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CRITICISM AND SYNTHESIS WITH SORGHUM



ICRISAT

International Crops Research Institute for the Semi-Arid Tropics
ICRISAT Patancheru P.O
Andhra Pradesh 502 324, India

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N. Seetharama, M.V.K. Shivkumar, F.R. Bidinger, S. Sardar Singh,
R.K. Maiti, B.V.S. Reddy, J.M. Peacock, S.J. Reddy, V. Mahalakshmi
and R.C. Sachan
ICRISAT, Patancheru 502 324 India

and

A. Shiv Raj, S.R.K. Murthy and A. Narayanan
APAU, Rajendranagar, Hyderabad 500 030, India

and

Tissa Kanangara, R.C. Durley and G.M. Simpson
University of Saskatchewan, Saskatoon, Canada S7N0W0



ICRISAT

International Crops Research Institute for the Semi-Arid Tropics
ICRISAT Patancheru P.O.
Andhra Pradesh 502 324, India

ABSTRACT

Although drought causes more yield losses than the combined effect of all biotic stress factors, the progress in increasing yield under water-limited environment is small. Major reasons for slow progress are listed and the relationships between crop productivity and drought resistance are examined. Adaptations to drought in sorghum are discussed in order of their utility in the immediate future: phenological, morphological, physiological and biochemical. Results of interdisciplinary research at ICRISAT in understanding drought resistance are discussed with respect to available screening methods, genetic variability and breeding methods. Breeding and management strategies should be aimed at increasing transpirational water use throughout the season and decreasing drought injury. Suggestions are made for promoting multi-disciplinary and inter-institutional cooperation and on training plant physiologists.

PROBLEMS AND PROSPECTS FOR INCREASING YIELD UNDER DROUGHT: CRITICISM AND SYNTHESIS WITH SORGHUM

1. INTRODUCTION

Crop production is limited more by unfavourable physiochemical environments than by all other factors combined (J.S. Boyer, University of Illinois, pers. comm.). Even in the United States of America, in spite of a great deal of research and inputs, the major cereal yields range from 1/4 to 1/7 of the potential yield (Wittwer 1975). In India, the average yields of major crops in farmers' fields are 10-30 folds less than those achieved by award winning "Krishi Pandits".

Dudal (1976) has estimated that 90% of the global land area has significant agricultural problem. Of these, the most important is drought which is chronic, either due to the shallowness of the soil (24%) or due to mineral toxicity (23%) etc. All the international agricultural institutes are well geared to address the problems of drought. For instance, the sorghum improvement program at ICRISAT has given top priority in its 10 year research projections to work on genetic improvement for drought resistance and on management to increase yields in drought prone areas (ICRISAT, 1981a).

'Krishi Pandit' is the award given annually by the Ministry of Agriculture to an Indian farmer who achieves for a given crop the maximum yield recorded in a given year.

2. IMPROVEMENT FOR DROUGHT RESISTANCE: A MYTH?

Breeding plants resistant to drought or devising management strategies to increase water use efficiency is not new. Unfortunately the progress has not kept up with expectations, and research in these areas, especially breeding for drought resistance, is very frustrating. To quote Arnon (1980) "Breeding for drought resistance has been a consistent theme for as long as I remember and probably the greatest source of wasted breeding efforts in the whole field of plant breeding". Recently Asana (1981) also reviewed the literature on drought resistance and concluded that "irrigation is the best solution".

We wish to differ from these two opinions, even though these conclusions have been based on life-long pioneering work of the individuals in agricultural productivity, mainly on the following grounds: Firstly, only fairly recently has drought, with all its ramifications, been systematically analyzed at all levels of biological organization. Secondly, breeders have not extensively used diverse germplasm and novel breeding techniques such as the recurrent selection method for improvement of drought resistance. Thirdly, the tools available to us today such as remote sensing and dynamic modeling are far more superior and powerful than those employed by previous workers. Furthermore tools for quantification of stress such as infrared thermometers will greatly assist the screening efforts. The cost of these need not be prohibitively high and such tools can be simplified. For example, simple temperature sensitive adhesive paper can be used to measure and register leaf temperature. With the advance in electronics it should be soon possible to "video-tape" the leaf temperatures in the field and scrutinize the response in a quantitative way (and screen large number of genotypes in the field) Milburn (J.A. Milburn, University of New England, Australia; pers. comm.) has devised a sound equipment for monitoring cavitation in plants subjected to stress. Thus, as technology becomes more accessible, quantification of stress and mass screening in the field will soon be possible. Finally, in recent years new field screening techniques, such as the line source sprinkler irrigation system (Hanks et al 1976), have been introduced and statistical methods have been improved to deal with the higher levels of field sampling variability which is common under drought.

In this report we will examine the problems and prospects of breeding for drought resistance in sorghum, which is one of the five most important cereal crops of the world. We will also briefly examine the role of management factors which will influence yield under drought. Finally the directions for future research and training will be projected.

3. PROBLEMS IN CROP IMPROVEMENT FOR DROUGHT RESISTANCE:

Experimentally it is more difficult to incorporate drought resistance in crops than it is to incorporate disease or pest resistance. Earlier workers failed to distinguish the subtle difference between breeding for disease or pest resistance, and for drought resistance. The former kind of resistance can be handled independently of yield and in most cases the number of genes involved is quite small. In the case of drought, resistance, crop productivity is linked with water which is a substrate, constituent (e.g. of hydrophobic membrane) and the medium in which all cellular processes take place. Water is the energy for evaporative cooling of the plant. Furthermore, the flow of water in the soil-plant-atmosphere continuum (SPAC) is crucial for the flow of nutrients, hormones and other substances.

The specific problems in crop improvement for drought resistance are listed below

1. Even under the same management practices the profile of drought varies considerably from year to year, from location to location and on different soil types within a farm. Even when the soil and plant characteristics as well as management factors are known or controllable, the aerial environment (e.g. rainfall and atmospheric demand for water) is difficult to predict.
2. Several adaptations favouring water loss under drought seem to negate crop productivity. For example, both leaf rolling and stomatal closure conserve water but reduce either light interception or entry of carbon dioxide into the leaf.
3. Drought affects many morphological and physiological processes; hence consideration of a single character has not yielded any consistent results.
4. Sensitivity of drought varies considerably between stages of crop growth. Resistance at one stage (e.g. seedling stage) is not necessarily correlated with resistance at other stages.
5. In the absence of simple methods to quantitatively estimate the effects of drought, the measurements of reduction in yield under drought as compared to yield under optimum moisture supply is the only method

available so far. This is very laborious and time consuming.

6. Screening for drought resistance during 'rain-out' dry seasons may not correspond to the performance under drought occurring during a normal season of growth.
7. Some of the adaptations are difficult to transfer. For example, the Nigerian sorghums escape drought by completing heading at the end of rains regardless of their planting date because of their photosensitivity (Bunting and Curtis 1970), but this character is not universally acceptable and such genotypes cannot be easily transferred to other latitudinal zones.
8. Drought is frequently associated with high temperature stress. At higher elevation it is also associated with cold stress (which reduces water uptake) and high radiation stress. Drought also reduces nutrient uptake.

4. ECOPHYSIOLOGICAL CONSIDERATIONS IN IMPROVEMENT FOR DROUGHT RESISTANCE:

The outline of the complexity of the problem in section 3 serves as the basic diagnosis of the problem and there are several implications. The first and the foremost task of a drought researcher is to characterize the profile of water stress. The effectiveness of any attempt to improve drought resistance in a crop must be based on a thorough knowledge of, and an appreciation for locational and temporal specificity (rainfall, temperature, radiation, humidity, day length, soil characteristics, duration of crop growth, the stage at which stress occurs and the intensity and duration of stress that characterizes a particular drought condition. (Tomic and Chand 1979)

An example is the case of the wheat variety Pitic-62, which performs well under terminal drought conditions of the Canadian praires, but is of no obvious advantage in Britain, where the periodic stresses occurring throughout the growing season are quite mild (Jones 1979). Another example could be comparing the effect of soil moisture stress on transpiration under the following two environments:

- a) Sorghum grown during the rainy season (kharif) at Anantapur on shallow Alfisols (plant available water-holding capacity, PAWHC=5 cm)
- b) Sorghum grown during the post-rainy season (rabii) on deep Vertisols at Patancheru, Hyderabad. PAWHC = 23 cm

Figures 1 and 2 show the simulated relative transpiration (and hence stress) rates of sorghum (45 days to flower) planted at the beginning of the season when the rainfall on the day of sowing exceeded 2cms.

The time of sowing is very uncertain at Anantapur, while it is fairly earlier at Patancheru. The interannua variability is very high at Anantapur though the water availability at the end of the season is reasonably assured. At Patancheru, each year, in the beginning of the season water is relatively plentiful and stress increases continuously throughout the season. (Note that during 1977, when the profile was not fully recharged, the stress was slightly more in the beginning of the season).

Thus more uncertainty exists at Anantapur due to erratic rainfall and poor water-holding capacity of the soil and higher evaporative demand. At Patancheru, the moisture environment is more easily and accurately predictable and hence more rapid progress can be made in breeding or evolving management strategies to make best use of available water and to stabilize production.*

* However, the progress in breeding for better adapted rabi types has been very slow, indicating the possibility of involvement of other limiting factors such as daylength, temperature regimes etc.

5. EMPIRICAL SCREENING IN THE FIELD

1. Repeatability in the field tests: The ultimate test of drought resistance is yield measured in the field under typical drought conditions. It is very difficult to develop field techniques to evaluate large number of genotypes for drought resistance. In normal seasons in the tropics, rainfall is erratic and hence even at a given location it is very difficult to conduct field experiments which can provide results applicable over many years. To be very efficient, field evaluations ideally need one irrigated non-stressed control to compare the effect of stress per se on grain yield. The proportional reduction in yield under stress compared to the yield obtained under well-watered conditions is more useful as a selection criterion (Blum 1974; Asana 1976; Seetharama and Bidinger 1977) than mere absolute yield estimates under stress.

When using the information from multilocal testing programs, care should be taken to compare the test sites (environments) with those of target regions. If this is not done types which have a high degree of drought resistance across different environments, but much poorer local adaptability and productivity, may be selected. For example it is more valid to select or test under different depths of soil in the post-rainy season than to use multilocal trials in the rainy season. The problem of repeatability in practical breeding can be solved by selecting in large populations (Murd 1976). Selection of entries from field trials within a single season (even from several closely related sites) is often difficult.

Ranking of genotypes in drought screening trials for yield from one year to another or between similar locations is frequently found to be variable. A major problem lies in developing field sites and irrigation techniques to produce a required pattern of stress. Also ^{while} handling the within-test variability, differences in soil texture, depth etc. which are not very evident under non-stress conditions becomes a major problem under stress conditions.

The coefficient of variation (CV) of the trial mean (Fig. 3A) or CV of mean yield of a cultivar (Fig. 3B) increases as the stress level increases (or as mean yield decreases). Successful field testing involves a careful selection of site, ~~choice of sites~~ good control of irrigation and development of statistical methods to adjust for yield variability (e.g. use of covariance or moving mean using systematic checks). Use of 'hill plots' seems to be less advantageous in sorghum since the plant produces nodal or basal tillers under such conditions. The loss of competitive environment under hill plots may also increase the variability (work of Leisle quoted by Hurd 1976). With proper techniques, cultivar differences in drought resistance for rice and wheat have been demonstrated and this was repeatable over a number of seasons (O'Toole and Chang, 1978; Fisher and Maurer, 1978). At ICRISAT we have reasonably sound techniques to screen sorghum (Seetharama et al 1982) and pearl millet (Bldinger et al 1982) for drought resistance in the field.

2. Screening for drought resistance using a line source: The line source (LS) (Hanks et al 1976), as described earlier (ICRISAT 1979, Seetharama et al 1981) continues to be useful for screening sorghum cultivars for drought resistance since it can be used for maintaining a stress gradient with minimum land requirement and cost with a great degree of precision. An experiment was conducted during the 1980 rabi with 18 cultivars on medium deep Alfisols. From each of the two replications (on either side of LS) each row was harvested for grain yield and biomass estimation. Regression of grain yields against water applied through LS plus rainfall received until physiological maturity of each genotype (Fig. 4) was used to determine the yield potential (yield of rows nearest to the LS; intercepts in Fig. 4) and drought susceptibility (slopes). Since the actual water applied (which differed depending on maturity; 6 irrigations for early ones and 7 for late ones) rather than distance from LS is used as independent variable, nearly a fortnights' difference in maturity is ignored in this discussion.

The correlation coefficient between intercepts (yield potential) and slopes (drought susceptibility) in Figure 4, was very highly significant ($r = -0.813^{***}$). This apparently poses a serious problem to the breeders aiming at combining high yield potential with the low drought susceptibility. Hence the following approach was used to select drought resistant genotypes. The slopes from the regressions shown in Figure 4 were regressed against intercepts (yield potential in Figure 5). Genotypes showing above average yield potential (points on the right hand side of broken vertical line) and slopes less than regression predicted values (points above regression lines) were selected as drought resistant types (least reduction in yield per unit decline in water supply). Similarly the genotypes below the regression line and on the left hand side of the broken vertical line can be identified as susceptible types.

When the genotypes were selected using the above approach it was noted that the entries in the drought resistant group (CSM6, DJ1195 and SPV35) did not necessarily have a steeper slope than entries in the acceptable groups (CSV5, V302 and D71463). D71463 and D71464 are sister lines arising from the same cross. In the field ^{during} screening for leaf firing (ICRISAT 1981b; Peacock 1981) under hot and summer conditions D71464 was found to be more resistant than D71463, the former also recovered faster. From Figures 4 and 5 it is apparent that while the difference in the Yield potentials under moist conditions is very small, there is considerable variation in drought resistance. Studies conducted in collaboration with scientists at Haryana Agricultural University, Hissar during hot and dry summer ^{of 1981} indicate that the above differences may be primarily due to differences in phenology i.e., D71463 is late, especially under stress.

In order to compare the drought susceptibility alone amongst genotypes, without considering yield potential, yields were

expressed on a relative basis as fractions of the intercept (Fig. 6). The slopes in Figure 6 can be directly compared for drought susceptibility, uninfluenced by yield potential. Although the slopes for CSH6 and D71464 are quite different in Figure 4 they are similar when adjustment is made for the yield potential. Susceptible entries like V302 and CSV5 have far steeper slope than resistant lines (e.g. CSH6 and DJ1195). There were considerable differences between the two sister lines D71463 and D71464.

Since the applied irrigation water decreased continuously and linearly as the distance from LS increased, the stability analysis of Eberhart and Russels (1966) was adopted using each row as one '(moisture) environment'. The regression coefficients indicating stability (b's) and residuals were highly correlated with slopes ($r = -.976^{***}$) and coefficient of determination ($-.769^{***}$) respectively, obtained in the analysis described earlier (Fig. 4). Thus, the data collected on a small piece of land using a LS in a single location can be used to select drought resistant ('stable') genotypes. The stability model can also be used to categorise the genotypes in terms of their stability across moisture environments created at a single location.

The early hybrid check CSH6 showed the highest yield potential, and, in spite of having a steeper slope in Figure 4, out-yielded all varieties at all levels of water supply used in the experiments. This supports the common belief that hybrids are more productive than varieties even under stress.

6. YIELD POTENTIAL vs DROUGHT RESISTANCE

The higher yields^{of} advanced varieties (e.g. SPV 351) or hybrids (e.g. CSH6) are highly related to their overall yield potential per se rather than drought resistance. Garrity et al (1981) have quoted Quinby's earlier work (1974) which suggested that the higher yield of hybrids is related to their greater efficiency in dry matter production and to a higher harvest index. Within the plant kingdom xerophytes are generally less productive than mesophytes. Gaff (1981) has studied 31 resurrection grasses and found that most of them were low in dry matter accumulation. In their survey of drought resistant species in Rajasthan deserts, Ahmed and Sankhla (1981) found that those species which survive better are poorer in biological productivity. From Figures 4 and 5 it is clear that drought resistant cultivars like DJ1195 and IS12611 are less productive than CSH6 (although this conclusion doesn't hold good when biomass productivity, rather than grain, is considered).

High yielding strains of forage grasses under conditions of adequate moisture supply are not always high yielders under drought (Johnson et al 1981). Orians and Solbrig (1977) have reported that 'trade-off' exists between performance under well watered and stress environments. Reitz (1974) has implied that selection for wide adaptability may, in reality, result in selection for mediocrity. Bunce (1981) has reported that photosynthetic rate (and stomatal conductance) of Taraxacum populations under favourable conditions was negatively correlated with ability to grow in dry soil. Sullivan (1972) has also noted that sorghum plants with high drought tolerance are generally associated with decreased growth and development. Some of the traits which reduce the loss of water from the plant such as decreased leaf area (either by production of smaller and fewer leaves or by rapid senescence), leaf rolling or stomatal closure, waxiness etc. also reduce photosynthesis since less light is intercepted or less CO₂ absorbed (Table 2). Hanson and Nelson (1980) have thoroughly reviewed this aspect and concluded that a 'trade-off' exists between adaptability to drought and maximum growth or yield and they explained this from the view point of plant strategies or 'energy drain' caused by the production of a chemical or structural component regarded as unnecessary under non-stress situations. Parson

(1979) has pointed out that in selection for drought resistance care must be taken not to select just for small plants with limited growth potential.

Figure 7 conceptualizes the relationship between productivity and drought resistance. The relative growth efficiency of two hypothetical cultivars with or without drought resistance, but with high yield potential (RP and rP , respectively) and a third drought resistant one with low yield potential (Rp) are compared. Notice that the high yield potential cultivar RP always takes advantage of the growth opportunities (mostly limited by water supply), while the low yield potential type (Rp) lags behind. However the latter may sometimes appear more efficient than the former e.g., between 70 and 85 days. The RP would have a higher demand for water because of the higher leaf area developed and maintained over time. Rp on the other hand, may have less leaf area and hence more moisture remains untapped in the soil for later use. However, the high yield potential type also has mechanisms to cut down its water consumption temporarily when the supply is limiting and also to increase consumption if the water becomes available later in the season. The susceptible cultivar rP , which has a higher growth rate under well watered conditions (before stress starts), may run out of water at a critical stage after stress and collapse.

The above arguments imply that any further increase in drought resistance is difficult at higher yield potentials. However this is not necessarily true. Seetharama and Bidinger (1979) have shown that the correlation between yield potential and drought resistance (measured as maintenance of yield under stress) becomes weaker as the stress level increased. It is only under severe stress that the drought resistance attributes are completely expressed and yield 'maintained' in resistant types. This means that the survival mechanisms become more important than maintenance of productivity (yield potential) if the stress intensity is high or duration is long. In this way production steps in the developmental sequence will be totally disrupted. Boyer and McPherson (1975) have fairly rejected the Mederski and Jeffer's (1973) conclusion (that it is possible to select for drought resistance under optimum growth conditions) on similar grounds: to screen for physiological characteristics

that are only called into play during drought one must select under desiccating conditions.

Arnon (1975) has concluded that breeding for specific environmental conditions is not a worthwhile exercise. Instead, a high yielding broadly adapted variety should be used. However, it is well known that the material selected on the basis of international trials of international institutes is not suited to all countries which have served as a test location. High yielding maize varieties of CIMMYT do not grow well in Israel (A. Blum, Volcani Center, Israel, pers. commu.) or in India (D. Sharma, ICRISAT, pers. commu.) Hence strong local efforts are needed to produce material useful for any specific region giving due consideration to the local drought situation.

From the logic developed in section 4, it would follow that the kind of genotype which could perform well from year to year at Anantapur during the kharif season (Fig. 1) may not be the same as the one resistant to terminal drought at Patancheru during the rabi season (Fig. 2).

In order to evaluate the relative importance of yield potential (as well as wide adaptability) and drought resistance, and to establish whether specific adaptability exists for the particular pattern of drought, direct selections were made in different stress environments (see below) from the S_0 generation of NP9BR and Downs' populations and from F_2 's derived from single crosses between two resistant and widely adapted cultivars (CSV3 and CK60B) with a susceptible one (CSV5) for two generations.

The selection environments (in F_2 's, F_3 's etc.) included the following:

- i) Kharif stress (on light shallow Alfisols)
- ii) Rabi stress (receding moisture situation on medium deep Vertisols)
- iii) Summer mid-season stress (crop not irrigated during panicle development stage, shallow Alfisol).
- iv) Summer control (regularly irrigated summer crop).

Twenty-three selections made from each population and crosses during each of the seasons were tested for yield together with the CSH6 hybrid and CSV4 variety as checks, during kharif, rabi and summer of 1980-1981. The objective was to see whether the selections made during any particular season are in reality best suited only for that particular season. Table 1 shows the mean yields of kharif and rabi trials. The rabi selections are distinctly superior in rabi yield trial. Additionally rabi selections are also good for the kharif season; in fact they are even better than kharif selections. Yield differences between selections made during different seasons could not be explained in terms of phenology. For example, during the kharif, mean days to flower and physiological maturity for both groups were same (61 and 92 days, respectively).

The above anomaly can be explained in terms of the overriding effect of yield potential of the selections rather than gene effects responsible for drought resistance or adaptability. During the kharif test, terminal drought did occur because of lack of rains and poor water-holding capacity of shallow Alfisols. Thus, the stress profile was more conducive for rabi selections and adaptation for terminal stress, than kharif types. Seetharama et al (1981) emphasized that the ideotype for any given location can never be more precise than the quantitative and probabilistic description of the seasonal moisture environment and other factors influencing growth and productivity. Arnon (1980) has pointed out that variability within a given ecological niche can be greater from year to year, than between locations or seasons.

There was no difference in yield between the summer selections made under midseason stress or under regular irrigation. This points out the difficulty in selecting for each agroecological set of conditions. Although several distinct agroclimatic divisions exist in India (Murthy and Pandey 1978), widely adapted cultivars such as CSH1, CSH6, CSV4, SPV351, are found to yield far better in almost all years of testing in most of the locations, than the best local cultivars. Hence the conclusion has been made that the whole part of the country growing grain sorghum during the kharif can be

treated as one zone (Rao et al 1979). Only varieties with wide adaptability are likely to be retained after such tests.

While we may succeed in characterising a location on the basis of long term weather records, it is difficult to deal with the interannual variability. The problem is made more complex as the seasonal plant microenvironment is further subjected to management factors (e.g. date of sowing or plant population). As the seasonal rainfall decreases, the variations increase (Cocheme and Franquin 1967) and hence the problem of breeding for a specific plant type adapted to that location becomes more difficult. The profile of drought^{which} the plant undergoes during F_2 could be qualitatively and quantitatively far different from that for the selection of the F_3 generation. Hence only those adaptive features which are given a chance to express themselves during each year of the selection period are likely to be retained in the final selections. This emphasizes the need for choosing proper location or season where the relevant pattern of drought stress occurs on almost all years.

In planning a breeding program it is necessary to study a relative acreage under different kinds of drought as well as the stability of production potential of each region. Maximising production in favourable years to provide a buffer for the lean years, has limited applicability in solving the food problem especially in densely populated developing countries (Swindale and Bridinger 1981).

7. ADAPTATIVE MECHANISMS

To answer the question of which parameter best describes and explains plant response to water stress, and which adaptive feature is responsible for drought resistance requires an understanding of how plant water stress is transduced into plant performance (Steponkus et al 1980). There has been a great deal of published material in the form of proceedings of various symposia and workshops (Goodwin and Nottingham 1979, Mussell and Staples 1979, Turner and Kramer 1980, Paleg and Aspinall 1981, IRRI 1981, ICRISAT 1980, 81c Johnson 1981, Monteith and Webb 1981, Krizek 1981), books (Brown 1974, Lyons and Briedenbach 1979, Levitt 1980, Simpson 1981) and reviews (Boyer and McPherson 1975, Benboudian 1977, Begg and Turner 1976, Parson 1979, Jordan and Monk 1980, Jordan 1981) and hence we will confine ourselves to the general assessment of the significance of various mechanisms or adaptive features in the immediate as well as the distant future.

Several authors (Jordan and Monk 1980, Turner 1981 a & b, Seetharama et al 1981, Hanson 1981) have listed the various types of adaptive mechanisms found in sorghum (Table 2) which can be classified as:

- a) Phenological
- b) Morphological
- c) Physiological
- d) Biochemical

a) Phenological adaptations are of three kinds:

- i) Earliness
- ii) Photoperiod sensitivity
- iii) Developmental plasticity

i) Earliness: The most important and common change that occurs in high yielding cultivars bred for drought prone areas is earliness in maturity. Thus the early hybrids and varieties have replaced all locals in India under progressive farming and thereby achieved a quantum jump in the yield of sorghum (Rao et al 1979). Further, earliness has also made the crop more widely adapted across the country and offers better intercropping opportunities. However,

earliness has not been a successful strategy elsewhere, e.g. in Zimbabwe, where substituting the late with early cultivars has made harvest difficult at the end of the season when the unpredictable rains may cause damage by preventing harvest in time as well as by grain molds (J.H. Williams, ICRISAT; pers. comm.; also see below).

- ii) Photoperiod sensitivity: In West African countries like Nigeria, Mali and Upper Volta, the rainfall at the beginning of the season is very erratic, while at the end of the season it terminates abruptly. The local farmers take advantage of the photosensitivity of the sorghum since the plants flower at the same time irrespective of sowing date (Curtis, 1968). With an insensitive type this kind of flexibility in sowing date is not possible and a late sown crop would flower and fill the grains under both severe moisture deficits and cold conditions in many places every year. Also when sown early during wet years such genotypes will suffer from grain weathering. An additional advantage of photosensitive types is the prevention of severe buildup of pest populations (e.g. midge or earhead bug) since in all fields, irrespective of date of sowing, the crops flower simultaneously. If the insensitive types are grown, an early sown (and hence early flowering) crops will undoubtedly serve as the source of severe epidemics for the late sown crops. Hence the ICRISAT programs at West Africa will retain this feature of sorghum in their breeding efforts (J.F. Scheuring, ICRISAT, Bamako, Mali, per. comm.).

However, it is noted, in the case of India, that earliness has been the most extensively used strategy in contrast to photoperiod sensitivity. Photosensitive varieties have a limited range of adaptation. For example Webster (1972) reported that a sensitive variety developed at Samaru, Nigeria is adapted to an ecological zone no more than 80 to 120 kms wide north to south. (The length of wet season increases from north to south in Nigeria). Outside this zone the variety was too early or too late. Such an approach of breeding for extremely narrowly adapted varieties can only be useful if each location has a strong breeding program of its own; otherwise the crop improvement in such places will lag behind the

centralized programs where the widely adapted varieties are emphasized, at least initially.

- iii) Developmental plasticity: Stout et al (1978) have described stress induced changes in the length of growth stages. Seetharama and Bidinger (1979) studied 33 germplasm lines under well irrigated and midseason (approximately during panicle development stage or GS2) stress and found that the days to flower under stress could be either hastened by a day or delayed as long as 33 days. There was a positive and significant correlation ($r=0.55^{**}$) between days to flower under control and delay under stress. This association, however, appeared to be largely due to those cultivars which flowered earlier than about 80 days (Fig. 8A). In another experiment with 33 S_1 lines from NP9BR population, the correlation was not significant ($r=0.27^{NS}$; Fig. 8B). In both cases the delay approximately follows the normal distribution. Thus this response seems to be, partly at least, genotype specific and hence it may be possible to manipulate this character in a breeding program for a region where there is a good probability of adequate rains late in the season to complete an extended crop growth period.

Figure 9 shows the relationship between delay in flowering and grain yield under stress. In the first experiment, the stress yields were reasonably correlated with delay up to about 10 days in flowering. In the second experiment the same factors were unrelated (Fig. 9B).

The nontillering sorghum commonly grown in India lacks the degree of plasticity exhibited by other tillering cereals like wheat and pearl millet which can use tiller number (and head size) to buffer against the available water for fairly long periods during the season. However, some sorghums do produce nodal tillers and, if the midseason stress has reduced the main culm yield, the nodal tillers make up for the loss by producing grain rather quickly, once the stress is released by rains. During the 1976 summer experiment at ICRISAT, IS 1037 under

midseason stress produced 1.1 t/ha on the main shoot, and an additional 1.5 t/ha was produced on nodal tillers; the control only produced 2.1 tons. Similar observations were made in the U.S.A. in the case of sorghum undergoing stress early in the season (T.C. Hsiao, University of California, Davis, pers. comm.).

- b) Morphological adaptations: Morphological adaptations which increase water uptake (Table 2) as well as reduce consumption of water have been extensively discussed in the literature (see above). At ICRISAT resistance to wilting, leaf firing and recovery ability at seedling stage have been evaluated in the field, in wooden and brick flats, and in cylinders. Significant genotypic differences in response to drought were found both in the germplasm and breeder's elite lines (Figure 10A) as measured by scoring for wilting and recovery and survival after release of stress. Most of the seedling drought resistant lines had light green leaves with a 'glossy' surface, while the susceptible lines, in general, had dark green leaves (Malti 1980). Scanning electron micrography showed that the 'glossy' leaves (Fig. 10B) have smooth wax plates forming large crystals, whereas the non-glossy (Fig. 10C) ones have small needle shaped crystals. Hull et al (1978) have noted similar differences in wax structure amongst drought resistant and susceptible Eragrostis species. Currently more germplasm is being screened to test the wide scale applicability of the 'glossy' trait and epidermal wax deposition pattern in the breeding program.
- c) Physiological adaptations: Physiological adaptations have been under study for more than a century and the findings for sorghum are summarized in several recent reviews (Jordan and Monk 1980, Jordan and Sullivan 1981, Garrity et al 1981, Turner 1981a, Seetharama et al 1981). We want to emphasise that any single physiological characteristic independent of others is unlikely to be directly correlated with drought resistance in the field. Table 3 shows the various physiological characteristics of ten sorghum cultivars under typical rabi conditions at Patancheru. Although M35-1 and CSH8 are more resistant cultivars in the field than CSV5 and V302, no single physiological characteristic can match with that observation

perfectly.

The physiological traits can be suitably used in screening genotypes by adapting the following procedures:

- i) Measure the traits diurnally and or seasonally and use the integrated value, if needed, after "cleaning" data for field variability etc. Figure 11 shows the seasonal pattern of differences in leaf temperature between different irrigation treatments over fully irrigated control. The LI treatment had cooler leaves than the control during the later stages. This was because of reduced leaf area in LI compared with controls (and hence less stress). Even the dry matter yield of LI was marginally more than control suggesting that it is not merely total green leaf area, but also the activity of those leaves, which produce higher yield under stress. Thus the judicious loss of some leaf area is more beneficial than having a large area which subsequently undergoes more severe stress. Piara Singh (1981) has described the advantages of integrating various physiological stress parameters to predict yield quantitatively.
- ii) Measurement of several traits measured at regular intervals or during critical stages: If physiologists are able to devise a "battery of tests" for the given pattern of stress environment this would tremendously stimulate breeders to use physiological parameters-(L.R. House, ICRISAT, pers. comm.). Research at ICRISAT since 1976 has proved useful in formulating a hypothesis regarding such a "battery of tests" for rabi sorghum. For example, a capability for osmotic adjustment, remobilization of stem reserves to the grain, rapid phenological development (not delayed by stress) with proper management practices for high and stable productivity (Seetharama et al unpublished).
- d) Biochemical adaptations: During the course of evolution of mesophytes, most of the changes that have taken place are either morphological

or phenological and the basic biochemical apparatus has remained almost unchanged. Amongst higher plants there is a great variability amongst species (e.g. C4 vs C3 pathway; Good and Bell 1980) in efficiency of water use, but differences between genotypes within a crop species are rare. However there seem to be reasonable differences in the metabolism of small molecules: e.g. differential production of proline or betaine in response to stress (Hanson 1980) or changes in hormones (Milborrow 1981, Kannangara et al 1981b). Figure 12 shows changes in abscisic acid (ABA) phaeic acid (PA) and 3-indolylacetic acid (IAA) as the stress level increase. the threshold leaf water potential for inducing ABA synthesis is around -14 bars. Genotypic differences in hormonal levels are found even under normal conditions and changes under stress are also genotype - specific (Kannangara et al 1982). Phaeic acid levels decline with stress and are positively correlated ($r = 0.61^{**}$) with yield levels. The relationship between leaf water potential and IAA (Fig. 12B) is more complex. The IAA levels increase after the initial decline: this may be due to the fact the plants at the extreme levels are already acclimatized to stress, mainly by small size and reduced leaf area. In the above preliminary study with CSH8R under LS treatment, the correlation between ABA and yield ($r = -0.65^{**}$) was similar to the correlation between irrigation and grain yield ($r = 0.68^{**}$) except being opposite in sign. Thus leaf ABA content could be equally effective as irrigation to predict yield under different levels of stress (Kannangara et al 1982). However at this stage the technique has to be further perfected and simplified before being used on a large scale.

Physiologists envisage the control of transpiration by hormones as dynamic (Jones 1979, Walton 1980), responding quickly and favourably to the onset of stress and reversing to the original level once the stress is removed. Thus it is possible to select for a low natural level of hormones with a tendency to produce large amounts at the onset of stress (e.g. accumulation of ABA in response to stress) or enhanced sensitivity under stress conditions (e.g. increased stomatal

sensitivity to lower concentrations of ABA in prestressed efficient than obligatory irreversible adaptations. Increased research in this area is expected to produce rich dividends. In an earlier section we have discussed how the yield of the crop under stress is influenced by its yield potential. Obviously we need to know far more about the role of hormones in the various physiological processes and their interactions with the environment and also how they are integrated during ontogeny to produce a particular magnitude of yield (or yield reduction under stress).

Studies with mosses have shown that the ability of the plant to mobilize enzymatic defence against lipid peroxidation (Dhindsa and Matowe, 1981) and to conserve messenger RNA during drying (Dhindsa and Bewley 1978) are very useful in detecting differences in drought tolerance. Boyer (1981) and Lawlor (1981) have reviewed the potential for biochemical and physiological modifications of crops to yield under stress. Although they have identified a few areas for possible applications, the existing knowledge is not enough to be of immediate practical use in screening genotypes.

Hanson (1980) has listed three different reasons why the metabolic traits could prove far more useful than conventional ones (especially during the later phase of drought research program when the conventional approaches are exhausted). Walbot (1980) in a recent review has said "unfortunately, the agricultural sciences have captured the imagination of too few molecular biologists seeking new problems largely due to separate, insular environments of land grant colleges and of major research centers in molecular biology". However the scene has been changing as evidenced by the importance given to agricultural genetic engineering both worldwide and in India (GOI 1980). The United Nations Industrial Development Organization is planning to establish an International Center for Genetic Engineering (Stein 1981). Woolhouse (1981) believes that "physiology should be pressed from the description down to the level of metabolic fluxes and thence to the controlling enzymes, membrane constituents and their determinants so that breeders can consider specific attributes." However, Hsiao and

Acevedo (1974) have cautioned that over-emphasis on molecular biology sometimes leaves the basic essential work at cell and plant levels (e.g. role of turgor in growth) unexplored or overlooked. Thus a proper balance of work on all aspects at each level of biological organization must be ensured.

8. INTERDEPENDENCE OF ADAPTIVE MECHANISMS: ROLE OF INTERMEDIATE AND INTEGRATING ADAPTATIONS

The above discussion of various adaptations under the respective four headings should not give the impression that each of these four are distinct categories, independent of each other. Sinha et al (1981) have argued that crop productivity, including under stress, is a total sum of several interacting factors varying in quality, quantity and duration. The ultimate yield produced under stress depends upon the net results of all these interactions and it is necessary to have a complete picture of all processes and components to fully understand and remedy drought effects. Note that short term biochemical events such as ABA production have influences on both stomatal response (short term) and on vegetative and reproductive growth (long term; Quarrie and Jones 1977). Similarly many physiological responses to stress influence crop growth and yield through changes in phenology and morphology. Thus it is very important to learn about not only the primary effects of above adaptations, but also the interactions between them.

For the immediate future it is worthwhile to concentrate on those adaptive features which are intermediary in character (e.g. leaf area) or which have an integrative effect (leaf area duration or leaf area/ root length ratio; representing a balance between water demand and supply) as illustrated below.

1. Leaf area (Fig. 13 and 14).

On 22nd April 1981, six cultivars of sorghum were grown under irrigation for 10 days (5-leaf stage). From then on one treatment was left unirrigated (stress) while the other was irrigated twice a week (control). The emergence, expansion and senescence of all leaves were measured daily, even after the arrival of monsoon rains during mid June (53 days after planting). Figure 13 shows the area of individual leaves under control and stress for two contrasting cultivars. While the total number of leaves was unchanged under stress their sizes were different. In CSH8, there was not much delay in emergence of leaves under stress (delay of 0,3 and 4 days under stress for 10th, 15th and

20th leaf), although leaf sizes were reduced. In CSV5 only the leaves 7-15 were reduced in size under stress; on the other hand emergence of leaves was delayed to a greater extent (Fig. 14) (by 2, 14, and 15 days for 10th, 15th, and 20th leaf) under stress and the final few leaves emerged and expanded after the relief of stress by the advent of monsoon rains during late June. Since the environmental conditions were optimum for leaf growth after rains, the top several leaves actually grew bigger in size under "stress" than under control. Thus the phenological changes can markedly change the morphological, or even physiological responses. If water availability is expected later during the season the postponement of development could be a better strategy than production of smaller leaves.

2. Analysis of change in yield components under stress (Fig. 15).

The effect of three different patterns of stress during the panicle and grain development was studied during rabi 1979, using a line source on medium deep Alfisols (Figure 15). The seed number (Fig. 15A) as expected, was influenced only by stress during the panicle development stage (GS2). A linear decline in seed number was noticed under the gradient of stress (treatments GS/GS or GS/NS) but under the third treatment (US/GS) the seed number at different distances from the line source was not significantly different, though drastically reduced (no irrigation during GS2; line source irrigation applied only during GS3). On the other hand, seed size differences were found only in the treatments receiving variable amounts of water during GS3 (in GS/GS and US/GS; not in GS/NS). Such yield component analysis can help us to define the ^{/stress effects on} individual steps which occur sequentially during the season.

Following the arguments of Sinha et al (1981) it is also clear that phenological and morphological adaptations represent greater integrating effects than either physiological or biochemical adaptations, and hence in the immediate future use should be made of them. Measurement of physiological and biochemical parameters stipulate higher levels

of time and resources (Swindale and Bidinger 1981) and hence the progress in using them will be slower. Some of the morphological ('glossy') and developmental ('recovery ability') traits have more profound and integrating effects than others (Table 2).

Even the drought resistance mechanisms (Levitt 1972) are not mutually exclusive. Sullivan (1972), discussing the basis of selection for drought resistance, suggested combining all interacting mechanisms. Boyer and McPherson (1975) have argued that some 'avoidance' type responses may also act as pretreatment for developing greater tolerance. Blum (1979b) has shown that early sorghum genotypes not only escape drought but also avoid it because of reduced transpiration demand as a result of decreased leaf area and high root length - leaf area ratio.

9. PHYSIOLOGICAL APPROACH FOR BREEDING FOR DROUGHT RESISTANCE

Plant breeding has been most notably successful in improving characteristics that can be easily observed. So far as breeding for drought resistance is concerned, it has been singularly successful in breeding for earliness hence drought escape. However in spite of correction for maturity, stress conditions may occur at various yield-determining stages. The first reaction of a crop is to continue to grow and develop by avoiding stress. Initially this is done by the uptake of stored soil moisture and later, when soil water becomes limiting, water loss from the shoot will be curtailed by one or more adaptive mechanisms (Table 2). In addition to drought escape and avoidance the crops should be in a position to invoke tolerance mechanisms under continuous stress. It should also have capacity to recover after the restart of rains. Under field conditions crops make use of all these mechanisms to varying degrees, but until now breeders have been consciously selecting mainly for escape and other unidentified or suspected traits such as recovery from stress or deeper roots which are associated with good yielding ability under stress. There is no doubt that drought escape is the first line of defence but for any further improvement other mechanisms should be extensively made use of by consciously selecting for such traits.

Maunder (1972) pointed out that single trait responses do not offer a valid screening index, but rather the total plant function must be considered. Asana (1957) attempted to explain the lack of correspondence between single measurements of stress and drought resistance. According to him these traits only indicate the ability of the plants to survive (e.g. desiccation tolerance). In the normal seasons such traits may not be directly related to yield; nonetheless their importance cannot be ignored. Some breeders also felt that the 'package of adaptive traits' suggested is not satisfactory. However, the significance of the combination of these adaptations must be evaluated in the context of the ultimate environment in which the plant is expected to perform. Breeders should be ready to learn by trial and error in the absence of detailed quantitative information on the environment.

How can several traits be brought together, especially when some of them seem to be mutually exclusive? Sullivan (1972) has given an analogy from nutritional and baking quality research in wheat. Several factors which could not be identified visually have been identified and combined judiciously for maximum benefit. Since simple field screening techniques can now be combined with several short term measurements or responses indicating avoidance or tolerance mechanisms (Turner 1981c, Seetharama et al 1981) greater progress can be expected than has hitherto been possible.

Garrity et al. (1981) have recognized five distinct stages in the physiological approach for breeding for drought resistance:

1. development of hypothesis
2. search for genetic variability
3. establishing a rapid screening method
4. determination of mode of inheritance of the trait of interest plus breeding method
5. proving that high levels of the trait improve drought resistance in the field.

No doubt, it will be very difficult to satisfactorily complete all these stages with all the characters but an enterprising breeder would always be happy to extend his 'art' and work on as many traits as possible. It is necessary for the physiologist to work closely with the breeder and make use of his material and approach and pay more attention to 'ideotype verification' after 'ideotype formulation' (Fischer 1981). Great expectations were associated with the isogenic line or population approach to elucidate the role of individual character in drought resistance but some of the limitations have now become apparent (Garrity et al 1981, Hanson and Nelson 1980, Seetharama et al 1981) have suggested that the simple phenological and morphological traits should be used routinely while the complex physiological and biochemical ones can be used to screen parents or elite lines from the breeding program.

The population breeding approach (Doggett 1977, 1981) has proved to be useful (Garrity et al 1981). While such an approach is most

effective in combining several traits and can be used as a vehicle to widely disseminate broad-based germplasm from international programs to countries wherever expertise exists to handle these populations for local needs, it is unlikely that this will be used widely as a tool in many developing countries in the near future. The possibility of using populations directly on the farmers field, on the other hand, has started receiving some attention by breeders.

Populations have distinct advantage over hybrids and lines under low yielding environments. Fig. 161 Mercer-Quarshie (1979) has shown the advantages of growing sorghum mixtures over pure lines especially under conditions of uncertain rainfall in northern Ghana. Physiologists and breeders are interested in explaining this effect. It is well known that hybrids are far more uniform than varieties which are in turn more uniform than ^{populations.} Under high yielding environments it is this uniformity from emergence to maturity that makes the hybrids most productive (G.L. Wilson, University of Queensland, Australia; pers. comm.). On the other hand, the reverse would be true under a low yielding (stress) environment since the heterogenous population acting as a 'system' has great flexibility. The constituents of the populations vary greatly in phenology and morphology and perhaps even in physiology. The 'system' as a whole acts as a 'mixed crop' and is buffered against stress, although low yielding under favourable environments. This hypothesis is similar to that of the relative advantages of synchronous and asynchronous tillering in cereals under high and low yielding environments, respectively. The 'populations' are like 'nomads' and hybrids are 'city people'. Another analogy is the increasing advantage of intercropping under low input conditions. It is easier to incorporate both the constitutive and facultative (inducible) adaptations listed earlier (Seetharama et al 1981) into this approach of growing populations. This system is expected to be more stable across years and low yielding environments than cultivars, which have great potential under high yielding environments but lack the 'plasticity' of the populations.* In West Africa, wherever sorghum

* The relative advantages of populations over pure lines and hybrids under drought is being tested in the 1981 rabi trials at ICRISAT center.

is planted along the toposequence, populations can be expected to yield better than lines or hybrids, since the variation in the soil and effective rainfall can be more advantageous to the 'mixture' along the gradient than for pure culture.

In view of the difficulty in combining high yield potential with drought resistance, a first approach should be to estimate the acceptable yield level (Hartmann 1981) for a given region. This consists of determining production potential under average weather conditions using an appropriate level of management. If the expected level of yield is high, then yield potential should be combined with only the few most important drought resistance traits for the most marked sensitive stage of crop development. On the other hand, if the yield expectation is low characters related to survival, even if they are negatively associated with high yield, should be incorporated in sufficient doses ('vertical resistance'). In most drought resistance breeding programs, scientists are overly concerned with drought sensitive stages and may not take adequate care to enhance the opportunities to increase productivity under other growth stages when the incidence of drought is less common. Equal emphasis on the latter will increase the crop productivity without much decline in drought resistance. Binswanger et al (1980) have pointed out the great need for breeding high yielding sorghum for Indian SAT regions when kharif crop production is not only risky but also has detrimental effects on the more assured rabi crop. An appropriate genotype which can be sown earlier than existing common cultivars, and with longer growth duration can increase productivity since it can tap late rain for vegetative growth over a longer period and fill the grains with stored moisture. In addition early planting would encourage fertilizer use; photosensitivity can be incorporated to intain flexibility in planting date.

Fortunately current breeding material contains sufficient genes for drought resistance. Hence the use of wild types is not urgently required for several traits (Blum 1981). The CIMMYT maize populations contain great variability for sensitivity of leaf elongation to water stress (Fischer et al 1981) although direct selections have not been made for this trait. The range of values of several

physiological traits (e.g. stomatal resistance) in advanced material is as great as in the selected germplasm (Seetharama et al unpublished). Sobrado and Turner (1981) have found that modern commercial cultivars of sunflower are more drought resistant than ancient wild types. This is not surprising since the modern ones have, under empirical field selection, probably combined both drought resistance and high productivity.

10. ROLE OF MANAGEMENT FACTORS

Amelioration of stress is very much dependent upon management decisions prior to and during the cropping season (Arnon 1975, Kanwar 1977b, Jordan 1981, Jordan and Sullivan 1981). Under most circumstances, after exploiting the potential of matching crop maturity and phenology to the specific environment, alterations in management are likely to be the most powerful tool and the next logical step in increasing water use, efficiency and reducing stress injury. Any crop improvement program aimed at increasing drought resistance should envisage the use of each of the management factors listed by Seetharama et al 1981.

The above point is illustrated by reference to Figure 17 which indicates the interaction between fertility and irrigation for each of three characteristics. While the irrigation increased biomass and grain yield at both levels of fertility, the increase was significantly greater ($P < 0.01$) under high than under low nitrogen. However charcoal rot disease, which is prevalent under drought, was more with high levels of nitrogen than with low. The possibility of reducing terminal stress which causes charcoal rot disease, even at the cost of partly reducing early growth should be tested. The problem of saving water for grain filling can also be solved by employing wider rows (Blum and Havsh 1976).

Passioura (1981b) has suggested the equation as a conceptual framework to discuss crop yield under the water-limited environments:

$$GY = W \times WUE \times HI \dots\dots\dots \text{Eq. (1)}$$

where GY = grain yield/unit area

W = seasonal evapotranspiration (water used/unit area)

WUE = water-use efficiency (biomass/unit area/W)

HI = harvest index (fraction)

By converting to logarithms on both sides of the Eq (1) it can be rewritten in the additive form:

$$\log GY = \log W + \log WUE + \log HI \dots\dots\dots \text{Eq. (2)}$$

When an attempt was made to predict GY based on the three components on the right hand side of Eq.(2) using a step-wise regression model

It was noted that HI accounted for 75% or more of variation in grain yield over three rabi trials with 10 genotypes (Table 4). The contributions of the other two variables were approximately equal (about 12% each). This is not surprising since until now the major gain in yield of sorghum grown in the rabi season has been only through increasing HI.

The WUE term in the equation can be derived as follows:

$$\text{WUE} = \frac{\text{Total (aerial) Biomass}}{\text{Evaporation (E) + Transpiration (T)}} \dots\dots\dots\text{Eq. (3)}$$

Hence,

$$\text{Biomass} = \text{WUE} \times (\text{E} + \text{T}) \dots\dots\dots\text{Eq. (4)}$$

In the rabi, the total available water for the crop is almost fixed around the seeding/seedling stage, and the total biomass is then directly proportional to water use (Seetharama et al 1978). However, since it is only the transpiration that produces biomass, the way to increase the latter under the conditions of fixed water supply is to cut evaporation and use the maximum amount of water for transpiration. The evaporation component, once the soil is dry (after the seedling stage) is very small (Russell 1980) and the scope for increasing transpiration further to increase biomass in a well managed rabi crop is also small. On the other hand the pattern of transpirational water use during development will certainly influence both biomass production and harvest index, thereby determining grain yield (Seetharama et al. unpublished). Thus, saving reasonably some water by reduced transpiration until flowering is a desirable strategy for rabi ("pessimistic environment"; Jones 1981). During kharif, on the other hand, a rapid ground cover and full rates of transpiration from the very beginning of the season is advocated ("optimistic environment").

Characterization of the physical environment as well as the multicriteria approach suggests the amalgamation of expertise of different disciplines. An appropriate way to deal with locational (and temporal) specificity throughout the sorghum growing regions is to encourage the formation of inter-disciplinary teams to work in the

regional and national programs. Since its inception ICRISAT has recognized this need. Most of the ideas and results reported in this paper are made possible because of efforts of a team of scientists (Figure 18) initially brought together by M.B. Russell, ex-director of the Illinois Experimental Station, when he was a consultant to ICRISAT.

Whenever water is the limiting factor in crop production, the study of the dynamics of water movement through the soil-plant-atmospheric continuum (SPAC) is extremely important. The objectives of such a study are to understand the physical processes operating in the system and to measure in situ the quantities of water involved, the rates at which transfer occurs, and the quantitative effects of the system which control them. Quantification of terms in the water balance equation will help soil and water engineers and hydrologists to understand the effects of natural and man-induced physical properties of the soil-crop systems. Plant physiologists will benefit from such studies since they can relate time and depth pattern of moisture in the root zone to transpiration, growth, plant adaptations to stress etc.

Agroclimatologists can help the team in describing and classifying climate in agronomically relevant terms. Basically this consists of translating the intermittent (kharif) or continuously declining (rabi) water supply and the atmospheric demand for water into daily values of available water in the root zone. The data can then be used to model transpiration (Figure 1 & 2) and crop yield. It is our hope that such a process-based, weather-driven, soil and crop-modulated model will be useful in (i) explaining and generalizing the results of site and season-specific field experiments, (ii) identifying agroclimatic analogues and efficient 'ideotypes' and (iii) analyzing the likely consequences of alternative systems of soil, water and crop management under different sets of soil and climatic conditions (Huda et al 1980).

The traditional 'trial and error agronomy' has to be at least in part, replaced by newer system analysis and modeling approach (Nix 1980). An observation made once or a few times on a particular crop, grown

under a well characterized environment, should not be related solely to that crop or to that particular set of conditions. Our interest now lies in making inferences for crops that will be grown in the future, or under other environments which are known only to the extent that probabilities of rainfall etc. have been computed (Gold and Raper 1980). Fortunately the application of systems analysis (modeling) techniques to agricultural cropping system is becoming fairly widespread. Nevertheless expectations should not be too high initially. An explicit model contains, at best only, that portion of the system which is clearly understood. Every "failure" of the model conveys a message that clarifies that part of the system of plant process that needs to be studied further.

Model building, especially the process-based dynamic ones need a lot of input data from different disciplines to be accurate. Emphasis should be placed on the cooperative field research amongst scientists with different backgrounds. Efficient functioning of such a team is ensured by proper structure and management (Kanwar, 1977a; Moragan et al. 1981). It is absolutely necessary to follow the professional ethics very strictly, for example those of the type formulated by various professional bodies such as the American Registry of Certified Professionals in Agronomy, Crops, and Soils (ARCPACS, American Society of Agronomy, Wisconsin 53711 USA).

12. ROLE OF PLANT PHYSIOLOGY IN THE SERVICE OF AGRICULTURE

Physiology is judged primarily on how enlightening it is and whether this enlightenment provides leads or tools for breeders and agronomists (Passloura 1981a). Kramer (1980) has outlined eloquently how a plant physiologist could contribute to agricultural research of immediate value. However it must be understood that plant physiologists, especially in the present day context can not be content with enlightenment alone, and greater 'tilt' has to be made towards the application of their knowledge. This can be best achieved by physiologists, whenever possible, joining a team of agronomists, plant breeders and others. This has already taken place in the international crop research institutes. Turner (1981c) has given three good reasons why such a 'merger' of physiologists would be more fruitful:

Firstly, under such an arrangement the physiologist is bound to concentrate on immediate problems and 'midwifery' (Evans 1977) than in the mere seeking of enlightenment. Secondly, the merger will help encourage physiologists to use the tools and products of agronomists and breeders. Finally the physiologists will be in a better position to convince a counterpart of the need to produce tools and techniques e.g. isogenic lines or populations, and make additional measurements in any agronomic trial, etc.).

Physiology is a science and not a technology. It seeks explanations and its methods are universal in application. And like any other science it has two facets: spectacular (e.g. discovery of photosystems or phytochromes) and utilitarian (e.g. development of herbicides based on inhibition of photosystems or role of hormones in apical dominance or in breaking dormancy). However the future of plant physiology, especially the future of research funding lies mainly in balancing the above two facets with a tilt towards the latter. Unfortunately plant

physiologists are not always trained to do this task. Figure 19 suggests how the training of a plant physiologist might best be undertaken. While the physiologist is expected to master the sciences in the middle circle, it will only be possible to be acquainted with those in the outer circle. However enough opportunities should be provided to a recent Ph.D. to take courses or learn skills which can be of immediate benefit once on the job. The first sabbatical leave and other study leave early in the career can be best utilized by complimenting and supplementing earlier formal training. Thus on return to the job situation there is an enhanced possibility of interaction with his/her colleagues in other disciplines (L.D. Swindale, ICRISAT, pers. comm.). It is hoped that the present conference will stimulate educators to train more competent physiologists because they are badly needed for programs of food production in developing countries.

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Table 1: Grain yields of selections made under different environments during kharif and rabi trials (1980; see text for details).

Selection environment	Mean grain yield/q/ha) during 1980 yield trials	
	Kharif trial	Rabi trial
Kharif (shallow alfisols)	38.9	10.6
Rabi (medium deep vertisols)	40.1	13.3
Summer control (alfisol, regularly irrigated)	38.4	9.4
Summer stress (as under control but 3 irrigations missed during panicle development stage)	37.7	9.0
Overall mean	38.8	10.6
LSD (5%)	1.2	2.0

Table 2: Phenological, morphological, physiological and biochemical changes reported to contribute to drought resistance of sorghum and a qualitative assessment of their cost in terms of biomass or grain productivity. Modified from Turner 1979 and Jordan and Monk 1980.

Mechanism of drought resistance	Productivity reduced?	Reference
1. DROUGHT ESCAPE:		
A. <u>Phenological response</u>		
1. Rapid phenological development	No?	Blum '70
2. Development plasticity	Depends on conditions	Seetharama & Bidinger '79
3. Photoperiodic response	Biomass only reduced with delayed planting	Bunting & Curtis '68
B. <u>Carbon assimilation & remobilization</u>		
1. Remobilization of stem reserves	Biomass only reduced	Seetharama <u>et al.</u> '81
2. High growth rates	No	Garrity <u>et al.</u> '81
3. Low respiration rates	No	Rice '79
2. DROUGHT AVOIDANCE (TOLERANCE AT HIGH WATER POTENTIAL):		
A. <u>Reduction in water loss</u>		
1. Increase in stomatal resistance	Yes	Henzell <u>et al.</u> '75
2. Reduction in leaf area (death)	Yes	Seetharama <u>et al.</u> (unpublished)
3. Reduction in leaf area (rolling)	Yes	Begg 1980
4. Increase in epicuticular wax	No?	Ebercon <u>et al.</u> '77
5. Increase in cuticular resistance	No	Blum '79
6. Glossy leaf	No?	Maiti (unpublished)
B. <u>Maintenance of water uptake</u>		
1. Increased root density & depth	No?	Jordan & Miller '80
2. Increased liquid phase conductance	No	
3. DROUGHT TOLERANCE (TOLERANCE AT LOW WATER POTENTIAL):		
A. <u>Maintenance of turgor</u>		
1. Osmotic adjustment	No?	Seetharama <u>et al.</u> '81
2. Increase in cellular elasticity	No?	Turner & Jones '80
3. Decrease in cell size	No?	Turner & Jones '80
B. <u>Dessication tolerance</u>		
1. Protoplasmic tolerance	No	Sullivan & Blum '70
2. Maintenance of chloroplast integrity	No	Sullivan & Blum '70
3. Resistance to leaf firing	No	Seetharama <u>et al.</u> '81
4. Heat resistance	No	Sullivan & Ross '79

Table 3: Plant water stress parameters of 10 sorghum cultivars (B₂, 1979 rabi).
Seasonal water stress parameters measured around noon at 12th Feb
1980, 45 days after planting.

Genotype	i) Leaf water potential* (bars)	ii) Solute potential** (bars)	Turgor (bars) ^{***}	Stomatal conductance (cm/sec)	Leaf temperature (°C)
1. NK 300	-16.8	-11.2	5.6	0.58	28.6
2. CSH 8	-19.7	-12.1	7.6	0.52	28.3
3. CSV 5	-21.9	-13.1	8.8	0.75	25.1
4. CS 3541	-20.5	-11.7	8.8	0.76	25.1
5. IS 1037	-20.9	-15.4	5.5	0.59	26.3
6. M 35-1	-25.9	-19.3	6.6	0.50	30.6
7. CSH 6	-17.8	-13.7	4.1	1.14	27.0
8. SPV 86	-24.1	-15.7	8.4	0.47	27.9
9. V 302	-20.4	-15.9	4.5	0.56	29.6
10. CSH 1	-16.0	-13.8	2.2	0.92	28.5

* Measured with pressure bomb

** Measured with Wescor osmometer, corrected by multiplying by 1.2 for dilution effects of apoplastic water (Jones and Rawson, 1979).

*** Differences between two. i) and ii)

Table 4: Grain yield, seasonal water use, water use efficiency (WUE) and harvest index (HI) of sorghum cultivars (B₂, 1979 rabi).

Genotype	Grain yield (q/ha)	Water use (cm)	WUE Kg biomass/ cm water	HI (fraction)
1. NK 300	40.3	26.4	358	0.43
2. CSH 8	40.5	21.5	461	0.41
3. CSV 5	36.9	30.9	278	0.43
4. CS 3541	31.8	32.2	249	0.40
5. IS 1037	20.7	27.0	296	0.26
6. M 35-1	19.4	27.2	419	0.17
7. CSH 6	31.6	16.6	495	0.39
8. SPV 86	29.5	19.7	530	0.28
9. V 302	31.5	23.1	389	0.35
10. CSH 1	40.6	27.6	334	0.44

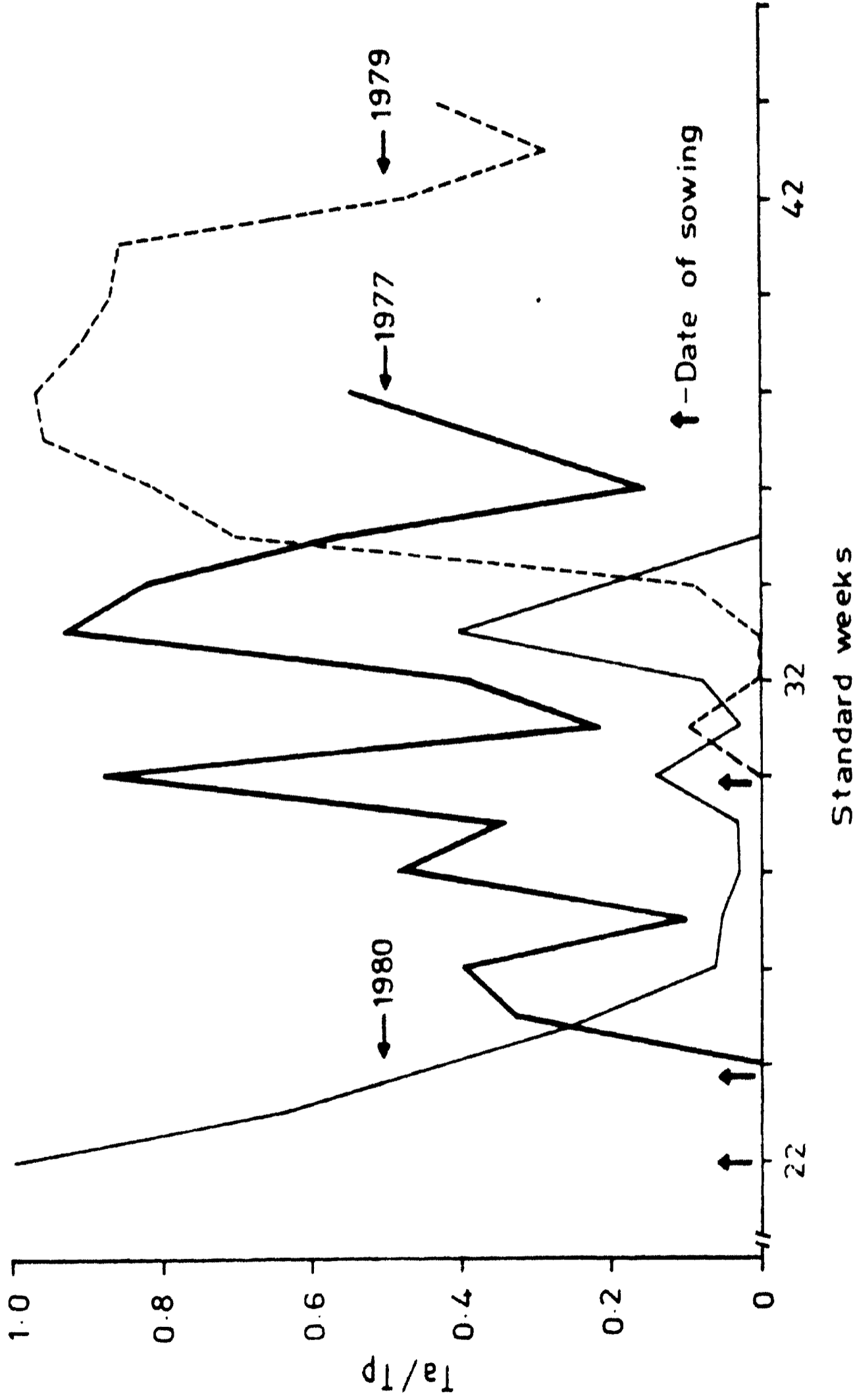


Fig.1: Relative transpiration during crop growth at Anantapur: 1977, 1979 and 1980 kharif (rainy season).
 T_a = actual transpiration (mm/week); I_p = potential transpiration; based on ICSMAB model of
 S.J. Reddy as modified by V. Mahalakshmi and G.D.P. Rao. Computations are on weekly basis.

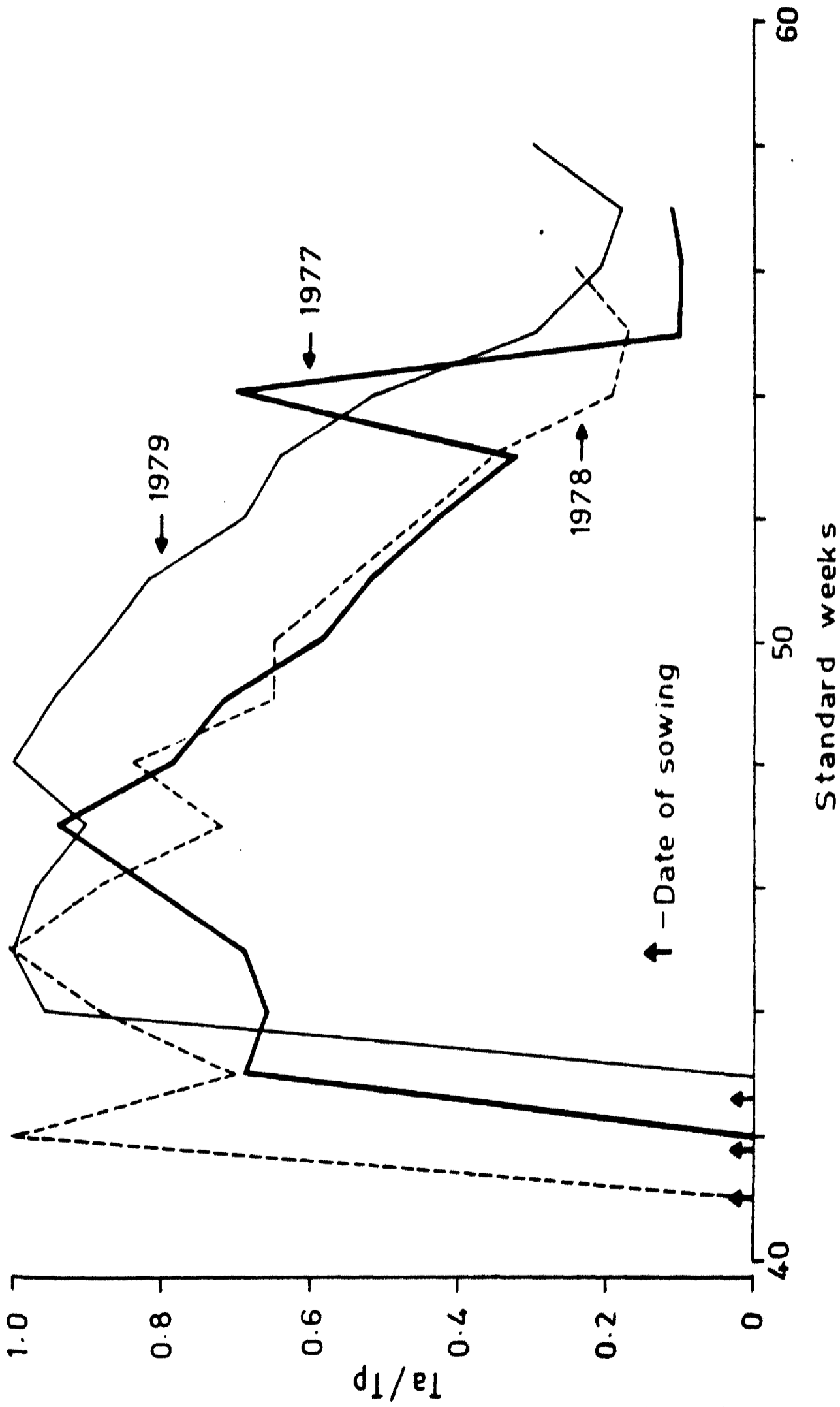


Fig.2: Relative transpiration during crop growth on deep vertisols at Patancheru, Hyderabad: 1977 (partially charged profile), 1978 and 1979 (fully charged) rabi seasons (post rainy). Based on ICSMAB model of S.J. Reddy as modified by V. Mahalakshmi and G.D.P. Rao. Computations are on weekly basis.

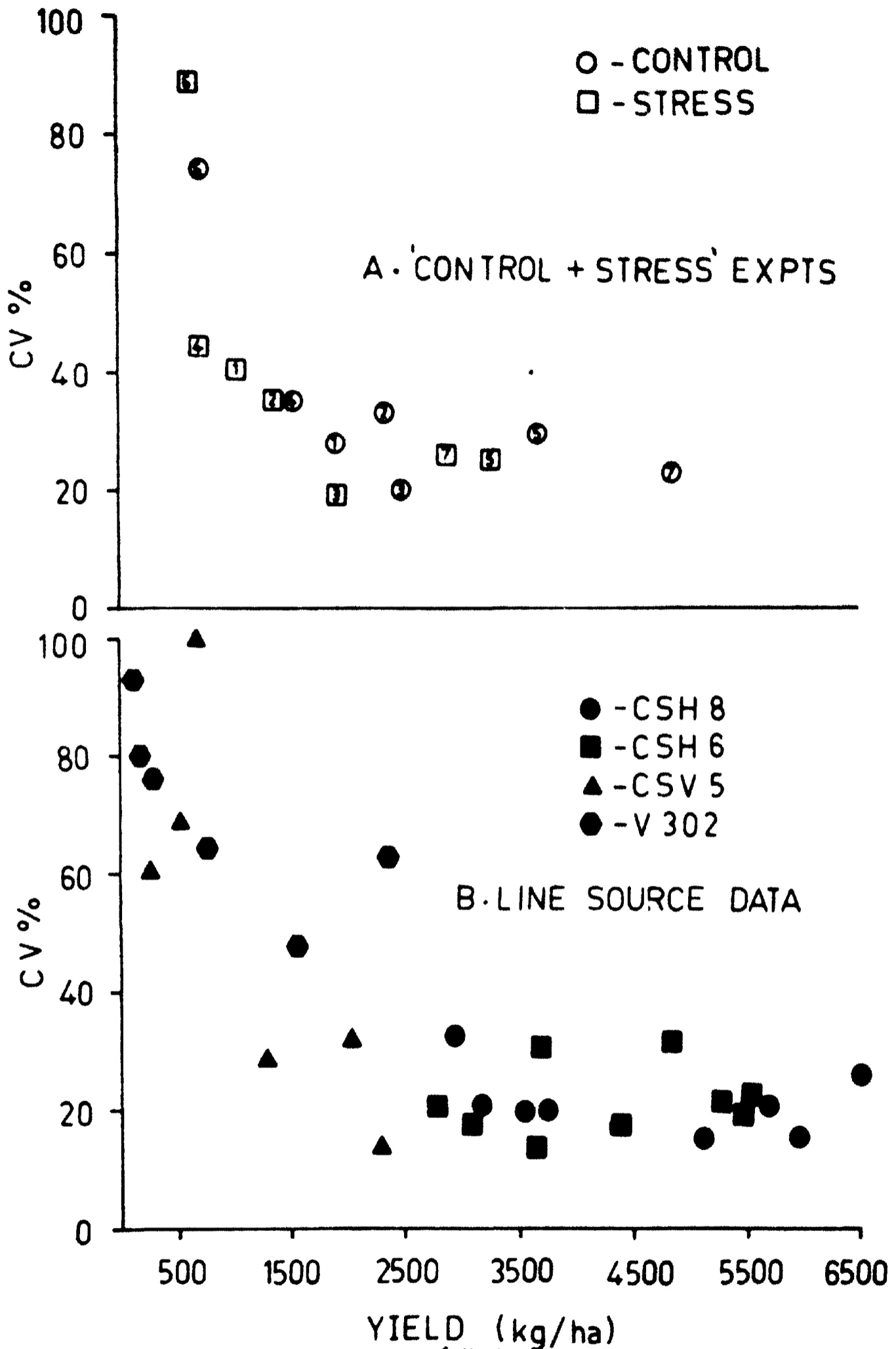


Fig.3: Relationship between ^{Coefficient of Variation} (CV %) and mean yield of cultivars. (A) CV (%) vs mean grain yields. The data are from different trials with irrigation treatments as main plots. The trial number appears within the treatment symbols. (B) CV (%) vs mean grain yields from the same irrigation level from a line source irrigation experiment.

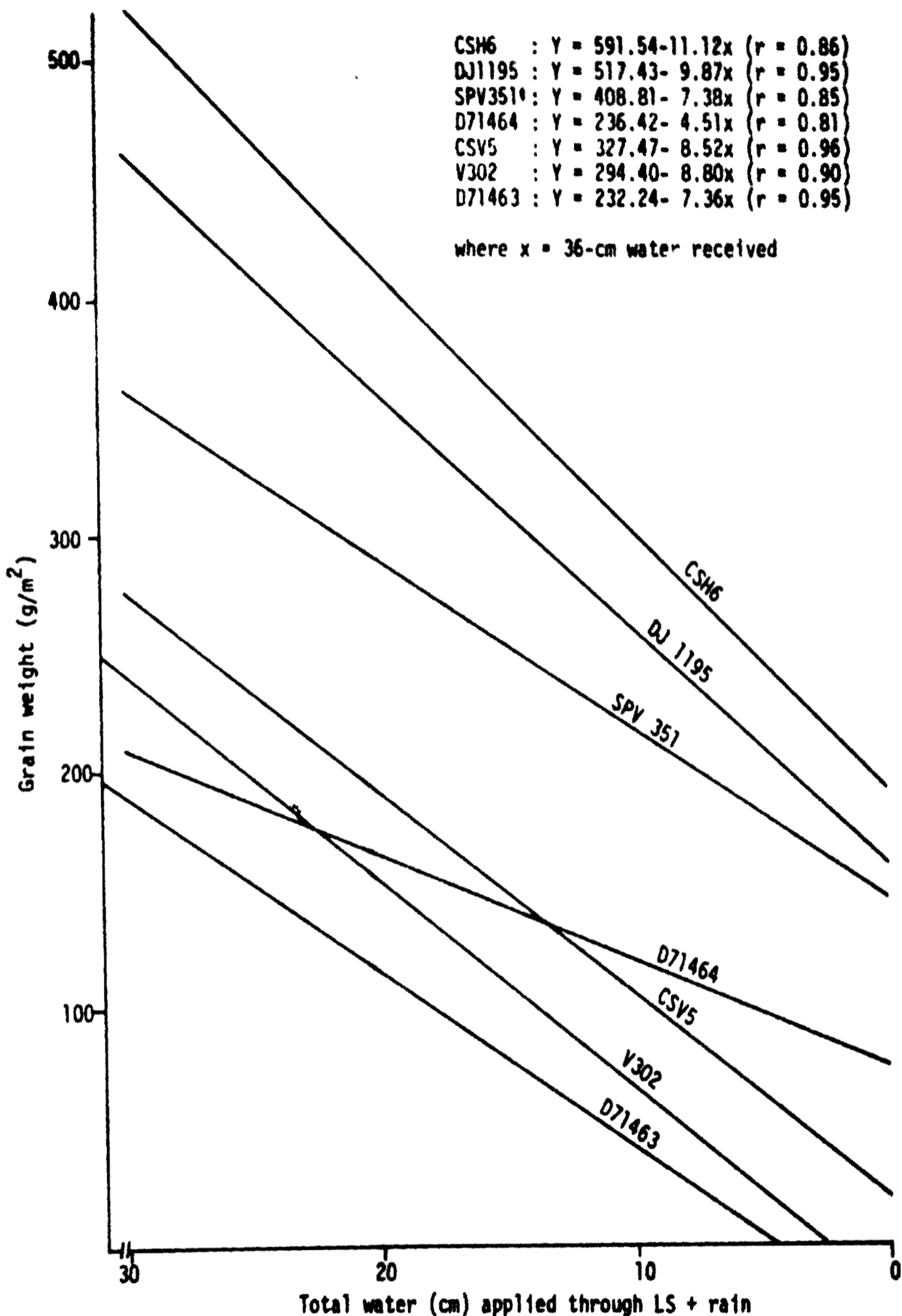


Fig.4: Genotype evaluation for drought resistance using line source (LS) sprinkler irrigation system: Relationship between irrigation water applied through LS plus rain (after 3 uniform furrow irrigations to recharge the profile during crop establishment phase) and grain yield. (Field RP11B, 1980 post-rainy season, regressions for only 7 (out of 18) genotypes are shown; for all correlations $n = 18$; $P < 0.001$).

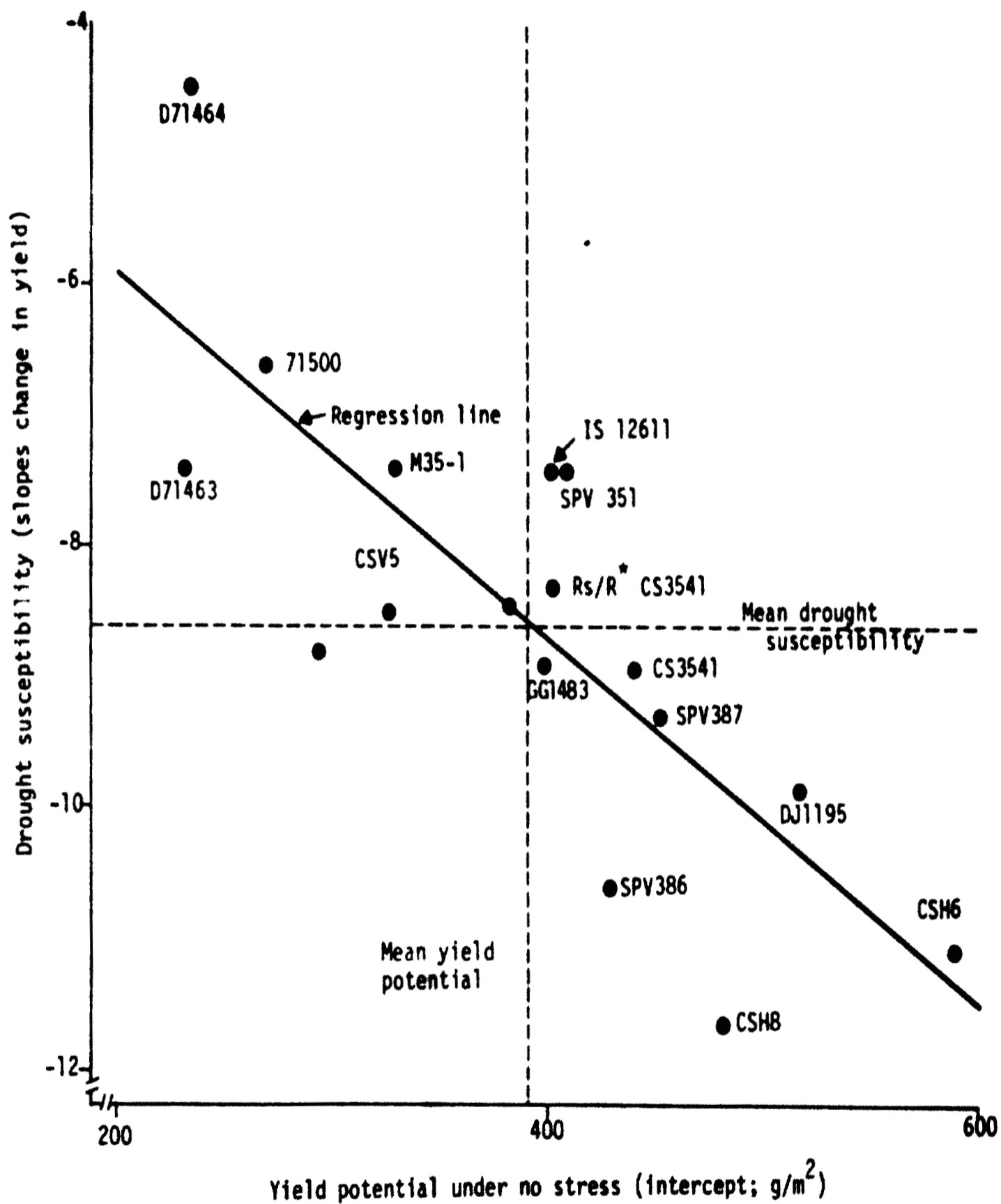


Fig.5: Relationship between yield potential and drought susceptibility (RP11B, postrainy season 1980 data for 18 genotypes are shown, unpublished data of N. Seetharama).

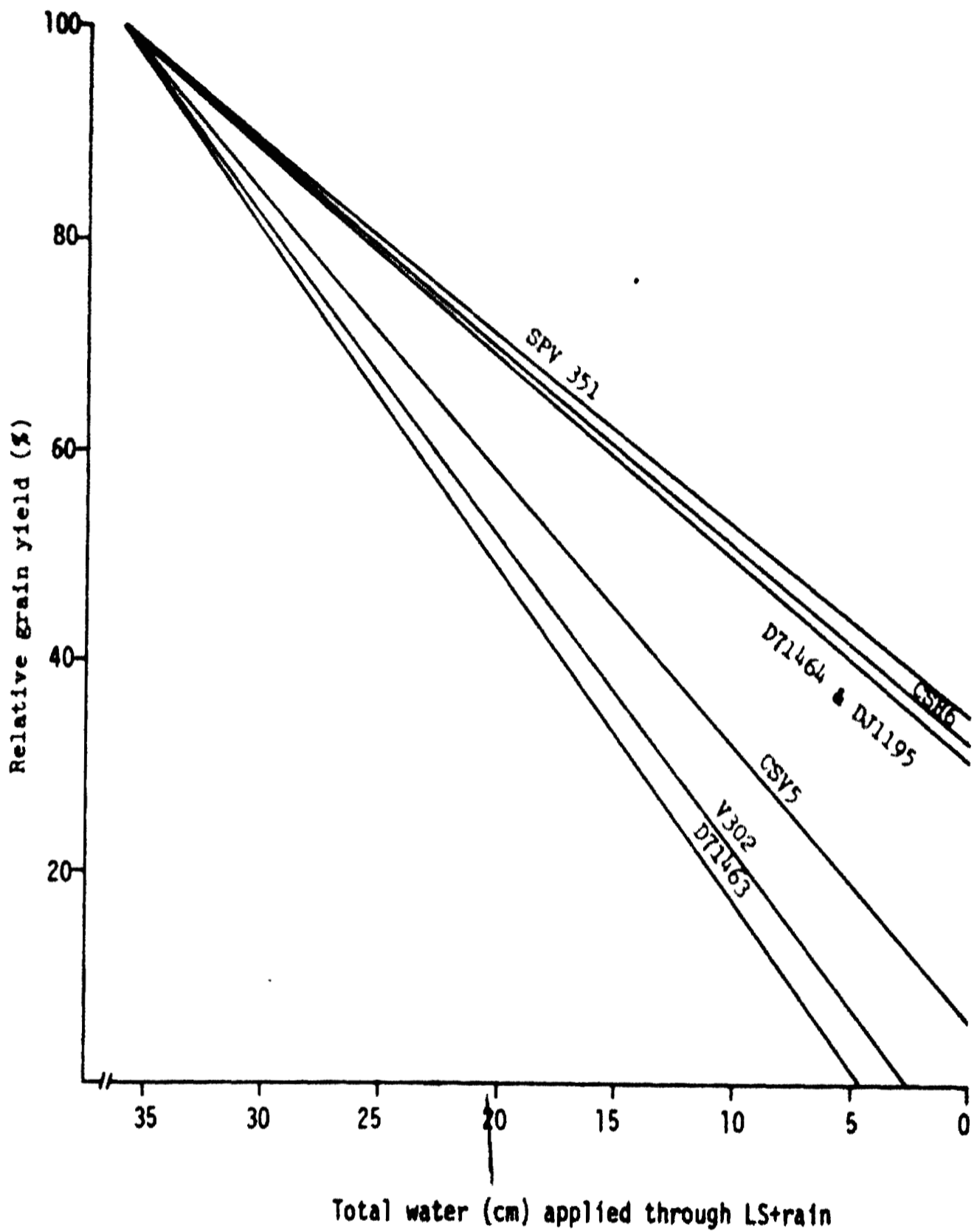


Fig.6: Relative grain yields at declining levels of water supply. (RP 11B, postrainy season 1980, data shown only for 5 selected genotypes. (Unpublished data of M. Seetharama).

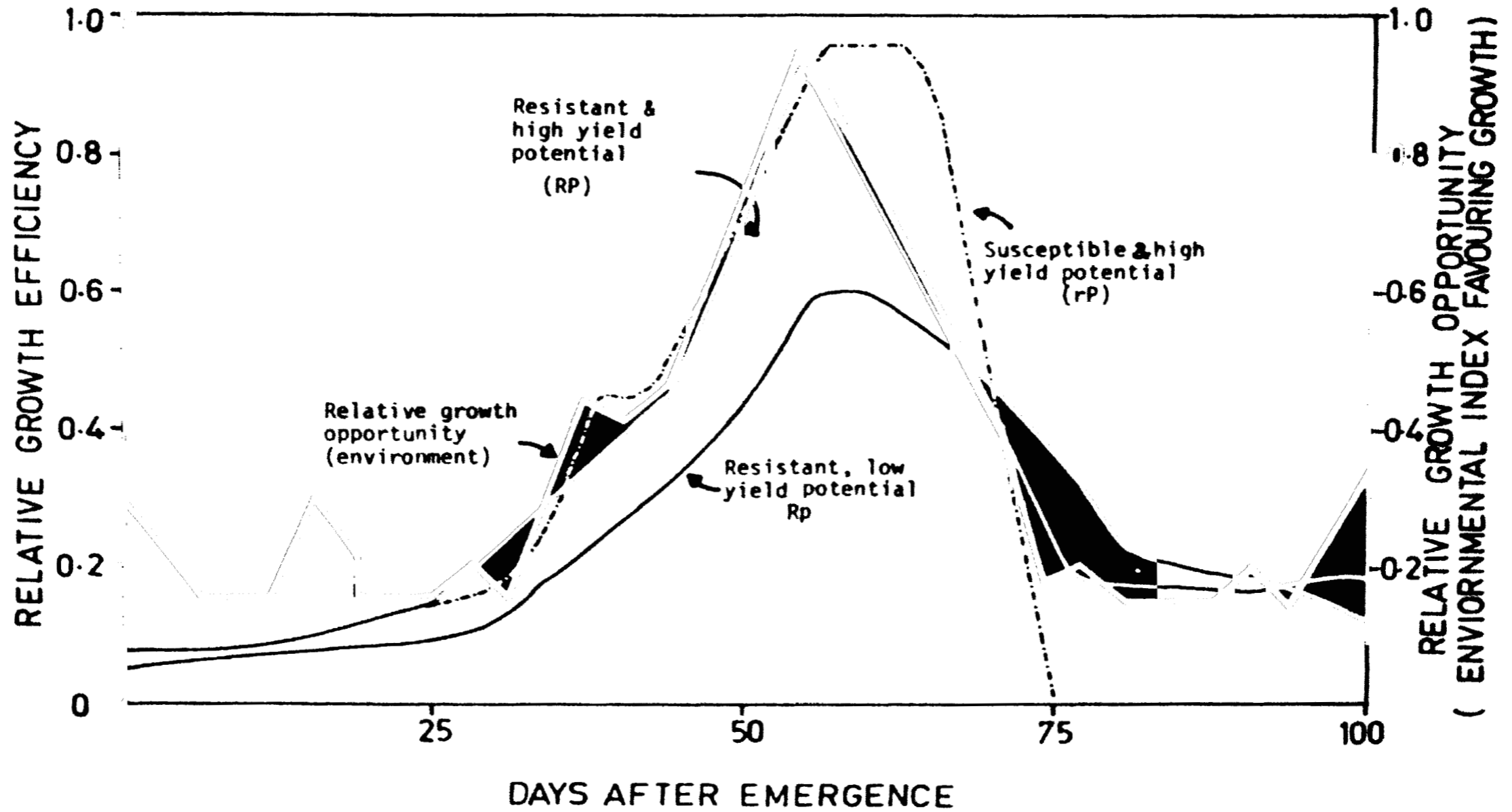


Fig:7 Resource use by various (hypothetical) sorghum genotypes (Relationship between growth opportunity and growth efficiency; see text for explanations).

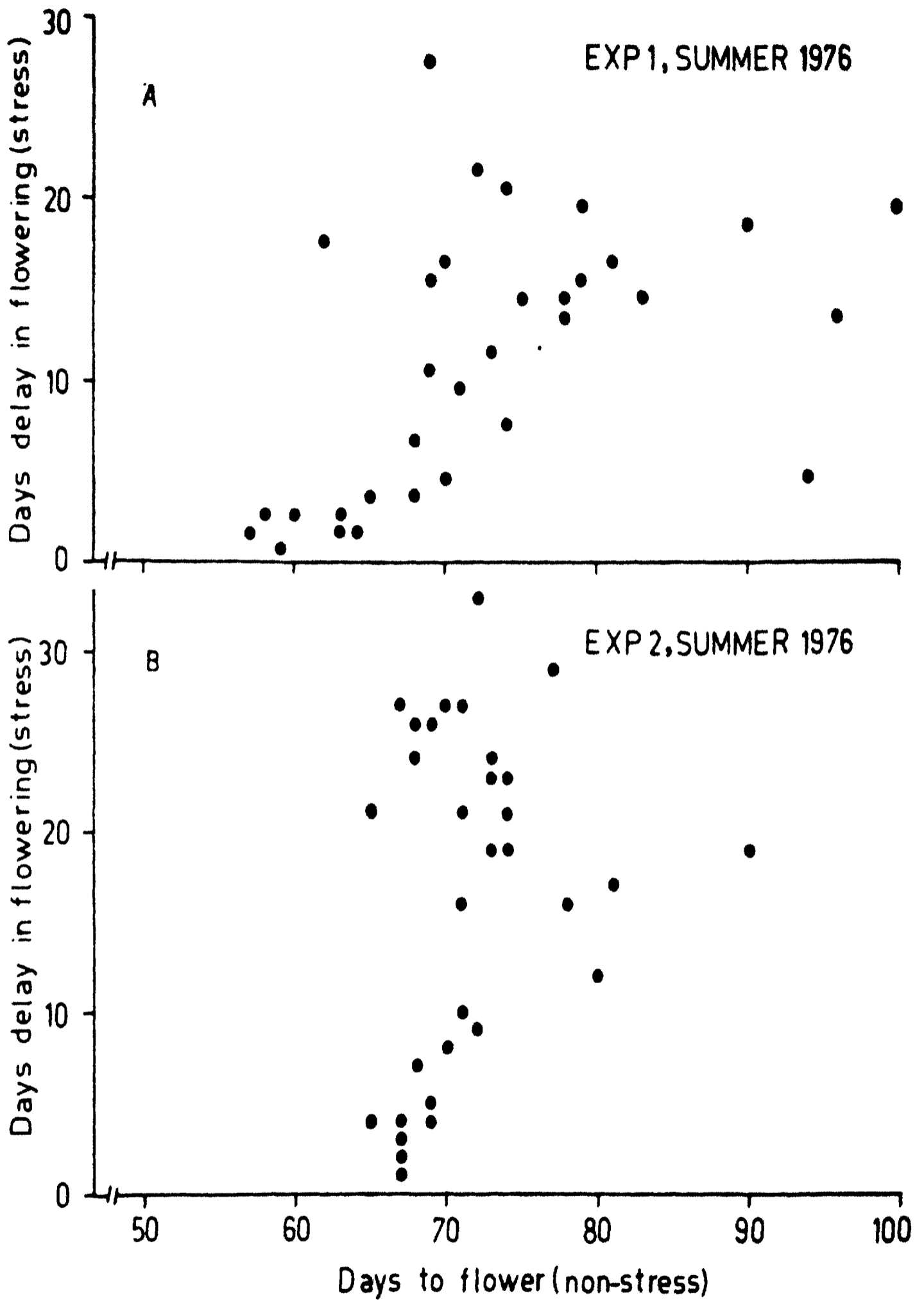


Fig.8: Relationship between days to flower (non-stress) and days delay in flowering under stress (Seetharama & Bidinger 1979).

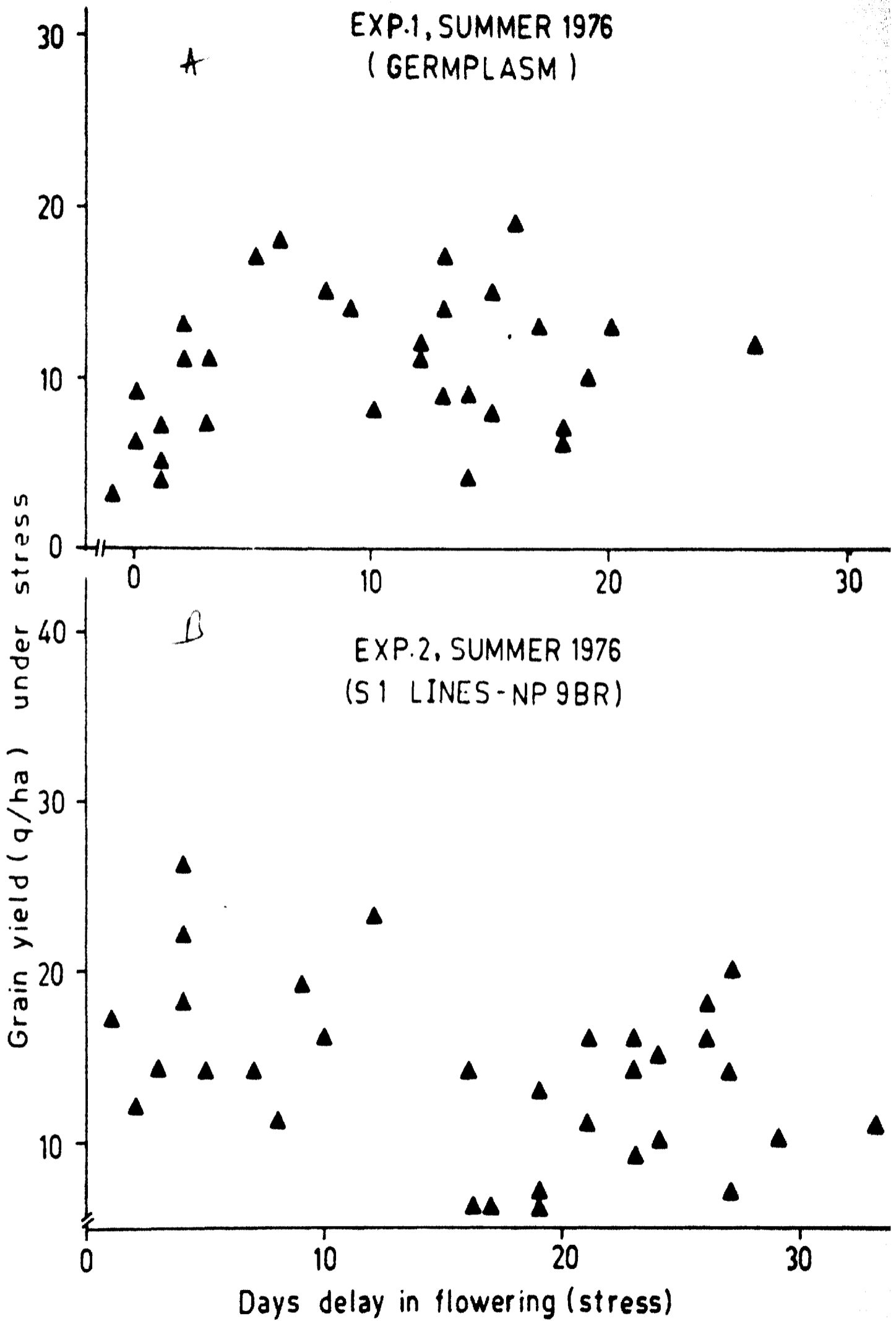
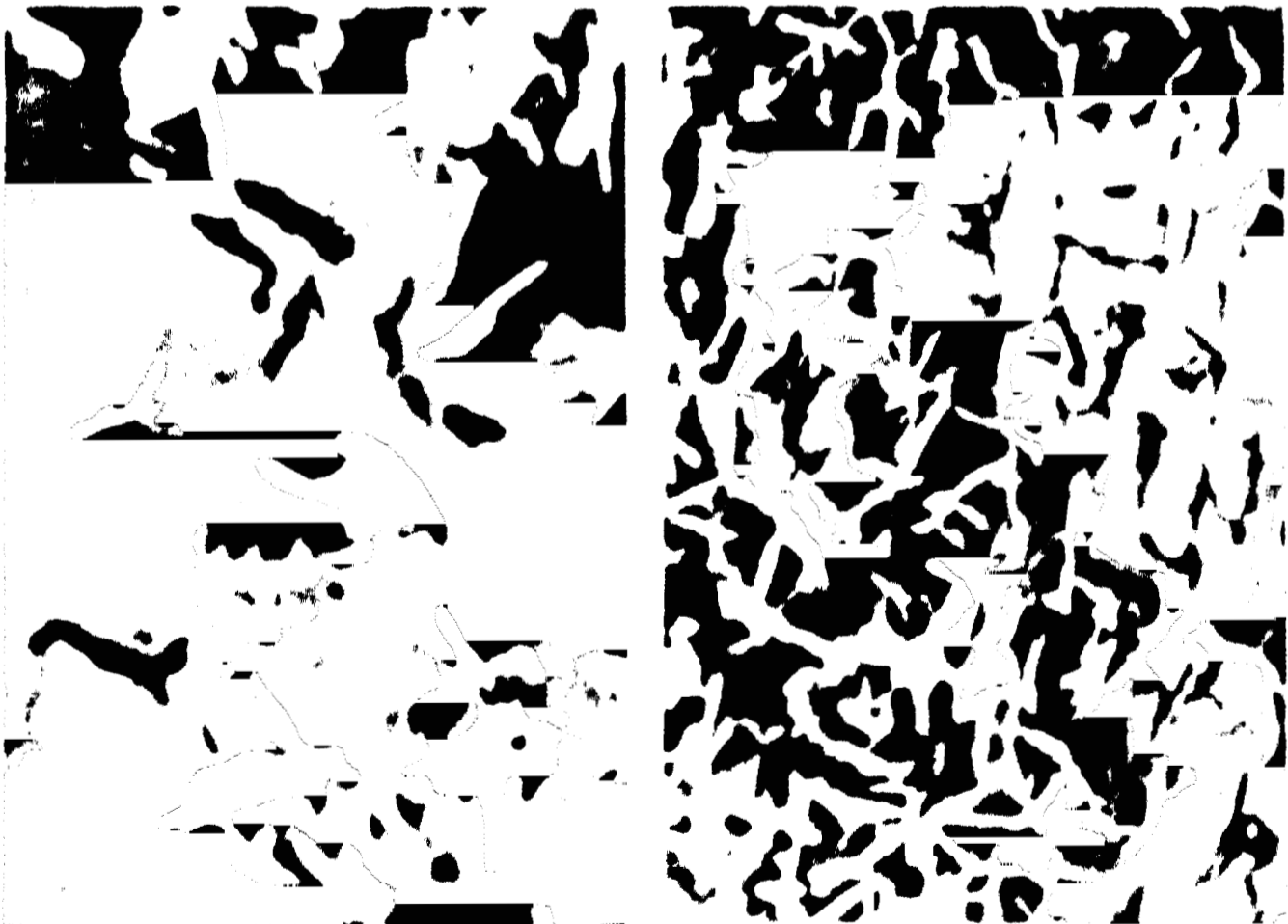


Fig.9: Relationship between days delay in flowering in stress and grain yield (Seetharama & Bidinger 1979).

CS 3541 IS 1160



Figure 10 (a) Screening for seedling drought resistance in brick flats (picture was taken after the release of stress by rewatering CS3541, a susceptible entry in the trial was killed due to stress IS1160, a resistant entry shows least damage due to stress and good recovery)



(b) & (c) Scanning electron micrographs (SEM) of glossy (b) and non-glossy (c) sorghum leaf surfaces. (Glossy leaf surface has flat wax plates forming large crystals, non-glossy surface has small needle shaped crystals:) (SEM by the courtesy of Dr. Susan Woodhead, Centre for Overseas Pest Research, London).

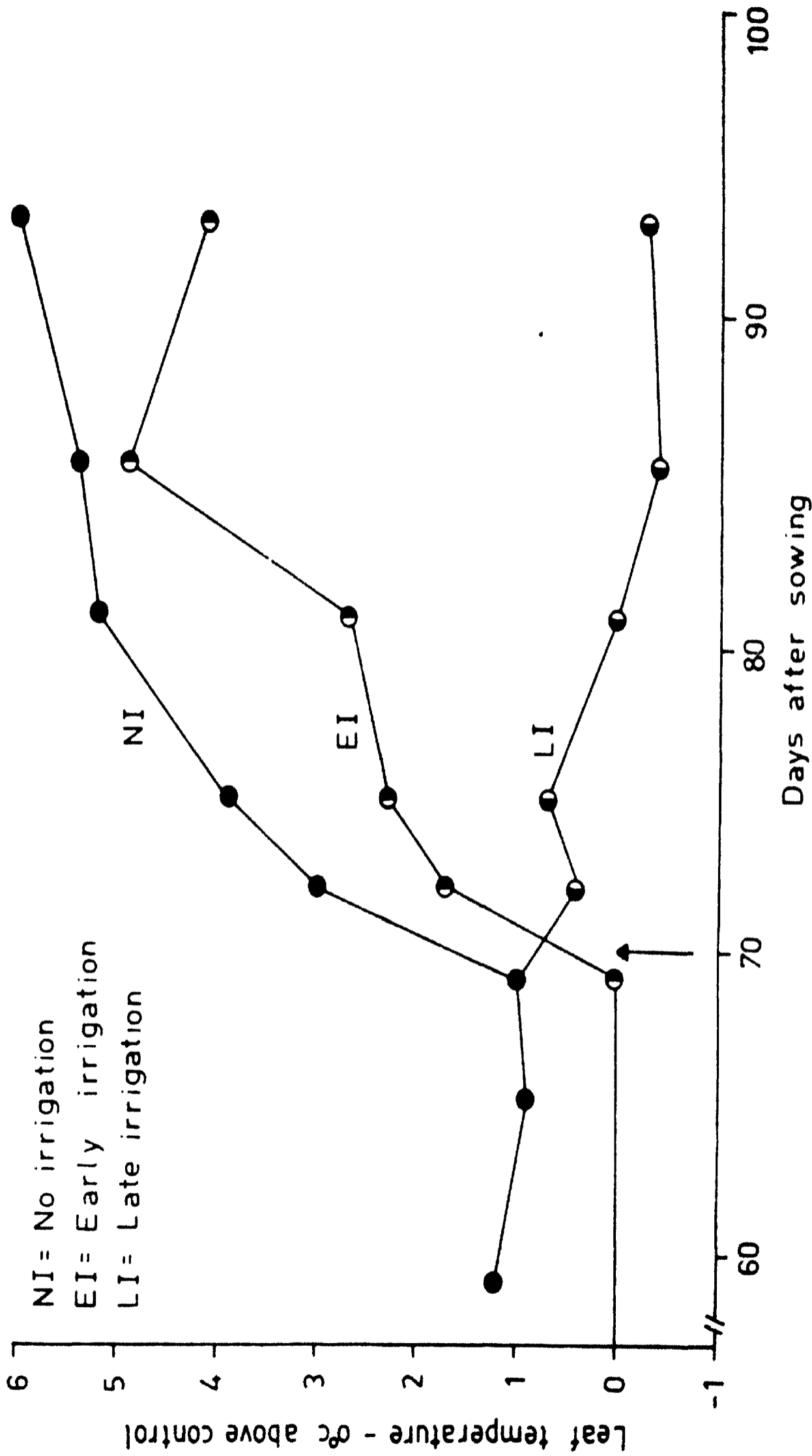


Fig.11: Seasonal (mid afternoon) leaf temperature of sorghum under different irrigation treatments. CSHBR sorghum was grown in RPI7 during rabi 1978 with uniform irrigation until 35 days. Control received 2 more irrigations on 47 and 70 DAS. Treatment EI received irrigation only 47 DAS and LI only 70 DAS. NI didn't receive any irrigation beyond 35 DAS. (F.R. Bidinger, unpublished).

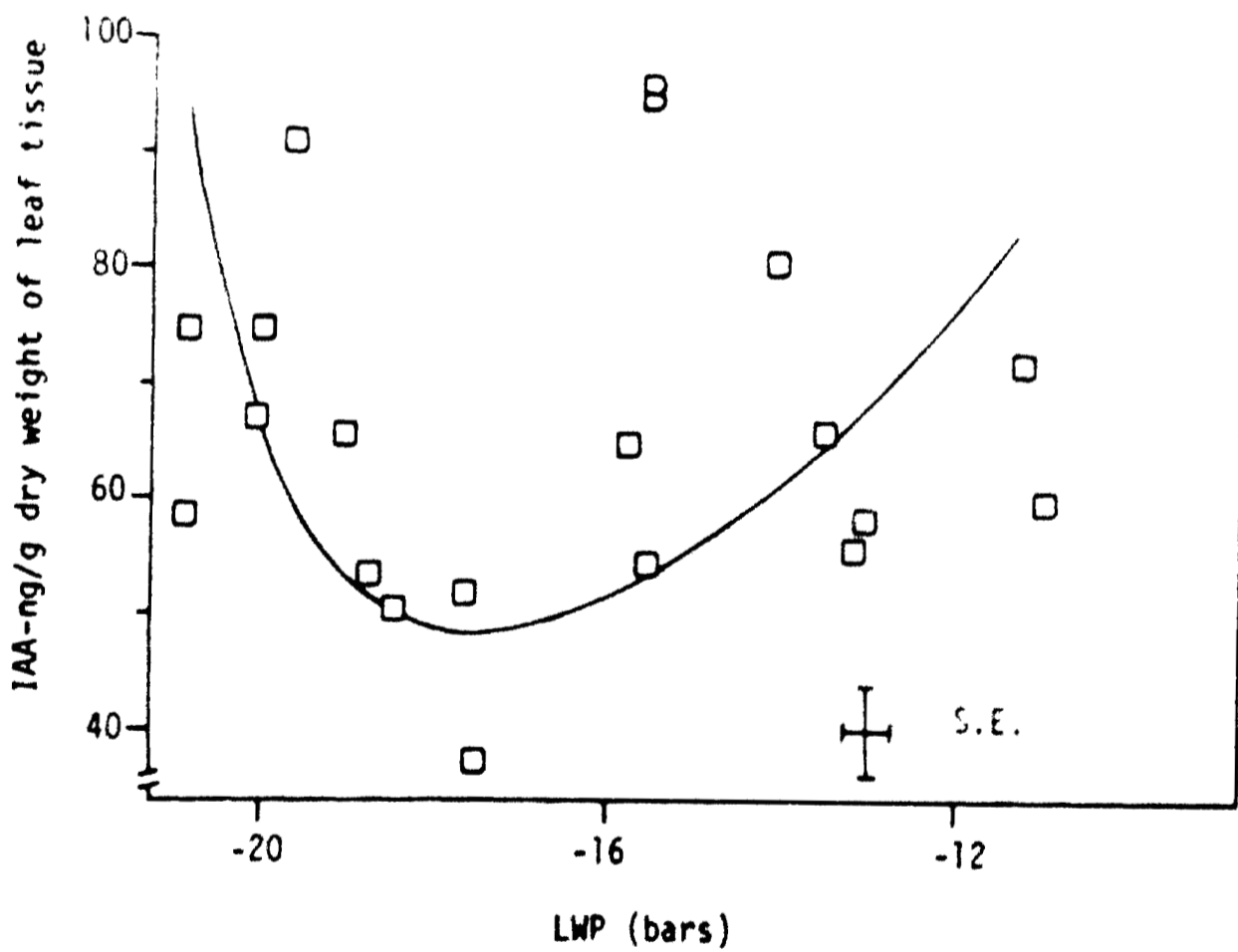
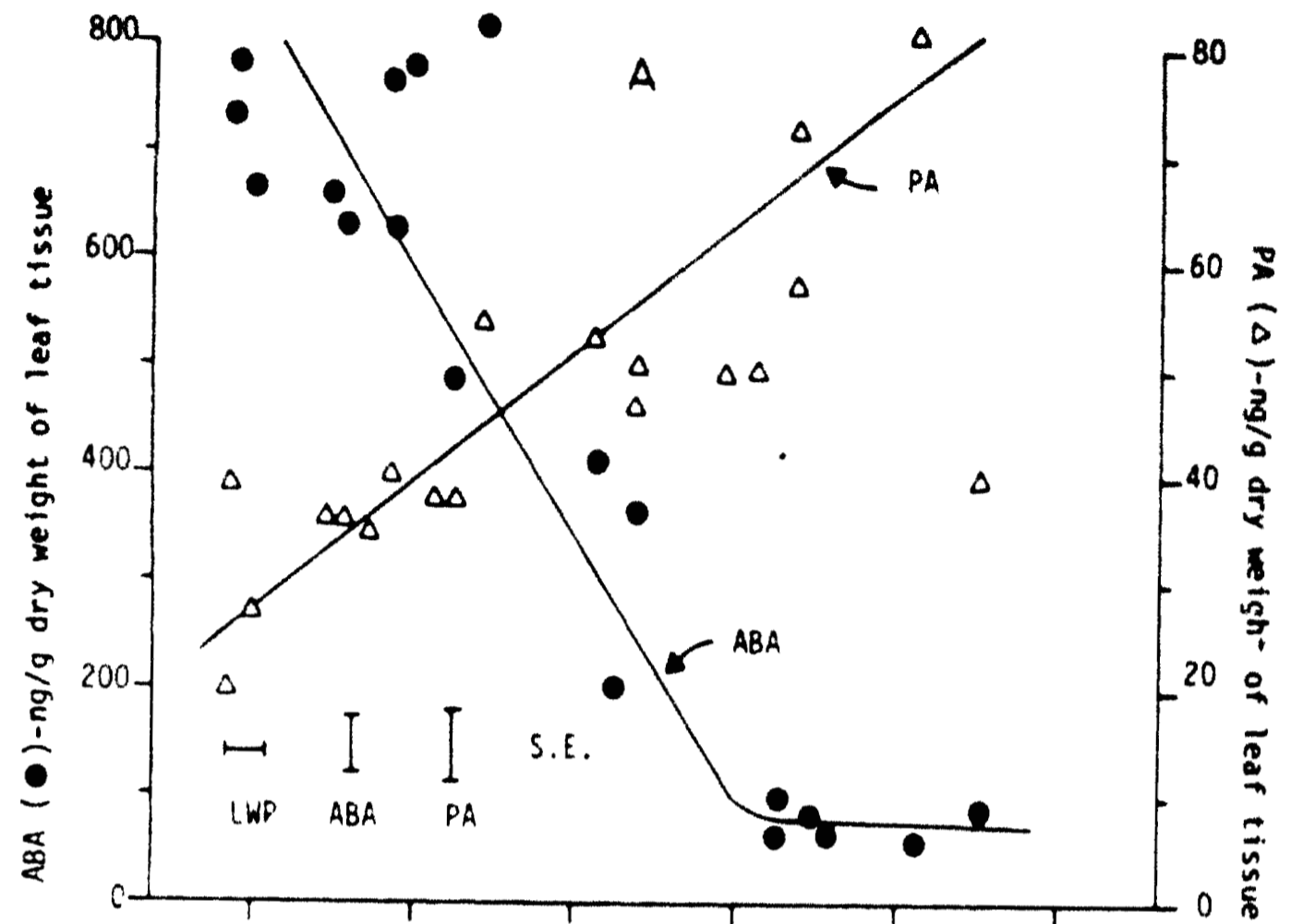


Fig.12. Relationship between Leaf water potential (LWP) and (A) Abscisic acid (ABA), Phaseic acid PA, and (B) Indolel-3-acetic acid (IAA) concentrations. (CSH-8; R6, 1980 Rabi, line source, unpublished data of T. Kannangara, R.C. Durley and G.M. Simpson).

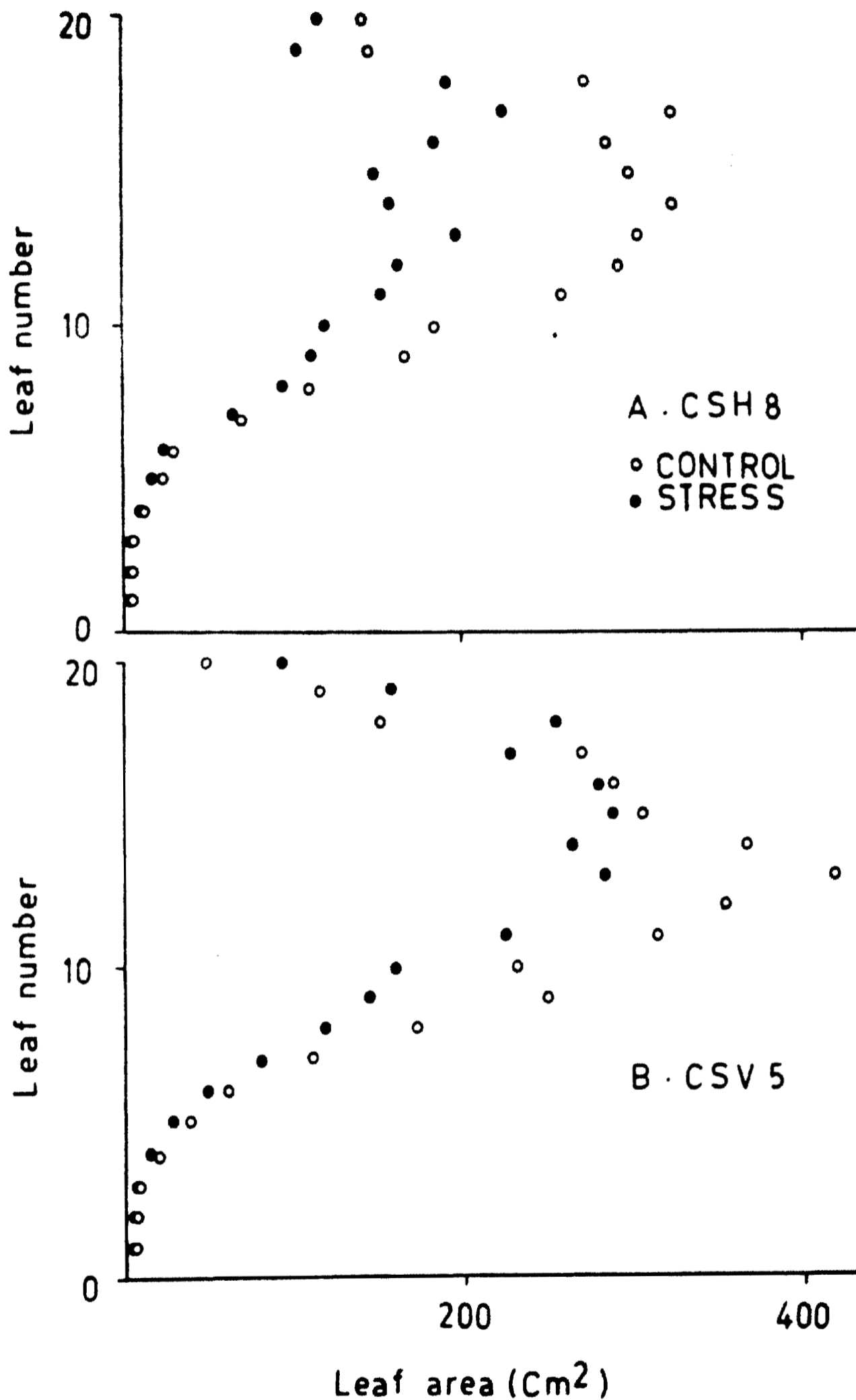


Fig.13: Area of individual leaves of two genotypes under irrigated (control) and unirrigated (stress) conditions (Botanical garden, Summer 1981, see text for details. Unpublished data of J.M. Peacock, P.K. Verma and N. Seetharama).

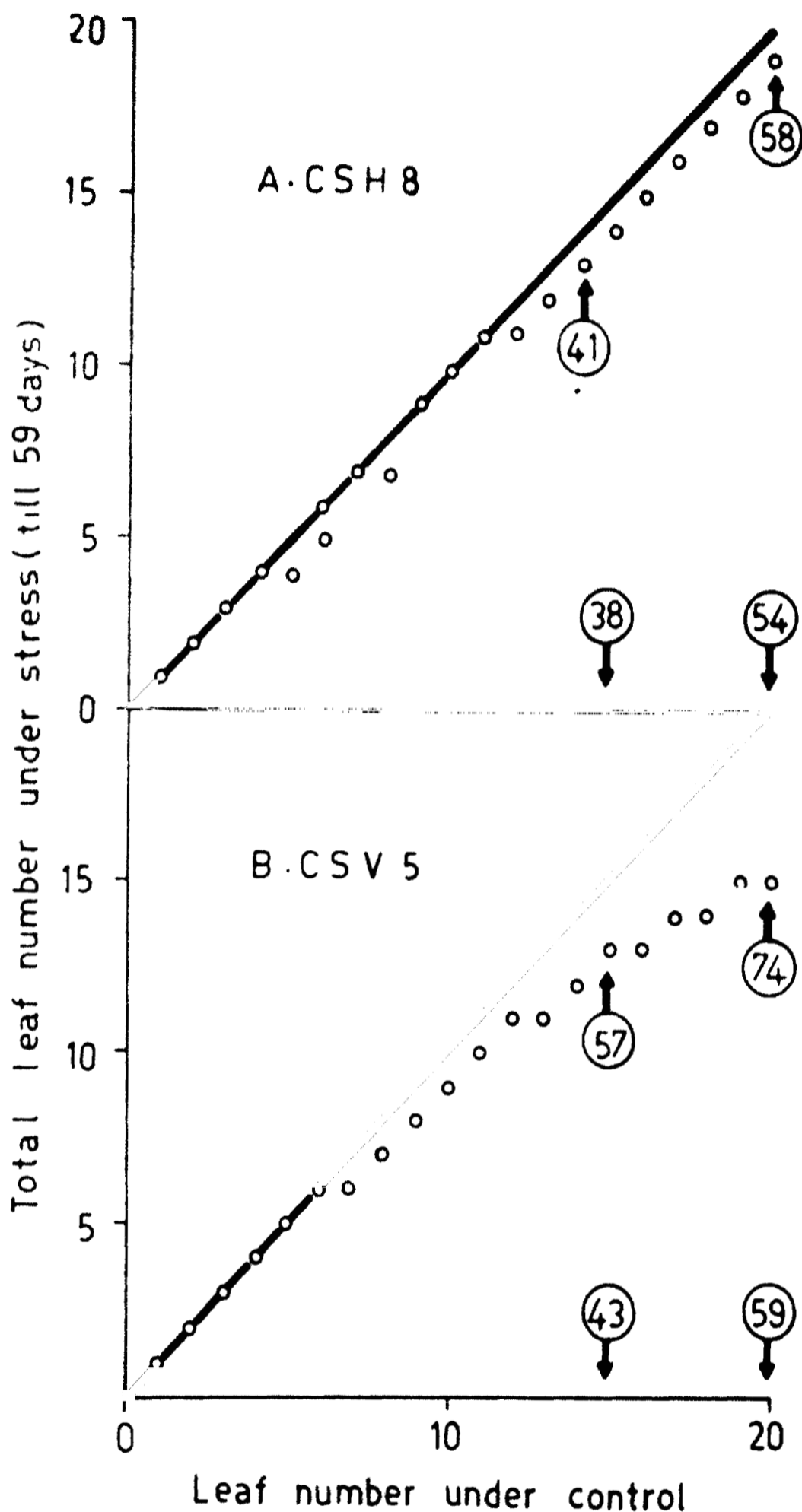


Fig.14: Relationship between number of leaves emerged in control and stress plots (Botanical garden 1981 summer; the final leaf under stress in CSH8 and CSV5 emerged respectively, 58 & 74 days after sowing; the circle with no. inside, denotes the no. of days from emergence of the particular leaf pointed out by the arrow under control (arrow pointing downwards) and stress (upwards). See text for details).

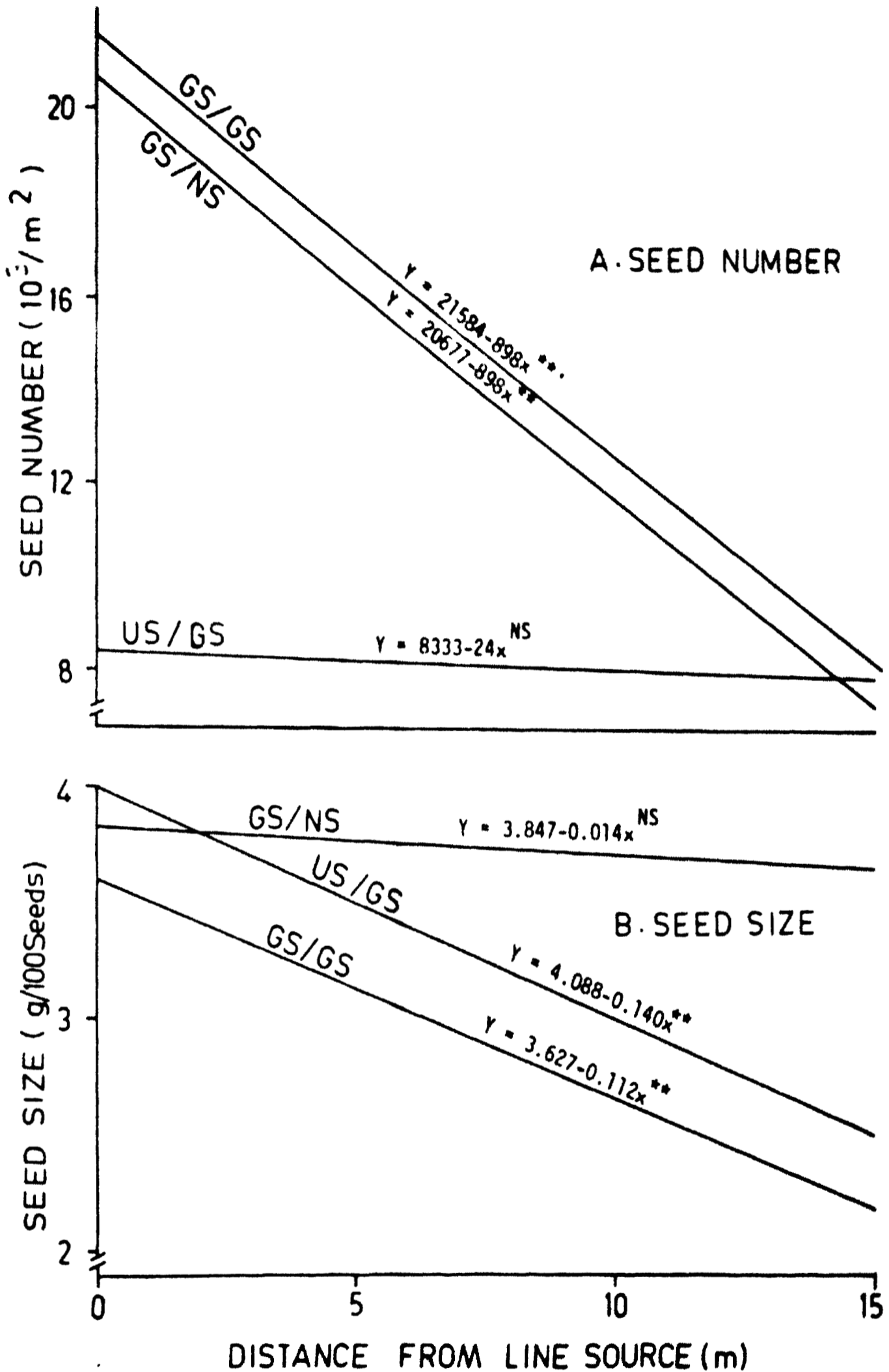


Fig.15: Changes in yield components as a function of distance from line source (LS) sprinkler and irrigation treatments. (Line source experiment, 1979 rabi, RCE3B. GS/GS - Gradient of moisture stress using LS in GS₂ and GS₃. GS/NS - Gradient only during GS₂, uniform irrigation (no stress) during GS₃. US/GS - Uniform stress in GS₂ (no irrigation) and gradient of stress with LS in GS₃. Unpublished data of R.C. Sachan).

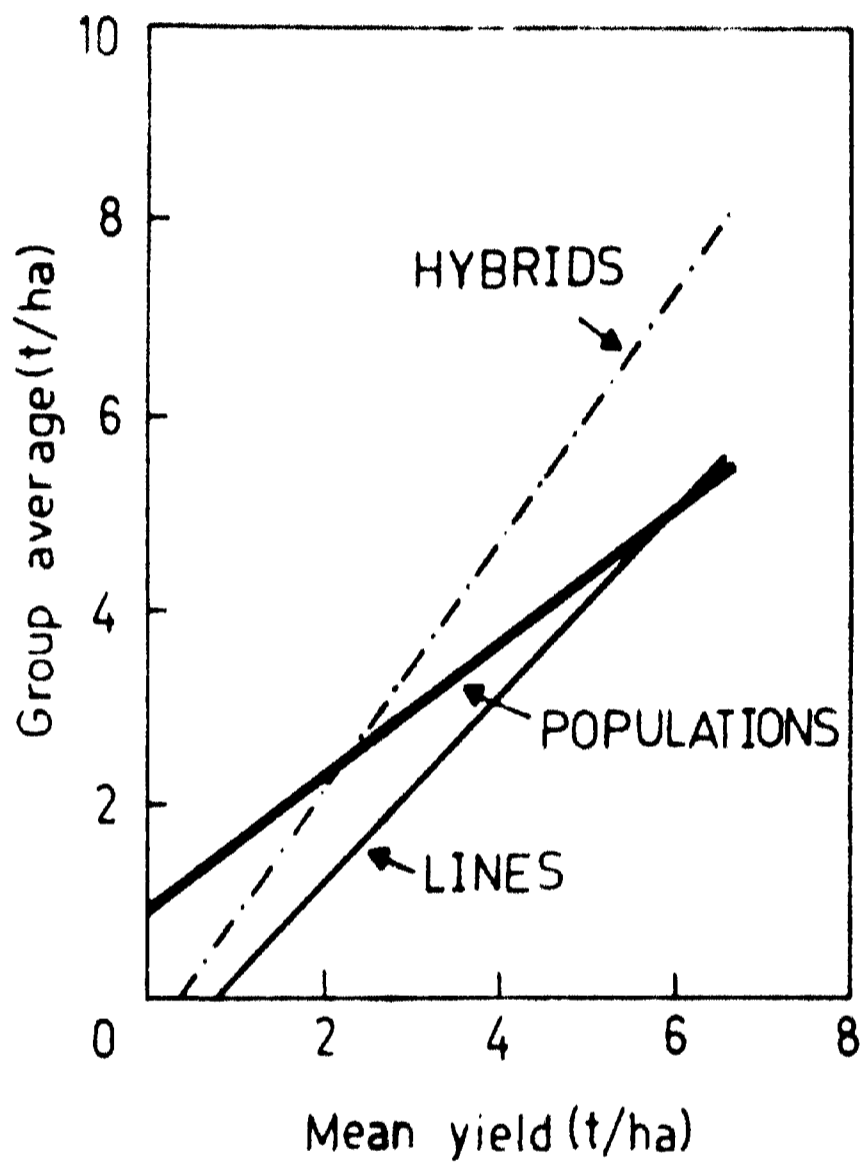


Fig.16: Stability analysis of sorghum hybrids, populations, and lines grown on an irrigation gradient at 6 research stations in Nebraska and Kansas, 1978 (Data of Francis et al. 1979; taken from Garrity et al. 1981).

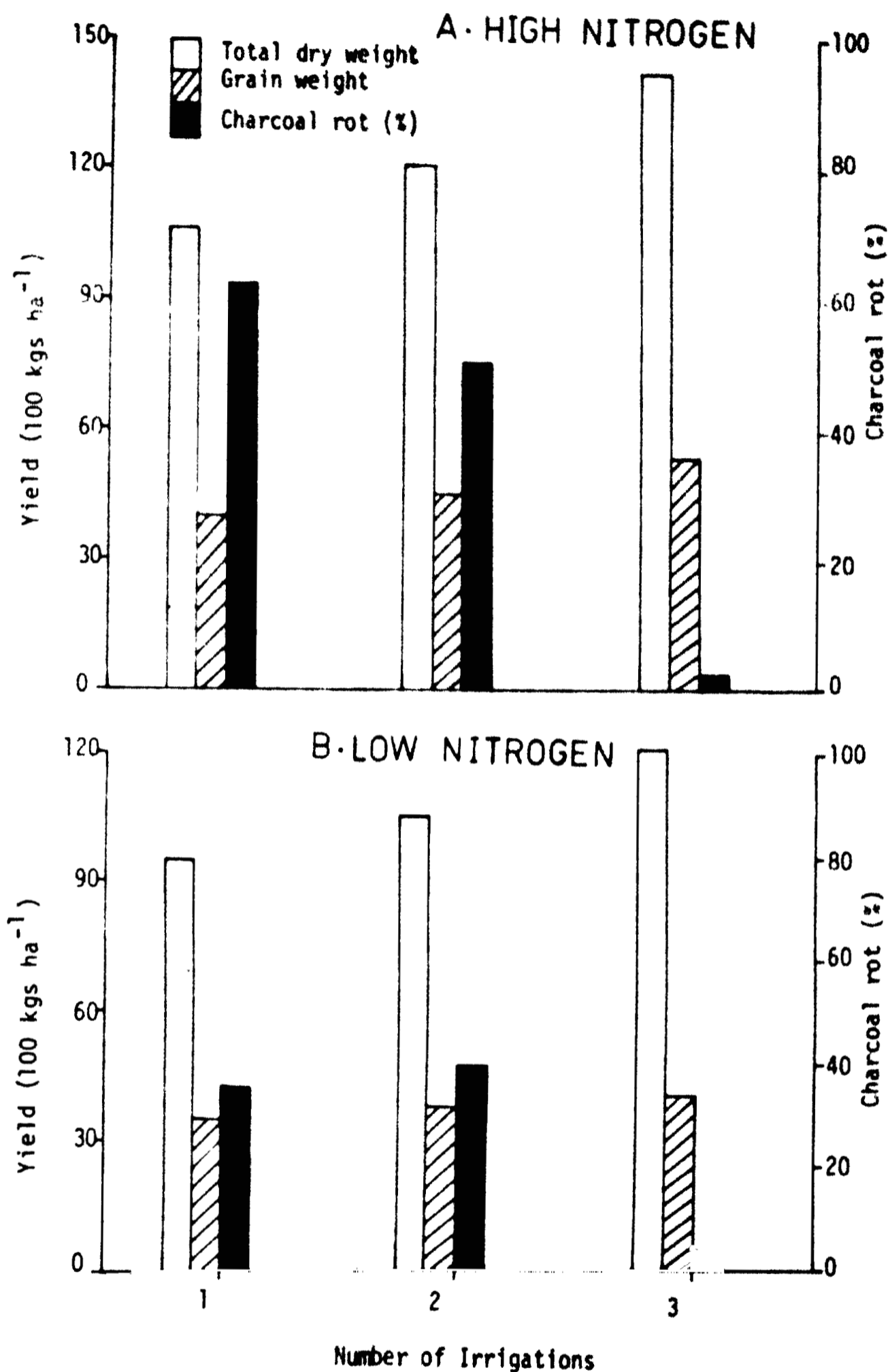
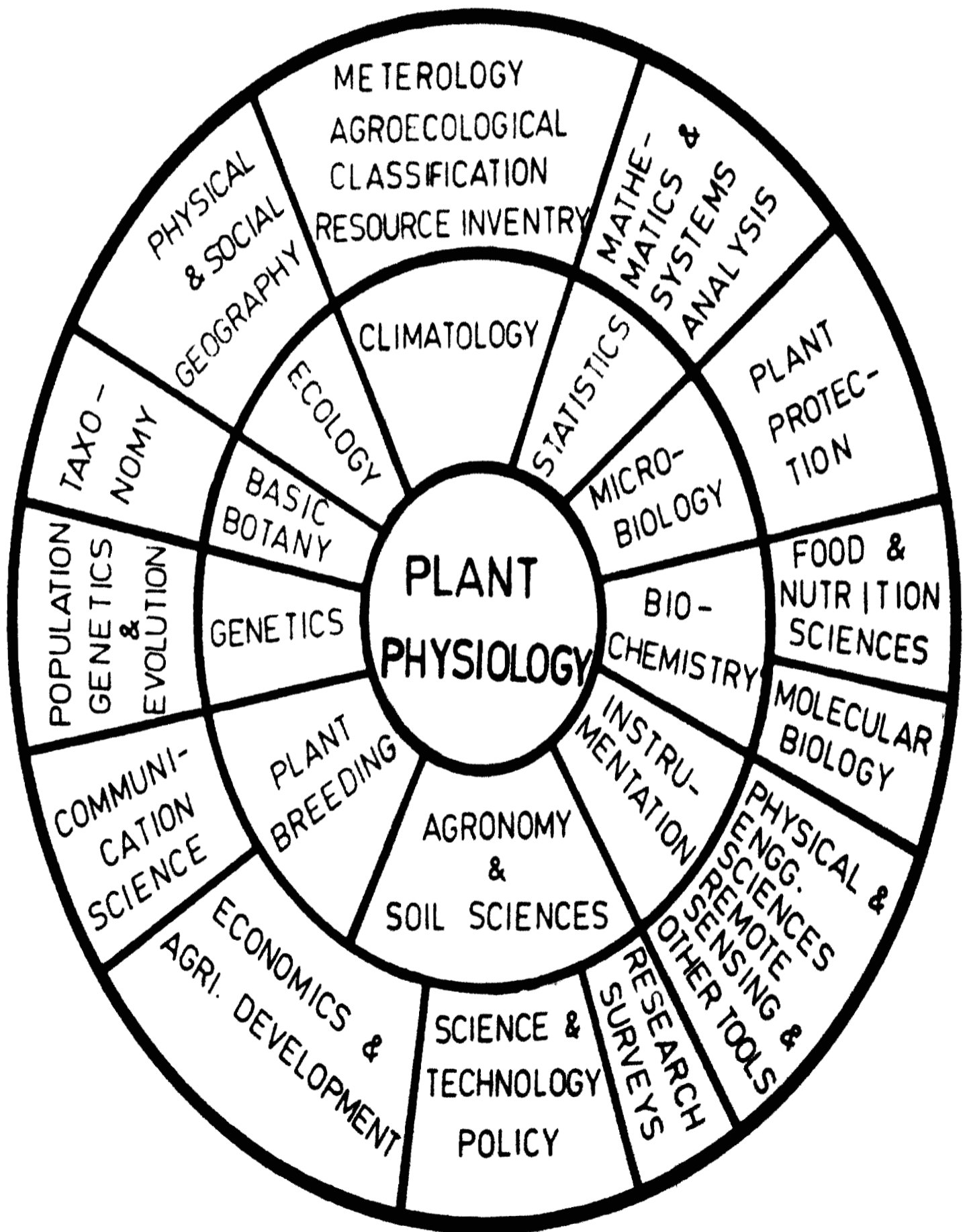


Fig.17: Effect of supplementary irrigations and nitrogen on grain and biomass yield and charcoal rot (% of soft stalk) incidence in sorghum (BW3A, 1980 rabi, unpublished data of Sardar Singh).

Fig:19 Training of a plant physiologist for assisting in crop improvement and production research programs.



3
Appendix I

PROBLEMS AND PROSPECTS FOR INCREASING YIELD UNDER DROUGHT
CRITICISM AND SYNTHESIS WITH SORGHUM*

N. Soetharama, M.V.K. Sivakumar, F.R. Bidinger, S. Sardar Singh,
R.K. Miti, B.V.S. Reddy, J.M. Peacock, S.J. Reddy, V. Mahalakshmi
and R.C. Sachan
ICRISAT, Patancheru 502 324 India

and

A. Shiv Raj, S.R.K. Murthy and A. Narayanan
APAU, Rajendranagar, Hyderabad 500 030, India

and

Tissa Kanungara, R.C. Durley and G.M. Simpson
University of Saskatchewan, Saskatoon, Canada S7N0W0

Although drought causes more yield losses than combined effect of all biotic stress factors, the progress in increasing yield under water limited environment is small. Major reasons for slow progress are listed and the relationships between crop productivity and drought resistance are examined. Adaptations to drought in sorghum are discussed in order of their utility in the immediate future: phenological, morphological, physiological and biochemical. Results of interdisciplinary research at ICRISAT in understanding drought resistance are discussed with respect to available screening methods, genetic variability and breeding methods. Breeding and management strategies should be aimed at increasing transpirational water use throughout the season and decreasing injury caused by drought. Suggestions are made for promoting multi-disciplinary and inter-institutional cooperation.

* Plenary

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