ADAPTATION OF CRAMBE SPECIES AS AN ALTERNATE BIOLOGICAL SOURCE OF OIL AND PROTEIN FOR ARID LANDS AGRICULTURE

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ABSTRACT

A preliminary study of the adaptation of Crambe spp. to arid lands agricultural conditions as an alternate biological source of oil and protein was made by: (1) obtaining crambe seed stocks of wide genotypic variation, (2) developing preliminary screening procedures and guidelines for evaluating the arid lands adapatation potential of Crambe spp., and (3) screening crambe germplasm for adaptability to water deficits, heat, and salinity. Approximately 1,740 entries of cultivars, experimental lines, and plant introductions of Crambe spp. were acquired and increased for screening purposes. Crambe plant-water relationships and screening techniques were evaluated under greenhouse conditions. Selected cultivars and experimental lines were field evaluated for adaptation to water deficits and heat in spring plantings in southern New Mexico using a line source sprinkler system to develop broad gradients of soil moisture. Evaluations included plant growth and development, plant-water relationships, earliness of maturity and seed yield. Results were generally discouraging although some variability for drought tolerance among the germplasm studied was indicated. Seed yields and seed quality from seed increase plantings and field tests were unacceptably low, casting serious doubt on the adaptability of crambe to the conditions under which the tests were made. Screening of germplasm for salinity tolerance was restricted because of unavailability of quality seed.

Key words: Germplasm, plant-water relationships, plant introductions, experimental lines, water deficits, drought tolerance, salinity tolerance, heat tolerance

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INTRODUCTION

Agricultural production in the United States has traditionally been limited to relatively few cultivars. Agricultural research, as well, has been confined primarily to the improvement of these cultivars. Advantages of having greater diversity in crops has been recognized, but recent experiences with disease, drought, water and energy shortages, and the growing necessity to improve agricultural productivity and the efficiency of production has increased the desirability of developing new cultivars.

In the arid and semiarid regions of the southwestern United States, water is one of the major limiting factors for crop production in an area that abounds in solar radiation, warm temperatures, and fertile soils. Development of underground water resources and river basins for irrigation purposes has resulted in a productive agricultural economy for much of the region. In many of the irrigated agricultural areas of the southwestern states, competition for these limited water resources from urban and industrial sectors of the economy is increasing rapidly. Declining water tables and escalating energy costs further limit the availability of these water resources to agricultural production. Salinity, the presence of excessive concentrations of soluble salts in both soils and irrigation waters, is another problem associated with arid and semiarid conditions. Salinity of irrigation water is becoming increasingly serious as water of less desirable quality is exploited for irrigation and as greater intensity of use leads to degradation. Salinity is a hazard on about half of the irrigated area of the western United States (Wadleigh 1968) and crop production is limited by salinity

on about 25 percent of this land (Bower and Fireman 1957; Thorne and Peterson 1954; Wadleigh 1968).

The potential for developing new crops specifically adapted to arid environments is relatively unexploited, as the traditional approach has been to use conventional cultivars and adapt the environment, the soil and water to meet the needs of the crop. However, this approach has become too costly in terms of dollars, good water, and energy. An alternative is to search for plant species with economic potential as crops which are adapted to the conditions of the xeric environment. One such potential crop is crambe (Crambe spp.) a new oil seed crop with potential economic value for the United States (Lessman and Anderson 1981; Nieschlag and Wolff 1971; Nieschlag et al. 1969; Nieschlag et al. 1964; Nieschlag et al. 1967). The adaptability of Crambe spp. to xeric conditions prior to this study were unexplored. However, the known sites of origin and the native habitats of this genus suggest a potential for adaptation to semiarid conditions. Limited yield data from irrigated field trials conducted at Las Cruces, New Mexico, in the late 1970s indicate that crambe is adapted to the general climate of the Southwest in terms of growing season and photoperiod. Additional research was necessary, however, to determine specific effects of water deficits and salinity on the growth and development of Crambe spp. and to evaluate its agronomic and physiological viability as a crop for arid lands agriculture.

The objective of this project was to evaluate Crambe spp. as an alternate biological source of oil and protein for adaptation to arid

lands agriculture with special emphasis on productivity under conditions of limited water and salinity by:

1. Obtaining Crambe seed stocks of wide genotypic variation and increasing the seed supply for screening purposes.
2. Developing preliminary screening procedures and guidelines for evaluating the potential of Crambe for adaptation to arid lands agriculture.
3. Screening the acquired Crambe germplasm pool for adaptability to water deficits, heat and salinity.

MATERIALS AND METHODS

Acquisition of Seed Stocks

Crambe seed stocks totaling 1,740 entries were obtained from the Purdue University crambe germplasm pool and the National Seed Storage Laboratories at Beltsville, Maryland, and Ft. Collins, Colorado. Irrigated seed increase plantings of 1,650 single plot entries and 90 replicated entries were made on 18 August 1980 at the New Mexico State University (NMSU), Plant Science Research Center (PSRC) near Las Cruces. The single plot entries were planted primarily as seed increases but preliminary observations on emergence and seedling vigor, days to first flower, height, leaf area, defoliation, and yield were recorded. Approximately 389 of 1,740 entries failed to produce seed as a result of either stand failure or lack of seed set. A number of those entries that failed to produce seed did not flower, indicating a possible photoperiod problem. Seeds were harvested by hand, threshed, and stored for future evaluation. In general, yields and seed quality were low. This was attributed to poor seed filling, possibly as a result of a relatively short growing season.

Plant-Water Relationships and Drought Screening Studies

A series of experiments were conducted under greenhouse and field conditions. The greenhouse studies were used to determine the plant-water relationships in crambe as well as to calibrate techniques specifically for crambe before going to the field. The greenhouse research was carried out at the facilities of the Department of Crop and Soil Sciences, NMSU, Las Cruces, New Mexico. Greenhouse experiments were conducted over the period of June 1980 through March 1981. The field research evaluated the response of several crambe genotypes to water

stress on the basis of the physiological parameters calibrated under greenhouse conditions. The field research was conducted at the PSRC, NMSU, Las Cruces, New Mexico, during the spring of 1981 and the spring of 1982. The methods used in the greenhouse experiments included the measurement of: (1) relative water content (RWC) in leaf tissue, (2) total leaf water potential (LWP), (3) leaf osmotic potential (LOP), (4) leaf diffusion resistance (LDR), (5) transpiration (TR), (6) leaf area (LA), and (7) dry matter production. In the field, earliness and seed yield determinations were included with the methods used in the greenhouse studies with the exception that total leaf water potential was not determined.

Relative Water Content

Weatherley's RWC approach (1950, 1951, Barrs and Weatherley 1962), which was used in this research, requires a minimum of three determinations: fresh weight (FW), turgid weight (TW), and dry weight (DW) of samples. In general, 10 leaf discs, 8 mm in diameter, were collected from well-developed mature leaves in each sample. All samples were taken from the leaf blade, avoiding the larger veins. Care was exercised in sampling to avoid damage to the edge of the leaf blade. In most cases, the fifth leaf acropetally was sampled, unless indicated otherwise. After sampling, the leaf discs were placed in sealed plastic containers and transported to the laboratory as soon as possible where they were weighed to obtain FW. Then the leaf discs were put in petri dishes containing distilled water. The discs were allowed to rehydrate for 4 hours (h) (unless indicated otherwise) to obtain TW. The temperature in the laboratory was 21±1°C during the time of floating under desk light. After floating, excess water on the leaf discs was removed with tissue paper before reweighing. A second turgid weight (TW2) was

recorded, generally at 16 h of floating, to estimate the rehydration kinetics of leaf discs. Dry weight was then obtained by dehydrating the leaf discs in a forced draft oven at 80°C for 48 h.

Consequently, two sets of response data were obtained from the RWC technique, RWC by itself and kinetics of rehydration (KR). In both cases, analyses of regression were used to estimate the functions of these response variables across the irrigation treatments or to other conditions under study. Dummy variables were included in the models to represent categorical independent variables (Draper and Smith 1966, Neter and Wasserman 1974). In the case of kinetics of rehydration, the nonlinear (linearizable) model used was:

$$Y = aT^{b}\ e^{E}$$

which transforms to

$$\ln Y = \ln a + b \ln T + E.$$

Thus, the function of rehydration through time (T) was estimated. The inclusion of treatment variables and their cross products yielded large models that were screened by backward or stepwise elimination of variables procedures (Neter and Wasserman 1974). Comparisons among treatments were then made on the basis of their water uptake through time. Otherwise, the classical analyses of variance for specified experimental designs were used (Steel and Torrie 1960).

Leaf Water Potential

In this study, leaf water potential was measured with a plant water console (Soil Moisture Equipment Corp., Model 3005). Special seals were made to fit the irregular shape of crambe petioles. Moist filter paper was placed on the inner wall of the cylinder to reduce loss of water

through transpiration, and all measurements were taken between 1400 and 1600 h (MDT) at the maximum evaporative demand. The fifth leaf, acropetally, was always used in the determination of LWP.

Leaf Osmotic Potential

The LOP in this study was measured with a vapor pressure osmometer (Wescor, Inc., Model 5100C). Samples were obtained from the same leaves used for RWC and porometric determinations. The tip 1/4 of the leaf was introduced into a plastic syringe which was immediately placed in a container of dry ice and quick-frozen. Samples were conserved in an ice chest usually for 4 to 5 h for subsequent analyses. To express tissue sap, the samples were allowed to thaw. As quickly as possible after thawing, pressure was exerted on the syringe plunger to express the sap which was collected in a plastic vial. An 8-µl sample was placed in the osmometer for the reading. This procedure has been outlined by McComb and Reding (1960), and Slavik (1974). Fixation by low temperature is advantageous, as it reduces the possibility of chemical changes such as hydrolysis or condensation. Killing by low temperature occurs mostly during thawing of the samples. The expressed cell sap is assumed to have the average osmotic potential of the leaf vacuolar solution which was *in situ* in a dynamic equilibrium with the cytoplasmic structures, all of them being under the same cell wall pressure.

Leaf Diffusion Resistance and Transpiration

Measurements of LDR and TR were obtained in this study for crambe as indicated for each experiment. An LI-1600 Steady State Porometer (LI-COR, Inc.) was used, which has a wide range in measuring diffusive resistance and concurrently measures photosynthetically active radiation, leaf temperature, relative humidity, diffusion resistance, and

transpiration. Porometer readings were always taken from 1000 h to 1500 h, MDT. The same leaf sampled for RWC and LOP was used for the porometric reading.

Growth

Growth, expressed as leaf area and plant dry weight, was measured as indicated for each experiment. Total leaf area was measured with a leaf area meter (LI-COR, Inc., Model LI-3000). The dry weight of plant components such as leaf, stems and roots were obtained by drying the tissue in a forced draft oven at 65°C for 48 h. Growth, measured as leaf expansion or dry matter accumulation, is one of the most sensitive parameters affected by water stress. Several ratios between growth components were analyzed in search of indicators of plant water responses. The ratios included leaf area/leaf dry weight (LA/LDW), leaf area/stem dry weight (LA/SDW), and leaf dry weight/stem dry weight (LDW/SDW). Top dry weight (TDW) which was obtained by adding LDW to SDW (TDW=LDW+SDW) was also evaluated. In one greenhouse experiment, the root dry weight (RDW) was measured. In this case, shoot/root ratios (S/R) were analyzed.

Germplasm

The germplasm used in these experiments was obtained from the seed stock of the Department of Crop and Soil Sciences, NMSU. It consisted of the registered cultivars, Meyer and Prophet, and advanced breeding lines obtained from the crambe seed stocks of Purdue University and increased at the NMSU PSRC at Las Cruces. In the greenhouse experiments, only the cultivars, Meyer and Prophet, were used as indicated for each experiment. In the field experiment of 1981 (F-1), 20 different plant genotypes were used as shown in Table 1.

Table 1. List of germplasm used in Exp. F-1. Spring 1981.

Field code	Pedigree	Group
G-1	I-1387	I
G-2	No. 36	I
G-3	No. 37	I
G-4	No. 38	I
G-5	No. 31	II
G-6	C-76-2xH-68-206	II
G-7	PI 281736-N3-N1	II
G-8	60456	II
G-9	No. 46	III
G-10	"Comm"	III
G-11	60507	III
G-12	60171	III
G-13	No. 41	IV
G-14	B-14-1xH-68-231	IV
G-15	No. 40	IV
G-16	60190	IV
G-17	Meyer	V
G-18	Propher	V
G-19	B-17-1-(x)	V
G-20	C-165-1-(x)	V

The 20 genotypes were selected from a group of 82 genotypes evaluated in a yield trial conducted at the PSRC with the seed increase plantings during the fall of 1980. Four different criteria were used to classify the genotypes into four groups of four genotypes each. The four criteria used were leaf area, plant height, earliness, and seed yield. Leaf area was graded visually in two subjective readings during the growing season. The score used was plus (+) for those genotypes showing comparatively more leaf area and minus (-) for the genotypes with visibly less leaf area. Seed yield was classified as (-) in those genotypes with less than 35 g/plot and (+) for genotypes with seed yield greater than 48 g/plot. Plant height was recorded at the maturation stage of plant development. The (-) class was given to the genotypes with heights less than 78 cm and the (+) class was assigned to genotypes taller than 88 cm. Earliness was determined by recording the number of days from planting to flowering. Genotypes that needed 36 or less days to initiate flowering stems were defined as (-) and genotypes that needed 40 or more days to initiate flowering stems were defined as (+). The characteristics of groups I to IV are shown in Table 2.

Group V consisted of two standard cultivars (Meyer and Prophet), plus two genotypes, C-165-1-(x) and B-17-1-(x) which were early (33 and 34 days to initiation of flowering stems, respectively), both having high seed yield in the fall 1980 trial.

During 1982, two field experiments were conducted at the PSRC. The germplasm used in Exp. F-2 consisted of only 10 out of the 20 genotypes used in Exp. F-1 in 1981, because of the very poor germination of the seed collected in the F-1 experiment (discussed later) and the amount of time required for field evaluation. The genotypes used in Exp. F-2 (1982 field experiment) are listed in Table 3.

Table 2. Group characteristics of crambe genotypes used in field experiments. 1981 and 1982.

Group	Group characteristics			
	Leaf area	Seed yield	Height	Earliness
I	+	+	+	-
II	+	-	+	+
III	-	+	-	-
IV	-	-	-	-

Table 3. List of germplasm used in Exp. F-2. Spring 1982.

Field code	Pedigree code	Group
G-1	I-1387	I
G-4	No. 38	I
G-5	No. 31	II
G-7	PI-281736-N3-N1	II
G-13	No. 41	IV
G-14	B-14-1-xH-68-231	IV
G-15	No. 40	IV
G-17	Meyer	V
G-18	Prophet	V
G-19	B-17-1-(x)	V

Greenhouse Experiments

The experimental period of the greenhouse experiments covered 10 months starting in June 1980. Air temperature and relative humidity were recorded by a hygrothermograph during the full experimental period. In general, air temperature ranged between 20°C and 30°C during the day (from 0800-2000 h, MDT) but occasionally reached 33°C at the hottest part of the day (between 1400 and 1600 h, MDT), At night, air temperatures ranged from 14°C to 20°C. The diurnal variation of relative humidity ranged from 50 percent to 90 percent during the summer months and from 25 percent to 75 percent during fall and winter months.

During the period in which the treatments were not under water stress, all the experiments were irrigated daily with an automatic irrigation system programmed to provide enough water to saturate the soil medium. Drainage of excess water was allowed in all pots. Water stress treatments were given by withholding water to individual pots (according to treatments) and allowing the soil medium to dry to the desired soil water potential. Standard plastic pots 17.8 cm in diameter with one plant per pot were used in all of the experiments. The growth medium was a mix of sand:clay loam soil:peat moss (1:1:1 by volume), except for the experiments in which plaster sand was used. Soil water potential (SWP) was estimated by in situ soil hygrometer/psychrometers, Model PT-51, and the Model HR-33T Dew Point Microvoltmeter, both manufactured by Wescor, Inc. Soil hygrometer/psychrometers were installed at approximately the center of the pots prior to filling the pots with the growing medium. The hygrometer/psychrometers were previously calibrated under laboratory conditions (Wiebe et al. 1971).

Experiment GH-1. In Exp. GH-1, the relationship of RWC and kinetics of rehydration with physiological age of the leaves was studied. Meyer crambe seed was sown on 20 June 1980 and harvested on 17 August 1980 when plants were at the flowering stage of development. The experiment was conducted in a split-split plot experimental design with three replicates in the main plots. Water stress treatments (SWP=close to 0 MPa and -1 MPa) were the main plots. Leaf age, as determined by leaves from the second, fifth, and eighth acropetal positions of the main stem, were the subplots. At the time of sampling, the old leaf (O) showed some chlorosis (aging symptoms) while the mature leaf (M) was complete healthy and the young leaf (Y) was at the rapid growing stage of development. Ten leaf discs, 8 mm in diameter, were obtained from each treatment. The floating times, in h, for leaf discs were 0.0, 1.75, 3.5, 7.0, 14.0, and 28.0, which constituted the sub-sub plots in the experiment.

Experiment GH-2. The objective of Exp. GH-2 was to evaluate the effect of time of floating (T) on the possible loss of dry weight by the leaf discs. Meyer crambe seed was sown on 10 August 1980 and harvested on 5 September 1980. The factorial combinations of drought (lightly stressed: SWP= -0.2 MPa; and stressed: SWP= -0.5MPa) and time of floating were the main plot treatments while samples (dried or floated) were the subplots in a split plot experimental design with three replicates. Samples were taken from the third leaf (acropetally) when plants were at the vegetative stage of development. Paired samples were obtained from one leaf by dividing it longitudinally and taking 10 leaf discs, 8 mm in diameter, from each side. Randomly, one of the two paired samples was allowed to float (floated), while the other was oven dried at 65°C for

48 h after obtaining its fresh weight (dried). The floated sample was weighed after 1, 2, 3, 4, and 5 h to obtain the turgid weights, then oven dried at 65°C for 48 h.

Experiment GH-3. This experiment was similar to Exp. GH-2 and was designed to explore the effects of time of floating on the possible loss of dry weight by leaf discs. Meyer crambe seed was planted on 10 August 1980 and harvested on 23 September 1980. Samples were taken from the fourth leaf, acropetally (mature and fully developed), when plants showed flower initials. A split plot experimental design with drought treatments (SWP= -0.3 MPa, and -1 MPa) as the main plots (replicated four times) and subplots represented by sample (floated or dried) was used in this study. Paired samples were obtained as in Exp. GH-2 and floating time was 2, 4, and 8 h.

Experiment GH-4. In Exp. GH-4, the relative water content and kinetics of rehydration of crambe plants were evaluated at two stages of development, vegetative (V) and flowering (F), combined factorially with drought treatments (stressed: SWP= -0.9 MPa; and nonstressed: SWP= -0.05 MPa). Meyer crambe seed was sown on 11 August 1980 and 29 August 1980 to achieve vegetative and flowering plants at the same harvest time. The treatments were arranged in a completely randomized experimental design with five replications for each treatment. The fourth and fifth leaves, acropetally, were sampled for vegetative and flowering treatments, respectively. Ten leaf discs per sample, 12 mm in diameter, were floated for 2, 4, and 8 h. After the turgid weights at 8 h were determined, all the samples were oven dried at 65°C for 48 h.

Experiment GH-5. This experiment was used to study the relationship of transpiration and leaf diffusion resistance with water stress in

the cultivars Meyer and Prophet during flowering. The two cultivars were arranged in a completely randomized experimental design with six replicates. Meyer and Prophet crambe seed were sown on 11 November 1980. All plants were well watered until the treatment period began. The treatment consisted of withholding water until a drought cycle was completed. Transpiration and LDR were recorded daily throughout the drought cycle, shortly after sunrise and at about 1400 h (MDT) in the afternoon from 27 December 1980 to 3 January 1981. The sixth acropetal leaf was sampled on the adaxial surface.

Experiment GH-6. In Exp. GH-6, a series of plant water stress indicators were evaluated in order to study the plant internal water relations. Meyer and Prophet crambe seed were sown on 4 November 1980 and harvested on 24 December 1980. Plants were subjected to four levels of drought intensity (SWP= 0, -0.08, -0.25, and -1.2 MPa). The experimental units were arranged in a randomized complete block experimental design, with eight replicates per treatment. The treatments were obtained by combining cultivars x drought levels, factorially. The fifth leaf was sampled for porometric analysis, RWC, and LOP. The sixth leaf was used to determine the LWP (pressure chamber method).

Experiment GH-7. The objective of Exp. GH-7 was to expand the information generated in Exp. GH-6 with respect to the evaluation of parameters associated with plant water stress in crambe. Meyer crambe seed was sown on 1 November 1980. Plaster sand was used as the growth medium and the study was irrigated with double strength "Hoagland's solution" (Hoagland and Arnon 1938). Five drought treatments (SWP= 0, -0.2, -0.4, -0.8, and -1.2 MPa) were examined in a randomized complete block experimental design with six replications. Treatments were given

by stopping irrigation and allowing each treatment to reach the desired SWP. The adaxial and abaxial leaf surfaces were read for porometric data on the fifth leaf acropetally. The same leaf was used for the RWC and LOP determinations. The sixth leaf was sampled for LWP (pressure chamber method). All the sampling was done from 1000 to 1600 h, MDT.

Experiment GH-8. In Exp. GH-8, the possible preconditioning effects of drought cycles were determined. The objective was to evaluate the response of crambe cultivars to an increased number of drying and wetting cycles in the soil medium. The growing medium and irrigation solution were similar to that used in Exp. GH-7. Meyer and Prophet seed were sown on 17 January 1981 and combined factorially with drought cycles (0, 1, 2, and 3 cycles) in a completely randomized experimental design with six replications. A drought cycle was defined by withholding water and allowing the soil water potential to decrease to -0.5 MPa before rewatering. Thus, there was one treatment that was not subjected to any drought cycle (control, SWP maintained close to 0 MPa) and treatments subjected to one, two, or three drought cycles. Enough time was permitted for the plants to visually recover from one drought cycle to another. The drought cycles were initiated at 30, 40, and 51 days after planting. The measurements taken on turgid plants included RWC, LOP, LWP, LA, LDR, TR, and plant dry weight divided into its components (leaf, stem, and roots).

Field Experiments

One field experiment was conducted in 1981 (F-1), and two in 1982 (F-2 and F-3). Land preparation included chiseling, plowing, floating, disking, and bedding (east to west) in both years. In 1981, deep

chiseling (45 cm depth) was also included. The plot area was laser-leveled in 1982. Fertilizer was applied at the rate of 86-67-18 kg/ha N-P-K in 1981 and 112-110-0 kg/ha in 1982 and was soil-incorporated during the disking operation. The herbicide Balan, at the rate of 1.68 kg active/ha, was applied and also soil-incorporated during the disking operation. In both years, cotton was the previous crop. Seeds were planted into dry soil in single rows on shaped beds 1 m wide in all three experiments. After seeding, furrow irrigation was applied to maintain high available moisture in the soil until emergence of seedlings was complete.

The 1982 experiments were located in an adjacent field to the F-1 experiment. The 1982 field size was equivalent to the F-1 experiment, where F-2 was established on the east two-thirds of the field and F-3 established on the west third of the field.

The soil where these experiments were conducted is a Glendale clay loam (mixed, calcareous, thermic family of typic Torrifluvent), as described by Beese et al. (1982). The clay loam is underlaid by a layer of medium sand at varying depths of 75 to 120 cm.

Experiment F-1. This experiment evaluated the field response of crambe genotypes to varying levels of available water. The evaluation which was based on the techniques and procedures previously calibrated under greenhouse conditions was used to catalog the response of crambe under water stress conditions. Crambe seed was sown on 6 March 1981 and furrow irrigated on 10 March and 24 March. Five irrigation treatments (IT) and 20 genotypes were evaluated in the four quarters of the experiment where the design criteria for water application were dictated by a

line source sprinkler irrigation system as described by Hanks et al. (1976). The use of the line source sprinkler plot irrigation system appeared to offer a reliable and convenient method of applying a continuous, uniformly varying level of water. The system is economical and simple to install and operate. However, no statistical test is available for the main effect of irrigation level on response variables because the irrigation amount is applied systematically with no randomization (Hanks et al. 1980). Because the irrigation effects are usually large and mean comparison is not critical, the use of analysis of variance, structured as a split-block design, may solve the analytical problem (Steel and Torrie 1960). Furthermore, because the comparison of means among irrigation treatments is of little interest in the present study, and the analysis of trends or tendencies is desirable, the response of genotypes can be analyzed through multiple regression as a response function, comparing the trends instead of the mean values for irrigation treatments (Neter and Wasserman 1974).

The layout of the experiment (Figure 1) was set to meet the requirements imposed by the line source sprinkler system as described by Hanks et al. (1976). The 20 genotypes were randomized within each irrigation plot (Figure 2). The plot size for individual genotypes was one row 5.18 m long. Only the central 3.05 m of each plot was considered usable plot area. The total experimental area consisted of 36 rows, 207.3 m long, with buffer areas of 15.2 m at each end (Figure 1). The sprinkler line was then installed between rows 18 and 19 in the middle of the plot area. Rainbird sprinklers, 70CW-TNT, with single 5.5 mm low trajectory (21°) nozzles were spaced 9.1 m apart. At an operating pressure of 0.3795 MPa, a wet diameter of 36.9 m with output

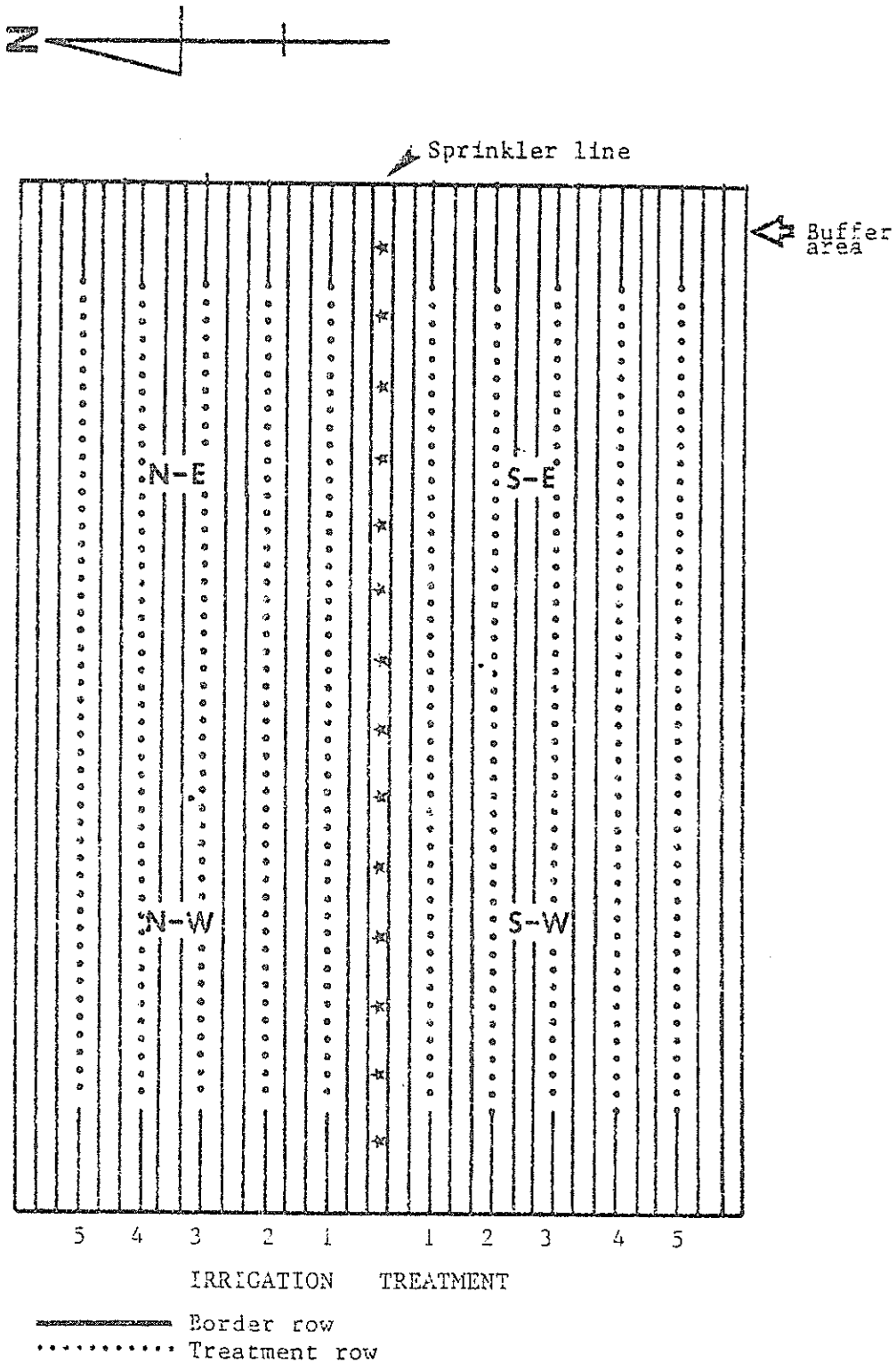

Fig. 1. Schematic field layout. Exp. F-1 and Exp. F-2. 1981 and 1982.

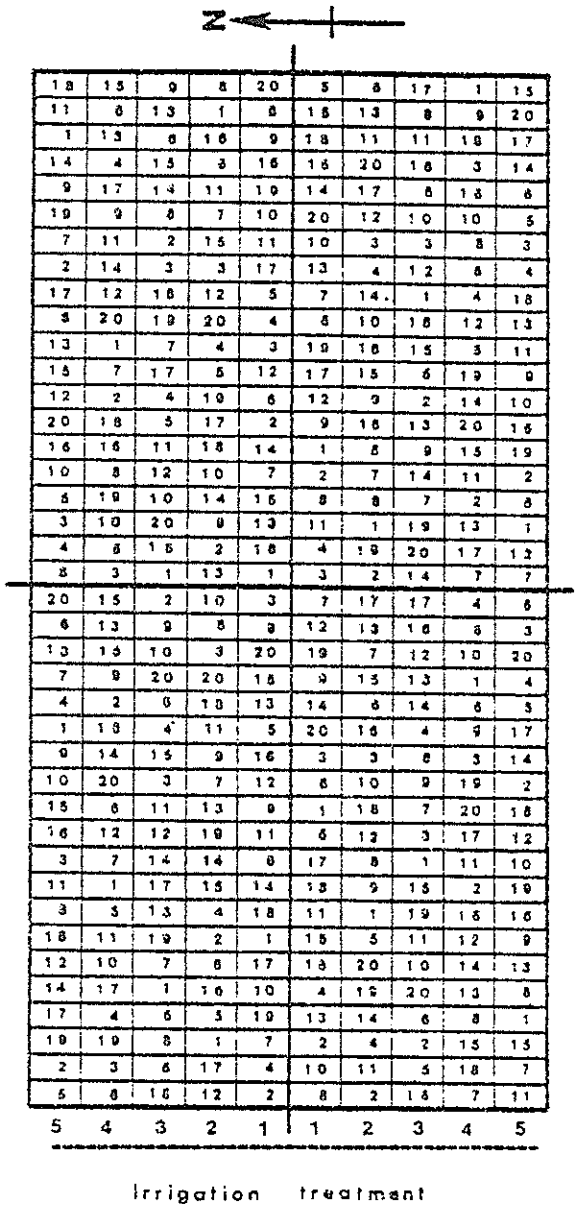

Fig. 2. Plot distribution of Exp. F-1. Numbers in the boxes indicate the field code of genotypes. 1981.

of 0.66 l/s per nozzle, is expected. The sprinklers were mounted on 46 cm high by 2.5 cm inside diameter risers attached to a 7.5 cm diameter quick coupling, portable, aluminum supply line.

The irrigation determinant was defined as -0.1 MPa soil water potential at 30 cm depth in irrigation treatment 1 (IT-1), which was the treatment closest to the sprinkler line. The irrigation treatments from IT-1 to IT-5 (the driest treatment) were evenly spaced (three rows apart) starting at the sprinkler line (Figure 1). Two aluminum access tubes were installed at each irrigation treatment to monitor the water content of the soil to a depth of 90 cm at 30 cm intervals. Soil moisture was monitored with a depth moisture gauge, Model 3222 (manufactured by Troxler International, Inc.), with SWP estimated from the soil moisture characteristic curve (Figure 3) obtained with the pressure plate apparatus (Hillel 1971). The moisture gauge was read twice a week. Catch cans, 9.8 cm in diameter, were used to estimate the amount of water applied to each irrigation treatment. One can per access tube was installed. The amount of water caught in each can was measured immediately after irrigation.

The average temperatures observed through the growing season in Exp. F-1 are shown in Table 4. Each month was divided into three periods of about 10 days each. The mean maximum temperature tended to increase steadily from 15°C in early March to 30°C in late May, with a sharp increase from 30°C to 35°C in early June. Thereafter, temperatures leveled off through that month. Minimum temperatures, however, had a different trend. From early March to early April, the mean minimum temperature increased from 1.4°C to 2.7°C, with a steep increase in mid-April to 9.1°C. Thereafter, the average minimum temperature

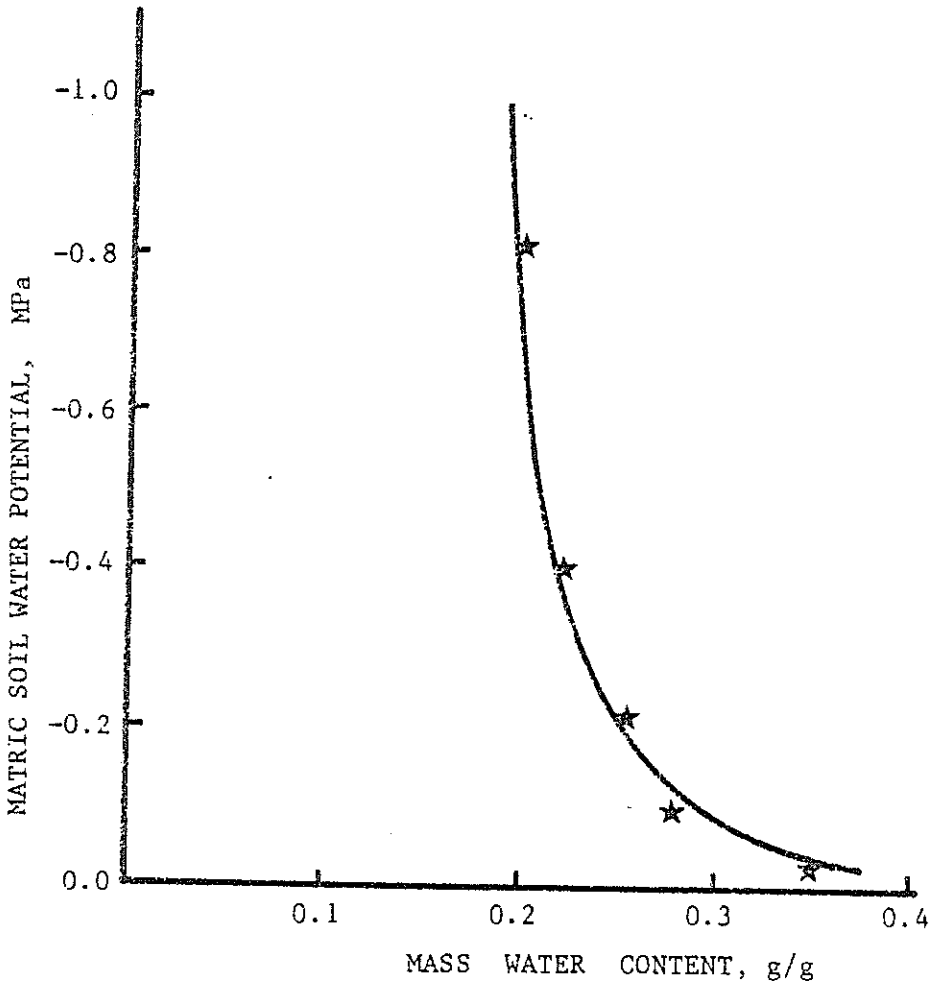

Fig. 3. Soil-moisture characteristic curve obtained from bulk samples at 30 cm depth. Exp. F-1. 1981.

Table 4. Growing season temperatures expressed as means per periods of about 10 days within each month. Exp. F-1. 1981.

Month	Period	Mean temperature Maximum	(SD)†	Minimum	(SD)
		C			
March	1	14.8	(2.4)	1.4	(3.4)
	2	19.6	(2.0)	1.4	(2.9)
	3	22.4	(3.2)	2.7	(2.3)
April	1	24.8	(4.3)	3.4	(2.2)
	2	25.7	(3.8)	9.1	(3.4)
	3	27.4	(4.0)	8.5	(3.6)
May	1	27.4	(2.0)	10.4	(1.5)
	2	29.6	(1.3)	10.3	(1.6)
	3	30.4	(1.6)	10.6	(2.7)
June	1	35.1	(3.3)	12.9	(1.8)
	2	35.7	(3.8)	13.2	(2.9)
	3	34.6	(4.3)	17.9	(1.5)

†Standard deviation.

increased steadily until mid-June to 13.2°C, with a further increase in late June.

Freezing temperatures (0.0°C) occurred in nine days during March, with extreme temperatures of -3.5°C, -2.0°C and -3.0°C for periods 1, 2 and 3, respectively. The frequency of days with freezing temperatures in March were 4, 4 and 1 for periods 1, 2 and 3, respectively. No visible damage due to low temperature was observed.

During late May, four days had temperatures above 32°C. In June, there were 4, 7 and 4 days with temperatures greater than 35°C during the periods 1, 2 and 3, respectively.

The irrigation pattern of the line source irrigation system is highly affected by winds (Hank et al. 1976). During this experiment, wind speed frequently exceeded 8 km/h during irrigation even though irrigations were applied early in the morning (starting before sunrise) in an attempt to reduce wind effects. The estimated pattern for the four irrigations applied in this experiment is shown in Figure 4. Individual irrigation patterns were highly affected by winds, but the average of all irrigations was only slightly offset from the expected pattern. The observed irrigation pattern implies that, on the average, the irrigation treatments were well differentiated, but individual irrigations had a nested effect with time and with development stage of the crambe plants.

The best fit polynomial was used to estimate the irrigation patterns. The complete model included, in the independent variables, IT up to the third power combined with a dummy variable which represented

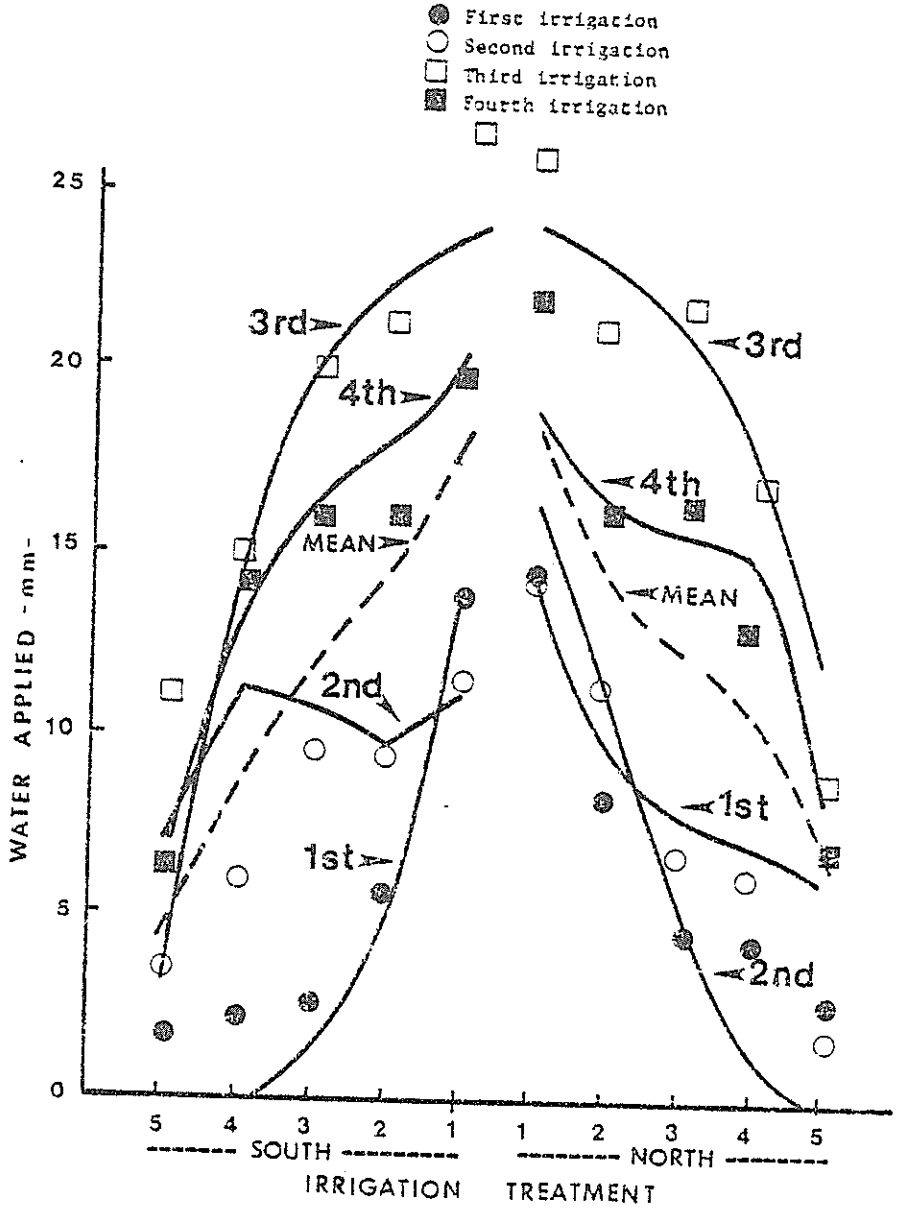

Fig. 4. Estimated irrigation pattern obtained in four irrigations applied with the line source sprinkler irrigation system. Exp. F-1. 1981.

halves (North=0 and South=1). The amount of irrigation water (IW) was then used as a dependent variable at each irrigation:

$$IW=f(IT, IT^2, IT^3, NS, ITxNS, IT^2xNS, IT^3xNS).$$

Table 5 shows the significant effect of NS (halves) in the model indicating the wind effects.

The amount of irrigation water received by each irrigation treatment (WA) and the average matric soil water potential (SWPm) observed at the time of sampling for physiological parameters is shown in Table 6. Because of the variability in SWPm and WA on the two sides (north and south) of the line source, it was not desirable to consider the plots equidistant from, but on opposite sides of the line source, as replicates (Miller and Hang 1982). Thus, the actual SWPm and WA were used as independent variables together with stage of development (SD) and pubescence (glabrous=0 and pubescent=1) as observed in the field.

Precipitation in the form of rain occurred on 15 April (5.1 mm), 30 April (7.9 mm) and 2 May (23.6 mm). The rain on 2 May significantly increased the amount of water in the soil; however, it was still possible to distinguish between treatments, based on the water content of the soil.

The plant population was thinned on 13 April to approximately one plant per 5 cm, whenever possible. Some genotypes showed slower emergence and weaker seedlings from the beginning of the growing season resulting in a higher rate of plant mortality, thus reducing final populations in those plots. The phenology of the plant was graded twice during the growing season with the first observation taken on 5 May and

Table 5. Estimated equations for individual and average irrigation patterns. Irrigations were applied through the line source sprinkler irrigation system. Exp. F-1. 1981.

Source	Sprinkler irrigation 30 April	12 May	22 May	4 June	Mean
Intercept	27.56	18.52	24.09	29.28	27.41
IT_2	-17.43	ns	ns	-15.37	-12.46
IT_3^2	5.00	-2.42	ns	5.64	3.73
IT^3	-0.48	0.33	-0.10	-0.67	-0.41
ITxNS	ns[†]	-11.95	ns	2.50	ns
IT_2xNS	-1.37	7.48	-0.19	-0.74	ns
IT^3xNS	0.23	-0.96	ns	ns	-0.02
R^2	94.3	75.2	73.1	85.2	94.1

[†]Nonsignificant at P=0.05.

Table 6. Total water applied (WA) through the line source sprinkler irrigation system and matric soil water potential (SWPm) observed at the time of reading of physiological parameters. Exp. F-1. 1981.

Concept	Irrigation treatment 1	2	3	4	5
			Northwest quarter		
WA (mm)	83.1	60.2	51.2	41.5	20.0
SWPm (MPa)	-0.43	-0.24	-0.39	-0.38	-0.71
			Southwest quarter		
WA (mm)	73.1	55.1	53.3	39.0	23.2
SWPm (MPa)	-0.46	-0.73	-0.27	-0.42	-0.67
			Northeast quarter		
WA (mm)	66.9	54.7	48.3	40.9	20.2
SWPm (MPa)	-0.15	-0.25	-0.30	-0.81	-0.31
			Southeast quarter		
WA (mm)	69.8	52.0	46.5	39.2	25.5
SWPm (MPa)	-0.80	-0.22	-0.71	-0.32	-0.17

the second on 19 May. Each experimental unit was given a grade according to the scale shown in Table 7. The stage of development was recorded as an auxiliary variable, as a very different developmental pattern was observed among genotypes and irrigation treatments.

Stages of development were defined in the following manner:

1. Vegetative - Complete absence of reproductive structures.
2. Buttons - First appearance of green flowering structures or buds.
3. Closed buds - Flower buttons were evident, but flower petals were still closed and white to cream in color.
4. Open flowers - Flowers were open with all the petals extended.

Table 7. Phenological stages in crambe used as an indicator of earliness in Exp. F-1. 1981.

Grade	Growth stage
0	Vegetative
1	Buttons
2	Closed buds
3	Open flowers
4	Seed set and flowering
5	Seed filling
6	Maturing and seed filling
7	Mature

5. Seed set and flowering - The flowering stem had grown and seed set was observed on the older part of the flowering stem, but the youngest part of the stem was actively producing flowers.

6. Seed filling - Flowering was almost completed and seeds were in the filling stage. Seeds were green in color.

7. Maturing and seed filling - Stage in which the first group of seed set was maturing (turning to golden-brown color), but seeds in the filling stage were still observed.

8. Mature - When all seeds and stems were a golden brown color due to maturation.

The physiological parameters used to evaluate the internal water status of the genotypes were measured on 19-21 May 1981. Three plants were randomly selected for porometric reading, RWC, LOP, LA, and top dry weight (TDW). Top dry weight was split into the components of leaf dry weight (LDW), stem dry weight (SDW) and specific leaf area (SLA) defined as the ratio of LA/LDS (cm^2/g). The sample for RWC consisted of 10 leaf discs 14 mm in diameter. The fifth acropetal leaf was used for samples in LDR, TR, RWC, and LOP. The readings were taken between 1000 h and 1500 h, MDT. Weather data for these three days are summarized in Table 8.

Because of the time required to measure the physiological parameters in each plot, only half of the experimental units were read. Seed from each plot was harvested by cutting off the plants at the base

Table 8. Weather conditions during the physiological sampling period for the evaluation of internal water status of crambe genotypes. Exp. F-1. 1981.

Weather variable	Date		
	19 May	20 May	21 May
Air temperature (C)			
Maximum	27.5	31.5	29.0
Minimum	8.0	11.5	6.5
Air humidity (%)			
Maximum	90.0	61.0	66.0
Minimum	26.0	9.0	15.0
Solar radiation			
mV	11243	11071	10986
ly/day	972.0	957.1	949.8
Wind			
km/24 hours	23.3	4.0	87.6
Pan evaporation			
mm/day	14.2	15.2	13.2
Precipitation			
mm/day	0.0	0.0	0.0

by hand and threshing with a nursery plot thresher. The number of plants per plot also was recorded. Harvest of plants from the field started on 11 June and ended on 25 June. Individual plots were harvested attendant upon their maturation stage.

Experiment F-2. Experiment F-2 was conducted in the spring of 1982 to validate the results obtained in Exp. F-1 in 1981. Due to the difficulty of reading a very large number of plots in the field, the number of genotypes was reduced to 10 and the number of irrigation treatments to three. The genotypes used in the F-2 experiment are shown in Table 3. The irrigation treatments were separated in the following way: IT-1 was three rows from the sprinkler line, IT-2 was six rows from IT-1, and IT-3 was six rows from IT-2. This arrangement would correspond to IT-1, IT-3, and IT-5 of Exp. F-1 (Figure 1). The same experimental layout was used for Exp. F-2 with respect to the line source sprinkler system. The plot distribution is shown in Figure 5.

Crambe seed was sown on 2 March 1982 and furrow-irrigated on 3 March and 12 March. The amount of seed sown per genotype was determined on the basis of the germination percentage obtained in the germination test conducted under laboratory conditions eight months after seed harvest. The lack of germination potential in genotypes was, therefore, compensated by increasing the amount of seed planted. Ten days after sowing the initial emergence of seedlings was noted, but by 19 March only a very poor plant stand was observed. Another furrow irrigation was applied on 22 March, but the plant population progressively declined to the point of becoming inadequate for the purposes of the experiment by 4 April.

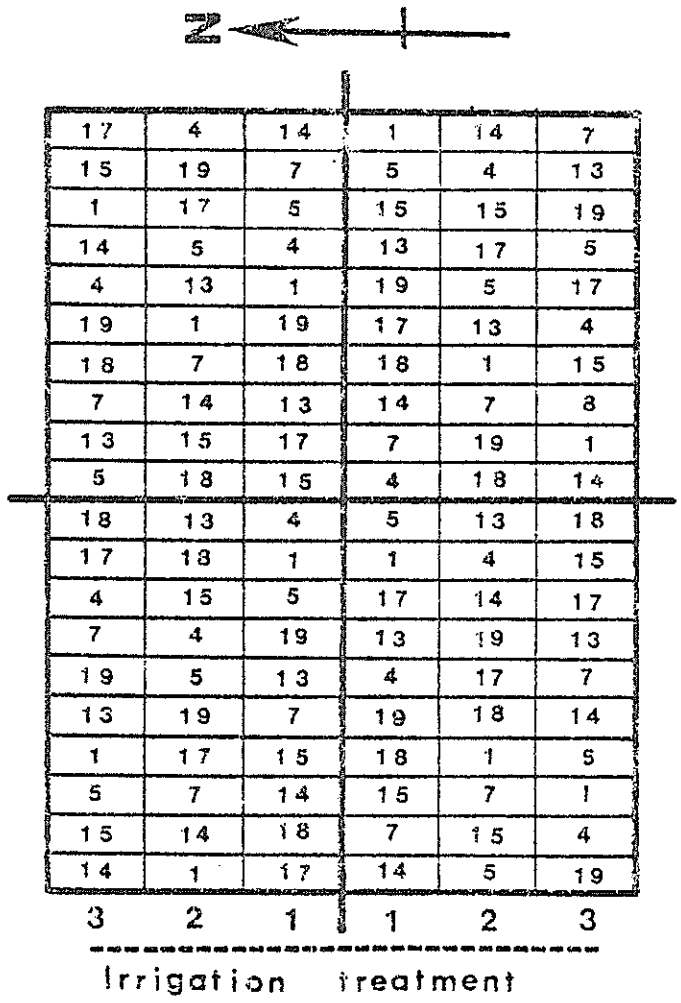

Fig. 5. Plot distribution of Exp. F-2. Numbers in boxes indicate the field code of genotypes. 1982.

The observed temperatures for the growing season of 1982 are shown in Table 9. The 1982 season was characterized by more extreme temperatures than in 1981 as there were warmer days and cooler nights at the beginning of the season. During the second period of March, six days had temperatures above 20°C; while in the third period of the same month, every day had temperatures above 20°C. In both periods, the highest temperature was 27°C. During the second period of March, only one day had freezing temperatures (-4°C), but seven days were registered with temperatures below 0°C during the third period of March with an absolute minimum of -2°C. Rains of 16.5 and 6.3 mm occurred on 23 May and 28 May, respectively.

Soil samples were taken during the installation of access tubes for the neutron moisture gauge. These samples were used to estimate the soil water matrix potential (SWPm) shown in the soil-moisture characteristic curve (Figure 6).

Soil samples were obtained to look into the possibility of salt damage, as well as the possibility of herbicide damage, since the plants showed chlorosis and browning of the foliage after the seedling stage was passed. Soil samples were taken at 18, 30, 60, 90, 120, 150, 180 and 210 m along the experimental field, from west to east. Three samples from each half of the field (north and south) were bulked, thus, there were 16 sites analyzed for each depth (0-20, 20-40 and 40-60 cm). The electrical conductivity (EC) analysis of the soil solution was conducted at the Soil, Plant and Water Testing Laboratory, NMSU. The estimated gradients of EC as a function of soil depth across the experimental area (west to east) is shown in Figure 7. Evidently, salt concentrations increased with depth of soil and also more salts accumulated

Table 9. Growing season temperatures expressed as means per periods of about 10 days each within each month. Exps. F-2 and F-3. 1982.

Month	Period	Maximum	Mean temperature (SD)†	Minimum	(SD)
		°C			
March	1	21.4	(4.1)	0.3	(4.1)
	2	21.7	(3.8)	3.7	(4.3)
	3	23.0	(1.3)	1.0	(3.4)
April	1	24.8	(2.0)	5.0	(3.2)
	2	28.2	(1.7)	4.6	(4.5)
	3	23.9	(5.7)	4.8	(3.2)
May	1	25.4	(2.9)	7.6	(3.7)
	2	28.7	(3.9)	5.7	(2.0)
	3	32.0	(2.0)	7.7	(3.2)
June	1	34.3	(1.5)	10.5	(2.4)
	2	28.1	(6.2)	13.0	(3.1)
	3	24.6	(2.1)	12.5	(3.6)

† Standard deviation.

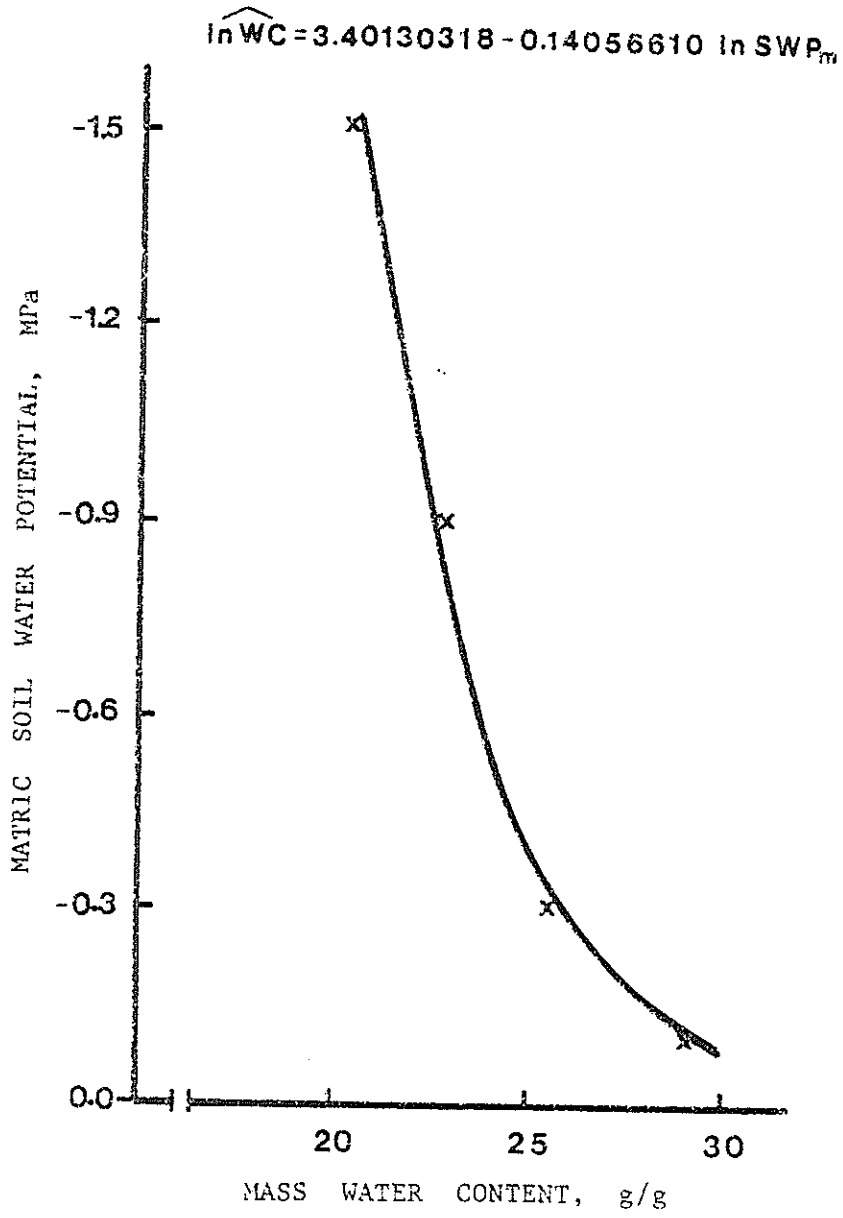

Fig. 6. Soil-moisture characteristic curve as estimated from 36 bulk samples from 0-30 cm depth. Exp. F-2. 1982.

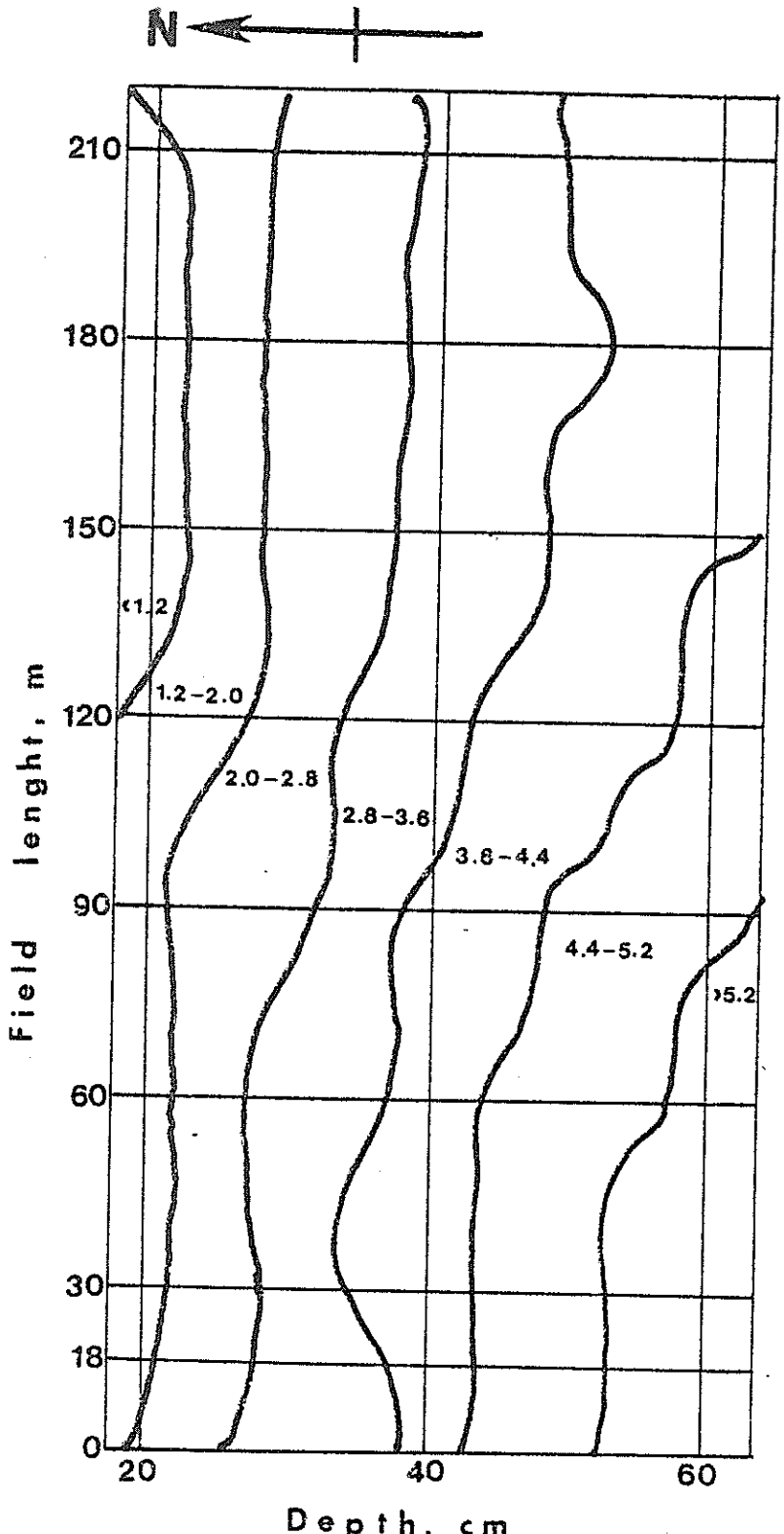

Fig. 7. Contour lines for soil solution electrical conductivity (EC, mmhos/cm) as a function of soil depth and field length (west to east). Exp. F-2 and Exp. F-3. 1982.

in the west part of the field. This field has been irrigated from west to east for several years. The mean EC values observed are shown in Table 10. The salt concentrations as indicated by the EC values do not appear to be critical at the 0-20 cm depth; however, the salt concentration at the 20-40 cm depth may be a detrimental factor for susceptible crops, mostly in the west part of the field.

Even though the EC gradient was fairly clear, it did not fit the injury pattern suffered by the crop as seedlings were mostly affected in the east part of the field. Furthermore, in Exp. F-2 (second planting) a root distribution study was conducted, in which it was found that 68 percent of the root mass of mature plants was located in the 0-20 cm depth (unpublished data).

Soil samples also were analyzed at the New Mexico Department of Agriculture State Chemistry Laboratory in search of Caparol (Prometryn) residues (Caparol is a herbicide commonly used in cotton fields). The Caparol concentrations found in the soil solution are shown in Table 11. Such concentrations were considered nontoxic for normal cropping; that is, the concentrations found were not high enough to promote a herbicide effect in plants, as presently known (W. P. Anderson, personal communication).

This experiment was reseeded in the same arrangement and on the same plots on 5 May 1982. In order to eliminate the deleterious effects of soil cracks from the seed track (observed in the first planting), sprinkler irrigation was used to provide moisture for germination and seedling emergence. Seeds were also sown at a depth of 1.5 cm to help seedling emergence. The soil was kept moist with light irrigations every day or every other day. Emergence was observed on 17 May, but it

Table 10. Mean electrical conductivity (EC) of soil solution observed at different depths across the experimental area. Exps. F-2 and F-3. 1982.

Field length (m)	Depth (cm) 0-20	20-40	40-60	Mean
	----------mmhos/cm----------			
18	1.61	5.38	5.12	4.04
30	1.63	4.10	4.85	3.53
60	1.83	4.52	5.19	4.02
90	1.35	3.59	5.53	3.49
120	1.37	2.57	4.92	2.95
150	1.31	3.12	4.48	2.97
180	1.28	2.26	4.21	2.58
210	1.28	2.26	4.21	2.58
Mean	1.50	3.55	4.90	3.32

Table 11. Residual concentration of Caparol (prometryn) in the soil solution at two soil depths. Exps. F-2 and F-3. 1982.

Field length (m)	Soil depth (cm) 0-30	30-60
90	0.3 ppm†	10 ppb‡
90	None detected	30 ppb
150	30 ppb	10 ppb
210	0.2 ppm	0.1 ppm

†ppm = Parts per million
‡ppb = Parts per billion

was uniformly adequate only in the border rows. Some genotypes in the treatment rows showed good emergence while others had no emergence at all. On 4 June, the irrigation treatments were started by using the line source sprinkler system. Flowering stems were observed on 21 June even though the plants were very small. As the season progressed, more and more plants died, reducing the stand to the point where only one reading on the best plots was possible on 28-29 June. Two plants per plot were sampled for porometry, RWC, and LOP. Weather data for these two days are summarized in Table 12.

Soil moisture showed no significant differences through the experimental period. Soil moisture was maintained at a high level in IT-1 according to the irrigation determinant (IT-1 = -0.1 MPa); however, irrigation treatments did not differentiate as expected.

Table 13 shows the observed means for soil moisture. The SWPm at the time of sampling for physiological parameters is shown in Table 14. These values were used to evaluate the response of crambe to drought. The average water applied by sprinkler irrigation is presented in Table 15. The expected pattern from the line source system is evident, although sometimes the pattern was shifted to the north and frequently to the east.

Plants showed a very drastic stress condition, leaves were rolled upward and fired. Even though adequate moisture was present in the soil, plants showed severe wilting during the hottest part of the day with recovery at night only sufficient to maintain turgid leaves early in the morning. The plants exudated a sticky material through the malformed flowering stems. Flowering stems curved downward, flowers did not open normally and many flowers became desiccated and dried. This

Table 12. Weather conditions during the period of physiological sampling for the evaluation of internal water status of crambe genotypes. Exp. F-2. 1982.

Weather variable	Date	
	28 June	29 June
Air temperature (C)		
Maximum	28.0	26.0
Minimum	12.5	14.0
Air humidity (%)		
Maximum	62.4	74.0
Minimum	4.0	7.0
Solar radiation		
mV	8689	7906
ly/day	751.2	683.5
Wind		
km/24 hours	134.3	127.9
Pan evaporation		
mm/day	12.7	10.9
Precipitation		
mm/day	0.0	0.0

Table 13. Mean soil mass water content observed through the experimental period. Exp. F-2. 1982.

Date	Depth	Irrigation treatment 1	2	3
	cm		%	
6-02-82	20	26.3	26.6	26.5
	40	30.8	31.0	30.8
	60	34.4	34.3	33.9
6-09-82	20	26.4	25.7	25.4
	40	30.8	30.7	30.5
	60	33.5	34.8	34.3
6-11-82	20	28.8	28.9	27.9
	40	29.5	29.5	29.3
	60	34.4	34.2	33.9
6-18-82	20	23.2	22.7	21.9
	40	29.8	29.9	29.5
	60	29.2	29.1	28.5
6-29-82	20	25.0	24.2	23.2
	40	30.8	30.8	30.7
	60	35.2	35.0	34.9
7-07-82	20	25.8	24.8	23.9
	40	34.6	34.3	34.8
	60	29.9	29.4	29.1

Table 14. Mean matric soil water potential (SWPm) observed at the time of sampling for physiological parameters, 29 June. Exp. F-2. 1982.

Experiment location	Irrigation treatment 1	2	3
quarter	----------MPa----------		
Northeast	-0.23	-0.16	-0.50
Southeast	-0.21	-0.29	-0.36
Northwest	-0.30	-0.62	-0.43
Southwest	-0.31	-0.30	-0.26

Table 15. Average water applied with the line source sprinkler irrigation system. Exp. F-2. 1982.

Date of irrigation	Water applied Irrigation treatment 1	2	3
	mm		
5-20-82	15.9	11.4	2.9
6-04-82	14.5	12.0	6.2
6-11-82	17.5	16.8	3.3
6-22-82	15.8	12.6	4.4
7-01-82	18.8	12.4	4.9
7-08-82	15.6	12.9	6.7
Total	97.5	78.9	28.5

experiment was terminated on 5 July 1982 because of high plant mortality, presumably due to heat stress.

Experiment F-3. This experiment was designed to explore the effect of water shortage on the internal water relations, growth and seed yield of two crambe cultivars, Meyer and Prophet. Crambe seed was sown on 2 March 1982. Land preparation was similar to the F-2 experiment. Three irrigations (not measured) were applied on 3 March, 12 March and 22 March to provide moisture for stand establishment. Seedling emergence was observed 10 days after planting. Plant stand was graded on 19 March and 26 March.

A split plot design with four replications was used. Main plots consisted of six irrigation schedules with the two cultivars as subplots. The main plots were six rows, 10.4 m long by 1 m wide. Each main plot was split into two subplots (cultivars), six rows wide by 5.2 m long. The usable plot area for each subplot was 3.05 m in the two center rows of the experimental unit with two border rows on each side of the central rows. The treatment matrix is shown in Table 16. All the treatments received the three irrigations required for stand establishment mentioned earlier. After the soil profile was filled to field capacity, the three irrigations applied for stand establishment had little additional significance in terms of water needs of the crop.

The subsequent three irrigations were applied on 3 May (60 days after seeding), 19 May (76 days after seeding), and 9 June (97 days after seeding). The average water applied to each irrigated plot was 59 mm, 75 mm, and 86 mm for the three irrigation dates, respectively. Soil water content was monitored through the season by weekly readings with a depth moisture gauge. Aluminum access tubes were installed to a

Table 16. Description of the irrigation treatments used in Exp. F-3. 1982.

Growth stage	Irrigation treatment 1	2	3	4	5	6
Planting	I†	I	I	I	I	I
Buttons	I	I	I			
Flowering	I	I			I	I
Seed filling	I					I
Water‡ applied (mm)	220	134	59	0	85	161

†Indicates irrigation applied at that growth stage.
‡Amount of water applied does not include water applied at planting.

depth of 90 cm and read every 30 cm. One access tube was installed in every plot in two of the four replications.

The northern row of the two usable rows was harvested for growth analysis samples. Each sample consisted of a block of five plants taken randomly. The sampling dates for growth analysis were 2 April (29 days after planting), 17 April (37 days after planting), 13 May (70 days after planting), and 30 May (87 days after planting). Plants were cut off at the crown and transported to the laboratory where leaves were removed from the plant, and leaf area was measured with a leaf area meter. Leaves and stems were oven dried at 65°C for 48 h to obtain the dry weight.

The pattern of soil water content is shown in Figure 8. The irrigation treatments in this case were well differentiated according to the irrigation schedules (Table 16). The matrix soil water potential at 30 cm depth is presented in Table 17. No water movement from one treatment to another was noticed; however, all the treatments tended to accumulate water at the 30-60 cm soil layer (Figure 9). At the second reading of LDR and TR (67 days after planting), IT-1, IT-2 and IT-3 were at about the same level of soil water depletion. Similarly, IT-4, IT-5 and IT-6 formed another group with similar soil water contents. By the time of the third reading of LDR and TR (85 days after planting), IT-4 had the lowest water content of all the treatments with no irrigation after stand establishment, followed by IT-3 with only one irrigation after stand establishment. On the other hand, IT-2, IT-5 and IT-6 showed a higher soil water content together with IT-1. The difference between the latter four treatments is that IT-5 and IT-6 were allowed to dry to about -0.5 MPa before irrigation, whereas IT-1 and IT-2 were kept at higher soil water potentials up to this part of the experiment.

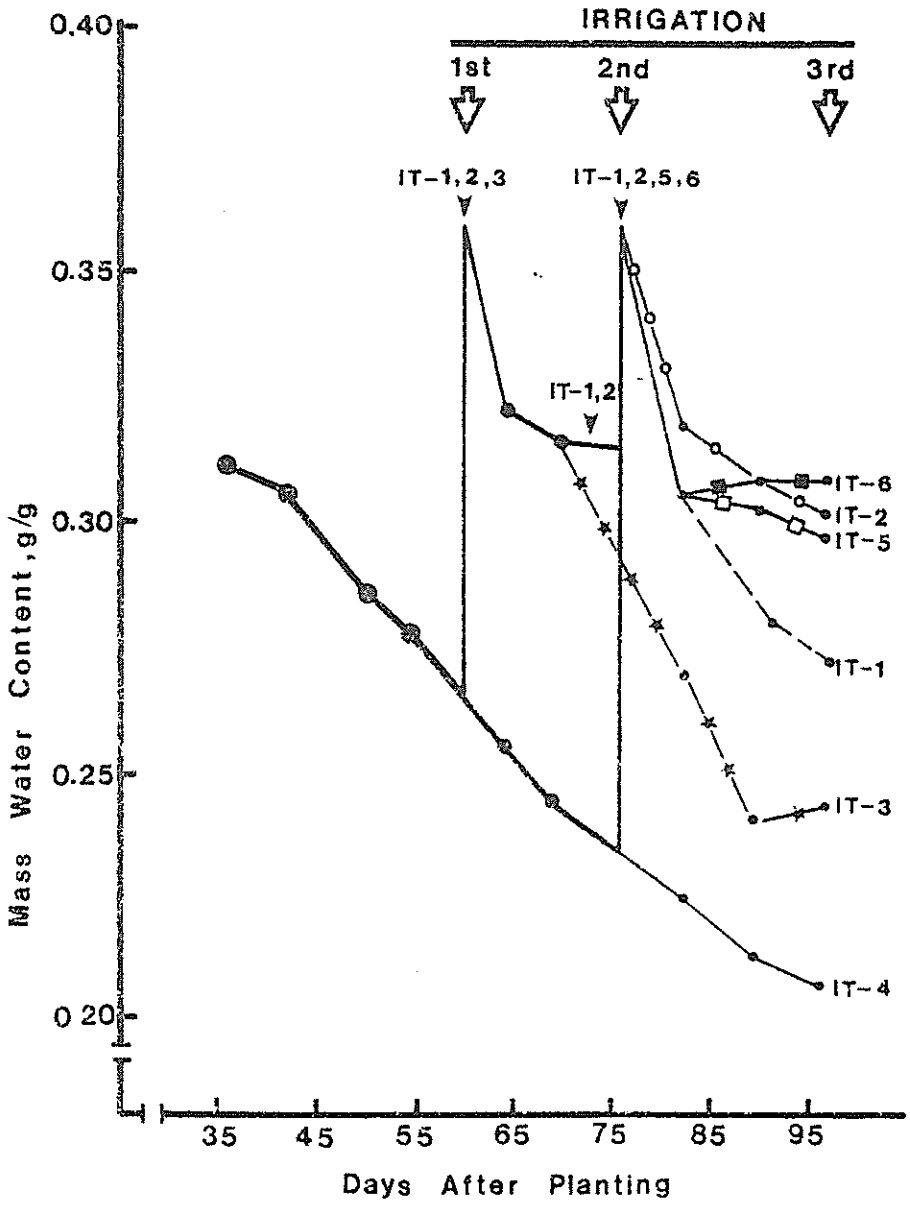

Fig. 8. Average soil water content for irrigation treatments at 30 cm depth through the growing season. Soil water content readings following the third irrigation were unavailable because of an error in reading the depth moisture gauge. Exp. F-3. 1982.

Table 17. Mean matric soil water potentials (SWPm) observed at the time of sampling for leaf diffusion resistance and transpiration. Exp. F-3. 1982.

Irrigation treatment	Sampling dates		
	4-28-82	5-10-82	5-26-82
	----------MPa----------		
1	-0.23	-0.06	-0.09
2	-0.11	-0.05	-0.06
3	-0.06	-0.04	-0.20
4	-0.14	-0.13	-0.77
5	-0.22	-0.28	-0.08
6	-0.16	-0.45	-0.07

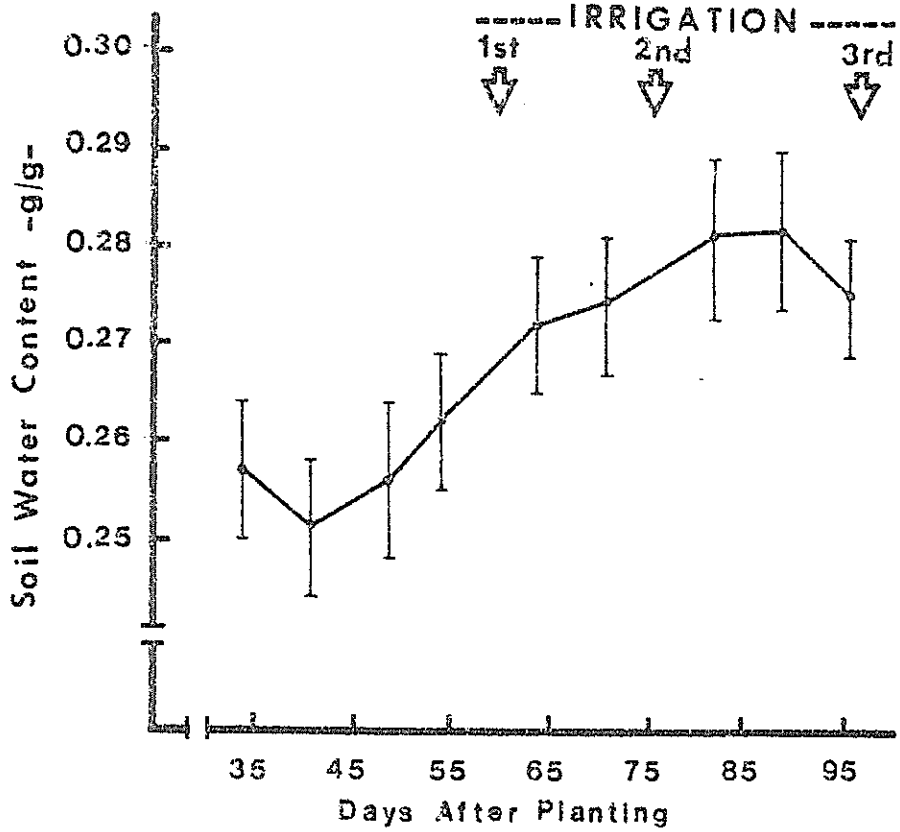

Fig. 9. Average soil water content for irrigation treatments at 60 cm depth throught the growing season. Exp. F-3. 1982.

Porometric readings were taken on 28 April and 10 May. Two plants randomly selected were read at each treatment. Measurements on LOP and RWC were taken only on 28 April; weather data for those two days are summarized in Table 18. Seed was collected on 21 June and machine threshed. The number of plants per plot at harvest was recorded.

This experiment was also affected by the syndrome described for Exp. F-2. As soon as the seedlings passed the cotyledonary stage of growth, they turned yellow and brownish. The symptoms were accentuated at the first irrigation (button stage of growth). Because of the swelling effects of the soil, big cracks were evident. The soil expansion, due to irrigation and subsequent cracking as the soil dried, suggested a damaging effect on the root system.

Germination Tests

Germination tests were performed on the seed harvested from the F-1 and F-3 experiments. Because seed viability appeared to be a serious problem in establishing crambe fields, the potential germination was studied in relation to the irrigation treatments and genotypes. Samples of 50 seeds with pod were placed in petri dishes containing two pieces of filter paper (Whatman No. 1) moistened with 4 ml of distilled water. Incubators were set at a constant 25°C and water was added to the petri dishes as needed throughout the incubation period. In general, the incubating conditions followed the recommendations of the Association of Official Seed Analysts (Bass et al. 1965, Larsen and Skaggs 1969, Skaggs and Larsen 1969, Clark and Bass 1973). Germinated seeds were defined as those germinants showing the radicle through the pod. In general, counts were made at 4, 7 and 10 days of incubation.

Table 18. Weather conditions during the physiological sampling period for the evaluation of internal water status of crambe genotypes. Exp. F-3. 1982.

Weather variable	Date	
	28 April	10 May
Air temperature (C)		
Maximum	29.0	26.5
Minimum	4.5	7.5
Air humidity (%)		
Maximum	81.0	80.0
Minimum	20.0	17.0
Solar radiation		
mV	8084	8195
ly/day	698.9	708.5
Wind		
km/24 hours	48.5	170.5
Pan evaporation		
mm/day	4.6	10.4
Precipitation		
mm/day	0.0	0.0

SALINITY STUDIES

An initial study to determine the sensitivity of crambe seed to salinity during germination was conducted using two cultivars of crambe, Meyer and Prophet, developed and released by Purdue University. The standard germination percentages (AOSA 1970) of the two lots of seed at the time of this study were 99 percent and 89 percent for Meyer and Prophet, respectively. Evaluation for salinity tolerance during germination was accomplished by placing samples of 50 seed in 90 x 15 mm glass petri dishes containing three circles of Whatman No. 1 filter paper to which 5 ml of an aqueous solution of isoequivalent amounts of NaCl and $CaCl_2$ had been added. The germination responses of crambe to concentrations of 0, 60, 120, 180, 240, 300, 360 and 420 meq/1 were evaluated. The range of concentrations was determined in preliminary tests. The covered petri dishes were arranged in a randomized complete block experimental design with one block for each of the five shelves of the germinator. Temperature was maintained at a constant 20±1°C (Skaggs and Larsen 1969) and counts were made at 2, 4, 6, 8, 10 and 12 days of incubation. Distilled water was added to the petri dishes as needed to provide adequate moisture and maintain salt solutions near the designated concentrations in all treatments. Analysis of variance was used to statistically analyze the data. A split-plot model was developed by considering the factorial combination of cultivars x salt concentrations as the main plots and incubation time (one level for each reading) as the subplots.

RESULTS AND DISCUSSION

GREENHOUSE EXPERIMENTS

Relative Water Content

Water uptake (i.e., rehydration) by floating leaf discs on water is a key factor in determining the time samples should be floated in order to obtain full turgor. It has been demonstrated that the process of rehydration includes two phases. Phase I, a rapid water uptake occurring passively, tends to result in the elimination of water potential gradients between leaf discs and distilled water and the establishment of diffusion equilibrium between the internal and external water (Barrs and Weatherley 1962, Slatyer 1962). The accumulation of solutes in the leaf in combination with cell and membrane properties is thought to be the major factor responsible for the increase of leaf water potential (Kramer 1955, Slatyer 1962, Cruiziat et al. 1980), which results from the rehydration process. Phase II is related to a continuous water uptake which depends on the physiology of leaf discs. Actually, Phase II includes the Phase I process, plus the biochemical changes which occurred in the cell tissue during dehydration. Those changes are thought to occur in two compartments, cell walls and membranes (Fereres et al. 1978, and Frederick and Lasko 1979).

Experiment GH-1. The variation found in Exp. GH-1 is presented in Table 19 where all the factors involved, such as drought treatments (D), leaf age (A), and time of floating (T) were nested and analyzed as a split-plot experimental design.

Weight of sample was taken as the response variable. In this analysis, 89 percent of the total variation is explained by the model. The relative distribution of the variability among sources gives a good

Table 19. Analysis of variance for weights of crambe leaf discs (sample) as affected by water stress, leaf age and time of floating in the process of rehydration. Exp. GH-1. 1980.

Source	DF	SS	OSL†
Total	107	4.46048	
Reps	2	0.11356	ns‡
Drought (D)	1	0.46360	ns
Error "a"	2	0.11093	
Age (A)	2	1.34031	0.01
D x A	2	0.00003	ns
Error "b"	8	0.30648	
Time (T)	5	1.65470	0.01
D x T	5	0.37698	0.01
A x T	10	0.02908	0.01
D x A x T	10	0.00875	ns
Error "c"	60	0.05606	

†Observed significant level.
‡Nonsignificant at P = 0.05.

idea of the most important effects in the model. The main effects of D, A, and T took 10.4 percent, 30.0 percent, and 37.1 percent out of the total variation, respectively. The most relevant interaction was that of DxT, which indicates a lack of parallelism between the wet and water-stressed treatments through time of floating. In other words, it indicates that the leaf discs from different water-stressed treatments behaved differently. This interaction took 8.4 percent out of the total variation. On the other hand, the interaction AxT was also significant indicating a lack of parallelism between leaf age in response to time of floating.

Figure 10 shows the relationship found between water uptake through time and leaf age. The data is presented in its original scale. The analysis was performed on water-stressed and nonwater-stressed treatments separately to illustrate the tendencies more clearly. The model used to estimate the trend through time was based on the power function mentioned earlier for kinetics of rehydration. In this particular case, the three categories of leaf age (old, mature, and young) were represented by dummy variables in the expanded model. Thus, the complete model for each treatment was:

$$\ln Y = \ln a + b D_1 + c D_2 + d \ln T + e(D_1 \ln t) + f(D_2 \ln T) + 4$$

where

lnY = Natural log of weight of sample
lna = Natural log of the intercept and reference line
b, c, d, e and f = Partial regression coefficients
D_1 = Dummy variable for old leaf
D_2 = Dummy variable for mature leaf
lnT = Natural log of time of floating.

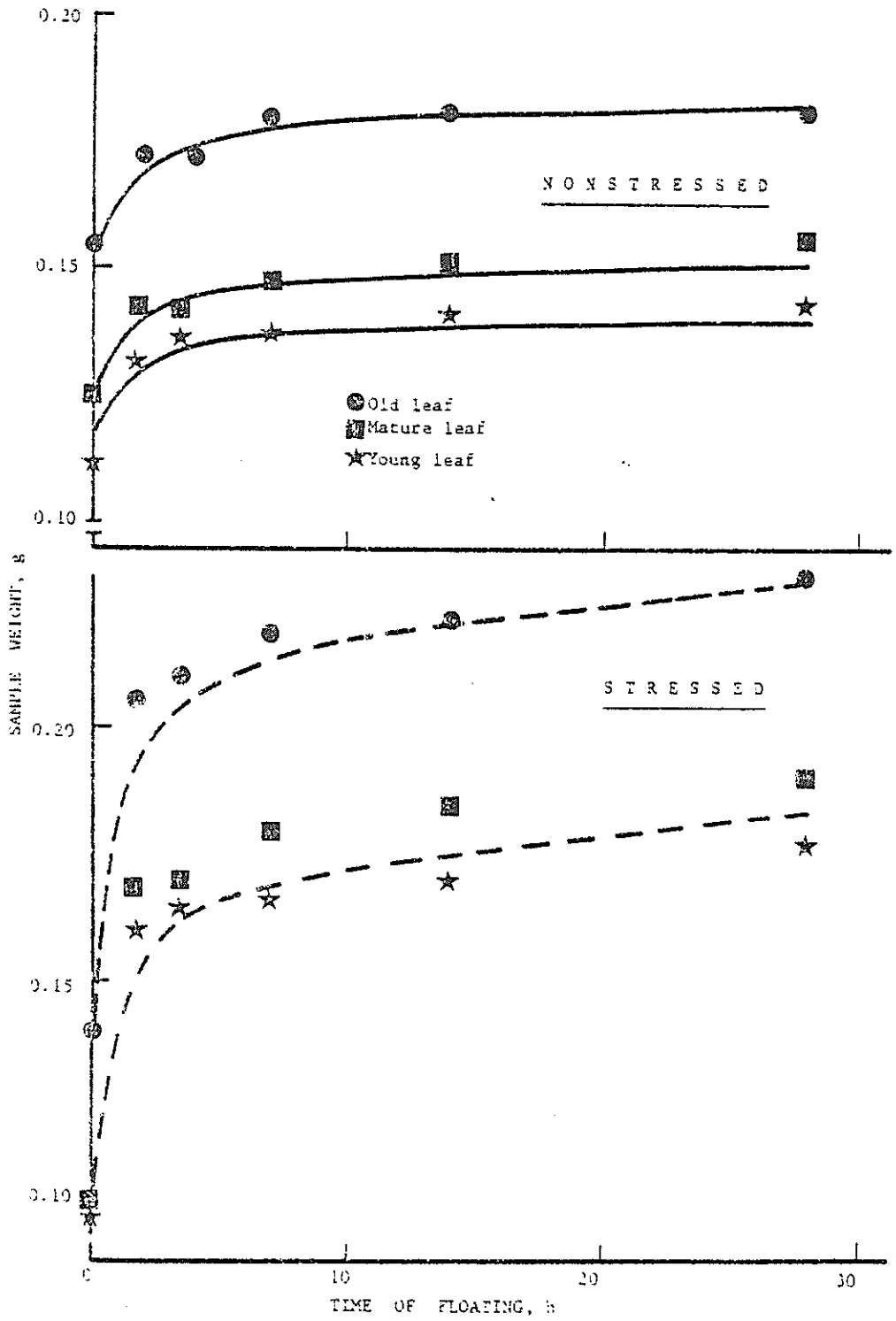

Fig. 10. Kinetics of rehydration of leaf disc samples as a function of floating time at three different leaf ages and two drought treatments. Each data point represents the mean of three samples. Exp. GH-1. 1980.

To meet model requirements, the young leaf was set at the reference line against the other two lines that were compared. Also, to meet the requirements of natural logarithms, the time given to the FW sample was 0.001 h.

The linearized function of each model internally tests for differences among the independent variables and automatically pools the variation associated with nonsignificant variables into the reference line. Table 20 contains the estimates of the significant parameters of each model.

The analysis of these models included tests for lack of fit and serial correlation, as well as residual analysis. None of the tests was significant, so the models were accepted as adequate to describe the process of rehydration. The old leaf sample was significantly heavier in both stressed and nonstressed treatments, whereas mature and young leaves behaved very similarly in both treatments and they were nonsignificantly different in the water-stressed treatment (pooled in one line). Parallelism existed for the lines of each treatment, since the cross products in the models were nonsignificant. Even though the fresh weights of samples were nonsignificant between drought treatments, the response of samples coming from the drought treatments showed a steeper increase in water absorption as compared to the nonstressed treatments (Fig. 10). These results are consistent with those obtained by Kassam and Elston (1976), and by Fereres et al. (1978) in Vicia faba. This effect is attributable to stomatal closure proceeding acropetally as the stress becomes more severe (Jordan et al. 1975) and to the changes in physical and chemical properties of tissue with age (Kassam and Elston 1976, Davis et al. 1977). The more rapid water uptake in samples from

Table 20. Summary of statistics associated with the significant effects in the regression analysis for kinetics of rehydration. Exp. GH-1. 1980.

Parameter	Parameter estimate	Standard error	OSL†
Nonstressed (R^2 = 91.2%)			
Intercept	-2.02854	0.0106	0.01
Old leaf	0.26425	0.0150	0.01
Mature leaf	0.07711	0.0150	0.01
Time	0.01929	0.0018	0.01
Stressed (R^2 = 79.4%)			
Intercept	-1.87549	0.0200	0.01
Old leaf	0.22786	0.0345	0.01
Time	0.05292	0.0048	0.01

† Observed significant level.

water-stressed treatments, as evidenced by the curves in Fig. 10 and by the partial regression coefficients (Time) in Table 20, was attributed by Frederick and Lasko (1979) to a lower LOP, which suggests a more active solute accumulation in the dehydrated leaf tissue. The LOP reduction would explain the rapid water uptake during Phase I (first few hours after flotation started); but during Phase II, where more water is being taken by stressed samples after turgidity was attained, suggests that cell elasticity was modified by the treatment. On the other hand, the higher rates of water uptake found in older leaves may be explained by the higher concentration of osmotically active cellular components, as compared to younger leaves (Kassam and Elston 1976).

Experiment GH-2. Experiment GH-2 was designed to look into the possible changes of dry weights in tissue samples while floating in the rehydration process. The results are shown in Table 21.

The results obtained in the statistical analyses are shown in Table 22. None of the sources of variation were significant for the analysis of dry weight. This means that the variation observed (Table 21) is mostly due to random effects or uncontrolled factors. The loss of dry weight observed between floated and dried samples was not significant at the 0.05 critical level of probability. Fresh weight of samples, however, was highly affected by drought intensity (DI) and time of floating (T).

The significant difference found due to drought intensity is understandable on the basis of plant water losses due to shortage of water in the rooting media. On the other hand, the variation associated with time of floating is related to an intrinsic variability in leaf samples. This variation is evidence of the need of determining the leaf water

Table 21. Mean weights of leaf disc samples through time of crambe plants grown at two soil water potentials in the study of tissue dry weight changes due to floating time in the relative water content technique. Exp. GH-2. 1980.

Floating time	Stress (-0.5 MPa)		Stress (-0.2 MPa)	
	Floated	Dried	Floated	Dried
h	----------	mg	----------	
		Fresh weight		
1	120.3	122.2	133.6	132.7
2	154.5	156.5	153.7	155.7
3	116.7	109.2	126.3	124.1
4	119.8	119.1	134.9	139.3
5	123.7	123.9	133.2	136.7
Mean	127.0	126.2	136.4	137.7
		Dry weight		
1	17.16	18.83	18.18	19.15
2	19.13	18.96	18.82	20.58
3	17.58	18.12	17.18	17.50
4	18.87	19.15	20.78	18.65
5	18.23	19.20	18.17	19.33
Mean	18.20	18.85	18.82	19.33

Table 22. Analysis of variance for fresh weight and dry weight of leaf disc samples in the study of dry weight changes due to the floating time in the relative water content technique. Exp. GH-2. 1980.

Source	DF	Fresh weight		Dry weight	
		SS	OSL†	SS	OSL
Total	59	16454.2	ns‡	276.41	
Rep	2	78.1	ns	74.7	< 0.01
Drought (DI)	1	1639.1	< 0.03	2.5	ns
Time (T)	4	8919.2	< 0.01	31.7	ns
DIxT	4	553.7	ns	5.1	ns
Error "a"	18	4897.9		86.2	
Sample (SA)	1	1.0	ns	2.9	ns
DI x SA	1	18.1	ns	0.7	ns
TxSA	4	102.1	ns	9.1	ns
DIxTxSA	4	37.9	ns	4.7	ns
Error "b"	20	207.1		58.8	

†Observed significant level.
‡Nonsignificant at P = 0.05.

content by dry weight. None of the interactions was found to be significant, which means that the rehydration of leaf discs of the treatments was parallel through time.

Experiment GH-3. Similarly to Exp. GH-2, this experiment was conducted to explore the possible changes in dry weight that crambe tissue may experience during the floating time in the RWC technique. In Exp. GH-3, paired samples were studied as in Exp. GH-2, but, the DW for floated samples was recorded at the end of 8 h of floating. Partial TW readings were taken at 2, 4, and 8 h of floating. The partitioning of variances among treatments is shown in Table 23. No significant differences were found for sources of variation in FW of samples. The sensitivity of the analysis was low because 65 percent out of the total variation was absorbed by experimental error (a+b). Yet, 18 percent of the total variation was explained by one degree of freedom of the DI source. The dry weight of floated and dried samples, however, was found to be significantly different. Floated samples had a mean DW of 18.3 mg/sample, while the dried sample had a DW of 19.9 mg/sample. This indicates a net loss of DW when samples were floated for 8 h. The interaction DIxSA in both cases explained little of the total variation (Table 23), which indicates independence between the two factors.

Kinetics of rehydration was also calculated for Exp. GH-3. The model approach had the same general form as described above. The two-line model was obtained by considering DI as a categorical variable, as follows:

$$\ln WT = \ln a + b \ln T + c\, DI + d(DI \times \ln T) + E$$

Table 23. Analysis of variance for fresh weight and dry weight of leaf disc samples in the study of dry weight changes due to the floating time in the relative water content technique. Exp. GH-3. 1980.

Source	DF	Fresh weight		Dry weight	
		SS	OSL†	SS	OSL
Total	15	1689.6		71.80	
Reps	3	292.4	ns‡	17.90	ns
Drought (DI)	1	300.2	ns	14.16	ns
Error "a"	3	891.1		22.17	
Sample (SA)	1	2.5	ns	10.97	0.02
DI x SA	1	0.2	ns	0.51	ns
Error "b"	6	203.2		6.09	

†Observed significant level.
‡Nonsignificant at P = 0.05.

where

WT = Weight of sample

T = Time of floating

DI = Dummy variable for drought treatment (0 if -0.3 MPa, SWP; and 1 if -1 MPa, SWP) a, b, c, and d=Partial regression coefficients.

All four partial regression coefficients were significantly different from zero (hypothesis tested), which indicated the influence of the variables under study on the sample weight. Parameter estimates of these sources of variation are shown in Table 24.

The variation explained by the model as indicated by R^2 was 79.7 percent. Figure 11 shows the behavior of both drought treatments. The significant interaction indicates a lack of parallelism between the two lines. This lack of parallelism was due to the more rapid water uptake by samples from the more water-stressed treatment (i.e., -1 MPa, SWP treatment). In fact, the higher rate of water uptake in more heavily stressed samples is important in determining the time of floating to obtain turgid weights. From Figure 11, it is evident that the plateau was reached after 2 h of floating. This was also observed in Figure 10. Similarly, the more severely stressed samples maintained a higher water uptake rate throughout the flotation period. Only 2 h after incubation started, the more severely stressed samples had absorbed significantly more water than those less severely stressed.

Relative water content calculated for each time of floating (2, 4, and 8 h) was found to be statistically insignificant for time of floating, but the differences between drought treatments were statistically significant, as shown in Table 25.

Table 24. Summary of statistics associated with the significant effects in the regression analysis for kinetics of rehydration. Exp. GH-3. 1980.

Parameter	Parameter estimate	Standard error	OSL†
Reference	4.974739	0.019560	<0.01
lnT	0.024514	0.005304	<0.01
DI	0.088060	0.027674	<0.01
DI x lnT	0.023455	0.007501	<0.01

†Observed significant level.

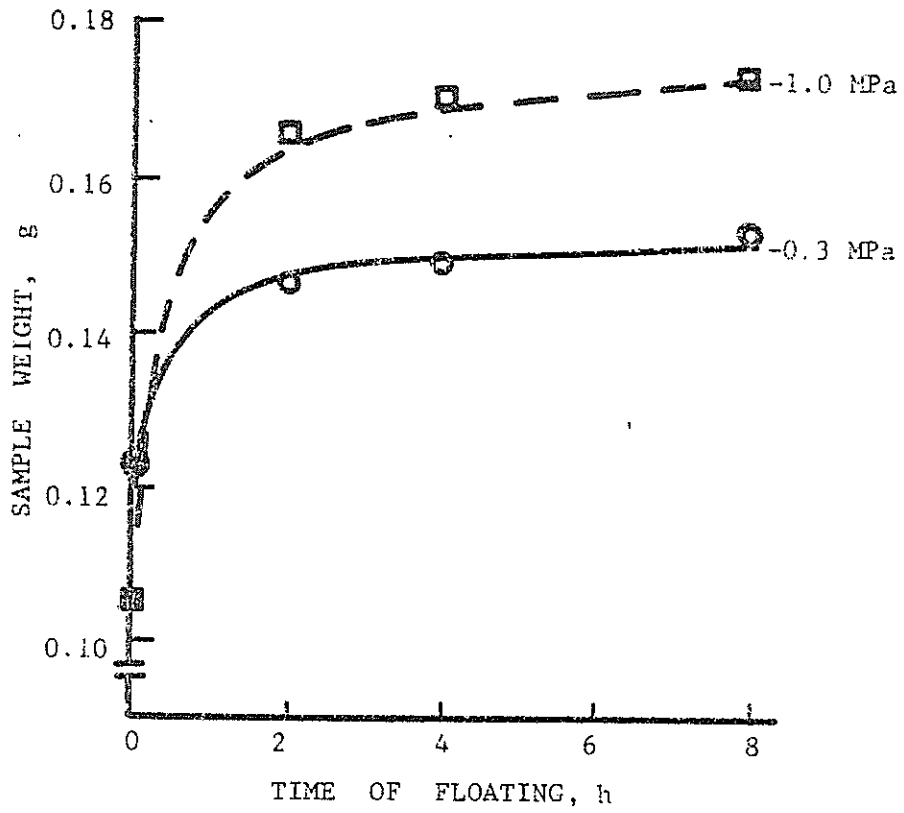

Fig. 11. Kinetics of rehydration of leaf disc samples as a function of floating time for two water stress treatments. Each data point represents the mean of four samples. Exp. GH-3. 1980.

Table 25. Analysis of variance for leaf relative water content (RWC). Exp. GH-3. 1980.

Source	DF	SS	OSL†
Total	23	339.5	
Rep	3	1084.1	<0.01
Drought (DI)	1	1591.5	<0.01
Time (T)	2	77.4	ns‡
DI x T	2	0.2	ns
Error	15	586.3	

†Observed significant level.

‡Nonsignificant at P = 0.05.

Stressed plants at -1 MPa (SWP) had a RWC of 63.5 percent, whereas plants stressed at -0.3 MPa (SWP) had a RWC of 79.8 percent. The relative water content of plants at different stress levels was clearly separated by the use of the RWC technique. Even though statistically nonsignificant, the RWC means had a tendency to decrease with time of floating (Table 26). The overall means for RWC at 2, 4, and 8 h of floating were 73.7 percent, 71.9 percent, and 69.4 percent, respectively. This effect is intrinsically related to the manner in which RWC is calculated and to the fact that leaf discs continue to absorb water through time.

Mean RWC values for stressed treatments crossed with time of floating are presented in Table 26. It should be noticed that similar amounts of RWC were lost through time by both stress treatments, although the absolute amount of water absorbed by the treatments was substantially different. This analysis demonstrated the value of calibrating the RWC technique in order to determine the optimum time of floating under a particular set of conditions.

The very poor interactive effect between drought treatments and time of floating (DIxT) is evident in Tables 22 and 26. This indicates that Phase I in the rehydration process has been completed and that Phase II will behave in a parallel manner between drought treatments. In turn, these trends would guarantee the validity of the RWC technique in comparing water deficits or water status in plants. Furthermore, Figures 10 and 11 revealed that Phase I of the rehydration process is highly interactive, since leaf disc samples coming from stressed treatments may take up twice as much water as less severely stressed or nonstressed leaf samples.

Table 26. Observed means of leaf relative water content (RWC) and absorbed water at two water stress treatments. Exp. GH-3. 1980.

Floating time	Drought treatment, SWP	
	-0.3 MPa	-1 MPa
h	RWC (%)	
2	81.8	65.7
4	80.2	63.7
8	77.5	61.2
Mean	79.8	63.5
	Absorbed water (mg/sample)	
0-2	24.4	50.2
2-4	2.5	4.8
4-8	4.7	5.9

Experiment GH-4. The leaf relative water content and kinetics of rehydration were evaluated in cultivar Meyer at two developmental stages and two water-stress treatments. The results obtained in the kinetics of rehydration at two different stages of development (Exp. GH-4) are summarized in Figure 12. The model used to analyze this set of data included two dummy variables characterizing the stage of development (0 if vegetative and 1 if flowering) and the level of drought (0 if non-stress and 1 if stressed at -0.9 MPa, SWP). Time of floating represented again, the continuous variable with levels at 0, 2, 4, and 8 h. The complete model was analyzed in the form:

$$\ln WT = \ln a + b\ DI + c\ SD + d\ \ln T + e(DI \times \ln T) + f(SD \times \ln T) + E$$

where

WT = Weight of sample (mg)

DI = Dummy variable for level of drought

SD = Dummy variable for stage of development

T = Time of floating (h)

ln a = Intercept and reference line

a, b, c, d, e and f = Partial regression coefficients.

The complete model was reduced only in one independent variable (SDxlnT) which showed no significant effect on weight of sample. Table 27 shows a summary of statistics on the regression analysis of kinetics of rehydration for this experiment.

The model explained 85.7 percent of the total variability. The behavior of samples coming from different stages of development and different drought treatments is shown in Figure 12. It should be

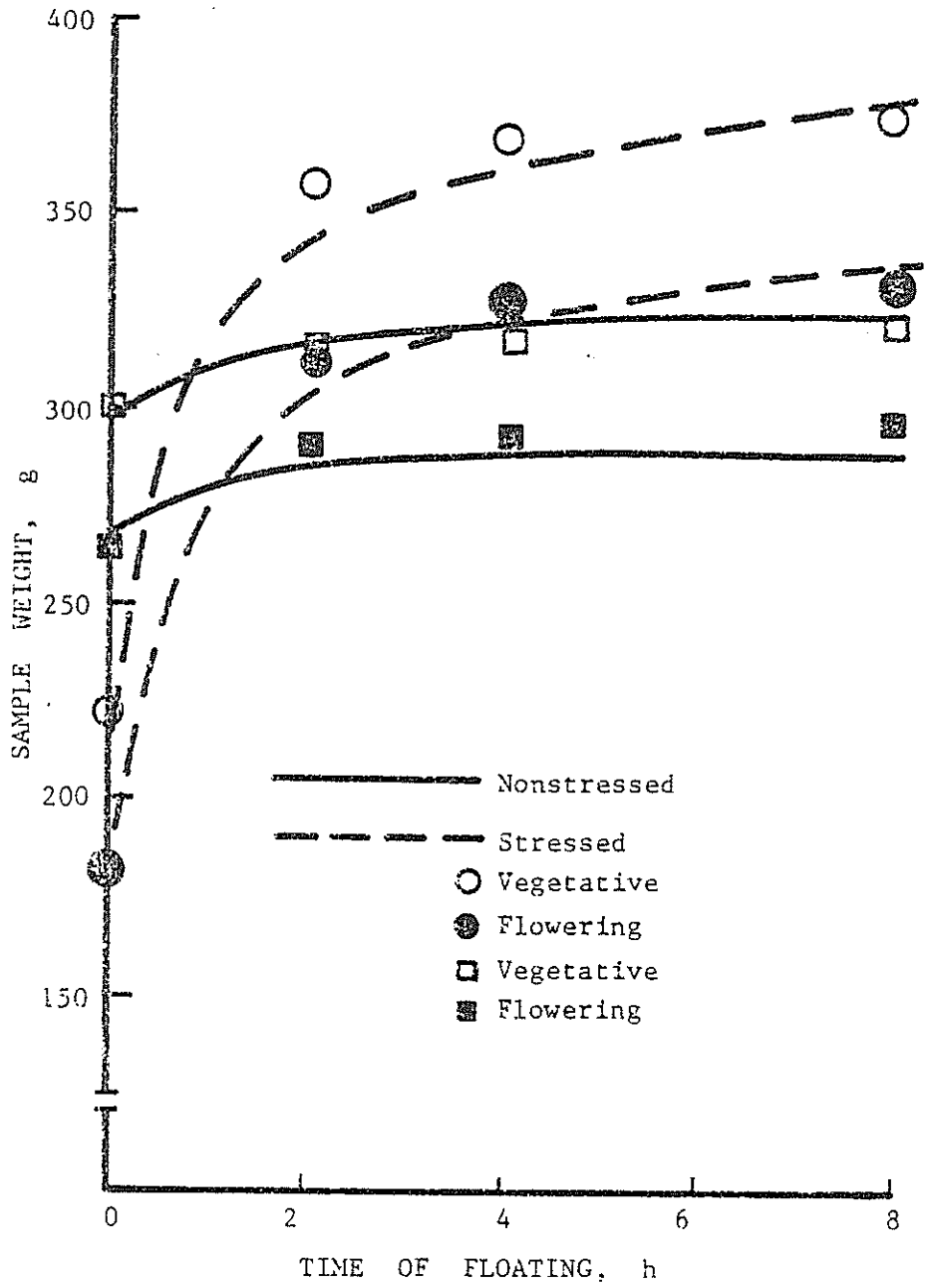

Fig. 12. Kinetics of rehydration of leaf disc samples as a function of time of floating for two water stress treatments at the vegetative and flowering stages of development. Each data point represents the mean of five samples. Exp. GH-4. 1980.

Table 27. Summary of statistics associated with the significant effects in the regression analysis for kinetics of rehydration. Exp. GH-4. 1980.

Parameter	Parameter estimate	Standard error	OSL†
Reference	5.768252	0.014696	0.01
DI	0.041210	0.017068	0.02
SD	-0.114395	0.011670	0.01
lnT	0.008876	0.003271	0.01
DI x lnT	0.056103	0.004626	0.01

†Observed significant level.

remembered that the sample in this experiment consisted of 10 leaf discs, 12 mm in diameter, while in previous experiments the disc diameter was 8 mm. This is the reason the sample weight is substantially larger than in previous experiments. The stage of development was found to affect the rate of water uptake per sample. This corroborates the requirement of using leaf samples at a similar stage of development.

The cross product DIxlnT was significant in this case, indicating that the rate of water uptake (slope coefficient) of the stressed sample was significantly larger than the nonstressed sample. This effect is applicable in both stages of development since the effect of SDxlnT was nonsignificant (Table 27), leading to the inference of parallel behavior through time.

The calculated RWC was found to be significantly different for the main effects DI and SD, but nonsignificant for the interaction DIxSD at each evaluated time of floating (2, 4, and 8 h). The average values of RWC are shown in Table 28. The differences between treatments within factors (DI and SD) were found to decrease proportionally through time. This effect is evidenced by the lack of significance in the regression analysis conducted on the complete data set that included DI, SD, and T, as well as all the possible interactions among them.

The complete model of seven independent variables was reduced to contain only the significant variables, SD, DI, and T. The reduced three-variable model explained 98.1 percent of the total variation. All partial coefficients of regression were negative, which indicates that RWC decreases with time of floating, drought stress and age of the plant (Table 29). As was shown in Table 28, the rate of decrease in RWC is much larger for drought, followed by stage of development and minimized for time of floating.

Table 28. Observed leaf relative water content (RWC) means in two water stress treatments at the vegetative and flowering stages of development. Exp. GH-4. 1980.

Treatment	Time of floating (h)		
	2	4	8
	----------%----------		
Stress			
0 MPa	92.9	91.9	90.4
-0.9 MPa	54.5	53.1	51.4
Stage of development			
Vegetative	75.5	74.1	72.6
Flowering	72.0	70.9	69.2

Table 29. Summary of statistics associated with the significant effects in the regression analysis for leaf relative water content (RWC) as a function of water stress treatments and stage of development. Exp. GH-4. 1980.

Parameter	Parameter estimate	Standard error	OSL†
Intercept	95.93	0.907	<0.01
SD	-3.39	0.712	<0.01
D	-38.71	0.712	<0.01
T	-0.45	0.143	<0.01

†Observed significant level.

The plot in Figure 13 reveals the goodness of fit of the model describing this phenomenon. Parallelism between lines exists for both categorical variables (SD and DI), which confirms the clue that the relative proportions of this measurement will decrease slightly with time, but with a parallel tendency. Thus, the determination should be at the same time for all the treatments under study.

The kinetics of rehydration in short-time measurements is dominated by the resistance of the xylem to water flow in the sense of water transport to the leaves; however, once the water is in the leaf, the rehydration kinetics can be explained by two cellular compartments in series (Cruiziat et al. 1980) in which the bulk elasticity modulus increases substantially during rehydration. The first compartment might be associated with the phloem and bundle sheath cells. Water rehydrating the second compartment, consisting of the remainder of the leaf cells, must pass through the first compartment by a transcellular pathway.

Basically, the rate of rehydration depends on two parameters that are related to each other: one is the resistance to water flow in the leaves and the other is the "water potential isotherm" of the individual cells. The first parameter can be neglected when leaf discs are in the rehydration process, but the second parameter controls the kinetics of rehydration. Therefore, if the leaf water potential is assumed to be

$$LWP = LOP + LTP$$

then at LTP=0, for all practical purposes, LWP is dominated largely by LOP which becomes the driving force of water uptake. Evidence for this relationship is presented by Frederick and Lasko (1979) for diurnal

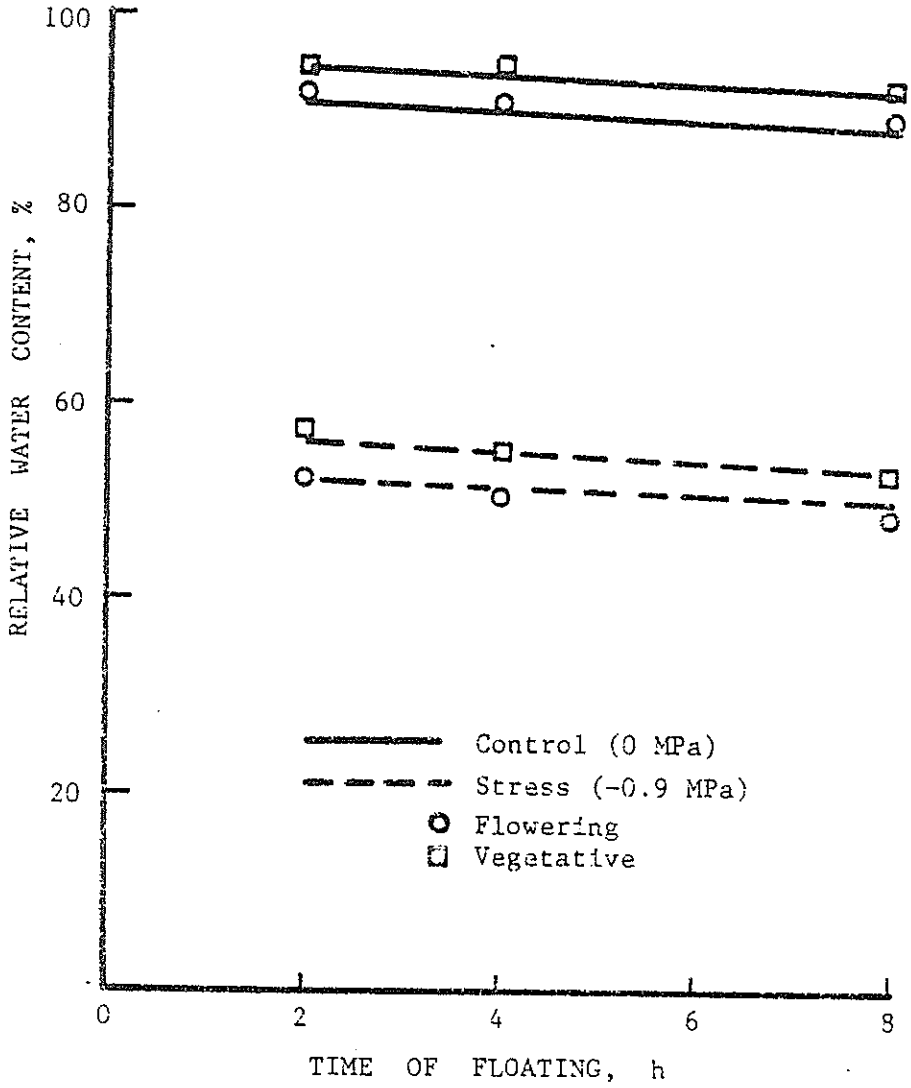

Fig. 13. Leaf relative water content (RWC) as a function of time of floating in two levels of water stress and two stages of plant development. Each data point represents the mean of five samples. Exp. GH-4. 1980.

changes in LWP, LOP, and RWC of apple trees. The RWC decreased from 100 percent to 75 percent during a day cycle from predawn to 1645 hours in the afternoon. Concurrently, the LOP decreased from -20 to -28 bars, and the decrease of LWP due to dehydration was estimated as 98 percent, 49 percent, 77 percent, 106 percent, and 88 percent in observations taken at 0645, 0845, 1155, 1445, and 1645 h, respectively. This indicated that leaf turgor (LTP) is maintained through decreases in LOP (due to active solute accumulation), osmotic adjustment, or to concentration of solutes via water loss.

Thus, the larger rate of water uptake observed in Figures 10, 11 and 12 may be explained by the loss of water from leaf tissue and the solute accumulation as LWP decreased with drought stress. When leaves undergo changes in water content (Cruiziat et al., 1980), the bulk elasticity modulus changes substantially. Therefore, the kinetics of rehydration is different for leaves suffering water stress from those leaves that are not subjected to water deficit, as shown in this research for crambe.

Summarizing, the use of the RWC technique in crambe is appropriate. Sample size of 10 leaf discs of about 8 to 12 mm in diameter can be used, which represent no problems for leaf size in these species. The environmental conditions used (i.e., standard laboratory light and temperature) did not greatly affect RWC determinations, for all practical purposes. The statistical models used (combination of power functions with categorical variables) were very efficient in describing the kinetics of rehydration.

Porometry

Four experiments were considered for the analysis of porometric responses (diffusion resistance and transpiration). Some time course characteristics of these experiments are shown in Table 30. In all the experiments, LDR and T were measured in one day, except for Exp. GH-5 in which readings were taken during eight consecutive days.

The statistical analysis performed on the porometric data was framed within the regressional approach. The physiological basis of stomatal behavior (Vaadia et al. 1961, Raschke 1975) suggests a two-line model, one line covering the phase at which stomata are relatively insensitive to water stress, and the second line for the falling phase when stomata closure progressively increases diffusion resistance and reduces transpiration rate. That behavior can be described by the "Piecewise Linear Regression" (Draper and Smith 1966, Neter and Wasserman 1974). The statistical model associated with this formulation is

$$Y=a+B\ SWP+c\ (SWP-A)D_1+E$$

where

Y = Leaf diffusion resistance or transpiration

a = Intercept

b = Slope of the first line

SWP = Soil water potential

c = Slope of the second line

A = Breaking point of the two lines

D = Dummy variable (0, if $SWP \leq A$; and 1, if $SWP \geq A$)

E = Error term.

Table 30. Dates and periods of porometric readings (leaf diffusion resistance and transpiration) in four greenhouse experiments. 1980 and 1981.

Experiment	Planting	Reading	Plant age
	----------date----------		days
GH-5	11-04-80	12-27-80 01-03-81	53-61
GH-6	11-04-80	12-24-80	50
GH-7	11-01-80	12-27-80	58
GH-8	01-07-81	03-27-81	59

For this model, A (the breaking point) is assumed to be known. In order to find the value of A, a regression analysis was performed with the complete model for breaking points from -0.25 to -0.6 MPa, at 0.05 intervals. The analysis, showing the minimum mean square error, was then chosen. The selected model was then passed through the "backward selection of variables procedure" to eliminate the nonsignificant variables (significant level=0.05 level of probability) from the model. Routine tests used for each analysis included lack of fit, Durbin-Watson for correlated errors, residual analysis and plot of residuals.

For those experiments with two cultivars, the model was extended to one more dummy variable (CV), plus the cross products of this variable with all of the others in the model.

Experiment GH-5. In Exp. GH-5, the response of leaf diffusion resistance and transpiration during a soil-drying cycle was evaluated in two cultivars. The average soil water potential measured with thermocouple psychrometers in Exp. GH-5 is shown in Figure 14. During the first four days of the drying cycle, only insignificant changes in SWP occurred. Thereafter, a very steep decrease in SWP with time was observed.

Trends of LDR for the morning and afternoon measurements are shown in Figure 15. Leaf diffusion resistance was found to increase linearly as SWP decreased if the measurement was taken in the afternoon when the evaporative demand was high. However, when LDR was measured during the morning, the LDR response followed the expected trend. Stomata were relatively insensitive to decreasing SWP to a threshold of -0.6 MPa, then a rapid increase of LDR occurred. No significant differences were

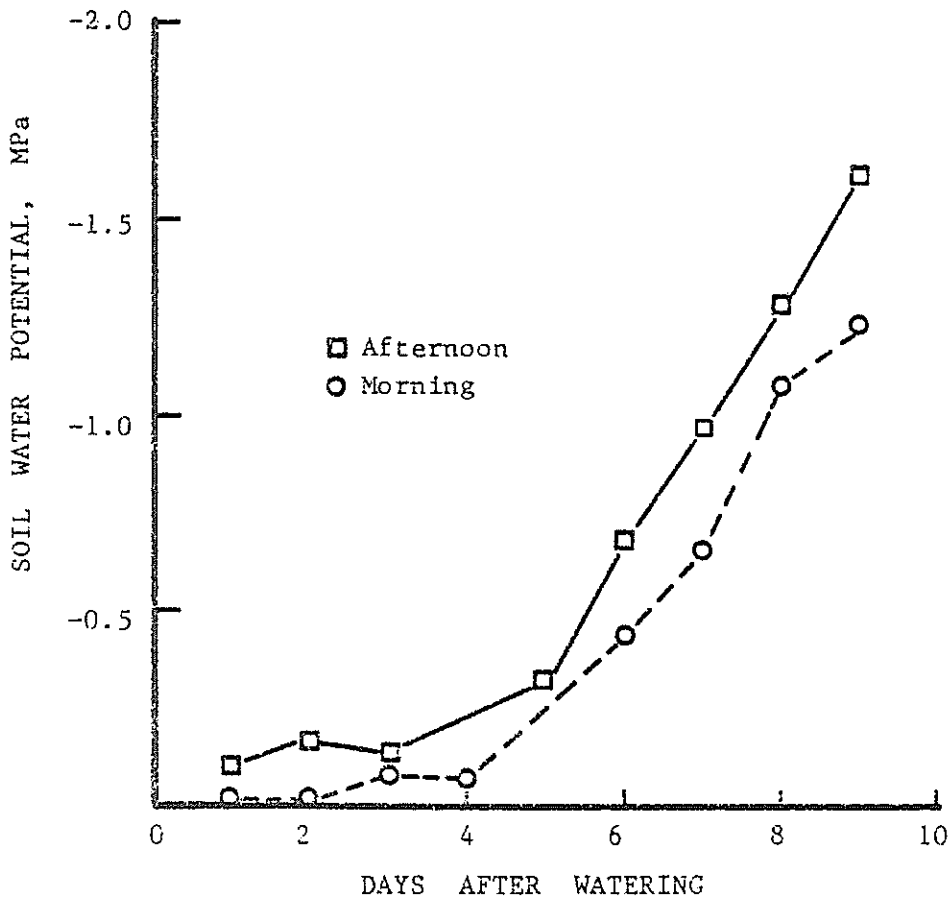

Fig. 14. Total soil water potential (SWP) measured with thermocouple psychrometers as a function of time. Observed morning and afternoon means of SWP through one drying cycle. Exp. GH-5. 1981.

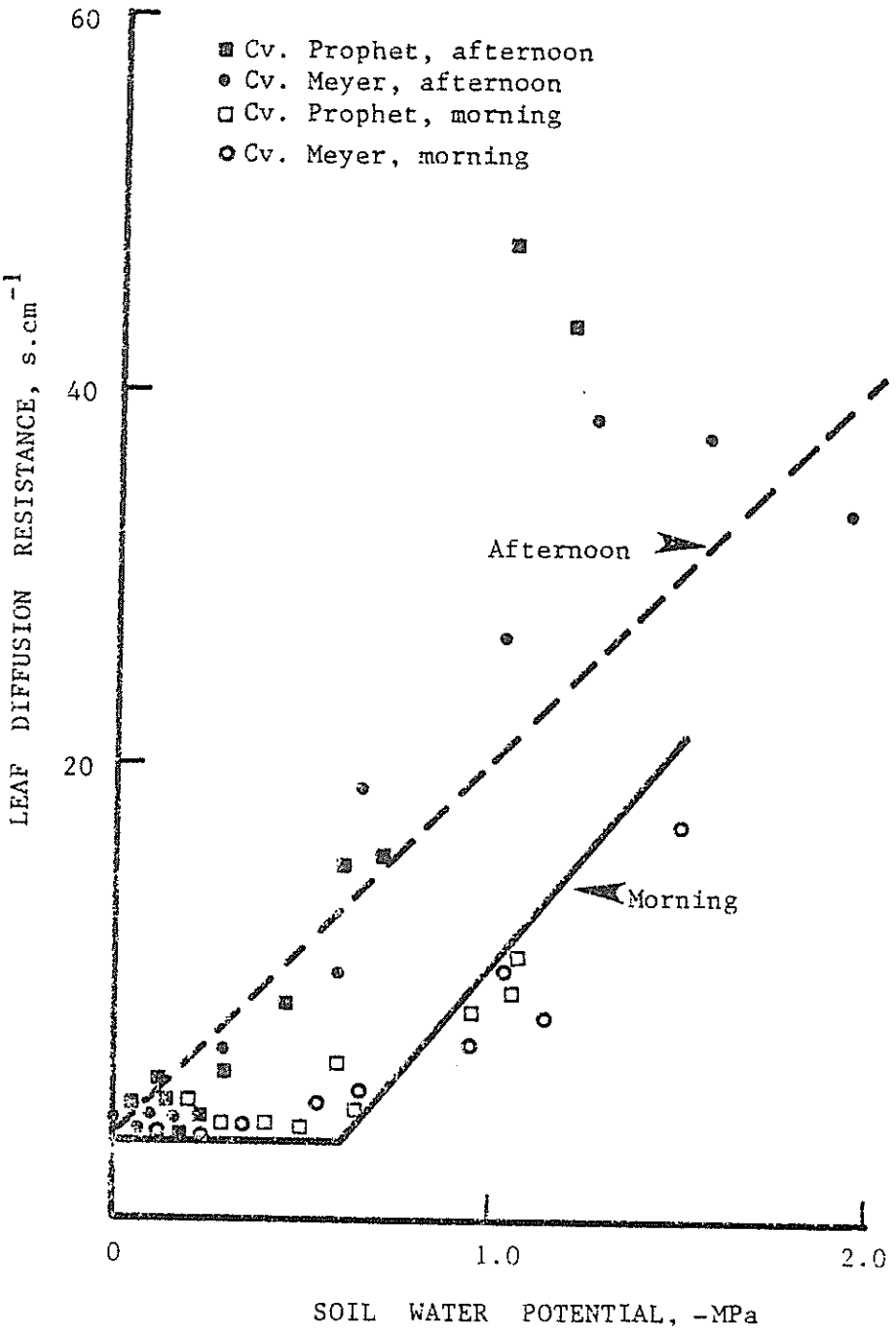

Fig. 15. Leaf diffusion resistance (LDR) as a function of soil water potential in the morning and afternoon during one soil drying cycle. Each data point represent the observed value. Exp. GH-5. 1981.

found between cultivars (Meyer vs. Prophet). The proportion of variation explained by the models was 85.4 percent for the afternoon and 74.4 percent for the morning. Parallelism between afternoon and morning behavior is noticeable as the slopes are 2.01612 ± 0.143 in the afternoon, and 2.426 ± 0.142 in the morning. This implies that in both cases the rate of LDR increase per unit change decrease in SWP is about the same; but when LDR was measured in the morning, stomata remained open even if SWP had decreased to -0.6 MPa. On the balance of effects, as shown in Figure 15, LDR became higher during the afternoon than in the morning at any given SWP, except at 0 MPa, at which no significant LDR was measured.

Transpiration trends for Exp. GH-5 are shown in Figure 16. Differences in cultivars appeared to be insignificant. Transpiration had a tendency to decline as SWP decreased from 0 to -0.4 MPa. Thereafter, transpiration maintained a steady decreasing rate. This is the typical performance expected by this phenomenon. In the morning, however, even if the general trend was similar, the rates of transpiration were different between cultivars. The amount of water transpired under conditions of no water stress was much higher during the afternoon than during the morning, which is very likely related to the evaporative demand and the availability of water at that time.

During the first phase of stomatal behavior, the decrease in transpiration per unit change of SWP between afternoon and morning are parallel, but on different magnitudes. The rate of change was $-3.375\ g.cm^{2}\ .s^{-1}$/MPa in the morning and $-7.475\ g.cm^{-2}\ .s^{-1}$ /MPa in the afternoon. The breaking point was found to be very different for the morning measurements (-0.25 MPa). It appeared that transpiration

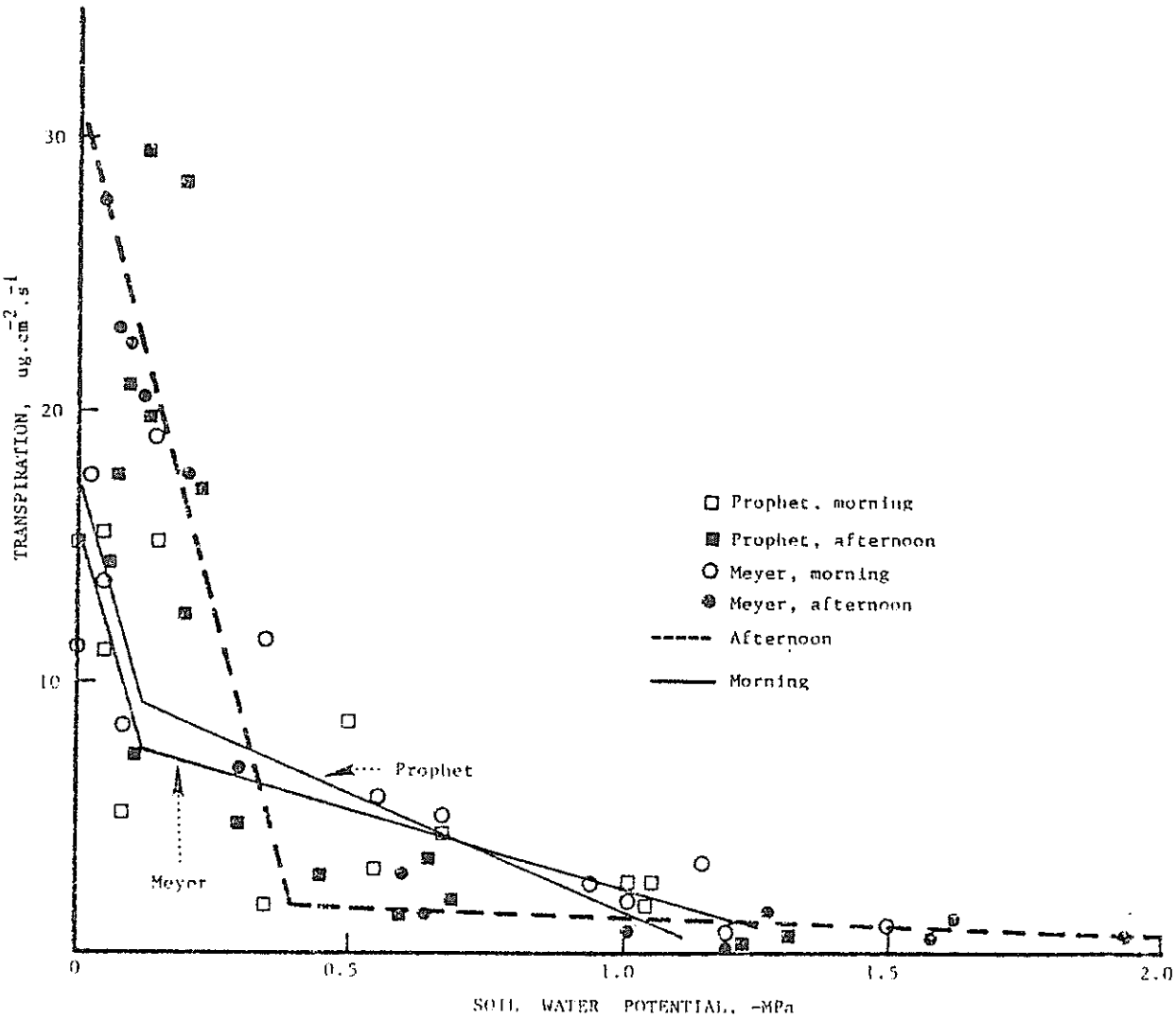

Fig. 16. Transpiration (TR) as a function of soil water potential in the morning and in the afternoon during one soil drying cycle. Each data point represents the observed value. Exp. GH-5. 1981.

decreases are slower in the morning than in the afternoon, probably because the sensitivity of the stomate was not drastically affected by the evaporative demand as it was in the afternoon, at least until the available water was depleted (SWP of -1.1 MPa or lower) in the root zone. Then, transpiration reached a very low rate simulating the afternoon rates. Indeed, these transpiration rates suggested that these plants were suffering from a high degree of water stress. Usually, plants started wilting between -0.4 and -0.5 MPa, SWP.

Differences in stomatal behavior between morning and afternoon are explained by changes in the evaporative demand to which the plants were subjected (Heth and Kramer 1975) firstly, and secondly, by the available water in the growing media (Davies 1977). In the morning, when available water is not limiting because the evaporative demand is not high, transpiration is a function of evaporative demand. In the afternoon, when available water becomes limiting because of a high evaporative demand, transpiration is a function of available water or is limited by the availability of water. Thus, when transpiration exceeded water uptake, stomata closed, maintaining a steady transpiration rate as a function of LDR. A similar trend was found for wheat (Sojka et al. 1979).

Experiment GH-6. The internal plant water status related to SWP was studied in Exp. GH-6. A series of plant water stress indicators was evaluated in two crambe cultivars, Meyer and Prophet. The relationship between LDR and SWP for Exp. GH-6 is shown in Figure 17. Significant differences in LDR were found between cultivars with the abaxial surface always higher in LDR than on the adaxial surface of the leaf. A similar response was reported for rice (O'Toole and Cruz 1980) but the reverse

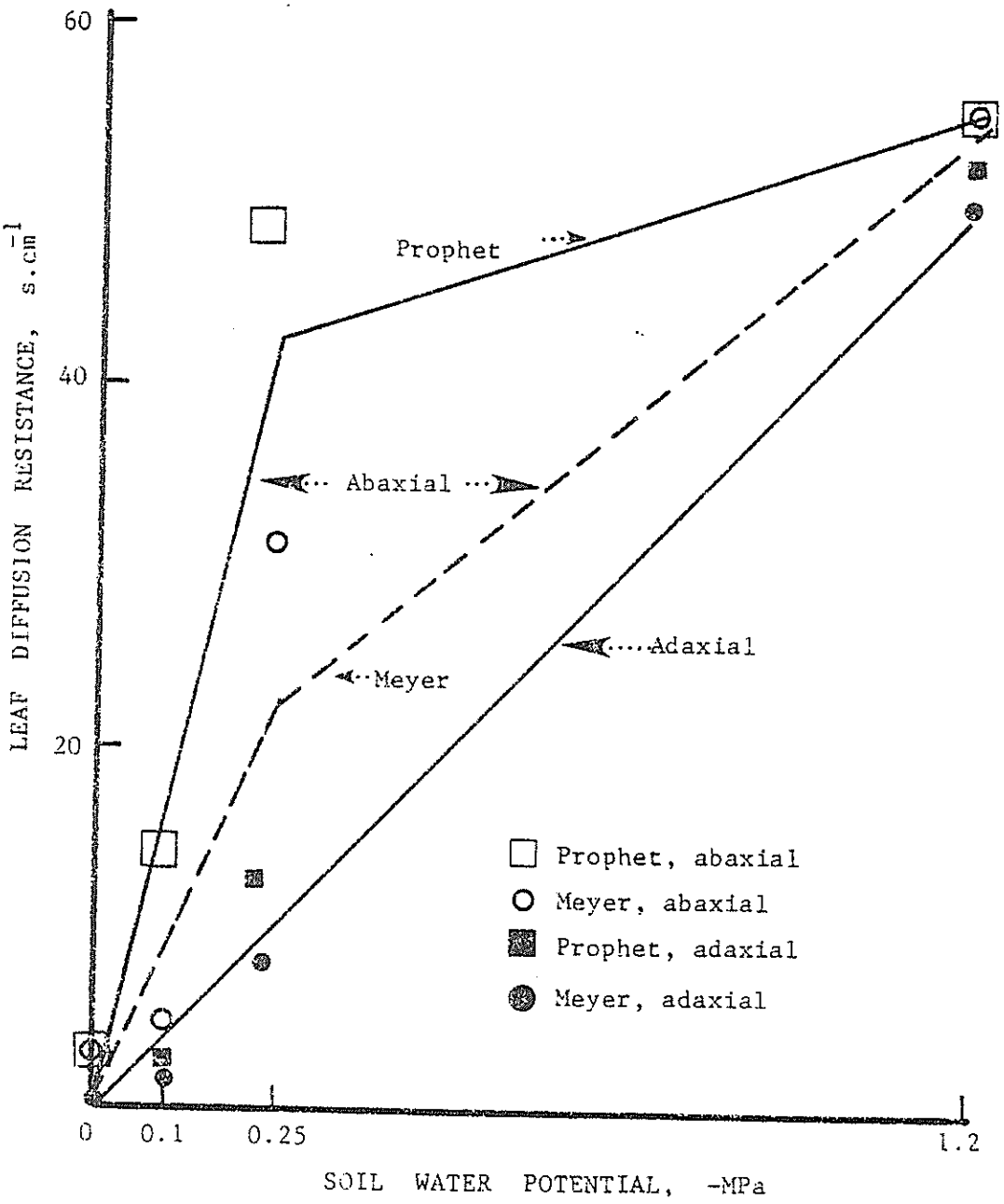

Fig. 17. Leaf diffusion resistance (LDR) as a function of soil water potential in two crambe cultivars (Meyer and Prophet) at the adaxial and abaxial leaf sufaces. Each data point represents the mean of eight samples. Exp. GH-6. 1980.

was found in cotton (Davies 1977) and no difference was detected in tomato (Hsiao 1973). In this experiment, LDR did not show the first phase of stomatal behavior for either adaxial or abaxial surfaces, where there was a well-defined tendency for LDR to increase as SWP decreased. Although the final value for LDR at the lowest SWP was similar for all treatments, the main difference remains at higher SWP where Prophet showed the highest abaxial LDR, followed by the abaxial leaf surface of Meyer, and then the adaxial surfaces of both cultivars (pooled). The amount of variation explained by the models was 93.3 percent for the abaxial analysis and 95.5 percent for the adaxial.

Transpiration, on the other hand, followed the first and second phases of stomatal behavior (Figure 18) on both the adaxial and abaxial leaf surfaces. It shows that TR is higher on the adaxial surface, which directly corresponded to the LDR observed. The breaking point (-0.25 MPa) was the same for both surfaces in spite of the fact that the intercepts and slopes are quite different, as shown in Table 31. The proportion of variability explained by the models was 87.8 percent for the adaxial and 58.4 percent on the abaxial.

The reason for the higher abaxial LDR in these cultivars of crambe is not known, but it can be speculated that a smaller stomatal density on the abaxial surface may be the cause. This was noted in rice (O'Toole and Cruz 1980). If the LDR for the abaxial was similar to the adaxial (close to zero) under high SWP, the difference in transpiration for that treatment should be given by the difference in stomatal behavior among leaf surfaces, as was observed in cotton and soybean (Davies 1977).

Experiment GH-7. Using a different soil medium (plaster sand) and only the cultivar Meyer, the same plant water stress indicators were

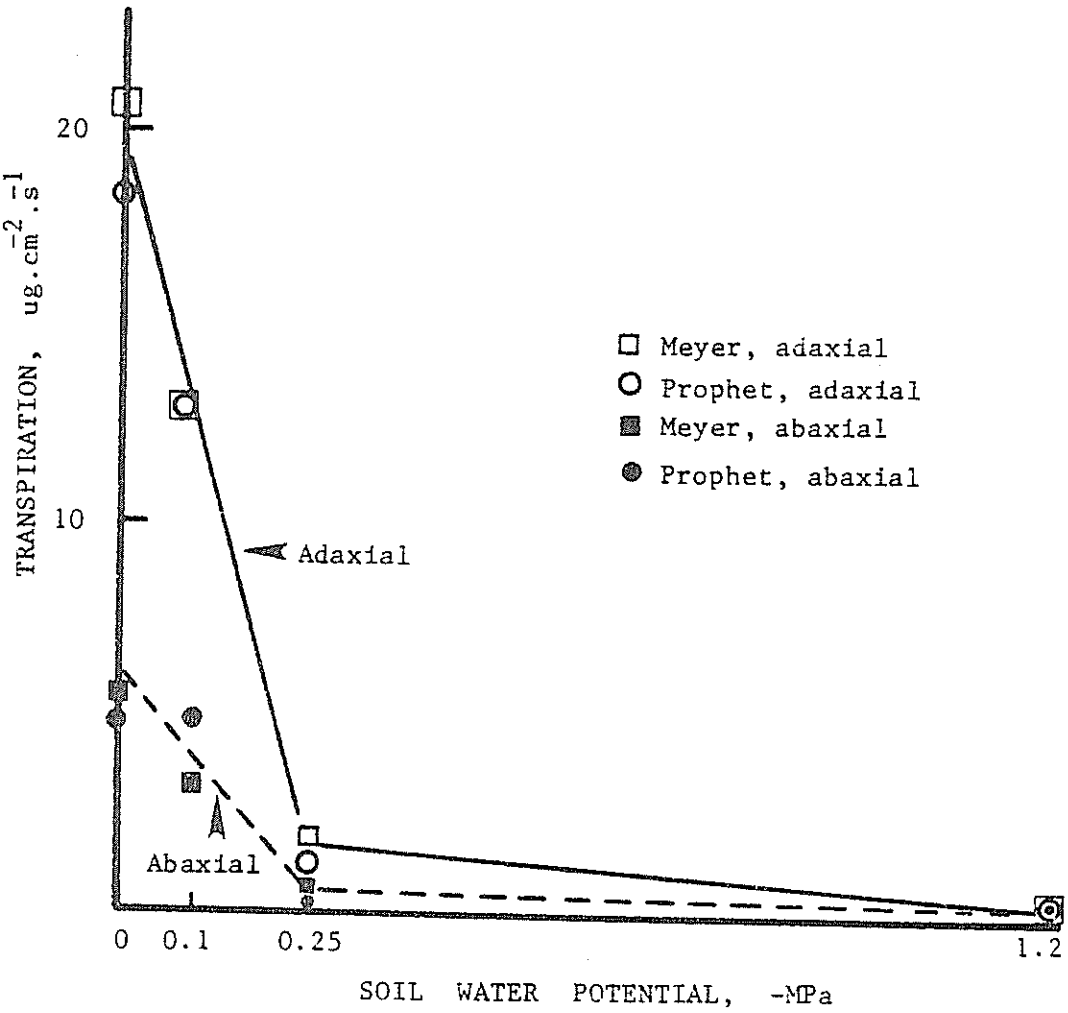

Fig. 18. Transpiration (TR) of the adaxial and abaxial leaf surfaces as a function of soil water potential. Each data point represents the mean of eight samples. Exp. GH-6. 1980.

Table 31. Summary of statistics associated with the significant effects of the regression analysis for leaf diffusion resistance (LDR) and transpiration (TR) of the adaxial and abaxial leaf surfaces as a function of soil water potential in two crambe cultivars (Meyer and Prophet). Exp. GH-6. 1980.

Parameter	Parameter estimate	Standard error	OSL†
LDR (Adaxial)			
SWP	4.189	0.160	<0.01
LDR (Abaxial)			
SWP	11.171	1.473	<0.01
SWP x CV	5.868	1.941	<0.01
(SWP-2.5)D	-8.263	1.883	<0.01
(SWP-2.5)CV	-7.412	2.497	<0.01
TR (Adaxial)			
Intercept	20.123	0.880	<0.01
SWP	-7.293	0.712	<0.01
(SWP-2.5)D	7.133	0.849	<0.01
TR (Abaxial)			
Intercept	6.323	0.591	<0.01
SWP	-2.245	0.478	<0.01
(SWP-2.5)D	2.205	0.570	<0.01

†Observed significant level.

evaluated in Exp. GH-7 as in Exp. GH-6. The purpose of this experiment was to broaden the knowledge of the internal water relations in crambe. Figure 19 shows the estimated trends of LDR on the adaxial and abaxial surfaces. In this case, both surfaces displayed the first and second phases of stomatal behavior, with the abaxial surface again having a higher LDR than the adaxial. It should also be noted that the rate of increase of LDR was about three times higher on the abaxial surface than on the adaxial surface. The breaking point (-0.3 MPa) was the same for both leaf surfaces.

Transpiration (Figure 20) followed the two phases of stomatal behavior. The adaxial transpiration was higher than the abaxial, which corresponds well to the LDR presented in Figure 19. It is interesting to note that TR-abaxial broke at -0.5 MPa, while TR-adaxial broke at -0.6 MPa. This effect has been observed before in rice (O'Toole and Cruz 1980).

Experiment GH-8. The effects of drought cycles in preconditioning crambe plants to subsequent water stress was explored in Exp. GH-8. Plants were subjected to drought cycles by allowing the soil medium to dry down to -0.5 MPa. One, two and three drought cycles were compared to a control treatment that was maintained in a well watered state throughout the experimental period.

In Exp. GH-8, all the measurements were made after the visual effect from the last drought cycle was passed. The cumulative number of days without watering (days of drought) were considered as the quantitative variable for the statistical analysis instead of number of drought cycles.

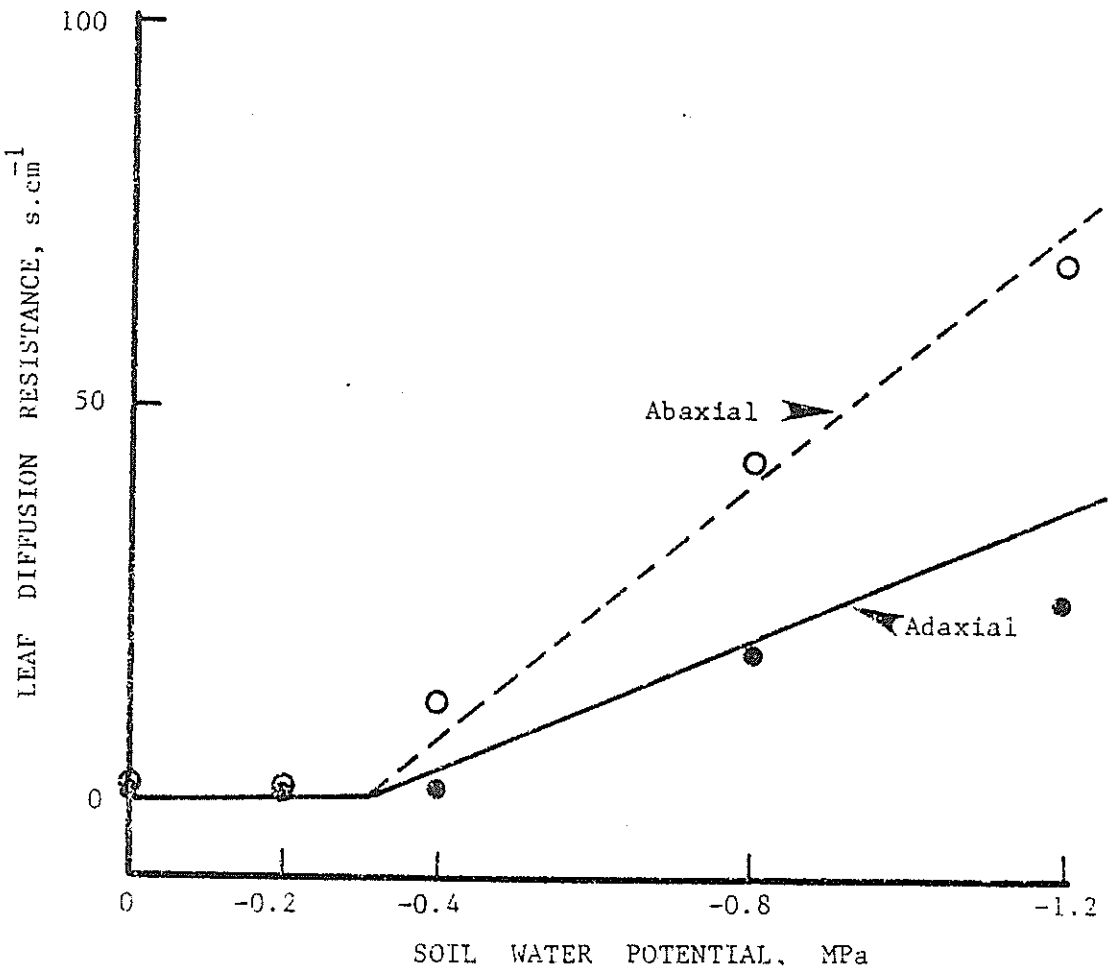

Fig. 19. Leaf diffusion resistance (LDR) of the adaxial and abaxial leaf surfaces of Meyer crambe as a function of soil water potential. Each data point represents the mean of six samples. Exp. GH-7. 1981.

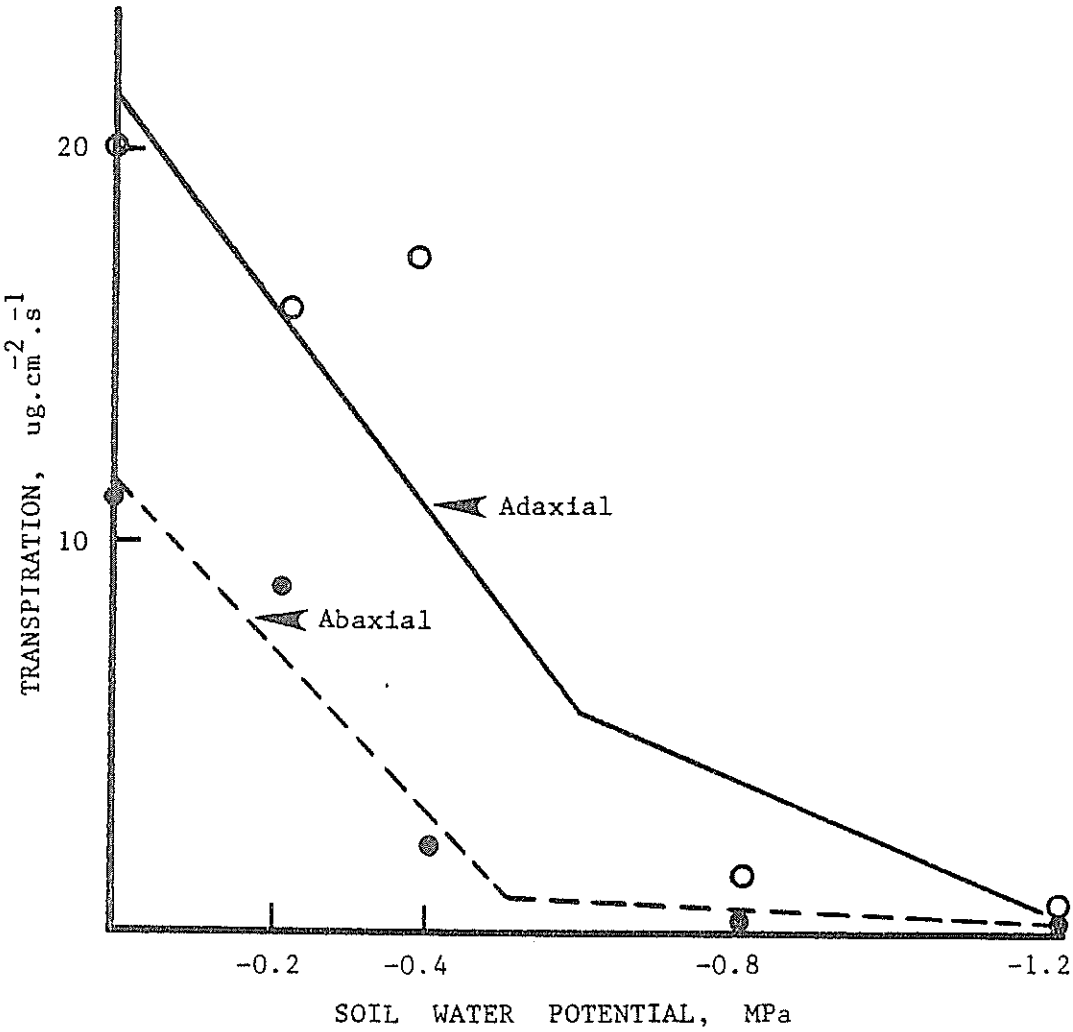

Fig. 20. Transpiration (TR) of the adaxial and abaxial leaf surfaces as a function of soil water potential of Meyer crambe. Each data point represents the mean of six samples. Exp. GH-7. 1980.

The general form of the model was:

$$Y=a+b\ Day+c\ CV+d\ S+e(DayxCV)+f(DayxS)+E$$

where

Y = Leaf diffusion resistance or transpiration

Day = Days of drought

CV = Cultivar (0=Meyer; 1=Prophet)

S = Leaf surface (0=Adaxial; 1=Abaxial)

a,b,...,f = Partial coefficients of regression

E = Error team

Adaxial LDR (Figure 21) was not significantly affected by treatments. However, LDR on the abaxial surface showed a linear trend to decrease as days of drought accumulated. Leaf diffusion resistance was significantly different between cultivars for both leaf surfaces, although the parallelism between lines indicates a similar trend through the experimental period. Meyer had a higher LDR than Prophet.

Transpiration related to cumulative days of drought (Figure 22) did not show any significant difference for cultivars, but it did show differences for leaf surface. The adaxial surface had a higher transpiration rate. Both surfaces, however, had a tendency to increase in transpiration as the number of days of drought increased, even though the adaxial LDR did not decrease in resistance. Cotton responded in a similar manner in the study by Cutler and Rains (1977).

The scale used in Figures 21 and 22 must be brought to the reader's attention. The magnitude changes for the abaxial surface was 1 $s.cm^{-1}$ for LDR and about 3 $g.cm^{-2}\ .s^{-1}$ for TR. These changes are very small

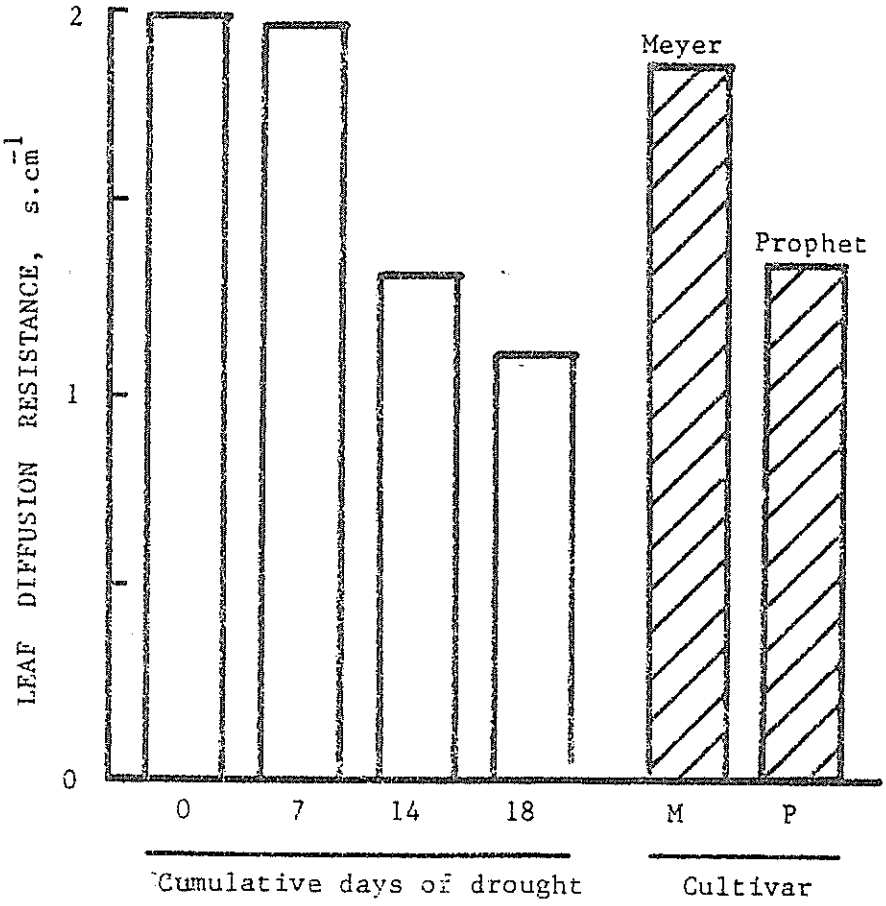

Fig. 21. Leaf diffusion resistance (LDR) of the adaxial and abaxial leaf surfaces of two crambe cultivars (Meyer and Prophet) as a function of drought cycles. Exp. GH-8. 1981.

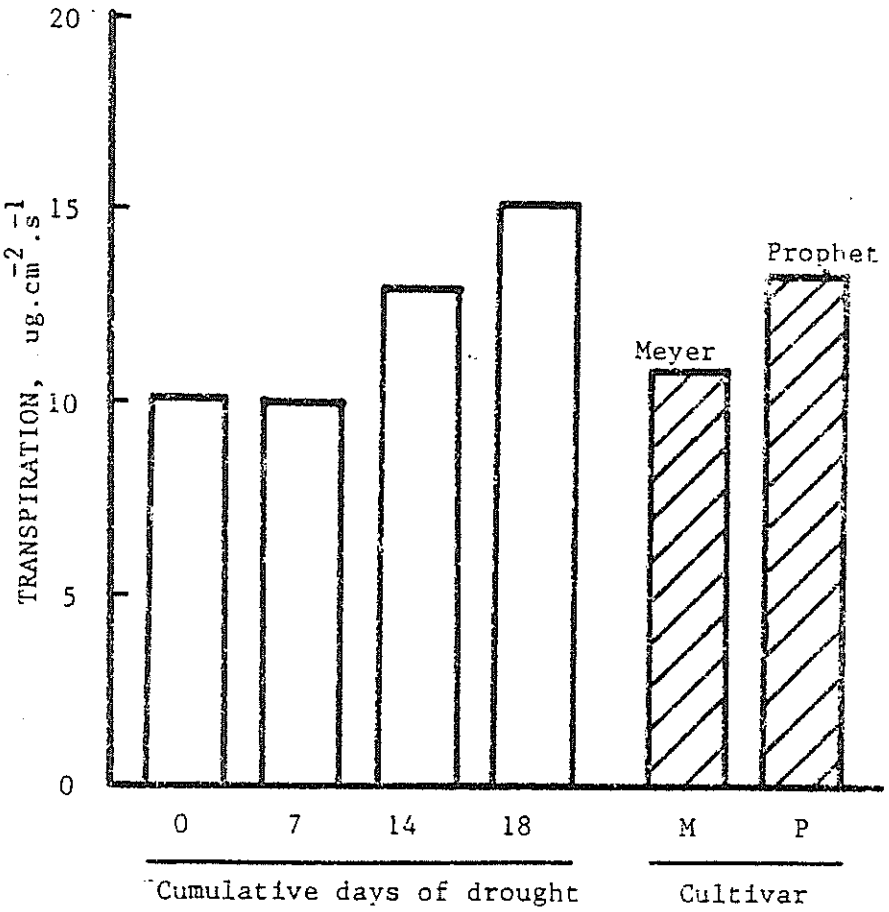

Fig. 22. Transpiration (TR) of the adaxial and abaxial leaf surfaces of two crambe cultivars (Meyer and Prophet) as a function of drought cycles. Exp. GH-8. 1981.

compared with those in Exps. GH-5, GH-6, and GH-7 because in Exp. GH-8, plants were fully turgid at the time of sampling. The measured differences are thought to be due to the preconditioning effect of drought cycles.

This set of experiments (GH-5, GH-6, GH-7, and GH-8) indicates that stomatal behavior in crambe, in relation to drought, is similar to that of other crop species. An increase in LDR can be expected as SWP decreases. If the evaporative demand is high, the increase in LDR will be more rapid as SWP decreases from 0 MPa; or under low evaporative demand, LDR will maintain a low rate until a threshold occurs (between -0.3 and -0.6 MPa), then will increase rapidly. Transpiration, on the other hand, will be high at high SWP, but it will decrease rapidly between -0.25 and -0.5 MPa SWP. Thereafter, it will continue to decrease at a very low rate.

Internal Water Relations

The interactive effects of plant water status, water content, and physiological processes contribute to the plant water balance, which in turn will respond to the environment. Among the factors commonly measured as indicators of plant water balance, LWP, LOP, RWC, LDR, and TR are the most popular. As expected, all of these factors are closely related as shown in Table 32 for Exps. GH-6, GH-7, and GH-8.

Soil water potential was found to be highly correlated with the variables included in this analysis. The general trends are that as SWP decreases, LDR increases and TR, LWP, and RWC decrease (Exps. GH-6 and GH-7). All of the coefficients of simple correlation were high, which indicates a high association among the variables. In Exp. GH-8, however, LDR and TR had about the same tendencies with respect to number of

Table 32. Correlative analysis among the physiological indicators of plant water status, leaf diffusion resistance (LDR), transpiration (TR), leaf water potential (LWP), leaf osmotic potential (LOP), relative water content (RWC) and soil water potential (SWP) or cumulative number of days of drought (DC). Exps. GH-6, GH-7 and GH-8. 1980 and 1981.

Physiological parameters	Physiological parameters			
	LWP	LOP	RWC	SWP
		Exp. GH-6		
LDR Adaxial	-0.93**	-0.94**	-0.95**	-0.97**
TR Adaxial	0.80**	0.69**	0.76**	0.76**
LDR Abaxial	-0.88**	-0.81**	-0.86**	-0.85**
T Abaxial	0.64**	0.55**	0.59**	0.61**
LWP	1.00	0.88**	0.91**	0.89**
LOP		1.00	0.93**	0.92**
RWC			1.00	0.92**
		Exp. GH-7		
LDR Adaxial	-0.77**	-0.63**	-0.69**	-0.79**
TR Adaxial	0.76**	0.59**	0.69**	0.78**
LDR Abaxial	-0.87**	-0.86**	-0.95**	-0.92**
TR Abaxial	0.80**	0.51**	0.65**	0.81**
LWP	1.00	0.81**	0.87**	0.93**
LOP		1.00	0.94**	0.77**
RWC			1.00	0.87**
	LWP	LOP	RWC	DC
		Exp. GH-8		
LDR Adaxial	ns†	ns	ns	-0.36*
TR Adaxial	ns	ns	ns	ns
LDR Abaxial	ns	ns	ns	-0.53**
TR Abaxial	ns	ns	ns	0.53**
LWP	1.00	ns	ns	ns
LOP		1.00	0.47**	0.65**
RWC			1.00	ns

*, **, Significant at P = 0.05 and 0.01, respectively.
†Nonsignificant at P = 0.05.

days of drought (DC), but there was no significant correlation with either LWP or RWC. A significant negative correlation was found between DC and LOP. The correlations among porometric data and SWP or DC were discussed previously. The response of LWP, LOP and RWC with decreasing SWP are well documented for many other crop species. The decrease of LOP as plants suffered more drought cycles is part of the osmotic adjustment mechanism operating in plants suffering water stress. This appeared to be an interesting finding in relation to osmotic adjustment in crambe for adaptation to drought. All other responses among the studied variables parallel the response described for SWP. In Exp. GH-8, porometric data were not correlated with LWP, LOP, nor RWC. This was very likely because of the narrow range of responses as measurements were taken on turgid, well-watered plants.

The relationship between LWP, LOP, and RWC was highly significant in all cases for Exps. GH-6 and GH-7. Leaf water potential behaved as a linear function of SWP in both experiments. Figure 23 shows the parallelism observed between the two experiments with the LWP measured for Exp. GH-6 at the same level of SWP being lower at the same level of SWP than that of Exp. GH-7. This response was also observed in soybean (Brady et al. 1974) at the podding stage, but with smaller slope and higher intercept, since that study was conducted under field conditions. The difference in magnitude of LWP between Exps. GH-6 and GH-7 are explicable on the basis of the water-holding capacity of the rooting medium used for each experiment (Exp. GH-6= soil mix; Exp. GH-7= plaster sand) and the time involved to reach the desired SWP after watering was stopped. In this case, Exp. GH-6 required approximately double the time to reach a given SWP as Exp. GH-7.

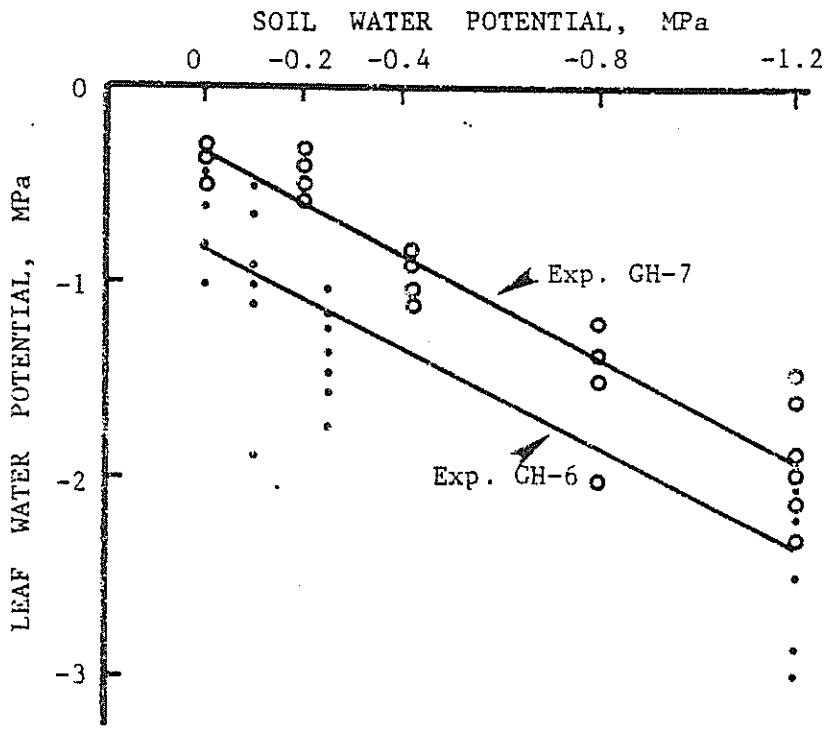

Fig. 23. Leaf water potential (LWP) as a function of soil water potential. Each data point represents the observed value. Exp. GH-6 and GH-7. 1980.

Figure 24 shows the differential capability of crambe cultivars to decrease LOP as SWP decreased (Exp. GH-6) where Meyer had lower LOP than Prophet, even though LWP was not significantly different for the two cultivars. In Exp. GH-7, however, a very slight decrease of LOP was observed at comparable SWP.

Leaf osmotic potential decreased as a response to drought with Prophet maintaining a higher LOP than Meyer (Figure 25). The decrease of LOP in response to drought cycles has been named "osmotic adjustment" (Ruf et al. 1963, Jones and Turner 1978), or "osmoregulation" (Meyer and Boyer 1981). The osmoregulation mechanism is of prime importance in maintaining the flow of water through the plant, in order to supply the necessary water for transpiration and physiological processes (Turner and Begg 1981). The osmotic adjustment was observed in crambe cultivars (Fig. 25) as they were hardened through drought cycles.

The analysis of RWC revealed a pattern very similar to that of LOP in Exps. GH-6 and GH-7 (Figure 26). The RWC of the leaves confirms the differences between cultivars and explains the higher LOP of Prophet due to its ability to conserve more water in plant tissue by increasing LDR more rapidly in response to soil water deficit than Meyer (Figure 17). The analysis of variance for RWC in Exp. GH-8 indicates that the only significant source of variation was cultivars with an average RWC of 75.8 percent and 81.2 percent for Meyer and Prophet, respectively.

The observed yield components (LA, SDW, RDW, S/R ratio) in Exp. GH-8 were highly affected by drought cycles. Prophet showed a significantly higher LA and LDW than Meyer. Both cultivars showed a decrease in LA (Figure 27) and LDW (Figure 28) with an increase in the number of

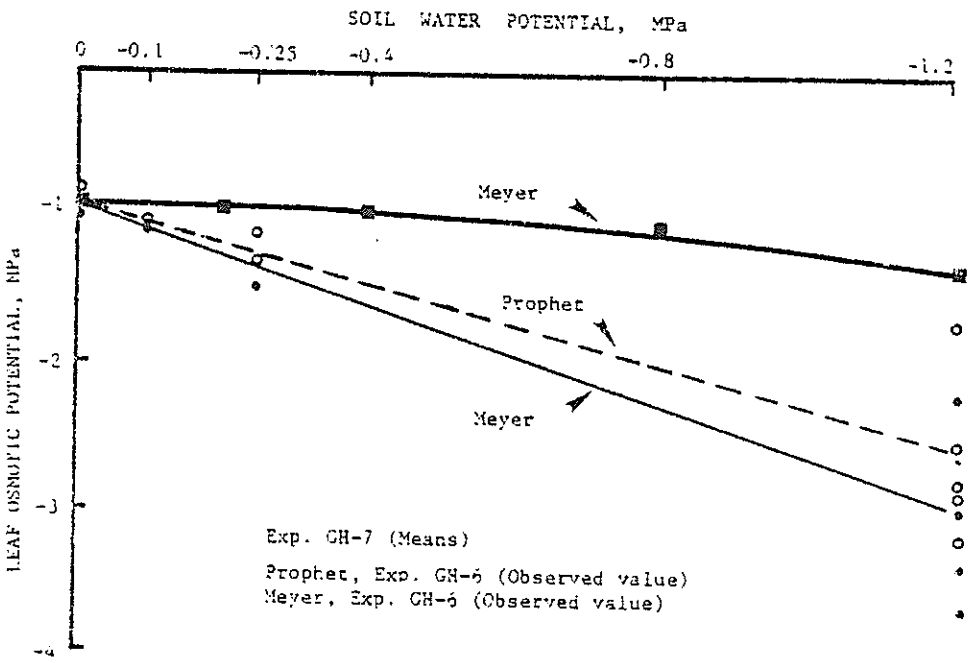

Fig. 24. Leaf osmotic potential (LOP) as a function of soil water potential. Exp. GH-6 and GH-7. 1980.

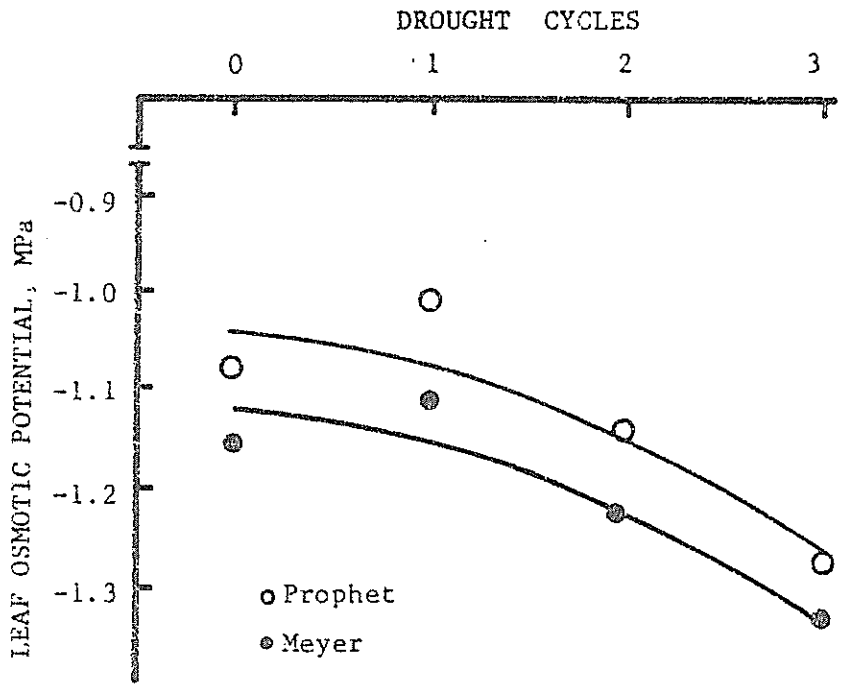

Fig. 25. Leaf osmotic potential (LOP) of two crambe cultivars (Meyer and Prophet) as a function of drought cycles. Each data point represents the mean of six samples. Exp. GH-8. 1981.

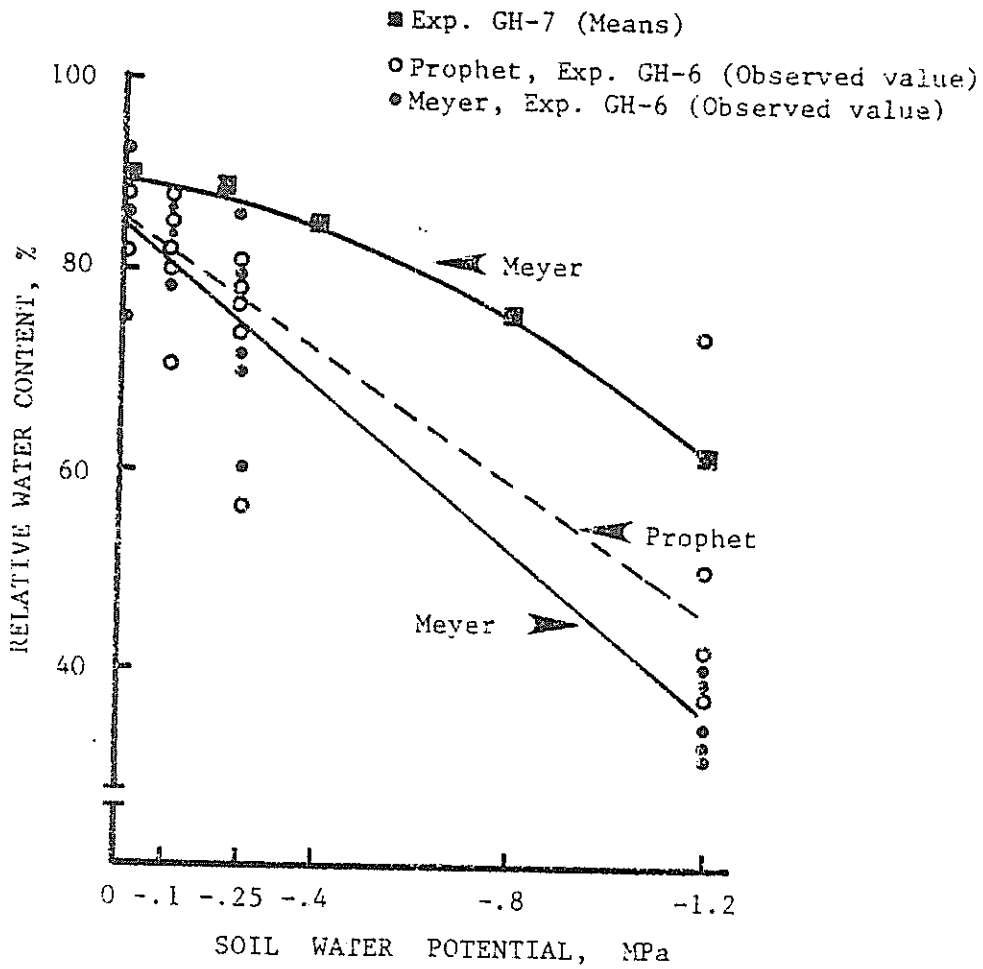

Fig. 26. Relative water content (RWC) as a function of soil water potential. Exp. GH-6 and GH-7. 1980.

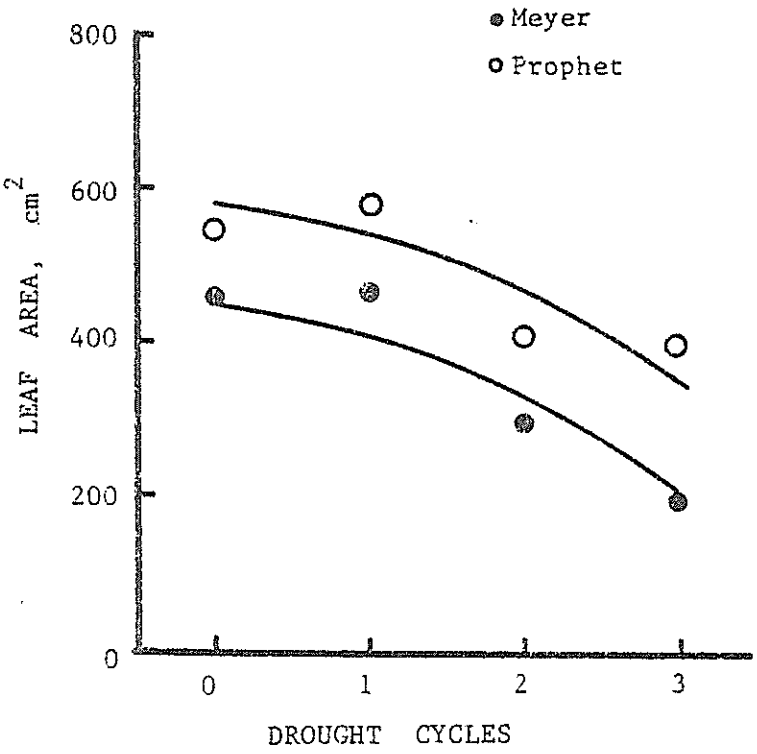

Fig. 27. Leaf area/plant (LA) of two crambe cultivars (Meyer and Prophet) as a function of drought cycles. Each data point represents the mean of six samples. Exp. GH-8. 1981.

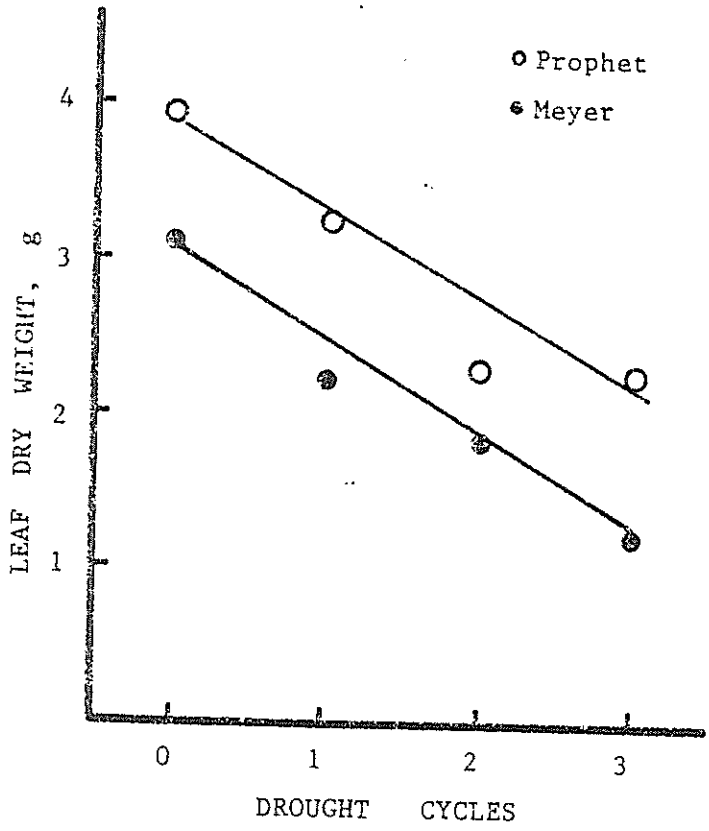

Fig. 28. Leaf dry weight/plant (LDW) of two crambe cultivars (Meyer and Prophet) as a function of drought cycles. Each data point represents the mean of six samples. Exp. GH-8. 1981.

drought cycles. However, Meyer had greater SDW than Prophet (Figure 29). This effect is closely related to the ontogeny of crambe, as Meyer was observed to produce flowering stems 10 days earlier than Prophet. In this experiment, flowering was not significantly affected by drought cycles.

Differences between cultivars were not significant for root dry weight (RDW), but drought cycles had a drastic effect in reducing root mass. Quantitatively, the most important effects were observed at the first and second drought cycles, since very little root growth inhibition was observed from the second to the third drought cycle. The third drought cycle coincided with the flowering stage which, in general, caused root growth to be restricted (Figure 30).

The shoot/root ratio (S/R), consequently, was heavily affected by drought cycles. Furthermore, significant differences were also found between cultivars (Table 33). Shoot/root ratio showed a linear trend to increase as plants were subjected to more drought cycles. Thus, drought cycles affected top growth as well as root growth, and cultivars appeared to respond differently.

The loss of dry weight relative to the control was evidently different between cultivars. Shoot dry weight losses were greater in Meyer with a decrease of 30 percent on the first drought cycle down to 56 percent after three drought cycles. Prophet, on the other hand, showed a loss of shoot dry weight of about 21 percent, relative to the control, after the first drought cycle, and 46 percent after three drought cycles. Root dry weight was more drastically affected as root dry weight loss relative to the control for the first and second drought cycles was about 57 percent and 70 percent, respectively, for both cultivars.

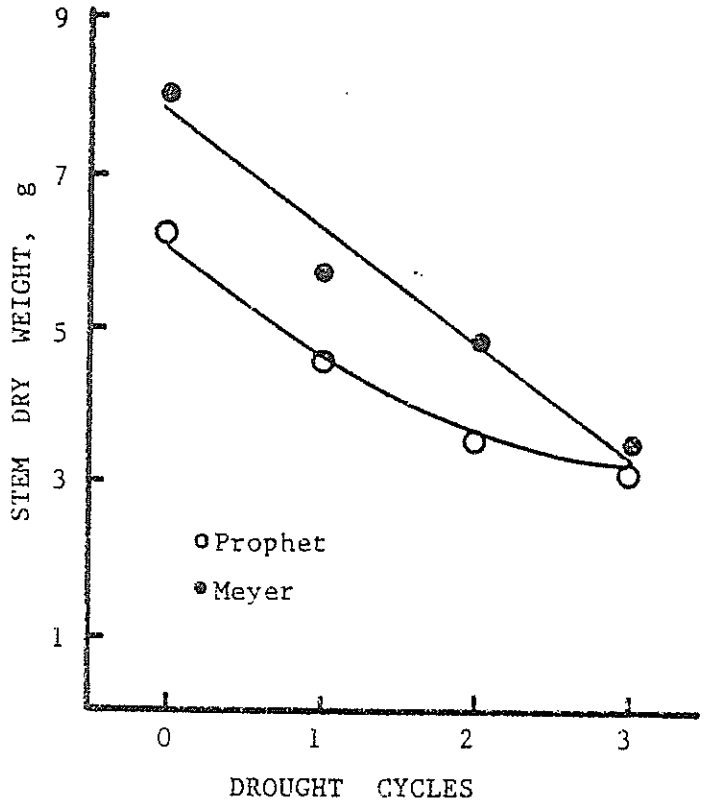

Fig. 29. Stem dry weight/plant (SDW) of two crambe cultivars (Meyer and Prophet) as a function of drought cycles. Each data point represents the mean of six samples. Exp. GH-8. 1981.

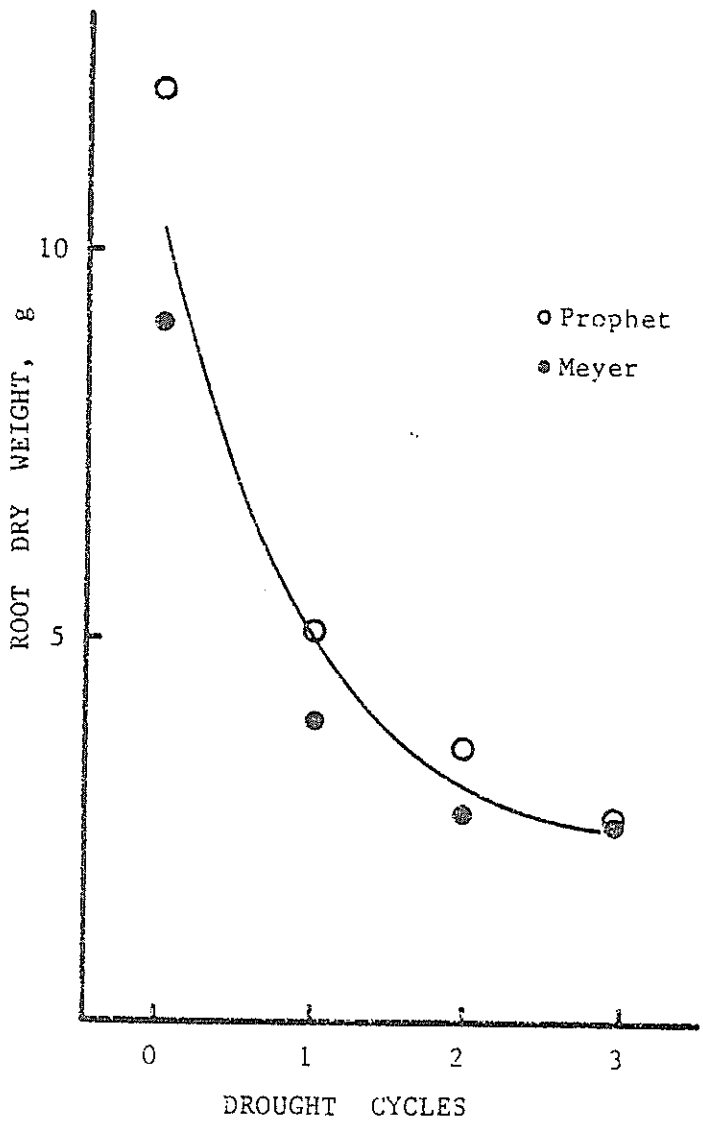

Fig. 30. Root dry weight/plant (RDW) of two crambe cultivars (Meyer and Prophet) as a function of drought cycles. Each data point represents the mean of six samples. Exp. GH-8. 1981.

Table 33. Mean root dry weight, shoot dry weight and shoot/root ratios observed in two crambe cultivars (Meyer and Prophet) subjected to drought cycles. Exp. GH-8. 1981.

Drought cycle	Shoot dry weight	Root dry weight	Shoot/root ratio
	g		g/g
	Meyer		
0	11.22	9.03	1.24
1	7.81	3.86	2.02
2	6.62	2.70	2.45
3	4.94	2.54	1.94
	Prophet		
0	10.28	12.21	0.84
1	8.10	5.17	1.57
2	5.81	3.61	1.61
3	5.54	2.49	2.22

The greater susceptibility of Meyer to water stress has been consistently evident through several plant indicators (i.e., LDW, T, LWP, RWC, and S/R ratios). In fact, the ability of Prophet to maintain a better water balance under water stress indicates a distinct difference in drought resistance between these genotypes.

FIELD EXPERIMENTS

Experiment F-1. The objective of Exp. F-1 was to characterize the plant water relations and to development guidelines for screening drought-resistance germplasm through field evaluation in order to evaluate the interactive effects imposed by the environmental conditions on the plant response. The physiological parameters under study--RWC, KR (kinetics of rehydration), LOP, LDR, T, LA, TDW, and SDW--were evaluated on 19 May through 21 May 1981 before the third sprinkler irrigation.

The complete model used included SWPm or WA development and pubescence plus 19 dummy variables representing the 20 genotypes evaluated. Genotype 20 (G-20) was set as the reference genotype in the model. The cross products between those variables were also included. Stepwise analysis was used in each model to select the significant variables.

The general formulation of this model was used for all the analyses except where indicated otherwise. The systematic water application imposes some statistical constraints upon the analysis of data. Such constraints affect the measure of uncertainty in the statistical analysis, but the design used here is justified by significant logistical advantages.

The trends observed in RWC (Figure 31) indicated that the majority of the genotypes were not significantly different from the reference set, and were also not significantly affected by the observed SWPm at

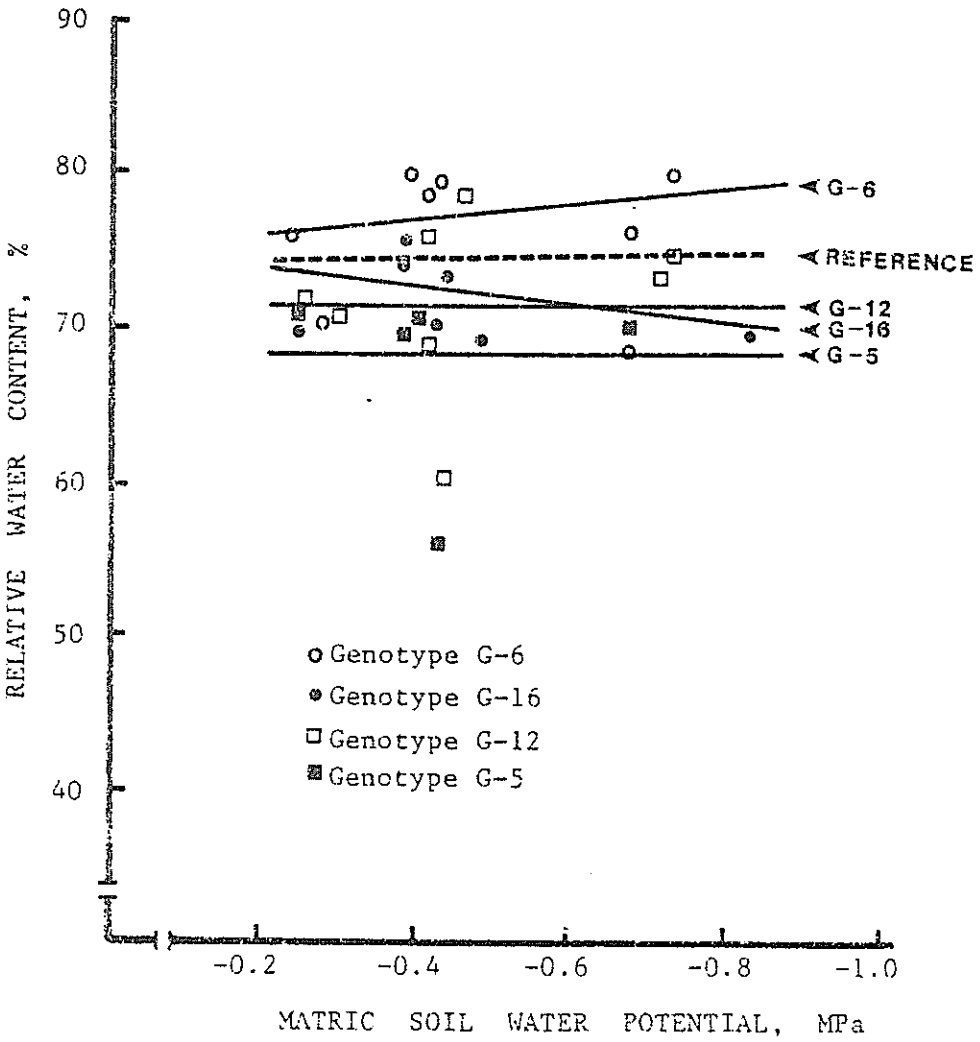

Fig. 31. Leaf relative water content (RWC) as a function of matric soil water potential. Each data point represents the observed value. Exp. F-1. 1981.

sampling time. The average estimate of RWC for the reference set of genotypes was 74.6 percent. Genotypes G-5 and G-12 showed a significant lower RWC as compared to the reference set with an estimated value of 68.6 percent and 71.6 percent, respectively, but these two later genotypes were also not significantly affected by the observed SWPm at sampling time. Only genotypes G-6 and G-16 were significantly affected by SWPm as genotype G-6 showed the tendency to increase RWC as SWPm decreased (Table 34), whereas the RWC of genotype G-16 decreased as SWPm decreased. The main effect of SWPm was not reflected by the plants in the experiment. The RWC was observed to be higher than 70 percent on the average for all the genotypes at all the observed SWPm, except in genotype G-5 which had a slightly lower RWC. At high levels of leaf water content, stomatal response appeared to be largely independent of leaf water content (Vaadia et al. 1961).

The analysis for kinetics of rehydration similar to that of RWC showed no significant differences for SWPm (Table 34). Only time of floating (TM) and the interaction lnTxG-6 were significant. This response is similar to the analysis of RWC, where genotype G6 had the highest RWC at the lower SWPm. Genotype G-6 absorbed significantly more water than the rest of the genotypes in the rehydration process.

The effect of drought on stage of development was analyzed following the model structure described for RWC. The parameter estimates in the model for stage of development are shown in Table 35. The selected model explained about 70.4 percent of the total variation. Figure 32 shows the tendency of crambe genotypes to remain vegetative as drought increased. Drought stress tended to delay development of genotypes G-2, G-4, G-5, G-8, G-9 and G-16. These genotypes were more vegetative in

Table 34. Summary of statistics associated with the significant effects in the regression analysis for leaf relative water content (RWC) and kinetics of rehydration (KR). Exp. F-1. 1981.

Parameter	Parameter estimate	Standard error	OSL†
Relative Water Content (R^2 = 16.2%)			
Reference	74.61	0.33	<0.01
G-5	-6.03	1.46	<0.01
G-12	-2.99	1.38	<0.04
SWPmxG-6	-0.70	0.31	<0.03
SWPmxG-16	0.65	0.26	<0.02
Kinetics of Rehydration (R^2 = 77.1%)			
Reference	6.2464	0.0036	<0.01
lnTM	0.0334	0.0008	<0.01
lnTMxG-6	0.0085	0.0038	<0.03

†Observed significant level.

Table 35. Summary of statistics associated with the significant effects in the regression anaylsis for stage of development (SD). Exp. F-1. 1981.

Parameter	Parameter estimate	Standard error	OSL†
Reference	2.0737	0.0827	< 0.01
G-1	-1.4740	0.1648	< 0.01
G-3	-0.7737	0.1774	< 0.01
G-7	-2.0737	0.1849	< 0.01
SWPmxG-2	0.1208	0.0350	< 0.01
SWPmxG-5	0.1776	0.0398	< 0.01
SWPmxG-6	-0.0959	0.0367	< 0.01
SWPmxG-8	0.1562	0.0299	< 0.01
SWPmxG-9	0.0895	0.0386	< 0.03
SWPmxG-16	0.2136	0.0327	< 0.01
$SWPm^3xG-4$	0.0028	0.0010	< 0.01
Pubescence	0.5558	0.0960	< 0.01

†Observed significant level.

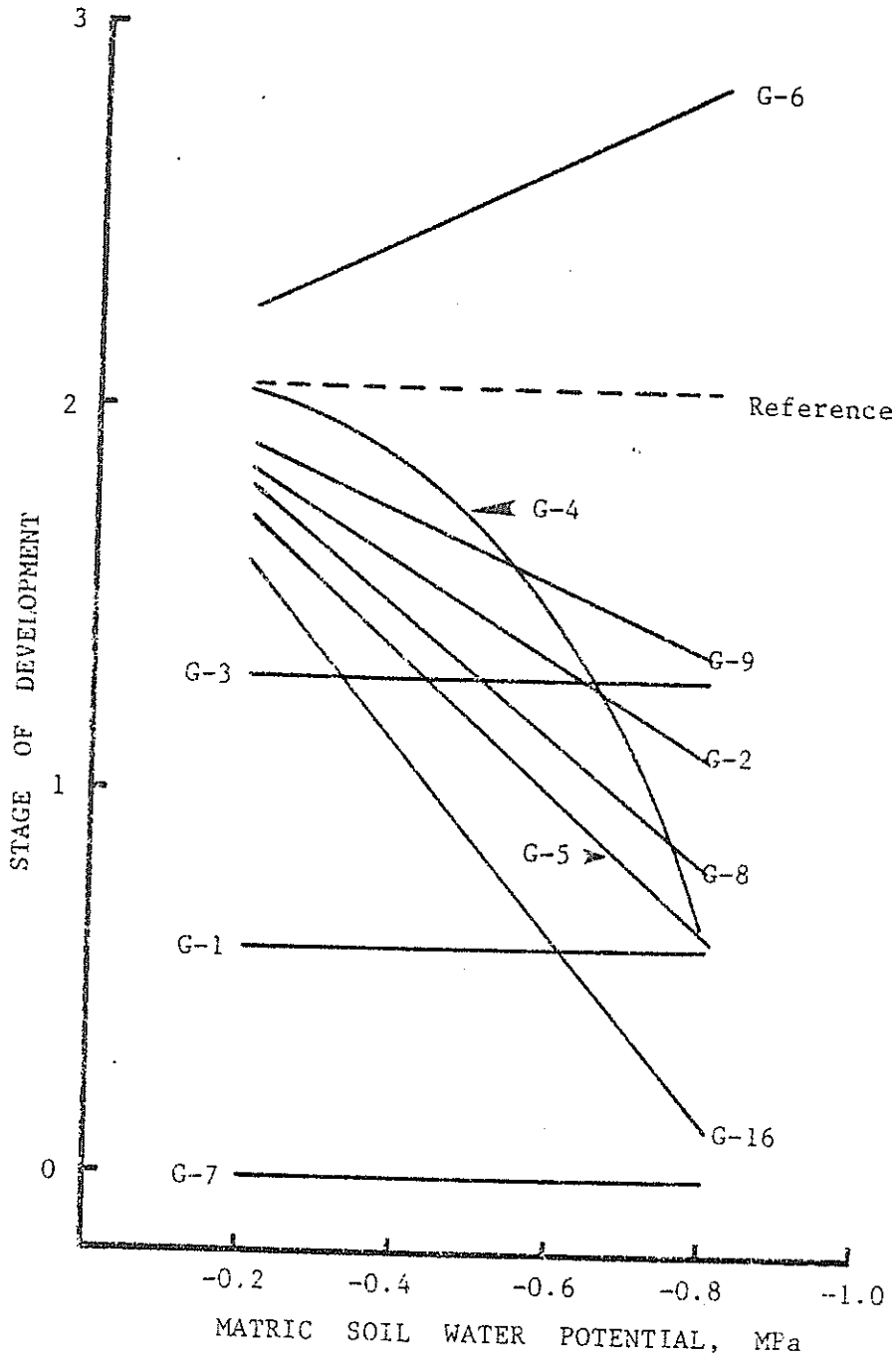

Fig. 32. Stage of development (SD) as a function of matric soil water potential at the time of sampling for physiological parameters. Exp. F-1. 1981.

the driest treatments. Genotype G-6 was the earliest genotype in terms of time to first open flowers and combined the highest RWC and water uptake in the process of rehydration. On the other hand, genotype G-7 was the latest genotype.

The analysis of stage of development is evidence of the variability among the genotypes included in this experiment. Earliness may play an important role in water use efficiency when the water resources are limited (Begg and Turner 1976). Three main tendencies can be identified in Figure 32: (1) one group of genotypes that was not affected in development by drought includes all the genotypes in the reference set plus genotypes G-1, G-3 and G-7; (2) a second group that responded interactively to drought which had the tendency to remain vegetative at the drier treatments but with about the same earliness as the reference set at the higher SWPm; and (3) a third group formed solely by genotype G-6, which showed a tendency to early maturity as drought increased. Both tendencies, enhancing or delaying maturity with increased water stress, may play an important role in a crambe improvement program.

Leaf osmotic potential was significantly associated with leaf pubescence. On the average, pubescent genotypes were about 0.081 MPa higher in LOP than glabrous genotypes. Leaf osmotic potential was also influenced by SWPm, as only genotypes G-1 and G-4 decreased in LOP as drought increased (Figure 33). All other genotypes were pooled at the reference set (Table 36).

The two genotypes showing a significant decrease in LOP with increasing drought were also grouped with the later genotypes (Figure 32), with the exception of G-7. The effect of SWPm in decreasing LOP has been observed in many other plant species (Ackerson 1981; Meyer and

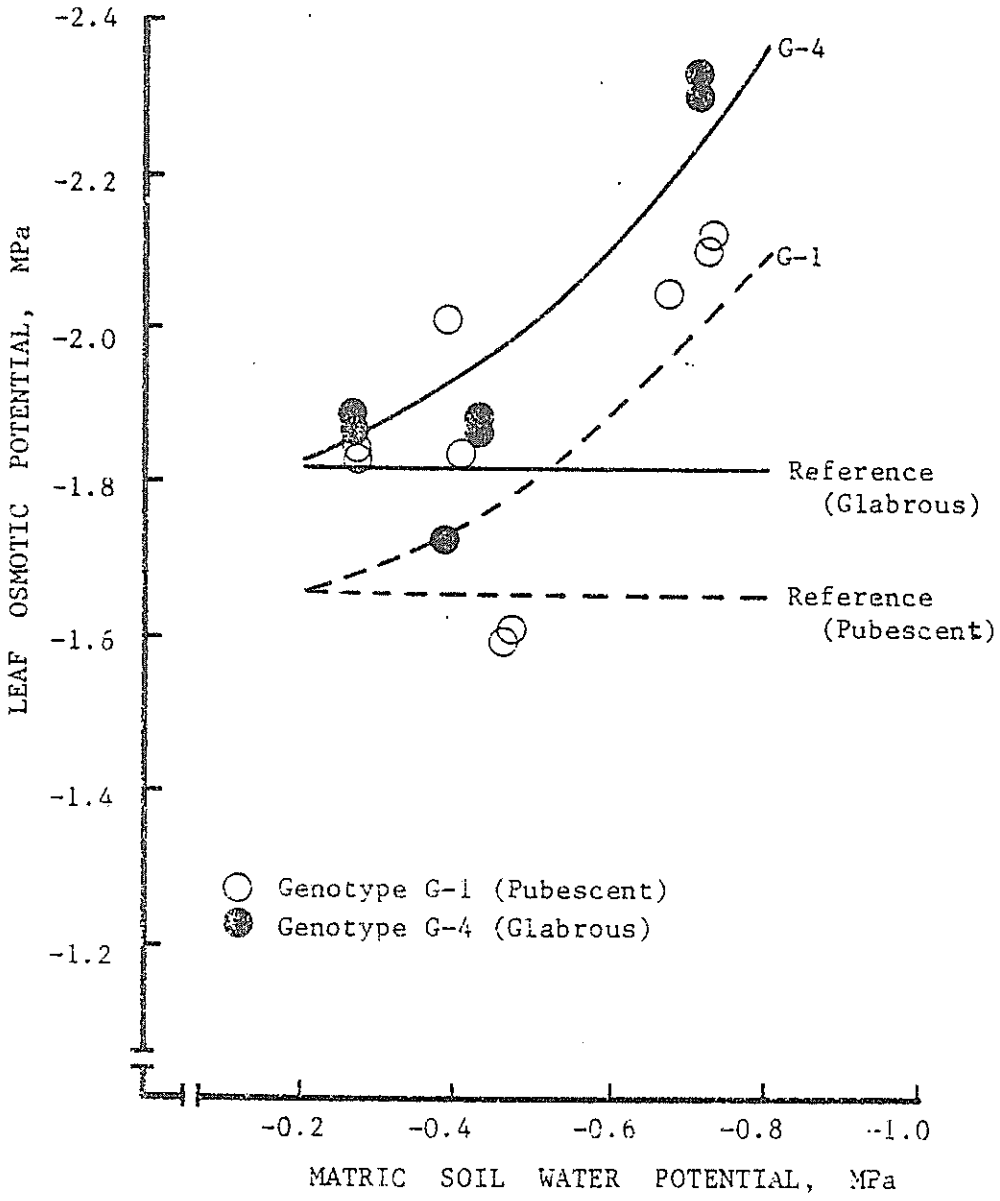

Fig. 33. Leaf osmotic potential (LOP) as a function of matric soil water potential. Each data point represents the observed value. Exp. F-1. 1981.

Table 36. Summary of statistics associated with the significant effects in the regression analysis for leaf osmotic potential (LOP). Exp. F-1. 1981.

Parameter	Parameter estimate	Standard error	OSL†
Reference	-19.1204	0.1879	<0.01
$SWPm^3$xG-1	0.0053	0.0025	<0.04
$SWPm^3$xG-4	0.0090	0.0031	<0.01
Pubescence	0.8116	0.2527	<0.01

†Observed significant level.

Boyer 1981) in which the mechanism of osmoregulation appears to be associated with genotypes (Jones and Turner 1978). The trends shown in Figure 33 are consistent with the results obtained in the greenhouse experiments (Figure 25) where the cultivar Prophet (glabrous) maintained higher LOP than Meyer (pubescent) when subjected to drought stress.

The model used to analyze leaf diffusion resistance and transpiration responses included the setup described for RWC with addition of the variables Leaf Temperature (LT), Relative Humidity (RH), and Photosynthetic Active Radiation (PAR), which were concurrently measured with LDR and TR. Also, PAR at the top of the crop (PARtop) was included with the independent variables. This measurement was taken with the porometer every hour during the sampling time.

In order to find out if leaf ambient RH had any association with the treatments under study, RH was taken as a dependent variable. There were no significant effects of treatment variables on RH, pubescence, stage of development, nor NS halves. This is shown in the main effects ANOVA in Table 37.

Consequently, the association of RH with LDR and TR is an intrinsic correlative effect of the sampling conditions as ambient RH increases as plant transpiration increases and vice versa. This is evident in Table 38, as the estimated partial coefficient of regression was negative for RH versus LDR and positive for RH versus TR.

As a general trend for all the genotypes under study, leaf diffusion resistance showed a significant increase as relative humidity decreased. Transpiration, on the other hand, was positively affected by LT and RH for most genotypes. Genotype G-15 followed a cubic trend to increased transpiration with increased drought. The increase in TR with

Table 37. Main effects analysis of variance for relative humidity (RH) of ambient leaf environment as measured with the porometer. Exp. F-1. 1981.

Source	DF	SS	OSL†
Total	175	8121.4	
Model	27	965.1	0.82
IT	4	28.3	0.96
NS	1	1.8	0.84
Genotypes	19	819.8	0.59
Pubescence	1	50.8	0.31
SD	2	64.4	0.51
Error	148	7156.3	

†Observed significant level.

Table 38. Summary of statistics associated with the significant effects in the regression analysis for leaf diffusion resistance (LDR) and transpiration (TR). Exp. F-1. 1981.

Parameter	Parameter estimate	Standard error	OSL†
Leaf Diffusion Resistance (R^2 = 47.5%)			
Reference	5.8460	0.2590	<0.01
RH	-0.1540	0.0122	<0.01
Transpiration (R^2 = 66.0%)			
Reference	-34.6391	3.3700	<0.01
LT	0.9764	0.0909	<0.01
RH	0.8938	0.0503	<0.01
$SWPa^3$ x10-15	-0.0152	0.0057	<0.01

†Observed significant level.

increasing drought cycles was also observed in the greenhouse experiments (Figure 22), given that no water shortage existed. Drought cycles, as they occur naturally in the field, appear to precondition the stomata to remain open under subsequent water stress as found in sorghum (Thomas et al. 1976).

Growth response was expressed through the determination of leaf area/plant (LA), leaf dry weight/plant (LDW), stem dry weight/plant (SDW), and top dry weight/plant (TDW [Table 39]). Leaf area and LDW were found to be associated with SWPm and earliness (SD) for all the genotypes. Stem dry weight did not show a relationship with any of the variables under study and top dry weight was significantly affected by earliness. All these analyses explained a very low proportion out of the total variation (Table 39).

Leaf area had a tendency to decrease as SWPm decreased (Figure 34), whereas both LA and LDW tend to increase as flowering was delayed. The response to these two variables (SWPm and SD) indicate that LA and LDW decreased in a linear manner as drought increased and that the genotypes that were more vegetative at the time of sampling had the higher leaf area and leaf dry weight. The decrease in LA and LDW due to drought has been frequently reported in a wide range of species (Hsiao 1973; Adjei-Twum and Splittstoesser 1976; Begg and Turner 1976; Read and Barttlet 1977; Constable and Hearn 1978; and Horton et al. 1982). Reduction of LA is thought to be a mechanism by which the plants tend to reduce the water demand. On the other hand, the increase in LA observed in later genotypes is related to the process of maturation in crambe. The phenological stages of crambe are well defined, as was observed in both greenhouse and field experiments. As the floral stem of crambe appears,

Table 39. Summary of statistics associated with the sigificant effects in the regrssion analysis for leaf area (LA), leaf dry weight (LDW), stem dry weight (SDW) and top dry weight (TDW). Exp. F-1. 1981.

Parameter	Parameter estimate	Standard error	OSL†
Leaf Area (R^2 = 25.0%)			
Reference	457.95	37.25	<0.01
SWPm	11.56	5.37	<0.04
SWPmxG-5	-19.35	9.67	<0.05
$SWPm^3$xG-3	0.44	0.18	<0.02
Pubescence	-44.04	21.01	<0.04
SD	52.00	12.59	<0.01
Leaf Dry Weight (R^2 = 27.2%)			
SWPm	2.6190	0.2158	<0.01
G-7	5.0049	1.8562	<0.01
SWPmxG-5	-0.1249	0.0542	<0.03
SWPmxG-7	0.6931	0.3371	<0.05
$SWPm^2$xG-4	-0.0034	0.0013	<0.01
SD	-0.2889	0.0661	<0.01
Stem Dry Weight (R^2 = 2.0%)			
Reference	6.5825	0.1674	<0.01
$SWPm^3$xG-10	0.0091	0.0048	<0.05
Top Dry Weight (R^2 = 3.6%)			
Reference	9.599	0.565	<0.01
SD	-0.647	0.254	<0.02

†Observed significant level.

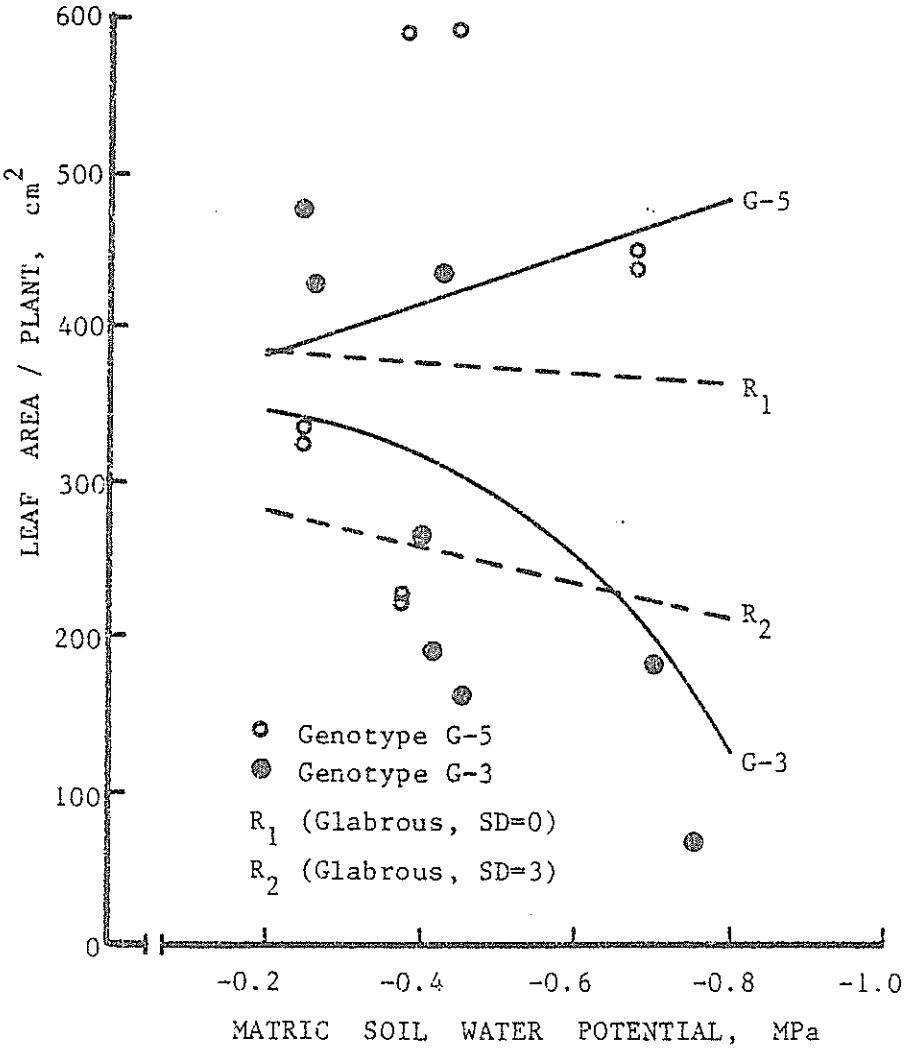

Fig. 34. Leaf area (LA) as a function of soil water potential. Characterization of grenotypes with respect to pubescence. R1 and R2 indicate the reference set for glabrous genotypes that were at stage of development 0 and 3, respectively. Each data point represents the observed value. Exp. F-1. 1981.

leaf enlargement is minimized; however, abundant new leaves are produced but they remain very small through plant maturation. These observations support the analytical inference that the later the genotype, the higher the LA and LDW, as the later genotypes invest more time in accumulating photosynthetic area.

Pubescence appeared to be highly associated with earliness. Pubescent genotypes were significantly earlier than glabrous genotypes. Pubescent genotypes also had significantly smaller LA. However, the differential response in leaf area of Genotypes G-3 and G-5 in LA (Figure 34) is of particular interest in this study as both genotypes are glabrous. Genotype G-3 was intermediate in earliness while Genotype G-5 tended to remain vegetative as water stress increased (Figure 32). This characterization explains the linear trend of Genotype G-5 to have more leaf area at lower SWPm. Leaf area of Genotype G-3, however, drastically decreased with increasing drought as compared to the reference set.

Leaf dry weight showed a different response than LA in all genotypes with the exception of Genotype G-5 which had a similar trend in both LA and LDW. Leaf dry weight was not significantly associated with pubescence, but earliness played a role similar to that in the LA response. Genotype G-7 had a significantly higher LDW at the higher SWPm with a tendency to decrease as SWPm decreased. Genotype G-7, the latest genotype in the experiment, was observed to be among the most succulent, with thicker leaves and petioles. Genotype G-4 also showed an increase in LDW as SWPm decreased, as it also showed a curvilinear response to SWPm in development (Figure 32). The effect of increasing LDW as SWPm decreased was also observed in Genotype G-5 (Figure 35).

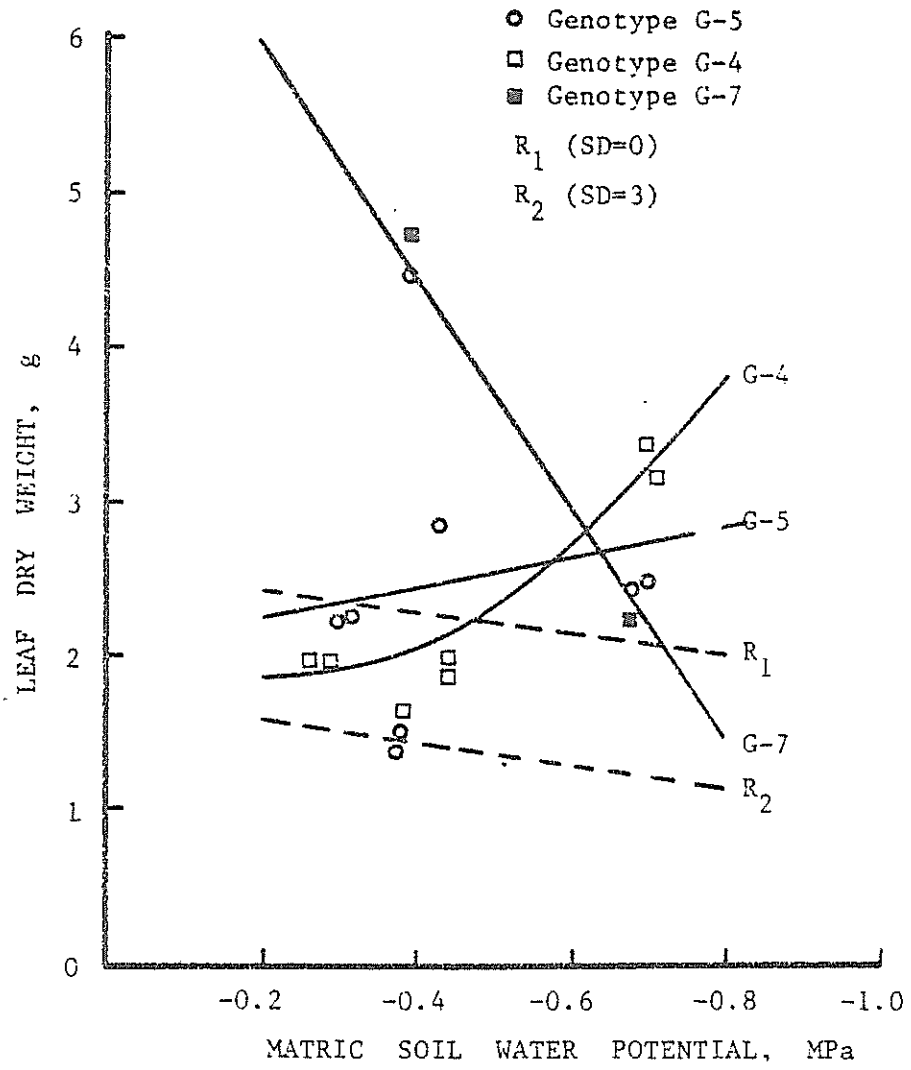

Fig. 35. Leaf dry weight (LDW) as a function of soil water potential. R1 and R2 indicate the reference set of genotypes that at time of sampling were at stage of development 0 and 3, respectively. Each data point represents the observed value. Exp. F-1. 1981.

The increase in LDW with decreasing SWPm may be directly related to CO_2 exchange rates that change with developmental stage. Silvius et al. (1977) found that CO_2 exchange rates decreased more rapidly in soybean plants at a more advanced stage of development (i.e., flowering and pod filling) than at the vegetative stage.

Seed yield was analyzed for those plots that had more than 60 plants or approximately 1 plant/5 cm. The number of plants per plot ranged from 60 to 90. The parameter estimates for the variables included in the selected model are shown in Table 40. The number of plants per plot (PPP) included in the analysis as a covariable was nonsignificant. In general, all genotypes increased in seed yield as more water was applied; however, three genotypes were found to react differently to the amount of water applied (Figure 36). Genotype G-19 was the lowest yielding genotype at the lowest level of water applied because seed yield increased in a parallel manner to that of the reference set of genotypes but always with a lower seed production. Genotype G-6 showed a lack of response to irrigation level, but with higher yield than G-19 at the lower irrigation level. Genotype G-18 expressed a higher yield potential by increasing in yield as the irrigation level increased.

The ratio of seed yield/water applied through the line source system was used as an indicator of water use efficiency (WUE = kg seed/mm water/ha). Water use efficiency decreased as more water was applied for all the genotypes under study, but Genotype G-18 (cultivar Prophet) responded with a slower decreasing rate in WUE as more water was applied (Figure 37).

Table 40. Summary of statistics associated with the significant effects in the analysis of seed yield. Exp. F-1. 1981.

Parameter	Parameter estimate	Standard error	OSL†
Reference	172.49	17.92	<0.01
WA	1.81	0.34	<0.01
G-19	-97.85	25.60	<0.01
WAxG-6	-1.62	0.51	<0.01
WAxG-18	0.97	0.38	<0.02
(R^2 = 27.1%)			

†Observed significant level.

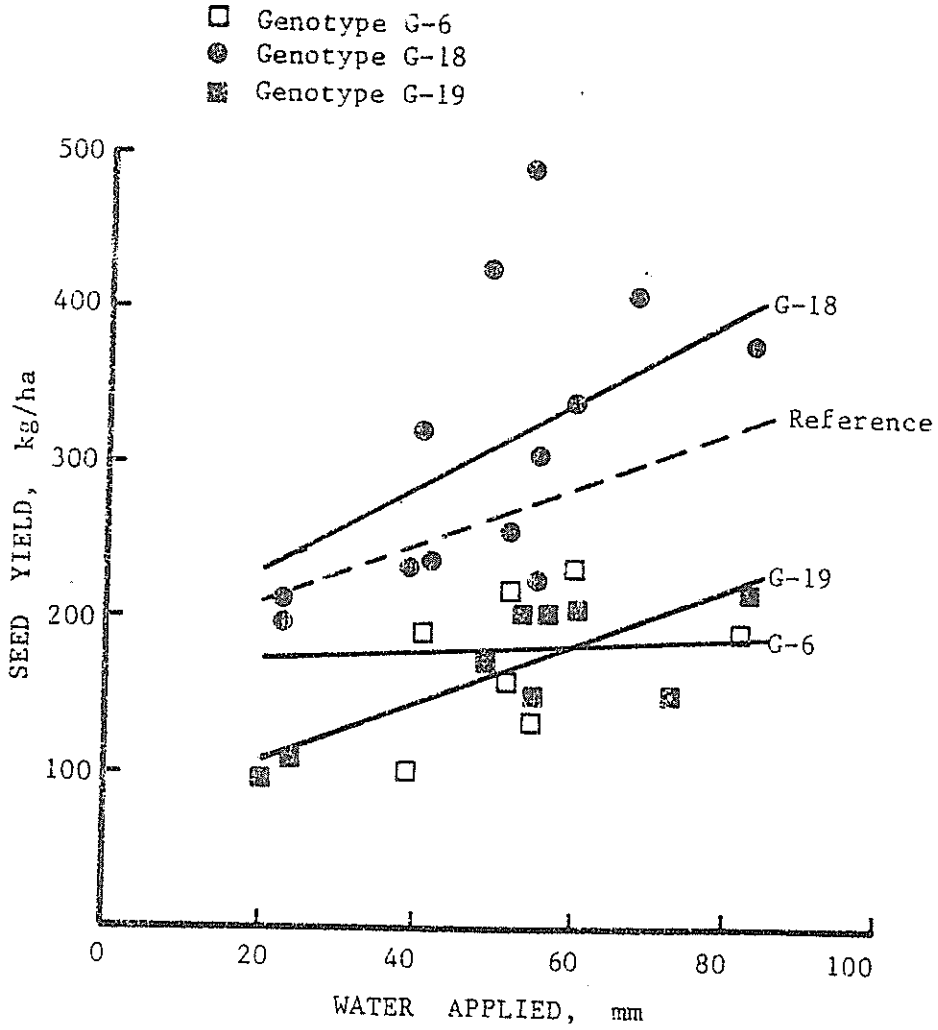

Fig. 36. Seed yield as a function of total water applied through the line source sprinkler irrigation system. Each data point represents the observed value. Exp. F-1. 1981.

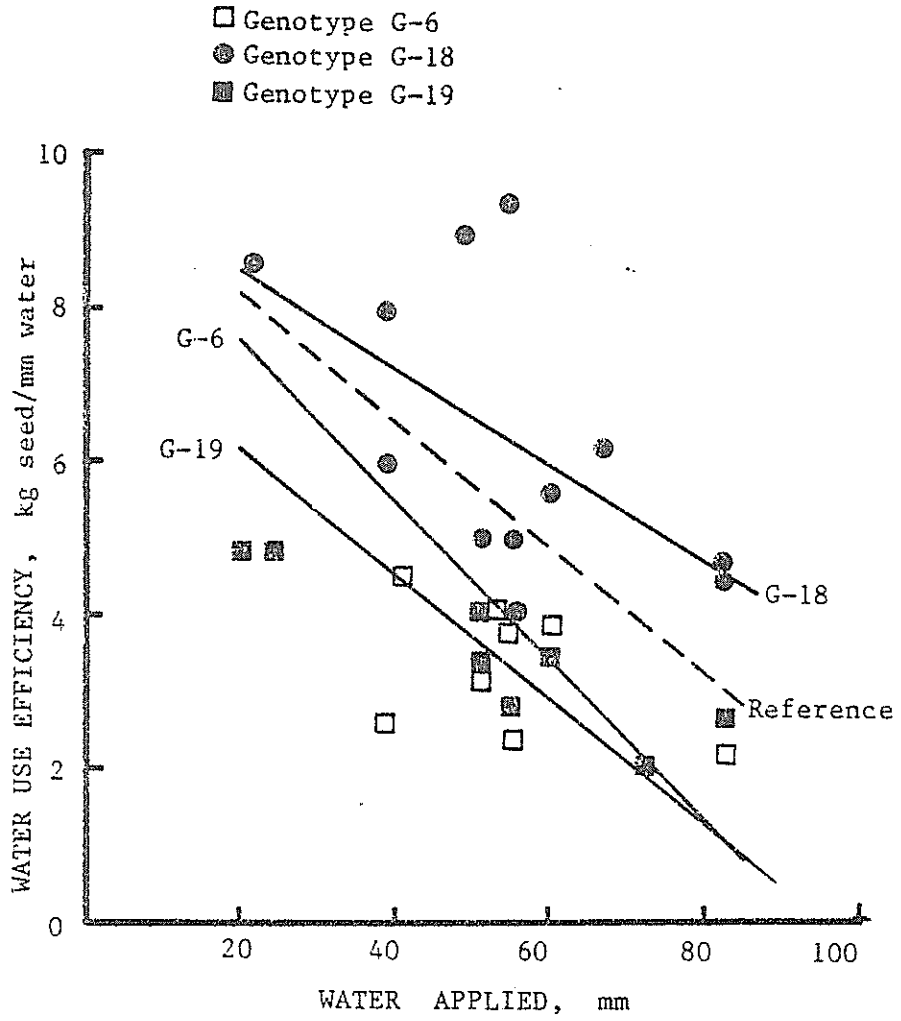

Fig. 37. Water use efficiency (WUE) as a function of total water applied through the line source sprinkler irrigation system. Each data point represents the observed value. Exp. F-1. 1981.

Adaptation of crop production to limited water supply requires at least two characteristics from plants. Firstly, plants must be capable of efficiently using the available water under limited conditions and secondly, the same plants should also be capable of increased yield with increased availability of water. Based on these requirements, the final analysis of Exp. F-1 as related to the adaptation of crambe to limited water supply, suggests that genotype G-18 has comparatively more yield potential as water availability becomes more favorable. Genotypes G-6 and G-19 were the lower yielding genotypes in the group; however, they behaved differently with respect to their response to water application and with respect to plant water relations. Genotype G-6 had a high plasticity and maintained a high RWC through decreasing SWPm. It was the only genotype that significantly absorbed more water in the process of rehydration, and initiated an earlier flowering as a response to decreasing SWPm. These mechanisms have been reported as indicators of plant adaptation to water stress (Begg and Turner 1976). In light of this information, genotype G-6 may be catalogued as well adapted to water stress. These peculiarities are of prime importance for survival and species perpetuation. In terms of economic yields, however, genotype G-6 is of little value, as it did not increase in yield as more water was applied.

The techniques and procedures used in this experiment allowed the detection of differential responses of crambe to drought stress. These responses were delineated in terms of both irrigation treatments (SWPm or WA) and genotypes. The general trend of plant water deficit to increase as soil matrix water potential decreased, or applied irrigation water decreased, was evidenced by means of different parameters.

Genotype differentiation was successfully based on the response to the imposed treatment and suggests that crambe genotypes can be screened for drought resistance on the basis of the parameters studied. There appears to be a differential potential between genotypes to withstand soil and plant water stress.

In general, the water deficits shown by the plants under study were not severe since RWC values were around 75 percent for the majority of the genotypes (reference), with the lowest estimated RWC of 69 percent for Genotype G-5, and the highest of 79 percent for Genotype G-6. The RWC was not significantly affected by irrigation treatment. This technique was not sensitive enough to detect small differences across SWPm, under the conditions of this experiment. With the use of kinetics of rehydration, it was not possible to separate the effects of SWPm among genotypes.

Genotypes G-1 and G-4 were observed to maintain a higher leaf osmotic potential as drought increased. This mechanism appeared to be related to the plasticity of these two genotypes, as they remained vegetative when drought increased.

Leaf diffusion resistance and transpiration responses also indicated low water deficits in the plants. This is evidenced by the low LDR (2 to 4 s $.cm^{-1}$), and high transpiration (approximately 12 $g.cm^{-2}.s^{-1}$). Growth characteristics, together with porometric data, showed high uncontrolled variability. Nevertheless, it was possible to detect certain differential trends on the basis of leaf area and leaf dry weight. Genotype G-5 had the most LA and LDW of all the genotypes, even though the RWC of G-5 was the lowest of all genotypes. An important consideration is the fact that genotype G-5 was grouped among the later

maturing genotypes at the lower SWPm. All other genotypes decreased in LA with decreasing SWPm, but genotype G-3 showed the most drastic LA decrease with decreasing SWPm.

The earliest genotype, G-6, together with genotype G-19, were the lowest yielding. On the other hand, genotype G-18 (cultivar Prophet), the highest yielding genotype, was in the medium range of earliness. Furthermore, genotype G-18 was the only genotype in the group that significantly increased in seed yield and had a better WUE as more water was applied in comparison with other genotypes. Moreover, cultivar Prophet, under greenhouse conditions, showed physiological mechanisms for conserving water which were based mostly on stomatal action.

Experiment F-2. The objective of Exp. F-2 was an intent to validate the information generated in Exp. F-1 in 1981. This experiment was reduced in number of treatments as compared to Exp. F-1 because of the time required for evaluation of the physiological parameters.

The relative water content in the five observed genotypes (only five genotypes out of the 10 planted had enough plants for sampling) decreased linearly as SWPm decreased. There were no significant differences among genotypes (Table 41). The selected model explained only 7.0 percent of the total variation, which indicates the presence of high uncontrolled variability around the estimated function.

The rate of water uptake, measured through kinetics of rehydration, showed no significant differences among SWPm levels. The only significant effect was time of floating (TM) and the interactive effect of TM x genotype G-17, which increased the rate of water uptake as SWPm decreased in comparison to the rest of the genotypes.

Table 41. Summary of statistics associated with the significant effects in the regression analysis for relative water content (RWC), kinetics of rehydration (KR), leaf osmotic potential (LOP), leaf diffusion resistance (LDR) and transpiration (TR). Exp. F-2. 1982.

Parameter	Parameter estimate	Standard error	OSL†
Relative Water Content (R^2 = 7.0%)			
Reference	71.59	3.3156	<0.01
SWPm	1.43	0.7372	<0.05
Kinetics of Rehydration (R^2 = 68.2%)			
Reference	5.9198	0.0097	<0.01
TM	0.0442	0.0024	<0.01
TMxG-17	-0.1129	0.0057	<0.03
Leaf Osmotic Potential (R^2 = 14.4%)			
Reference	-15.8906	0.8185	<0.01
SWPm	0.7117	0.2359	<0.01
Leaf Diffusion Resistance (R^2 = 82.5%)			
LT	0.3078	0.0375	<0.01
RH	-0.4257	0.0679	<0.01
$SWPm^3$xG-14	-0.0152	0.0062	<0.02
Transpiration (R^2 = 96.7%)			
LT	-0.3973	0.0657	<0.01

†Observed significant level.

The leaf osmotic potential, on the other hand, responded to SWPm in a linear fashion. Similar to the response of RWC, no differentiation of LOP among genotypes was found. The rate of decrease of LOP per unit SWPm change was about -0.07 MPa.

Leaf temperature and relative humidity were the most significant variables in the analysis of porometric data and genotype G-14 had a significant interaction with SWPm with a tendency to decrease LDR as SWPm decreased (Table 41). These two variables (LT and RH) were discussed earlier as correlated with the processes of LDR and TR. The factor analysis, which measures the association of variables within factors, is shown in Table 42. This correlative analysis was conducted with the "principal factor method" in order to assign variables to a factor (Harman 1976). This analysis demonstrated that all of the variables of LT, RH, LDR and TR together with IT were loaded on the most important factor. The conclusion indicated by this method of analysis confirms that as LT and LDR increase, RH and TR decrease (see the signs of loadings, Table 42), but they are also correlated positively with irrigation treatment, which means that as drought increased, LT and LDR also increased, and RH and TR decreased. Photosynthetic active radiation (PAR), on the other hand, had its more important loadings on factors II and III.

In this case, PAR is a measure of the incoming photosynthetic active radiation at the sampling point and at the sampling time. The negative association between LT and PAR in Factor II may be explained by the poorer foliage observed in the drier plots, but it could also be a higher albedo present in drier plots. Irrigation treatment has a significant loading on Factor III together with PAR. This indicates that

Table 42. Factor analysis of porometric data. Each factor contains the correlative loadings which indicate the magnitude of association and its direction (positive or negative). The principal factor method was used. Exp. F-2. 1982.

Source	Factor pattern		
	Factor I	Factor II	Factor III
LT	0.70	-0.41	0.17
RH	-0.85	-0.28	0.12
PAR	-0.36	0.46	0.46
LDR	0.82	0.05	0.14
TR	-0.88	-0.14	0.03
IT	0.45	-0.15	0.41

even though the irrigation treatment has a close relationship with the variables significantly loaded on Factor I, IT also has a separated effect, although less important, for the conditions in which this set of data was collected.

Experiment-F-3. This experiment was used to study the effects of soil water shortage at different stages of development in two crambe cultivars (Meyer and Prophet) and included the evaluation of the internal plant water relations, growth and seed yield.

Treatment means of LDR and TR were not significantly different for irrigation treatment in all three readings, except for the main effect of cultivars at the third reading for transpiration. The average transpiration for cultivar Prophet was 9.4 $g.cm^{-2}.s^{-1}$, while cultivar Meyer had a mean transpiration of 7.9 $g.cm^{-2}.s^{1}$. Even though the soil water potential was well differentiated among irrigation treatments, the stomatal behavior did not follow the same trends found in the greenhouse experiments. This response is very likely due to the progressive adjustment of plants to their environment under field conditions or to the availability of water at deeper soil layers.

The greenhouse results and field observations of this study have suggested that cultivar Prophet has a more extensive root system than Meyer. These observations may explain the greater water extraction by Prophet (Figure 38), which extracted more water than Meyer at the end of the growing season, as indicated by the greater water depletion in Prophet plots. This is also supported by the significantly higher transpiration shown by Prophet during the third reading and the significantly higher leaf area of Prophet during the later part of the growing season.

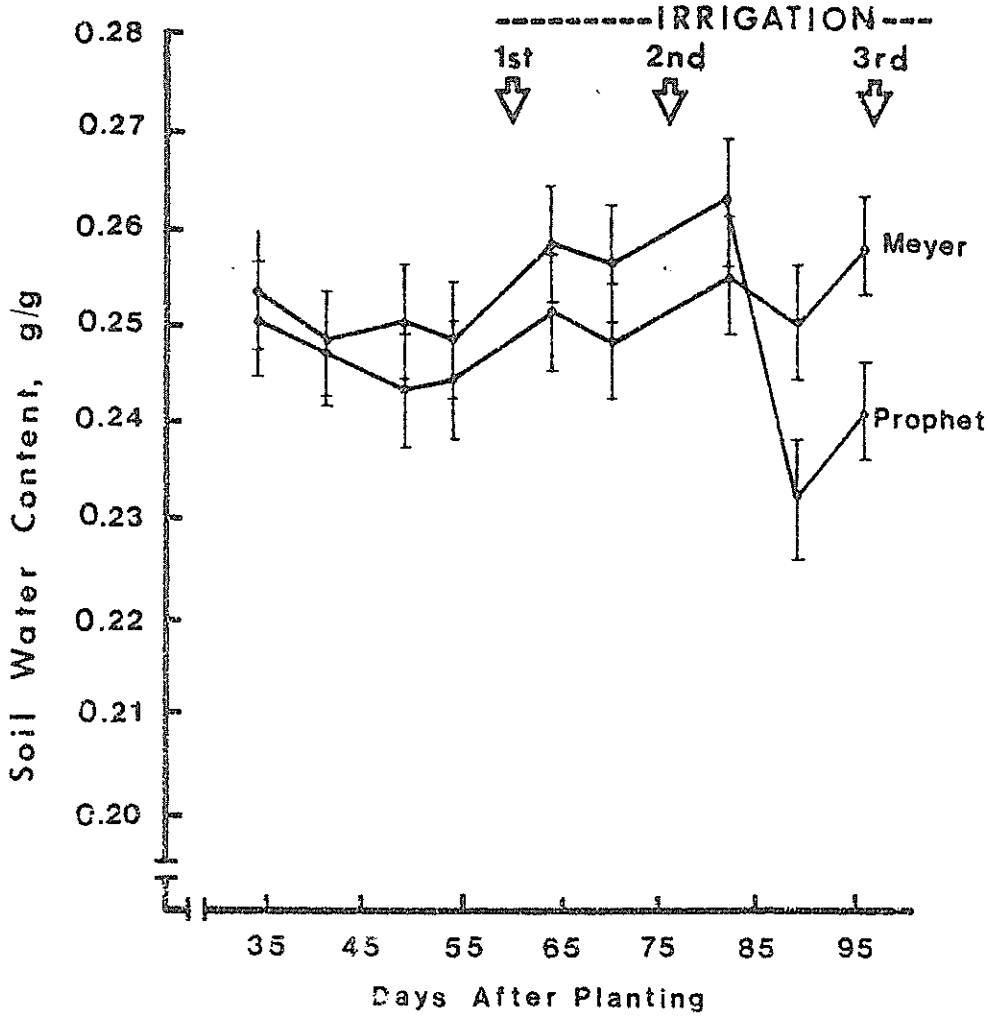

Fig. 38. Soil water content for two crambe cultivars (Meyer and Prophet) through the growing season averaged over all the irrigation treatments at 30 cm depth. Exp. F-3. 1982.

The analysis of variance for growth components was conducted at each date of sampling. A summary of significance levels is presented in Table 43.

According to the separation of effects in the statistical analyses, cultivars were different in terms of ontogenetic response to the environment in this experiment. The observed means for cultivars are shown in Table 44. Prophet had a greater growth potential than Meyer. This is based on the accumulation of dry matter throughout the vegetative growth period and on its later maturity. Earliness is also evidenced by the shift of SDW between cultivars, where Meyer had a larger SDW than Prophet at 90 days after planting. This means that Meyer had produced more flowering stems than Prophet.

Irrigation treatment had a significant effect on specific leaf area (ELA) only at 73 days after planting and on LA/SDW and LA/TDW at 90 days after planting (Table 45). The irrigation treatment had a definite effect in developing more leaf area per gram of leaf dry weight (specific leaf area). This is shown in IT-4, where leaf expansion was inhibited by drought by about 20 percent as compared to the well-irrigated treatments. Furthermore, the importance of supplying water at the vegetative stage of development to promote leaf expansion is shown by the ELA differences among irrigation treatments.

At 90 days after planting, excluding irrigations for stand establishment, IT-1 and IT-2 had received two consecutive irrigations; IT-3 had received one irrigation at the button stage; and IT-5 and IT-6 had received one irrigation at flowering, skipping the button stage irrigation. Three groups of treatment means were found statistically different (Duncan's test). One group, consisting of IT-1, IT2, and IT-3, was

Table 43. Observed significant levels (OSL) for the analysis of variance of growth components in two crambe cultivars (Meyer and Prophet). Exp. F-3. 1982.

Growth component	Source of variation			
	Rep	IT	CV	ITxCV
	----------OSL----------			
At 31 days after planting (4-02-82)				
LA	ns†	ns	ns	ns
LDW	ns	ns	ns	ns
SDW	ns	ns	ns	ns
TDW	ns	ns	ns	ns
LA/SDW	0.01	ns	ns	ns
LA/TDW	ns	ns	ns	ns
ELA	ns	ns	ns	ns
At 46 days after planting (4-17-82)				
LA	ns	ns	ns	ns
LDW	ns	ns	ns	0.01
SDW	0.01	ns	0.05	ns
TDW	0.01	ns	ns	0.01
LA/SDW	ns	ns	ns	ns
LDW/SDW	0.01	ns	0.03	0.03
LA/TDW	ns	ns	ns	ns
ELA	ns	ns	ns	ns
At 73 days after planting (5-13-82)				
LA	ns	ns	0.01	ns
LDW	ns	ns	0.01	ns
SDW	ns	ns	ns	ns
TDW	ns	ns	ns	ns
LA/SDW	ns	ns	0.01	ns
LDW/SDW	ns	ns	0.01	ns
LA/TDW	ns	ns	0.01	ns
ELA	ns	0.01	ns	ns
At 90 days after planting (5-30-82)				
LA	ns	ns	ns	ns
LDW	ns	ns	ns	ns
SDW	ns	ns	ns	ns
TDW	ns	ns	ns	ns
LA/SDW	ns	0.03	0.01	ns
LDW/SDW	ns	ns	0.01	ns
LA/TDW	ns	0.01	0.02	ns
ELA	ns	ns	ns	ns

†Nonsignificant at P = 0.05.

Table 44. Observed means of growth components in two crambe cultivars (Meyer and Prophet), at four sampling dates through the growing season. Exp. F-3. 1982.

Growth component	Days after planting			
	31	46	73	90
Leaf area (cm^2)				
Meyer	9	435	325	204
Prophet	8	459	492	255
Leaf dry weight (g)				
Meyer	0.054	3.01	2.74	1.78
Prophet	0.049	3.03	4.08	2.24
Stem dry weight (g)				
Meyer	0.007	0.73	4.22	7.82
Prophet	0.006	0.41	4.33	7.24
Top dry weight (g)				
Meyer	0.061	3.38	6.96	9.60
Prophet	0.055	3.44	8.42	9.48
Leaf area/stem dry weight (cm^2/g)				
Meyer	1474	1186	74	25
Prophet	1370	1115	116	36
Leaf dry weight/stem dry weight (g/g)				
Meyer	7.71	8.20	0.64	0.21
Prophet	8.16	7.47	0.96	0.32
Leaf area/top dry weight (cm^2/g)				
Meyer	154	128	57	19
Prophet	154	132	45	26
Specific leaf area (cm^2/g)				
Meyer	174	145	120	99
Prophet	173	150	122	104

Table 45. Observed means of growth components at six irrigation schedules in two sampling dates. Exp. F-3. 1982.

Irrigation treatment	Days after planting		
	73	90	
	ELA	LA/SDW	LA/TDW
	cm/g		
1	130	41.3	30.6
2	130	36.7	28.2
3	131	39.0	27.1
4	105	29.0	21.7
5	112	17.6	13.6
6	120	16.6	13.4

significantly different from IT-4, and this treatment was significantly different from IT-5 and IT-6. The sharp decrease of the ratios was associated with the irrigation treatments. The irrigation given in IT-5 and IT-6 apparently enhanced plant maturation as indicated by the shift of ratios at 90 days after planting.

The yields in this experiment were too variable. The covariance analysis included the number of harvested plants per plot (PPP) as a covariable, which weighted the effects of irrigation treatments (coded as dummy variables) and cultivars. The covariable itself was not significant, even though PPP varied from 25 to 43. The only significant independent variable was the interaction of PPP^2 x IT-1. In other words, the only significant trend of yield was in IT-1 with a tendency to increase yield with PPP in a quadratic manner. The estimated model was, however, of poor predictive potential with an R^2 of 11.9 percent.

$$\text{Yield} = 182.1 + 0.079\ PPP^2$$

The predicted yields for IT-1 were estimated for a PPP equivalent of one plant every 10 cm, up to one plant every 7.5 cm in the row. Using these values for PPP, estimated seed yield increased from 253 kg/ha to 308 kg/ha, respectively. All other irrigation treatments had a predicted value of about 182 kg/ha. These PPPs would correspond to plant populations of about 97,000 plants/ha and 130,000 plants/ha, which are very low populations if compared with normal crambe plant populations used in commercial production (approximately one million plants/ha).

Germination Potential of Seed Harvested From Exp. F-1 and F-3. The germination potential of crambe genotypes was researched because of two reasons: first, information was needed on the effects of plant water

stress during the growing season on seed germination; and second, it was necessary to assess the potential germination in order to program (setup) the F-2 experiment.

The potential germination of crambe seed harvested from Exps. F-1 and F-3 was determined under laboratory conditions. The analytical procedure was structured similarly to the analysis used for seed yield. The parameter estimates for the model used in Exp. F-1 are shown in Table 46, where the important variable influencing seed germination was stage of development (SD), which in this situation is a reflection of earliness of maturity.

Germination potential one month after harvest was directly affected by the earliness of the genotypes. In general, the earlier the genotype to flower, the larger the germination potential observed (Figure 39). However, the amount of water applied had a slightly negative effect on germination potential (Figure 40) with the treatments receiving more irrigation water showing a definite lower germination. The lowest germination was observed in genotype G-7 which was the latest genotype along with genotype G-2. The highest germination was observed in genotypes G-9, G-14 and G-15 (about 31 percent, 34 percent and 38 percent, respectively), and the majority of genotypes had about 24 percent germination (reference set). Only the germination of genotype G-14 seed was positively affected by water applied to the parent plants. This same genotype was in the reference set in development (Figure 32). Germination of genotype G-4 seed, on the other hand, showed a linear trend to decrease as water applied increased. This tendency was significantly different from the reference set.

Table 46. Germination potential of crambe seed genotypes evaluated one month after harvest. Exp. F-1. 1981.

Parameter	Parameter estimate	Standard error	OSL†
Reference	14.6462	2.2492	<0.01
WA^3	-0.00001	0.000005	<0.01
G-2	-6.5641	3.3029	<0.05
G-7	-9.6870	3.7545	<0.02
G-9	8.0953	3.2362	<0.02
G-15	10.0556	3.2658	<0.01
WAxG-4	-0.1349	0.0617	<0.03
WA^3 xG-14	0.00004	0.00001	<0.01
Pubescence	5.9026	0.9336	<0.01

†Observed significant level.

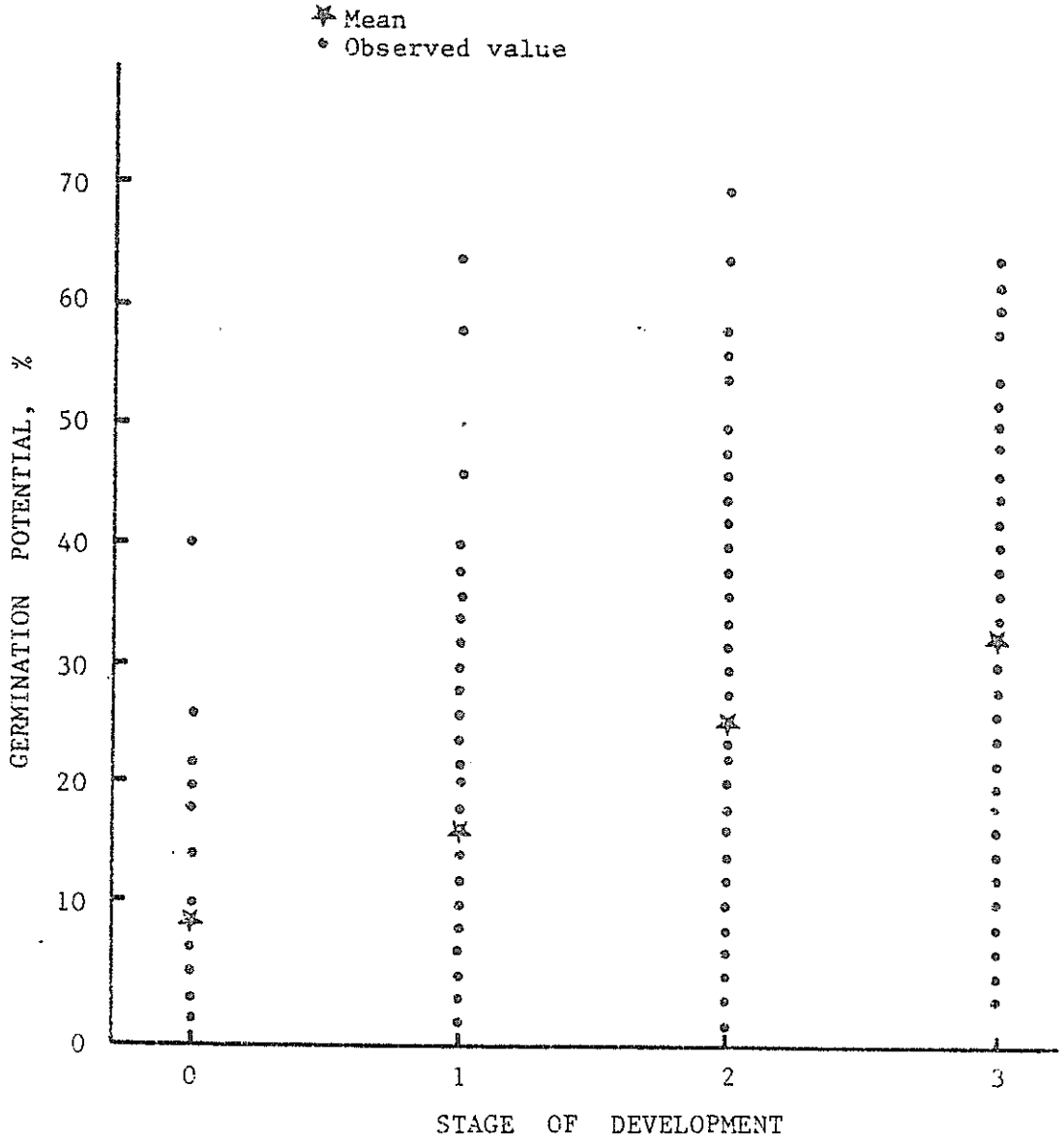

Fig. 39. Germination potential of crambe seed one month after harvest as a function of earliness of maturity as determined by stage of development at 55 days after planting. Exp. F-1. 1981.

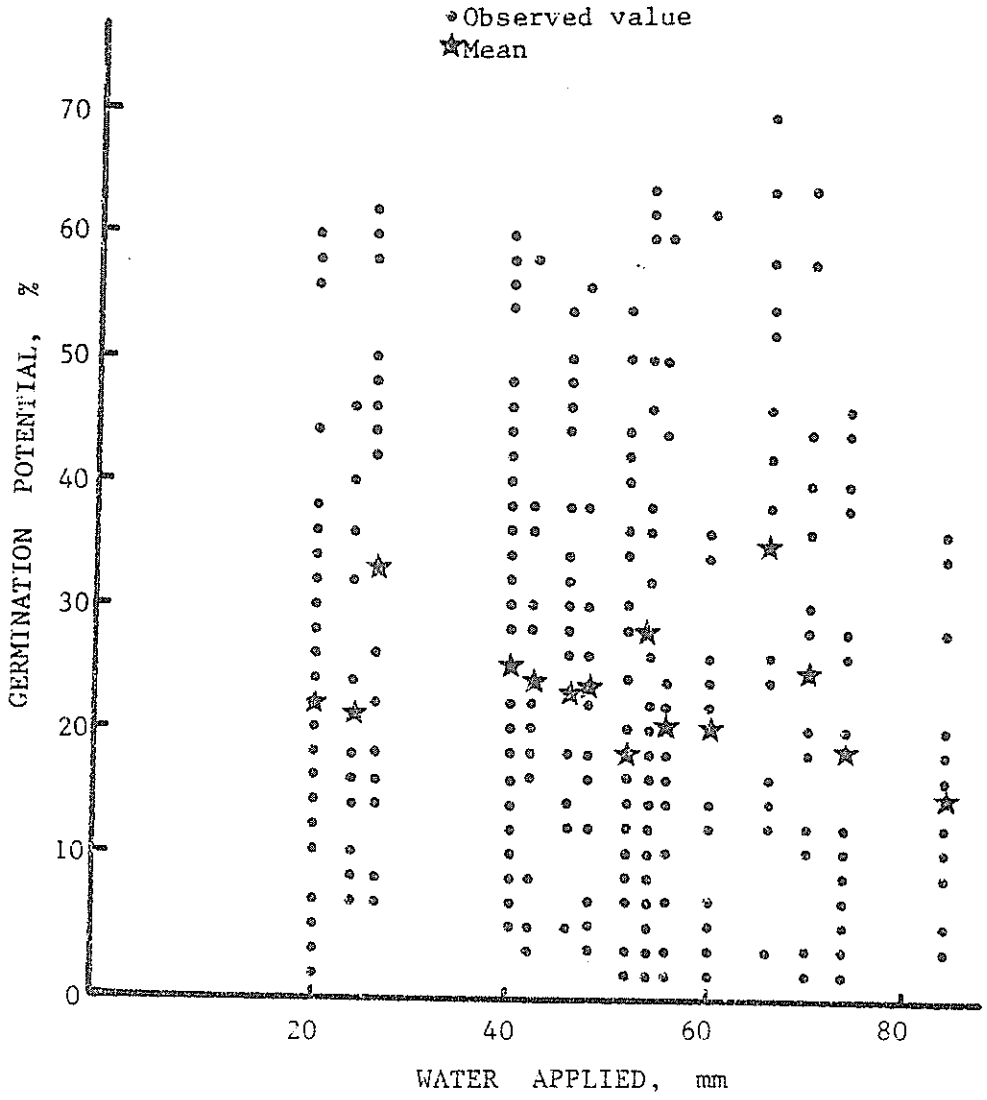

Fig. 40. Germination potential of crambe seed one month after harvest as a function of total water applied through the line source sprinkler system. Exp. F-1. 1981.

The lack of germination potential in crambe genotypes grown in the spring appears to be dependent upon both plant and environmental factors. Within the plant factors, the most important seems to be earliness. Among the environmental factors, high temperature and low relative humidity may play important roles in promoting poor seed quality or in developing seed dormancy, although the data to support this supposition are not available.

In selecting the genotypes to be used in Exp. F-2, another germination test was performed on the Exp. F-1 seed eight months after harvest. The variable time after harvest was then included with the residual effect of irrigation treatment on the 10 selected genotypes. Table 47 shows the significant parameters in the model. Time after harvest (T) compared the germination response of crambe seed at one and eight months after harvest. The interaction of T and genotypes was nonsignificant, which implies that all the genotypes had a parallel tendency in germination, with an improvement of about 18 percent eight months after harvest. Pubescence was also significant, which indicates that pubescent genotypes (G-1, G-13, G-14, G-15, G-17 and G-19) on the average had higher germination than glabrous genotypes (G-4, G-5, G-7, and G-18) by about 17 percent. Genotypes G-15, G-17, and G-19 showed a significantly higher germination with respect to the reference set genotypes G-1, G-4, G-7, and G-13). Genotypes G-5, G-14, and G-18 interacted with the amount of water applied (Table 48). There was a definite trend to increased germination at eight months after harvest as more water was applied. The most important response was observed in genotype G-18 across irrigation levels, where germination was estimated to be close to 0 percent at the lowest level of irrigation, one month after harvest and 75 percent, eight months after harvest.

Table 47. Germination potential of crambe seed genotypes evaluated 1 and 8 months after harvest. Exp. F-1. 1981.

Parameter	Parameter estimate	Standard error	OSL†
G-15	32.3287	4.9090	<0.01
G-17	19.6621	3.8400	<0.01
G-19	19.3287	3.8400	<0.01
WA_2^2xG-5	0.0051	0.0009	<0.01
WA_2xG-14	0.0046	0.0010	<0.01
WA_2^2xG-18	-0.0162	0.0083	<0.01
WA^3xG-18	0.0004	0.0001	<0.04
Pubescence	17.2239	2.6727	<0.01
Time (TM)	17.6711	1.9845	<0.01

†Observed significant level.

Table 48. Germination potential in ten crambe genotypes at 1 and 8 months after harvest. Exp. F-1. 1982.

Pubescence	Genotype	Irrigation level (mm) 46.3	52.0	53.0	55.1	69.8	73.1
		%					
		1 Month after harvest					
Glabrous	G-4	--	--	4	--	10	--†
	G-5	22	10	4	--	16	14
	G-7	4	4	4	8	0	2
	G-18	--	12	16	10	46	24
Pubescent	G-1	30	22	8	36	10	8
	G-13	14	20	26	14	26	28
	G-14	--	30	16	46	32	44
	G-15	30	--	--	56	--	44
	G-17	32	24	28	34	24	44
	G-19	26	24	34	60	20	56
		8 Months after harvest					
Glabrous	G-4	--	--	4	--	16	--
	G-5	41	28	24	--	67	37
	G-7	24	7	23	18	11	4
	G-18	--	43	25	21	74	58
Pubescent	G-1	44	22	51	41	25	23
	G-13	26	36	23	26	23	44
	G-14	--	37	42	65	69	52
	G-15	72	--	--	59	--	80
	G-17	72	31	74	77	35	56
	G-19	61	58	37	72	56	41

†Not available for analysis.

The variation among crambe genotypes in seed production and seed germination with respect to irrigation levels is evidence of the variation which exists among crambe genotypes, pointing to the potentiality of crambe species for improvement programs, as well as emphasizing the problems associated with crambe seed production in southern New Mexico during the spring. The presence of pubescence in crambe leaves has been used as a differential characteristic between species (Leppik and White 1975; and White 1975). This character was also related to other plant-water relations parameters, suggesting a possible approach to the classification of genotypes based on their response to this environment and the potential use of these species in other environments.

The significant increase in potential germination of all the genotypes suggests the presence of some kind of seed dormancy, but the differential response of genotypes to irrigation levels also suggests the presence of plasticity in that dormancy. The plasticity shown by genotypes may be used as a point of departure in future improvement programs for crambe species.

Seed collected from the F-3 experiment was also tested for potential germination, just after harvest. The interaction ITxCV was the only significant effect detected among the sources of variation (Table 49).

The average seed germination for cultivars (Meyer = 22±8 percent and Prophet = 21±6 percent) was very similar across irrigation treatments, but a clear-cut beneficial effect of irrigation during the early stage of growth is seen for Meyer (IT-1 and IT-2), while late irrigation was more important for Prophet (IT-6). Again, this relates well with the earliness of cultivars, since it is known now that Prophet is later than Meyer.

Table 49. Germination potential of the seed of two crambe cultivars (Meyer and Prophet) just after harvest. Exp. F-3. 1982.

Irrigation treatment	Cultivar	
	Meyer	Prophet
	----------%----------	
1	23	18
2	38	17
3	20	22
4	12	19
5	23	18
6	20	32

All of the germination percentages measured were very low. Thus, the germination potential was affected by irrigation treatment plus the environmental conditions present at seed maturation time. The latter factor (probably high temperature) appears to be of prime importance in reducing the potential germination. The increase in germination with time after harvest suggests the presence of germination inhibitors which deserve future study.

SALINITY STUDIES

Seed lots of the two cultivars, Prophet and Meyer, used in this experiment were selected for high germination and seedling vigor. Of the lots available, the two selected had the highest germination in a standard germination test (AOSA 1970) of 88.5 percent and 99.5 percent for Prophet and Meyer, respectively. All other seed lots available had much lower germination and larger differences between cultivars. The effects of salinity on the germination of these two cultivars is given in Table 50. The analysis of variance resulted in highly significant differences in cultivars, salinity levels, incubation time, and the interactions of cultivar x salinity level, cultivar x incubation time, salinity level x incubation time, and cultivar x salinity level x incubation time (Table 51). The interactions of cultivar x salinity level and cultivar x incubation time indicates that the two cultivars responded differently across salinity levels and across time. The salinity level x incubation time interaction also indicates that germination responses through time differed within salt concentrations.

The difference in the quality of the seed of the two cultivars as indicated by the standard germination test, in all probability, affected

Table 50. Cumulative germination percentages of Prophet and Meyer crambe seed as affected by solutions of isoequivalent amounts of $CaCl_2$ and NaCl.

Concentration of salt solution	Days of incubation					
	2	4	6	8	10	12
meq/l	----------	----------	----------	%----------	----------	----------
				Prophet		
0	62.0	77.6	82.4	84.4	85.2	85.2
60	45.8	75.0	82.2	83.0	85.4	85.8
120	32.0	62.8	74.0	74.0	75.6	75.6
180	5.2	34.4	55.4	56.6	59.8	60.6
240	0.0	6.4	27.8	28.2	33.8	33.8
300	0.0	0.0	8.0	8.0	8.4	8.4
360	0.0	0.0	2.8	2.8	3.6	3.6
420	0.0	0.0	0.0	0.0	1.2	1.2
				Meyer		
0	96.4	98.4	99.2	99.6	99.6	99.6
60	93.4	96.6	98.2	98.2	98.2	98.2
120	65.4	71.8	90.2	90.6	93.0	93.0
180	28.6	38.6	62.4	66.0	72.4	72.8
240	14.6	18.6	42.6	43.8	47.0	47.0
300	5.2	7.0	26.4	28.0	33.2	33.2
360	0.0	0.4	7.2	7.2	9.6	10.0
420	0.4	0.4	0.8	1.2	1.6	1.6

Table 51. Analysis of variance of observed germination percentages.

Source	DF	SS	MS	F
Total	479	670027.397	--	--
Reps	4	1174.491	293.622	1.48
Cultivars (CV)	1	20632.518	20632.518	104.14**
Salinity levels (SL)	7	569051.814	81293.116	410.31**
Cv x SL	7	5856.364	836.623	4.22**
Error a	60	11887.708	198.128	--
Time (TM)	5	33680.660	6736.132	410.21**
Error b	20	328.433	16.421	--
Cv x TM	5	1241.693	248.338	14.35**
SL X TM	35	16795.422	479.869	27.74**
Cv X SL X TM	35	4187.722	119.649	6.92**
Error c	300	5190.566	17.301	--

**Significant at the 0.01 level of probability.

the response of the two cultivars to both salinity level and to incubation time with the higher quality seed responding more favorably to both. In a preliminary test, another lot of Meyer seed (standard germination-60 percent) was compared with another lot of Prophet seed (standard germination-86 percent) over the same salinity levels and a similar incubation period. In that test, the Prophet seed responded more favorably to salinity levels than the lower quality Meyer seed and also more favorably across incubation times. These data point out the importance of comparing seed lots of comparable quality if relative comparisons of germination response to salinity are to be made.

Because of the extreme variability and poor quality of seed available from the New Mexico 1980 crambe seed increase and the apparent affect of seed quality on germination response to salinity, the decision was made to forego further salinity screening until seed of better quality was availabe.

SUMMARY AND CONCLUSIONS

The water relations in crambe were studied in a set of greenhouse and field experiments. The greenhouse experiments were important in developing the understanding of the behavior of crambe plants under water stress. The controlled conditions also permitted the calibration of techniques that measure physiological parameters.

The methods used to measure the response of crambe to water stress were successful in one way or another. The relative water content technique, which requires a minimum of instrumentation, was found to be very useful in measuring the water content of plants in the greenhouse where even small differences were detected among treatments. However, this technique was not as good when measuring water content in the

field. By including the kinetics of rehydration as an extension of the RWC technique, the sensitivity of the technique for discriminating effects of desiccation and rehydration as they relate to the water content in the plant was improved.

Determinations of leaf osmotic potentials were practical and meaningful in both greenhouse and field research. With increasing water deficit, leaf osmotic potential became more important in understanding the water relations. The process of solute accumulation in the leaves enables the plant to retain more water as plant water potential decreases. This mechanism appeared to be important in maintaining higher levels of productivity in the cultivar Prophet in comparison to the cultivar Meyer.

Leaf diffusion resistance and transpiration are closely related to the water status of the plant as was evidenced in the greenhouse experiments. However, this technique was of little value in the field experiments. Nevertheless, this technique has proven to be highly useful when drought treatments are beyond the threshold point of stomatal closure. Thus, the porometer is useful in research having treatments with large contrasts.

Leaf area and dry matter production in crambe are highly affected by water stress. Indeed, the understanding of ontogenetic development is crucial in order to interpret crambe water relations and growth. A clear tendency was found for the later maturing genotypes to produce larger leaf area and top dry weight. However, the later genotypes are the most affected by heat stress when planted in the spring and by frost damage when planted in the fall. This, in fact, has detrimental effects on seed yield and potential seed germination of crambe genotypes.

In conclusion, variation among crambe genotypes was found in both greenhouse and field-grown plants. The methods used are capable of bringing out these intrinsic differences among genotypes, although it is desirable to use more than one method in order to ensure the detection of these differences. In field research, the RWC-kinetics of rehydration plus leaf osmotic potential appear to be the most appropriate techniques. In the greenhouse, those two methods, plus leaf diffusion resistance and transpiration, may help in classifying the most drought-tolerant genotypes of crambe.

The variability found among crambe genotypes evidenced its potential for improvement. Rather than including specific genotypes in a classification list, the genotypes studied can be catalogued into well-defined groups. The character, earliness to flower, was an important variable in explaining specific behavior of crambe genotypes with respect to plant water status. There were four groups of genotypes: Early (G-6), Medium-Early (G-10, G-11, G-12, G-13, G-14, G-15, G-17, G-18, G-19, and G-20), Late (G-1, G-3, and G-7), and genotypes with plasticity that significantly modified their developmental processes as drought increased (G-2, G-4, G-5, G-8, G-9, and G-16). The group of genotypes showing plasticity may be of particular interest for imporving crambe, because the observed latency (delaying maturity under stress) could be used as a breeding character in rainfed areas, or wherever the irrigation water is not under complete control for scheduling irrigation.

Genotype G-6, the earliest, was observed to maintain good plant water relations; however, this genotype was the one with the lowest seed yield, as it did not respond to increasing water level. The majority of the genotypes fell within the medium range of earliness. This group

included genotype G-18, which was the leader in production and productivity (water use efficiency ratio). Among other genotypes in this group, G-15 was the only genotype that significantly reduced transpiration when SWPm decreased, indicating a possible mechanism of water conservation under stress conditions. The later genotypes appeared to have very low possibilities of adaptation to the spring planting, under the conditions of these experiments. This was evident in genotypes G-3 and G-7 which responded with a larger decrease in leaf area and leaf dry weight than other genotypes when drought increased. The group of genotypes showing plasticity showed various characteristics that can be used advantageously. For example, genotype G-5 tended to increase in leaf area with decreasing SWPm as a result of delaying plant maturation, whereas genotype G-4 maintained a higher leaf osmotic potential at the lower SWPm studied, very likely due to its latency to flower.

The response of Crambe spp. to salinity was not determined due to the problems encountered with the production and availability of quality seed. High quality seed of comparable germination and seedling vigor are necessary for valid comparisons of germination response among genotypes because of the apparent interactions of seed quality with germination response to salinity.

Many problems were encountered during the conduct of this project, which primarily concerned the culture of the crop itself. Most of these problems can be attributed to unknowns. No doubt, environment and the lack of well-developed cultural practices such as seeding rate, planting dates, fertility and irrigation requirements played significant roles. The future of crambe as a potential crop for arid environments such as southern New Mexico is uncertain. Other areas with cooler, more humid climates would appear to offer more suitable environments for the development of this potential new crop.

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STATEMENT OF POTENTIAL UTILIZATION OF THESE RESEARCH RESULTS

This preliminary study of the adaptation of Crambe spp. to arid lands agriculture provides a basic background of information concerning the plant water relationships of Crambe spp. and the adaptation potential of crambe germplasm to drought. This information should be of interest to crop scientists in general and specifically to those research scientists contemplating future agronomic studies of crambe, particularly as related to the adaptation of crambe to aridity. This information should also be useful to state and federal agencies in the evaluation of the potential of crambe as a new crop for the southwestern United States.