. Leaf temperatures would have tended to express yield limiting thresholds of water stress at this site. Significance

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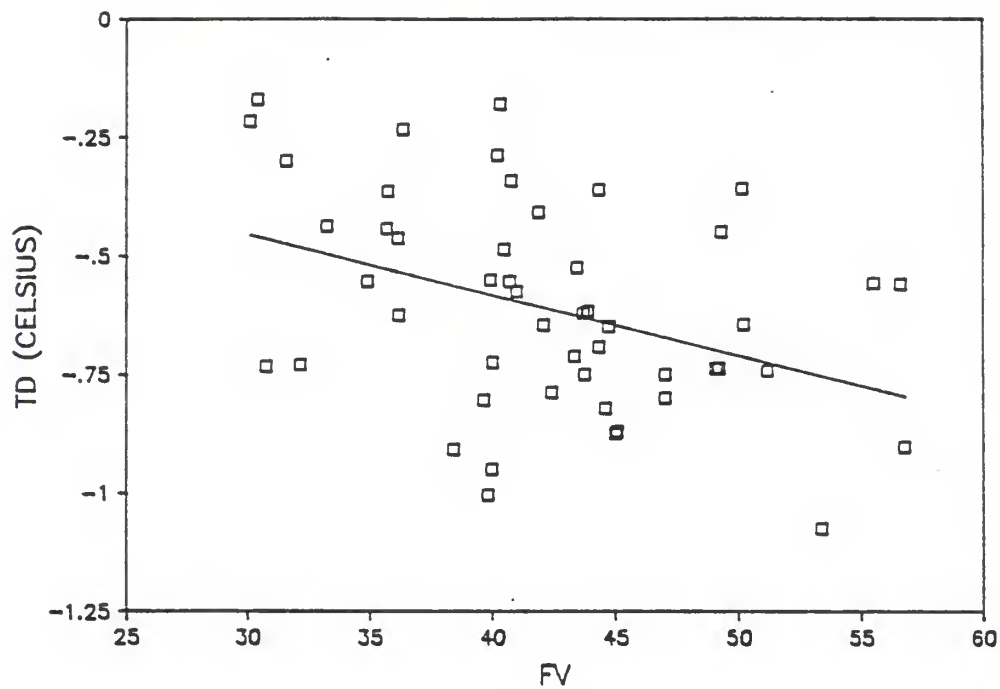
Fig. 7 1986 Relationship between T_D and F_V among inbred lines averaged over locations.

Table 18. Two factor regression analyses of F_v and T_D responses versus yield among parental lines.

LOCATION	P. Levels F_v	T_D	$B_1 \pm$ 95 % C.I. F_v	T_D	R^2
Ashland					
irrigated	.0008	.02	1.93 ± 1.1	-50.7 ± 40.5	.36
dryland	.005	.007	1.57 ± 1.1	-49.4 ± 35.3	.30
Rossville					
irrigated	.004	.01	1.23 ± .83	-21.6 ± 15.3	.38
Locations					
average	.0002	.0004	1.66 ± .83	-50.4 ± 26.4	.52

levels for F_v were relatively high among all two factor regression analyses. Fluorescence measurements probably quantified genotypic limitations and stress damage related to photosynthesis.

These two factor regression analyses had correlation coefficients higher than any single factor analyses which utilized either T_D or F_v responses for yield prediction. R^2 values increased from about .35 in the highest single factor regression analysis to approximately .50 for the two factor analysis. Simultaneous use of T_D and F_v in two factor regression analyses predicted yields among genotypes better than either physiological parameter used alone.

Responses for Inbred Lines

Average T_D, F_v and yield responses for the S_1 and S_2 entries are shown in Tables 19 and 20. Lines with cool T_D responses and high F_v values generally represented those

Table 19. 1986 F_V (relative), T_D (^{O}C) and yield (g/plant) means of S_1 lines averaged over locations.

Line	FV (relative)	TD ^{O} C	Yield
		C	g/plant
685-4	49.22	-.738	120.24
656-3	55.85	-.598	118.64
677-1	45.08	-.871	117.50
676-2	32.12	-.729	114.02
674-1	43.32	-.713	108.20
658-4	56.86	-.808	102.35
686-2	40.00	-.727	99.43
668-2	50.23	-.646	99.36
677-3	53.40	-1.08	98.60
655-4	39.75	-.997	98.14
657-1	50.70	-.660	95.81
660-2	44.70	-.761	90.95
662-4	40.33	-.588	89.58
686-1	43.89	-.617	86.41
701-2	38.39	-.908	78.27
662-3	45.74	-.750	77.39
665-1	47.03	-.750	76.06
665-2	41.92	-.771	74.14
672-1	31.56	-.300	64.61
706-1	42.10	-.646	62.00
697-1	35.72	-.363	61.32
683-3	42.41	-.788	56.75
698-2	39.90	-.550	46.00
697-4	40.20	-.288	28.86
692-2	30.37	-.171	24.29
LSD$_{.05}$	5.52	.46	26.84

Table 20. 1986 F_v (relative), T_D (^{O}C) and yield (g/plant) means of S_2 lines averaged over locations.

Line	FV (relative)	TD	Yield
		C	g/plant
685-4	49.33	-.450	105.00
656-3	43.43	-.525	98.20
686-1	49.10	-.788	94.07
657-1	50.15	-.358	92.55
668-2	47.02	-.800	90.24
674-1	43.71	-.621	88.01
677-1	39.62	-.804	85.91
701-2	39.97	-.950	83.35
677-3	44.74	-.650	80.15
686-2	36.13	-.463	78.04
683-3	41.88	-.408	77.67
672-1	35.67	-.442	72.98
660-2	45.34	-.783	72.41
658-4	55.52	-.558	71.92
662-3	44.36	-.692	69.43
662-4	40.71	-.554	68.81
676-2	30.74	-.733	62.12
665-1	44.20	-.469	58.92
697-1	34.88	-.554	51.00
706-1	40.79	-.342	50.78
655-4	33.22	-.438	50.64
698-2	36.35	-.233	50.46
665-2	36.17	-.625	39.80
697-4	41.17	-.286	33.66
692-2	30.07	-.217	13.89
LSD	5.64	.59	24.63

with the highest yields. Lines designated with entry numbers above 690 came from the hot S_0 population. Hot lines tended to yield lower, have lower F_v values and warmer leaf temperatures than lines from the cool population. Simultaneous use of chlorophyll fluorescence and infrared thermometry provided valuable selection criteria for improvement of environmental stress tolerance in maize.

A few lines with high yields had relatively high fluorescence values and warm leaf temperatures. Lines designated as 656-3, 657-1 and 685-4 are lines which had among the highest yields, high F_v values and relatively warm T_D responses. T_D responses may have been warmer due environmental variation. Increased stress tolerance may have allowed these lines to maintain high levels of F_v and yield. It is unlikely, however, that environmental variations would have affected the responses of the same S_1 and S_2 genotypes similarly. These lines also produced among the highest yielding hybrid combinations.

Perhaps physiological combinations of high F_v and warm T_D reflect better stress tolerance. Relatively warm T_D values coupled with high fluorescence responses indicated a particular line had combinations of photosynthetic maintenance and low transpiration. In some cases, warm leaf temperatures may indicate that a particular genotype had relatively low water requirements

rather than the ability to absorb and transpire water from the effects of drought. Lines with physiological combinations of warm T_D responses, high yields and high F_v values were rare.

F_v Responses from Seedlings

Results from the analysis of variance for F_v responses from S_1 and S_2 lines measured during their seedling stage of development are shown in Table 21. Effects due to the classification of entries based on their source from either the hot or cool population were significant. Analysis of variance which included effects due to individual entries were not significant. Replication effects in the analysis presented may account for variation due to reading fluorescence over different nights.

Mean F_v responses between stress tolerant and stress susceptible seedlings are presented in Table 22. Lines derived from the hot population had significantly lower values of F_v as seedlings.

Table 21.   Analysis of variance of F_v responses of seedlings of hot and cool parental lines, 1986.

Source	D.F.	M. S.	F value	P. Level
Populations	1	249.6	6.32	.01
Replication	1	528.9	13.39	
Error	93	39.5		

Table 22. Mean values of F_v (relative) responses of seedlings of hot and cool parental lines, 1986.

Population	F_v Mean (relative units)
Hots	45.59a
Cools	48.75b

Means followed by the same letter are not statistically different at the .05 level.

Stress susceptibility among lines which came from the hot population was detected in these phases of the fluorescence study. F_v responses may reflect seedling vigor or environmental stress sensitivities early in the season thus allowing one to concentrate efforts on superior lines.

Hybrid Analyses

Rossville Responses

Single factor regression analyses of T_D and F_v responses versus grain yields among hybrid combinations from the Rossville tests are presented in Table 23. The relationship between hybrid grain yield and T_D responses was not significant, but that between F_v and yield was significant.

Relationships between F_v and yield among hybrids were similar to the results obtained from parental lines. Relationships between hybrid yields and F_v responses are illustrated in Fig. 8.

65
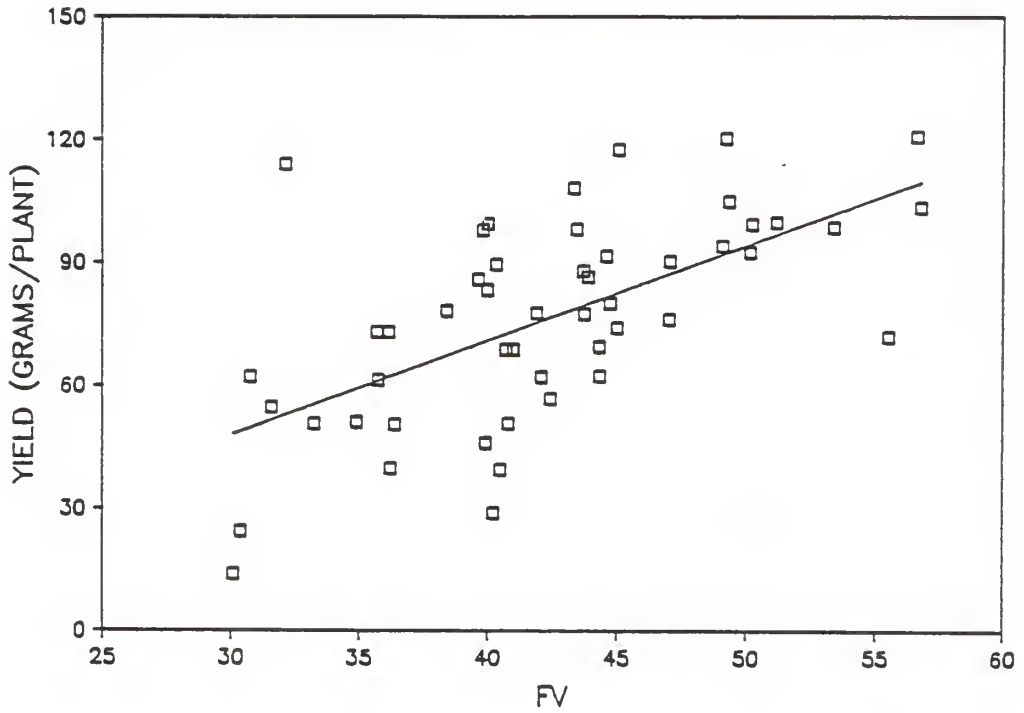
Fig. 8   1986 Relationship between F_v and yield among
Rossville hybrids averaged over replications.

Table 23. Single factor regression analysis of T_D and F_v responses versus grain yield among hybrids, Rossville, 1986.

Trait	P.Level	$B_1 \pm 95\%$ C.I.	R^2
T_D ($^{\circ}$C)	.91	$.001 \pm .02$	.00
F_v (relative)	.001	2.1 ± 1.18	.20

Midparent-Hybrid Correlations

Results from the single factor regression analysis of physiological midparent values versus hybrid grain yields are presented in Table 24. Only regression analyses which utilized averages of the physiological responses from S_1 and S_2 lines as midparent responses are shown. Analyses which utilized midparent data calculated from S_1 or S_2 lines separately were not statistically different from the analyses presented.

Relationships between the physiological midparent data and hybrid grain yield were significant. Yield variation among hybrid combinations were related to T_D and F_v responses from parental lines. These results indicate F_v and T_D responses of parental lines were controlled by genetic factors which effected the yield of their hybrid combinations.

The use of either T_D or F_v measurements from inbred lines as selection criteria for hybrid yield improvement would probably tend to be slow, as indicated by low R^2

Table 24. Single factor regression analyses of midparent
         values for T_D and F_v versus hybrid yield, 1986.

Trait	S. Level	$B_1 \pm$ 95% C.I.	R^2
T_D ($^\circ$C)	.03	-15.6 ± 14.2	.02
F_v (relative)	.02	1.0 ± 0.8	.02

values from each single factor analysis.

Two factor regression analysis using midparent values
for T_D and F_v to determine their relationships with hybrid
grain yields are presented in Table 25. Midparent data for
T_D and F_v were each highly significant in the two factor
regression model. Simultaneous use of IR and fluorescence
responses from inbred lines as selection criteria for
hybrid development would probably increase genetic gain for
hybrid yield improvement and stress tolerance. The R^2 value
of the two factor regression analysis was high compared to
values from either single factor model presented in Table
24. The effectiveness of the two factor model stems from
the low correlations between F_v and T_D regression variables.
Each of the physiological responses measure largely
independent plant factors related to yield.

Table 25. 1986 Two factor regression analysis of midparent
         responses for T_D and F_v versus hybrid yield.

| | Significance Levels | | $B_1 \pm$ 95 % C.I. | | |
Full Model	F_v	T_D	F_v	T_D	R^2
.0001	.0001	.0001	$2.1 \pm .41$	-30.3 ± 7.0	.47

<u>Hybrid Yields</u>

Average yields of the hybrid combinations are given in Table 26. Hybrids which showed superior performance generally involved parental lines which had cool T_D and high F_V responses. Hybrids which yielded among the lowest 50% tended to represent parental lines with warm T_D and/or low F_V values.

A few lines from the hot population, such as 701-2 and 702-4, produced hybrids with high yield performance. Data available on 701-2 shows this source had cooler leaf temperatures and higher fluorescence values than many of the parental lines derived from the cool population. Line 697-1 produced hybrids with superior performance when involved as the male parent in hybrid combinations.

Hybrids produced from 656-3 consistently yielded high. This line showed high fluorescence and relatively warm leaf temperatures. Line 657-1 had combinations of T_D, F_V and yield relationships similar to those of 653-3, yielded among the top 50% of hybrid combinations. Line 662-4 was another source among the highest yielding hybrids. It had relatively high fluorescence and warm T_D responses, but, unlike 656-3 and 657-1, its S_1 and S_2 yields were relatively mediocre.

Table 26. Mean yields (g/plant) of hybrids, 1986.

Hybrid		Yield	Hybrid		Yield
female	male	g/plant	female	male	g/plant
656\3 x 697\1		171.9	698\2 x 683\3		134.4
655\4 x 656\3		168.3	658\4 x 706\1		134.4
668\2 x 698\2		159.1	697\1 x 665\1		133.2
662\4 x 662\3		157.5	697\1 x 685\4		133.5
702\4 x 662\4		156.3	698\2 x 668\2		133.1
702\4 x 662\4		154.2	705\2 x 677\1		132.1
701\2 x 697\1		153.9	698\2 x 662\3		128.3
676\2 x 698\2		153.2	677\3 x 677\1		128.5
674\1 x 660\2		153.4	660\2 x 676\2		127.0
657\1 x 668\2		151.9	674\3 x 655\4		126.7
662\3 x 656\3		146.4	665\1 x 686\2		126.1
692\2 x 656\3		146.9	692\2 x 658\4		123.9
686\1 x 657\1		145.0	697\1 x 683\3		121.5
692\2 x 665\1		143.4	697\1 x 660\2		121.7
655\4 x 668\2		142.5	668\2 x 692\2		118.3
683\3 x 697\1		141.5	672\1 x 655\4		118.2
660\2 x 685\4		139.2	685\4 x 686\2		114.5
665\1 x 662\4		139.0	697\1 x 692\2		114.5
658\4 x 685\4		137.4	662\3 x 665\2		113.4
662\3 x 658\4		137.8	665\2 x 658\4		112.2
662\4 x 686\2		137.0	706\1 x 665\2		102.1
674\3 x 677\3		137.0	665\2 x 662\3		102.9
702\4 x 706\1		136.6	701\2 x 692\2		97.1
668\2 x 677\3		135.9	706\1 x 698\2		96.7
676\2 x 657\1		135.1	665\1 x 665\2		84.3
685\4 x 660\2		135.5	698\4 x 706\1		84.9

LSD = 28.54

Drought tolerance traits associated with inbred lines which have warm canopies due to low water requirements may cause the leaf canopies of their hybrids to remain active in CO_2 fixation and transpiration. These hybrids may therefore be better able to sustain relatively cool canopies through the entire duration of the season.

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Lines which have warm leaf temperatures due to increased water use efficiency rather than drought tolerance may be improved more readily by use of both IR thermometry and chlorophyll fluorometry in a selection index.

1986 Heritability Analyses

Yield

Parent-offspring regression analyses for yield are presented in Table 27. Regression coefficients, correlation coefficients and estimates of heritability among the analyses were statistically significant. The Ashland dryland test had the highest correlation (R^2), and regression (B_1) coefficients, and heritability (h^2) estimates in analyses involving parents and offspring from similar locations. A greater proportion of genotypic variation associated with drought tolerance and related to yield may have been expressed at the dryland site. Available soil water may have been more evenly distributed

Table 27. 1986 Parent-Offspring regression estimates of heritability for yield.

S_1	S_2	P.Level	R^2	$B_1 \pm$ 95% C.I.	$h^2 \pm$ 95% C.I.
Ross	Ross	.001	.38	.59 $\pm$ .32	.39 $\pm$ .21
Ash-irr	Ash-irr	.008	.27	.47 $\pm$ .37	.35 $\pm$ .25
Ash-dry	Ash-dry	.0001	.64	.65 $\pm$ .21	.43 $\pm$ .14
Ross	Ash-dry	.0002	.45	.66 $\pm$ .31	.44 $\pm$ .21
Ash-dry	Ross	.0002	.46	.48 $\pm$ .23	.32 $\pm$ .15

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over this location which would cause less masking of genetic effects due to environmental variation. Water supplied by rainfall probably was more evenly distributed than water from surface irrigation.

Estimates of heritability for yield from parent-offspring regression indicated that genetic factors were involved in the expression of this trait. Regression coefficients and estimates of heritability among parent-offspring analyses were not statistically different. Theoretically, estimates of heritability from analyses which utilize dissimilar locations provide the most accurate estimates of heritability (14,75).

Estimates of heritabilty from midparent-offspring analyses were not significant for yield, as shown in Table 28. Failure to detect significant heritability for yield by these analyses may have been due to the low heritability for yield. Genetic effects due to specific combining ability, dominance effects and/or heterosis probably have a greater effect on yield than additive genetic effects.

Estimates of heritabilty from parent-offspring regression were probably biased upwards due to non-additive genetic effects or common environmental factors. Midparent-offspring regressions tend to provide narrow sense estimates of heritability. Variations among environmental factors within locations may have masked additive genetic effects which may be present for yield.

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Table 28. S_1, S_2 and average midparent-offspring regression estimates heritability for yield, 1986.

Parent	P. Level	R^2	$B_1 \pm$ 95 % C. I. $= h^2$
S_1 Midparent	.33	.02	$-.17 \pm .34$
S_2 Midparent	.10	.03	$-.21 \pm .25$
Average	.17	.04	$-.24 \pm .32$

T_D Responses

Only parent-offspring analyses which involved the lines at the Ashland dryland site had statistically significant parent-offspring regression coefficients and estimates of heritability, as shown in Table 29. Analyses which utilized data from the irrigated sites had positive estimates of heritability, however, these estimates were not significant. Estimates of heritability for T_D had relatively large confidence intervals, but in general, heritability for T_D was not significant.

Table 29. Parent-Offspring regression estimates of heritability for T_D ($^\circ$C).

S_1	S_2	P.Level	R^2	$B_1 \pm$ 95% C.I.	$h^2 \pm$ 95% C.I.
Ross	Ross	.40	.03	$.19 \pm .47$	$.13 \pm .31$
Ash-Irr	Ash-Irr	.11	.11	$.37 \pm .45$	$.25 \pm .30$
Ash-Dry	Ash-Dry	.06	.15	$.37 \pm .38$	$.25 \pm .25$
Ross	Ash-Dry	.005	.29	$.29 \pm .19$	$.19 \pm .13$
Ash-Dry	Ross	.94	.00	$.03 \pm .84$	$.02 \pm .56$

Environmental factors which influenced T_D responses probably contributed to the masking of genetic effects.

Detection of heritability for T_D may also depend on whether plants had responded to severe water stress. Insufficient genetic variation may have been expressed for T_D due to insufficient stress during the 1986 season. High levels of soil moisture would tend to result in cooler leaf temperatures among all genotypes. Heritability for T_D may have been detected from analyses involving the dryland site because plants would have been stressed. Additionally, there probably were less environmental variations within the stressed site. Soil moisture was probably more evenly distributed from precipitation and moisture levels generally low.

Sensitivity towards detection of genetic factors possibly would have been improved if plant T_D responses had been adjusted by an environmental stress index. T_D responses from a common cultivar planted throughout each location and/or soil moisture data might provide an environmental stress index useful for accounting for environmental variation through the use of covariate analysis. The use of adjusted T_D responses from experimental lines might also have accounted for environmental variations and improved the sensitivity of responses in regards to detection of genetic effects.

Results from midparent-offspring regression analyses for T_D are shown in Table 30. Estimates of heritability were not statistically significant among midparent-

offspring. High stress thresholds of hybrids due to heterosis and environmental variation possibly contributed to the lack of significant estimates of heritability for T_D.

Table 30. 1986 S_1, S_2 and average midparent-offspring regression estimates of heritability for T_D (^oC).

Parent	P. Level	R^2	B_1 + 95 % C. I. = h^2
S_1 Midparent	.12	.05	$-.31 \pm .42$
S_2 Midparent	.41	.00	$-.24 \pm .72$
Average	.12	.05	$-.45 \pm .58$

Differences between lines derived from the hot and cool populations indicate that genetic factors were involved in the expression of T_D responses. Parent-offspring and midparent-offspring analyses indicate that T_D responses were not dependent on additive genetic factors and/or were masked by environmental variation.

F_V Responses

Results from parent-offspring regression for F_V are presented in Table 31. Estimates of heritability for F_V from these analyses were significant among all locations. Estimates of heritability for F_V indicated that genetic factors were involved in the expression of this trait.

Estimates of heritability among locations were lowest for Rossville. Comparisons of yield, T_D and F_V values of S_1 and S_2 lines from the different locations indicated that S_2

Table 31. 1986 Parent-offspring regression estimates of heritability for F_v.

S_1	S_2	P.Level	R^2	$B_1 \pm$ 95% C.I.	$h^2 \pm$ 95% C.I.
Ross	Ross	.006	.28	.47 $\pm$ .32	.31 $\pm$ .21
Ash-irr	Ash-irr	.001	.67	.84 $\pm$ .25	.55 $\pm$ .17
Ash-dry	Ash-dry	.0001	.58	.79 $\pm$ .29	.53 $\pm$ .19
Ross	Ash-dry	.0001	.58	.64 $\pm$ .23	.43 $\pm$ .15
Ash-dry	Ross	.001	.38	.68 $\pm$ .37	.45 $\pm$ .25

lines at Rossville had apparently suffered from more environmental stress while S_1 lines had superior performance at this location. Environmental factors which affected the relative performance of S_1 and S_2 lines at Rossville probably contributed to the lower heritability estimates obtained for this site. In addition, competition between S_1 and S_2 lines at Rossville may have influenced the expression of genetic relationships for F_v. Increased responsiveness of S_2 lines towards environmental stress relative to S_1 lines probably decreased genetic relationships among lines for F_v.

Parent-offspring regressions using data from different locations did not differ significantly from each other or from models which utilized data obtained from each location separately. Estimates of heritability from analyses of data obtained from different locations appeared to be relatively conservative when compared to analyses of data from the Ashland tests only. Relationships between parents and offspring from analyses of different environments are shown in Figs. 9 and 10.
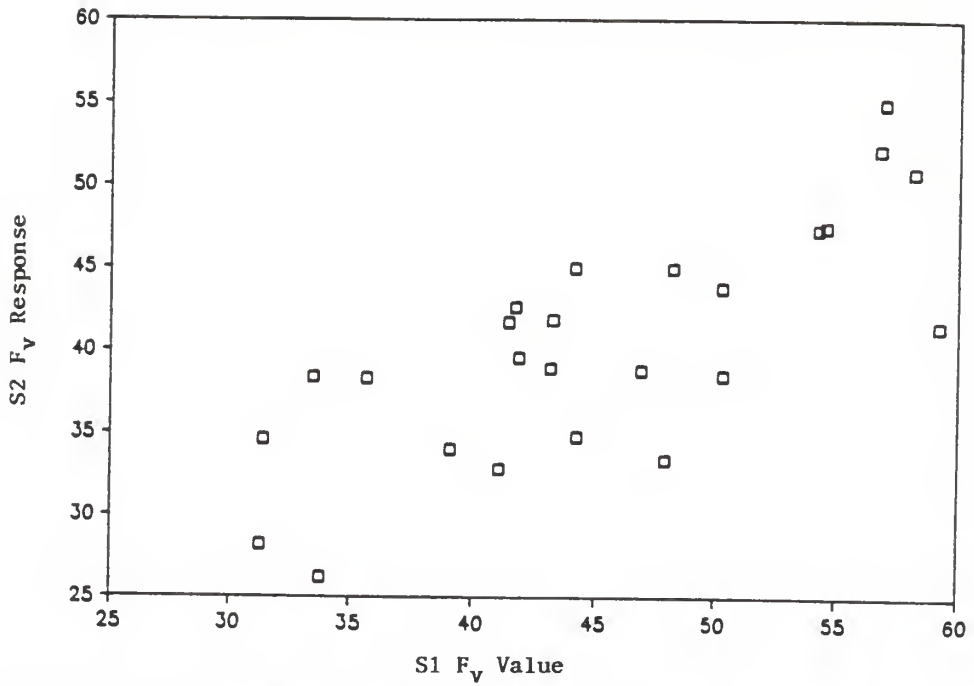
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Fig. 9 1986 Relationship between F_v responses of S_1 lines from Rossville versus the S_2 lines at the Ashland Dryland Site.
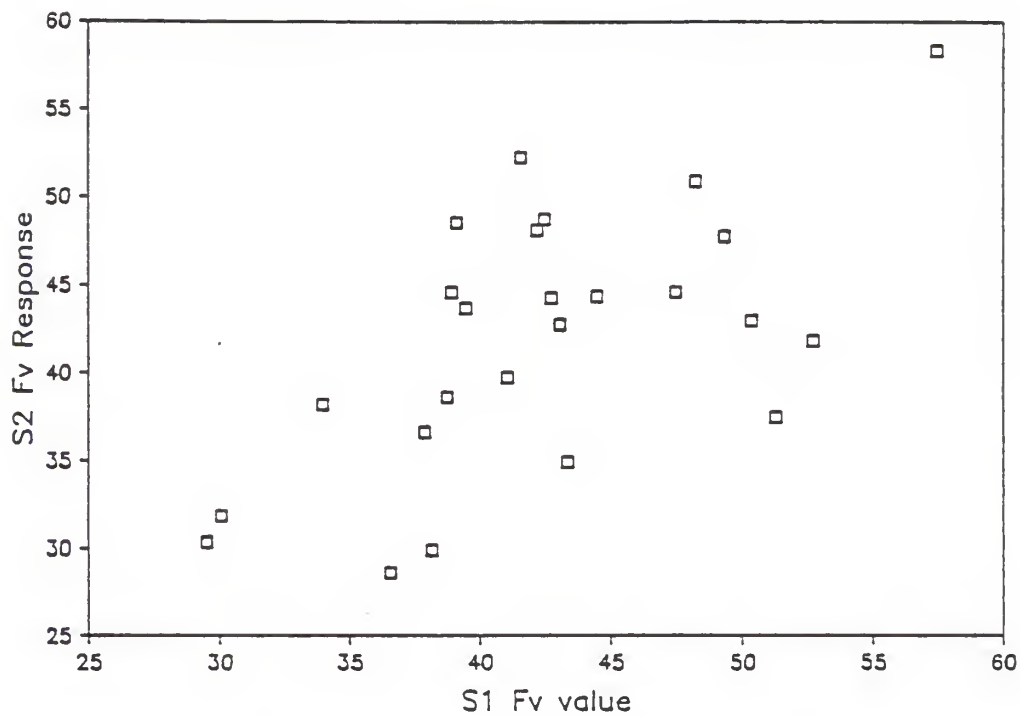
Fig. 10   1986 Relationship between F_v responses of S_1 lines from the Ashland Dryland Site versus the Rossville S_2 progeny.

Results from midparent-offspring regression analyses are presented in Table 32. The analysis of F_V responses of S_2 lines and hybrid combinations was significant. Estimates of heritabilty from analyses which utilized midparent values from S_1 lines were significant at the .075 level. Analyses of averages of S_1 and S_2 lines for midparent data gave a significant heritability estimate for F_v. Midparent-offspring analysis of midparent averages taken from S_1 and S_2 lines utilized the most F_V data available from parental lines. Average midparent-offspring relationships for F_V are illustrated in Fig 11. Estimates of heritability for F_V from midparent-offspring regression indicated that additive genetic factors were involved in the expression of this trait.

Chlorophyll fluorescence responses show potential for use as selection criteria for improvement of environmental stress tolerance in maize. Midparent-offspring and parent-offspring procedures generally indicated that additive genetic effects contributed to F_V expression among experimental maize genotypes. Relationships between F_V and yield determined that F_V responses reveal important plant attributes pertinent to breeding program goals.

Table 32. 1986 S_1, S_2 and average midparent-offspring regression estimates of heritability for F_v.

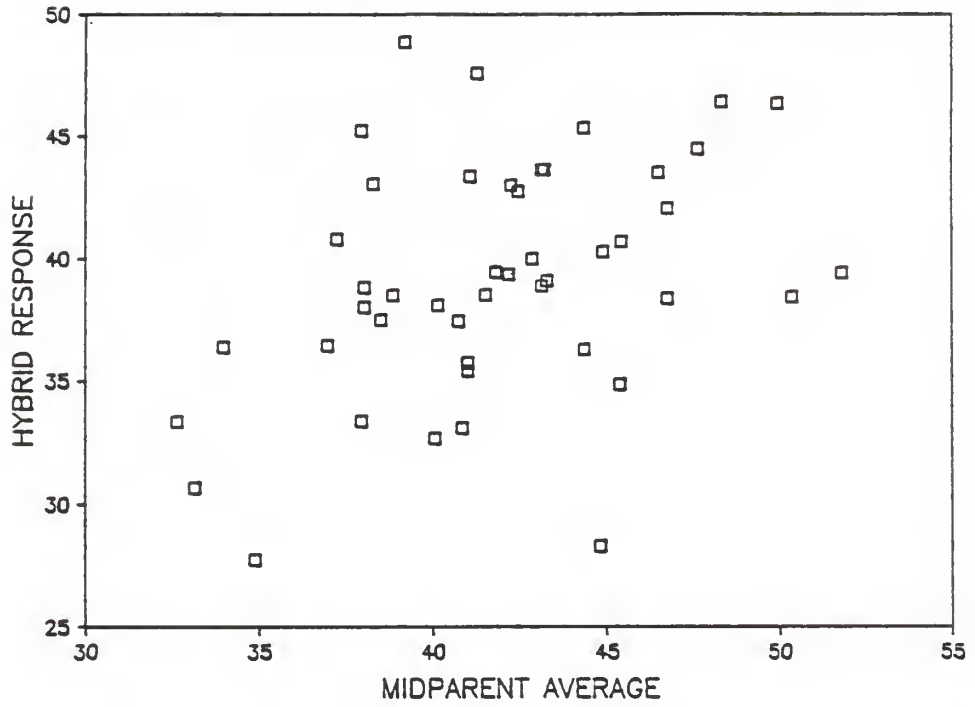| Parent	P. Level	R^2	B_1 + 95 % C. I. = h^2
S_1 Midparent	.069	.07	.26 $_+$ .28
S_2 Midparent	.0003	.14	.50 $_+$ .28
Average	.007	.15	.45 $_+$ .30

Fig. 11 Relationships from midparent-offspring regression analyses for F_V.

SUMMARY AND CONCLUSIONS

1. Plant responses to environmental stress factors imposed by hot and dry climatic conditions were measured in corn varietal tests. Root evaluation techniques were used in 1985, chlorophyll fluorescence in 1986, and infrared thermometry during both seasons.

2. Two experimental populations, designated as Hot and Cool, were planted in 1985 at the Ashland Agronomy Farm, Kansas State University, Manhattan, Kansas. Both populations consisted recombinations of selected families of previous genotypic selections from within the Kansas White Synthetic. Plants were self pollinated and evaluated for stress tolerance in the 1985 nursery. S_1 seed from selected lines were planted in a winter nursery to produce S_2 seed and a series of hybrid combinations of S_1 lines for progeny tests in 1986.

3. T_D responses of plants from the Hot Population in both 1985 and 1986 were significantly warmer than those from the Cool population. Root measurements taken in 1985 were significantly smaller for plants derived from the Hot population. These differences indicated that root development and T_D responses were related.

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4. The 1986 replicated tests were designed to determine the feasibility of using chlorophyll fluorometry and infrared thermometry as selection criteria for environmental tolerance. Genotypic effects and relationships of the physiological parameters with each other and with grain yield were evaluated. Heritability was estimated for fluorescence responses, canopy temperature responses and for yield by parent-offspring and midparent-offspring regression.

5. Canopy temperatures and chlorophyll fluorescence were related to each other and to yield among inbred lines. Canopy temperatures were inversely related to fluorescence and yield, and fluorescence responses were directly related to yields. Two factor regression analyses, which simultaneously used T_D and F_V responses from parental lines, were highly significant in their relationships with yield. Chlorophyll fluorescence responses of hybrids were related to grain yield.

6. Inbred lines which showed relatively warm canopy temperature responses and relatively high fluorescence values produced hybrid combinations with high yields. Inbred lines with these combinations of fluorescence and canopy temperature responses were rare. Generally, inbred lines which had cool canopy temperatures and high fluorescence values produced agronomically desirable

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hybrids.

7. Two factor regression analyses using T_D and F_V responses simultaneously from parental lines were highly significant in their relationship with hybrid yield. Midparent values of canopy temperature and fluorescence responses and hybrid grain yield were used as regression variables in these analyses. Two factor analyses using both physiological responses with hybrid yield had relatively high correlation coefficients.

8. Heritability for T_D responses estimated from parent-offspring and midparent-offspring were not significant. Differences among lines from the Hot and Cool populations indicated that genetic effects were involved in the expression of T_D values. Two factor analyses and/or selection indices which utilize both T_D and F_V responses provided important information for selection of superior lines.

9. Fluorescence responses gave significant estimates of heritability from both midparent-offspring and parent-offspring regression. The use of fluorescence responses as a selection criterion would result in genetic improvement for environmental stress tolerance of maize.

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APPENDIX

Hot versus Cool 1986 Inbred Sources

Individual S_1 and S_2 entries were grouped according to their original classifications of hot and cool and utilized in analyses of variance procedures. Results from these analyses are presented in Table A1.

Table A1. 1986 Sums of squares and significance levels for tests from the combined analyses of variance procedures for F_v, T_D and yields among hot and cool inbred lines.

Effect	D.F.	T_D	P.Level	F_v	P.Level	Yield	P.Level
Location	2	9.0	.0001	287.5	.10	27305.5	.0001
Populat'n	1	1.5	.01	1516.8	.0001	60961.8	.0001
Rep	3	17.6	.0001	70.9	.38	2992.3	.34
Pop x loc	2	.02	.94	79.9	.53	1023.0	.56
Error	295	61.66		18384.03		264308.41	

Each of the traits among inbred lines showed significant effects due to their origin. Variation in environmental conditions in the IR analyses would probably be accounted for better if lattice cross over designs or repeated measures designs were utilized to account for soil variation and effects due to time. T_D measurements from a common genotype planted throughout replications and locations could also provide a useful covariant variable for T_D adjustment for experimental lines.

Means of line from experimental populations are shown in the Table A2. Comparisons among all traits for the hot and cool populations were significant.

Table A2. T_D, F_v and, yield means for hot and cool groups, 1986.

Trait	Cool Group	Hot Group
T_D (^{O}C)	-0.64	-0.47
F_v (relative)	43.52	37.89
Yield (g/plant)	87.87	48.05

SELECTION PROCEDURES FOR THE GENOTYPIC IMPROVEMENT
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B.S., Kansas State University, 1985

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AN ABSTRACT OF A MASTER'S THESIS

Submitted in partial fulfillment of the
requirements for the degree

MASTERS OF SCIENCE

Department of Agronomy

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1988

ABSTRACT

Two experimental synthetic populations of maize were used in this study. These populations were designated as hot and cool based on the canopy temperature differentials (T_D) of their parental lines. Individual plants from each population were self pollinated during the first season. Genotypic selections for drought tolerance or susceptibility were based on T_D responses and visual rating of partial root systems. Nineteen lines which came from the cool population were classified as drought tolerant. These lines had large and highly developed root systems and cool T_D responses. Six lines from the hot population were selected and classified as drought susceptible. These lines had relatively poor root development and hot canopy temperatures. Differences in the overall root ratings and T_D responses from plants evaluated from the two populations were significant.

A winter nursery was used to produce S_2 seed and a series of hybrid combinations were from selected lines. A total of 50 S_1 and S_2 lines, and 52 hybrid combinations were produced. These were grown in randomized complete block designs at three locations in north-central Kansas, two replications per location. T_D measurements and chlorophyll fluorescence were used to identify superior lines having tolerance to environmental stress. Chlorophyll fluorescence (F_v) provided a measure of photosynthetic attributes and infrared thermometry identified plants able to utilize available soil water for transpiration.

Correlations among yield and physiological responses were determined for the parental and hybrid lines. Estimates of heritability for physiological responses and yield were estimated by parent-offspring and midparent-offspring regression analyses.

T_D and F_V responses correlated with yields among inbreds grown at all locations. F_V responses from hybrids grown at Rossville also related to yield. T_D responses of hybrids did not significantly relate to yield. Midparent data for F_V and T_D responses among inbreds were related to yield performance of their hybrids. Two factor regression analysis which simultaneously utilized both physiological parameters from inbred lines were highly significant in regression models with hybrid yield as the dependent response.

F_V and yield gave high estimates of heritability in the parent-offspring analyses. Estimates of Heritability for T_D responses were not significant, except when the dryland location was used in the regression model. Heritability estimates for T_D were unstable over locations which indicated that the estimates were dependent on environmental conditions specific to each location. F_V estimates of heritability were stable over locations. The only heritability estimate which was significant in the midparent-offspring analyses was F_V.