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THE PHYSIOLOGY OF STRESSED AND NON-STRESSED SORGHUM (SORGHUM BICOLOR (L.) MOENCH)

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THE PHYSIOLOGY OF STRESSED AND NON-STRESSED SORGHUM (*SORGHUM BICOLOR* (L.) MOENCH)

by

Wallace Craig Hofmann

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read

the dissertation prepared by Wallace Craig Hofmann

entitled The Physiology of Stressed and Non-Stressed Sorghum (Sorghum bicolor (L.) Moench)

and recommend that it be accepted as fulfilling the dissertation requirement

for the Degree of Doctor of Philosophy.

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Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

Albert K. Dobrenz Dissertation Director	27 Jan, 1982 Date

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SIGNED: Wallace C. Hoffmann

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ABSTRACT

Physiological responses of six sorghum (Sorghum bicolor (L.) Moench) hybrids and their respective parental lines were evaluated under high and low soil moisture conditions at Tucson, Arizona in 1980 and 1981. Apparent photosynthesis, transpiration, diffusive resistance, and temperature differential (ambient temperature minus leaf temperature) were measured under field conditions at weekly intervals. To measure apparent photosynthesis, a small plexiglas chamber was sealed over a section of leaf blade and gas was sampled with two syringes pulled at a 30 or 60 second interval. The gas samples were injected from the syringes into an infrared gas analyzer to measure CO_2 concentrations. Transpiration, diffusive resistance, and temperature differential were measured with a steady state porometer. Regression analysis was used to compare the physiological performance of the germplasm sources over a wide range of environmental conditions.

The physiological characteristics of the highest yielding sorghum hybrid in 1980 were the most stable across all environments. This hybrid was superior to both its male and female parent for all four physiological characteristics. In 1980, this hybrid was superior to the other hybrids in temperature differential and transpiration. The superior yielding hybrid had the highest mean apparent photosynthesis and the lowest mean diffusive resistance. All hybrids had higher yields than their respective male parents under both irrigation treatments.

Thirty-five days after planting, the superior yielding hybrid had the greatest leaf, stem, and root dry weights. This hybrid also had the highest relative leaf area expansion rate. Heterosis for stomatal density was not observed either year.

Regression analysis proved to be an effective tool for analyzing the sorghum germplasm over a diverse range of environmental conditions. By comparing the response of an individual germplasm against the mean response of the population under numerous environmental conditions, the slope, mean, and coefficient of correlation may be used to evaluate genotype-environment interactions.

INTRODUCTION

Present world population is estimated to be 4.5 billion and Cochrane (1969) has projected it to be in the range of 6 to 8 billion people by the year 2000. The present population is far more than the maximum predictions of Malthus who in 1798 estimated that massive famines would limit population to 1.5 billion. Such enormous growth must be paralleled by increases in agricultural production. Tragically however, food production often fails to meet the nutritional demands of the poorest nations (Food and Agriculture Organization, 1972). Meyer (1975) estimated that the food supply would have to double in order to feed the world by the end of the twentieth century.

Increasing world-wide agricultural production can be accomplished in two ways: (1) by increasing yields per unit land area and (2) by expanding land area devoted to crop production (Christiansen, 1979). With the availability of new arable land severely limited, crop plants must be improved to enhance production on existing land and to better adapt them to the marginal lands which must be put into cultivation.

Sanchez (1976) reported that the total cultivated land in Africa was only 8% and in Latin America 5%. This proportion must be expanded if extensive famine is to be averted. Water is the major limiting factor to plant productivity on 40% of the world's land area (Meigo, 1953). A substantial proportion of these arid and semi-arid lands are found in the poorest nations, the same regions which are struggling to feed ever expanding populations.

Sorghum is an extremely important grain crop worldwide and is a major food source for much of Africa and Asia. Estimates are that the world production of sorghum exceeds 120 million acres and that sorghum yields are surpassed only by those of wheat, rice, and possibly corn (Martin and Leonard, 1967). Fortunately sorghum is considered by most agriculturalists to be a drought resistant crop (Sullivan and Ross, 1979). Sorghums are grown under warm, natural rainfall conditions in many regions where precipitation is only 6.7 to 9.8 cm per year (Martin, 1941). Improved sorghum varieties, better adapted to severe moisture stress, would be an important step in increasing world food production. The purpose of this study is to evaluate the effects of soil moisture stress on sorghum hybrids and their respective parents.

REVIEW OF LITERATURE

The drought resistant qualities of sorghum have long been recognized and exploited. Its superior response to moisture deficits was recounted by J. B. Adams (Fields, 1914):

> "It (1911) was a season of unusual severity, the dryest and hottest in Kansas, as it was in Oklahoma since 1901. A pitiless sun burned up the Indian corn and parched the native grass upon the prairies. Throughout this trying ordeal, our unfailing friend, the hardy and indomitable kafir, stood sentinel upon the prairies with the patient fortitude inherent in its nature, born of centuries of hardship upon the desert; it bided its time and silently waited for rain, springing triumphantly into new life with the first downpour from the heavens. Our prairie hay turned out less than a third of a crop and our alfalfa only a little better than half a crop. But notwithstanding this accumulation of calamities, we pushed back the impudent face of famine, cheated the hot winds, and whipped the drouth to a standstill with kafir corn."

The inherent drought resistant characteristics of sorghum have been exploited for centuries. The underlying basis of this adaptation to water stress is poorly understood. Success in breeding for tolerance to drought depends on a fuller understanding of basic plant physiological processes and their interactions with each other and with their environment.

Numerous isolated plant processes are affected by moisture deficits. Cell elongation is one of the most sensitive and immediate (McCree and Davis, 1974). Acevedo, Hsiao and Henderson (1971) showed that cell elongation is initially arrested and later resumes at a slower rate when stress was imposed on corn and sorghum.

A rapid decline in protein synthesis is another documented response to stress (Bardzik, Marsh and Havis, 1971). This appears to be closely correlated with polyribosome formation. Several investigators have found rapid reductions in polyribosome levels in stressed cells (Hsiao, 1970; Nir, Klein and Mayber, 1970; Rhodes and Matsuda, 1976).

Proline and betaine, two amino acids often implicated in osmoregulation, appear to be synthesized in response to stress (Boggess et al., 1976; Hanson and Scott, 1980). Changes in hormonal activity have also been observed following moisture deficits. These include increases in ABA (Wright and Hiron, 1969) and ethylene (Ben-Yehoshua and Aloni, 1974; Guinn, 1976, 1977). Decreased cytokinin concentrations in response to stress have also been observed (Itai and Vaadia, 1971).

Activity of the mitochondria is altered when stress is imposed. Normally reduced oxygen uptake is observed, however increased respiration has been reported (Nieman, 1962). Photosynthesis appears to be more seriously affected by stress than respiration (Nieman, 1962). As moisture is depleted from the soil, photosynthetic rates show a rapid decline before respiration is affected. Both photosynthesis and respiration are adversely affected by stress induced changes in leaf resistances, stomatal behavior, transpiration, and leaf temperature.

While numerous stress induced responses have been isolated and documented, little is known about how they interact in field environments to affect yield. An important consideration, now being investigated in wheat by Matsuda, Sarmadnia and Adjei (Personal Communication, 1980), is how moisture stress at specific developmental stages affects yield. As concluded by Christiansen (1979) "...there has been a lack of integration among basic research, whole plant response studies, and field testing, especially as related to interaction of environmental factors."

Sorghum is an extremely important food crop for much of the world and fortunately is regarded by most agriculturalists to be relatively drought resistant (Stout, Kannangara and Simpson, 1978). There is, however, wide variability in the germplasm. A vast range of responses were recorded when over 200 sorghum germplasm sources were grown on an irrigation gradient system at Yuma, Arizona (A. K. Dobrenz, Personal Communication, 1981). In addition to yield and growth differences, transpiration rates of plants grown with adequate moisture ranged from 45.0 to 10.6 μg H_2O cm^{-2} s^{1} and under stressed moisture conditions from 32.2 to 1.1 μg H_2O cm^{-2} s^{1}. Leaf diffusive resistances with adequate moisture went from 0.7 to 4.2 s cm^{-1} and showed a range of 2.3 to 44.4 s cm^{-1} in the stressed plots.

These data indicate wide genetic diversity of gas exchange rates in sorghum germplasm. How this variability is expressed in terms of transpiration and photosynthetic rates has been the subject of extensive research. Much of this work has focused on the role of the stomatal pores.

> "In furnishing the needs of plant metabolism (light, water, CO_2, nutrients) a leaf is faced with a dilemma: it must assimilate atmospheric CO_2, but at the same time it must minimize evaporative losses. Some regulatory system is clearly needed and specialized epidermal organs (stomata) fill this role." (Leopold and Kriedemann, 1975).

The stomata have been the subject of extensive research because of their role as a variable control point located immediately between the plant and the atmosphere. How their behavior is influenced by environments, both within and external to the plant, was summarized by Burrows and Milthorpe (1976).

Several external factors influence stomatal behavior. Stomata open in response to increasing light intensity over the entire sensible range. This response in sorghum was studied by Turner (1970, 1973). Temperature has numerous influences on stomatal activity, affecting both the metabolism and the water relations of the guard cell. Evidence supports the premise that guard cells are very responsive to external CO_2 levels. There are indications that conductance is decreased with increased wind velocity.

Factors internal to the leaf and guard cell also influence stomatal behavior. There is a range of high leaf water potentials over which there is no influence on stomatal aperture. Reductions below this range leads to a rapid closure at a critical level. This sudden fall in conductance over a narrow range of decreasing leaf water potentials is followed by a more gradual reduction in conductance with further decreases in water potential.

Other internal factors which influence stomatal behavior are hormone levels and nutrient status. Closure is promoted by abscisic acid and there are indications that cytokinins and giberellic acid promote opening. Potassium levels in the epidermis are critical for stomatal function.

That temperature affects stomatal behavior was not supported in work by Troughton and Slatyer (1969). They found stomatal apertures to be unaffected by temperatures ranging from 22.5 to 38^{o}C in oxygen free air. However, these results could very easily be an artifact of the anaerobic environment.

Much of the drought resistant quality found in sorghum has been ascribed to its stomatal behavior. Glover (1959) investigated the behavior of maize and sorghum stomata in response to moisture stress. Plants were subjected to varying lengths of severe moisture stress and evaluated for changes in conductance. They found that maize stomata failed to recover after a one week period of drought. While turgidity and appearance seemed normal, stomatal behavior was permanently altered. Sorghum stomata however fully recovered after two weeks of severe moisture stress. Glover states that this "...ability of stomata to recover from severe drought in some measure accounts for the superiority of sorghum as a grain crop in dry regions."

Sanchez-Diaz and Kramer (1971) compared maize and sorghum stomatal resistances by withholding water until the plants became severely wilted. Maize had lower resistances under well watered soil conditions. However, as stressful conditions developed, the maize stomata began to close at higher water potentials than did sorghum stomata. The stomatal resistances of both species returned to approximately those of the well watered checks soon after rewatering. The authors felt that one critical response difference was that the maize tissue lost significantly more of its water before the stomata fully closed than did the sorghum tissue. Sorghum had a water saturation deficit of only 29% as compared to 45% for maize at the lowest measured leaf water potentials (-12.8 and -15.7 bars for maize and sorghum, respectively). The ability of sorghum to minimize tissue water loss is characteristic of a drought resistant species.

Beadle et al. (1973) compared maize and sorghum responses to moisture stress and confirmed earlier findings that at lower leaf water potentials the two species respond differently. In maize they observed a rapid increase in stomatal resistance over a narrow range of water potential. Sorghum showed a more gradual response.

This buffered response found in sorghum stomatal behavior was confirmed by Stout and Simpson (1978). They determined that leaf diffusive resistances measurements indicated open stomata in both stressed and non-stressed plants. They concluded that under imposed stress conditions, stomatal closure was not interfering with the transpiration or gas exchange requirement. They attributed this response to reduced leaf water potential caused by osmoregulation.

Work by Jones and Turner (1978) disputed the concept that osmoregulation is the key to low diffusive resistances at low water potentials. The authors compared the responses of a drought sensitive (Shallu) and a drought resistant sorghum specie (RS-610) which were well documented in the literature (Blum, 1974; Blum and Ebercon, 1976; Henzell et al., 1976). Jones and Turner found no significant differences in leaf water potential and concluded that "...the superior responses of 'RS-610' over 'Shallu' in the drought tolerance tests applied by Blum (1974) appear to be due to varietal differences in factors other than leaf tissue water relations, such as rooting habit, conductance of water in the xylem, or desiccation tolerance."

This ability to maintain open stomata at a lower leaf water potential may partially help explain the superiority of sorghum under stressed environments. Shimshi and Ephrat (1975) found that "...wheat cultivars having wider stomatal aperture produced higher yields without consuming more water."

The effects of illuminance on stomatal opening in sorghum was reported by Pasternak and Wilson (1973). Leaf resistances in sorghum showed a continuous decrease when light was increased from 0 to 11,000 foot candles. Very similar responses were observed for all the sorghum genotypes they evaluated.

The stomatal diffusive resistances and leaf water potentials at various heights within a sorghum canopy are not constant (Teare and Kanemasu, 1972). They found the resistance of the lower leaves was usually higher than found in the upper leaves. The actual level of minimum resistance within the canopy varied with time of day. This was confirmed by the study of Brun et al. (1972), which reported that the lower leaves of a sorghum plant had stomatal resistances as much as ten times greater than upper leaves. Turner (1974) again observed the differences with respect to height. He also reported that the upper leaves developed lower leaf water potentials before increases in stomatal resistance were evident.

The relation of leaf stomatal resistances as a function of height in the canopy is related to leaf age and the stage of development (Frank, 1981). Constable and Hearn (1978) found that soil moisture deficits during grain filling were most detrimental to soybean yields. Inuyama (1977, 1978) found that stress induced high stomatal resistances affected yields more dramatically during the boot stage of growth (Vanderlip and Reeves, 1972). The reductions in yield when stress was imposed during vegetative, boot, or milk stages were 26.9, 61.2, and 4.3 percent, respectively. Very similar results were reported by Lewis, Hiller and Jordan (1974) who found yield reductions of 17, 34 and 10 percent for sorghum stressed in the vegetative, boot, and milk stages, respectively. Eck and Musick (1979) reported yield reductions of 27 and 12 percent when stress was imposed during boot and early grain filling respectively.

Kramer (1963) outlined some of the reasons why plants respond differently at a given degree of soil moisture stress. He relates that water deficits can affect almost every process occurring within a plant. Because individual processes respond differently to degrees of moisture stress, whole plant response must also respond differently. Fortunately, genetic variability for drought resistance exists in sorghum.

Blum (1974) found several drought response patterns in sorghum. Using Levitt's (1972) system of categorizing these patterns he was able to find genotypes with low diffusive resistances under moisture stress which Levitt defined as "drought avoidant (avoidance of low water potential)". At the other extreme he defined the genotype 'Shallu' as being "drought susceptible" because of its high diffusive resistance and corresponding low soil moisture extraction. The range of stomatal resistances under soil moisture stress for the 14 genotypes evaluated in 1971 averaged 3.1 to 20.2 s cm^{-1}.

Henzell et al. (1975) confirmed that genetic variability existed for stomatal behavior in response to moisture stress in sorghum. The authors observed a wide range of stomatal response to low soil water potentials in the 23 sorghum genotypes tested. The authors found that there was an inverse relation between stomatal sensitivity and the drought resistance qualities of the genotypes. Henzell et al. suggest that measurements of diffusive resistance might be used as a screening technique for drought resistance but added that "...this fact does not constitute proof that drought adaptation consists in a relatively insensitive stomatal apparatus and further work to decide this issue is required."

Genetic variability does not account for all stomatal response characteristics. McCree (1974) determined that a stressful environment can induce a "water stress hardening" effect in grain sorghum. Plants which were subjected to five cycles of moderate soil moisture stress and hot, dry atmospheric conditions actually developed less sensitive stomatal responses to low leaf water potentials.

Evidence shows that there is a wide range of variability in sorghum for stomatal sensitivity and behavior to drought stress. There is, however, little understanding of what the most desirable patterns are for a stressful environment. Turner (1979) states "...it has been shown that a diversity of morphological and physiological mechanisms enable crop plants to escape or tolerate water deficits. In assessing the importance of these mechanisms it is important to distinguish between those that allow a plant merely to survive drought and those that allow it to tolerate drought and continue to develop and produce a harvestable yield."

While stomatal sensitivity to leaf water potential appears to be a very important component of drought stress resistance in sorghum, it is not the only factor. As summarized by Henzell et al. (1976) it is not "...the only criterion by which to distinguish genotypes in regard to adaptation to drought conditions."

Transpiration is the evaporation of water by plants from cell surfaces and its loss through stomata, lenticels and the cuticle (Bidwell, 1979). The relationship between transpiration and dry matter production has been the subject of numerous studies.

DeWit (1958) found that when soil water supply fluctuated over the growing season, as occurs under dryland small grain production, there is a one-to-one relation between transpiration and the production of dry matter. He states "As for drought resistance, it is shown that the relation between transpiration and total dry matter production is not affected by the ability of the plant to withstand periods of drought. Instead, the amount of marketable products and the total amount of water which is transpired during the growing period, may depend to a large extent on this ability."

Arkley (1963) confirmed that this relationship existed. Hanks, Gardner and Florian (1969) measured a very close correlation between evapotranspiration and yields in sorghum (r^2 = .98). They conclude that under dryland conditions there is "...strong evidence that for grain sorghum, dry matter production is directly proportional to transpiration." Hill (1976) also found a positive correlation between transpiration rates and yield in a random-mating population of grain sorghum under stressed and normal soil moisture conditions. Hsiao and Acevedo (1974) suggest that this relation could be partially explained by reduction in photosynthetic assimilation when leaf resistances are high.

There are of course limits to the concept that a linear relationship exists between transpiration and dry matter production. Both DeWit (1958) and Arkley (1963) acknowledge that it only holds true when available water is limiting maximum yields. Hillel and Guron (1973) found that in maize the relationship had a lower limit; "A threshold evaporation of 250 to 300 mm was indicated below which production was negligible and above which production rose linearly with the amount of water applied."

Fischer and Kohn (1966) stress that "...rapid vegetative growth leads to increased moisture usage (evapotranspiration) early in the season, and that less soil moisture is available to sustain grain growth after flowering." This they feel would explain the "...common observation in cereal crops grown with limited moisture that high levels of vegetative growth may depress the grain yields." This would be in agreement with the findings that were reported earlier (Inuyama, 1977, 1978; Lewis et al., 1974; Eck and Musick, 1979).

Passioura (1972) demonstrated that plants which are grown on stored water have an advantage if they have restricted transpiration rates during vegetative growth. By conserving water early in development there will be more water available for grain filling. He suggests that it might be possible to breed for this trait by increasing a crop root resistance.

The superior response to drought found in sorghum has often been reported (Rawson, Turner and Begg, 1978; Burch, Smith and Mason, 1978; Constable and Hearn, 1978; Slatyer, 1955; Downes, 1970). Slatyer (1955) suggests that this is due to a well developed root system and very effective internal control over transpiration. Sorghum is able to maintain relatively high turgor at low soil water potentials and shows a slower rate of decrease in turgor. By maintaining positive turgor, sorghum can maintain its growth rate under moderate stress.

Attempts to equate photosynthetic rates with yield have been numerous and with inconsistant conclusions. The concensus has been that the two variables are not well correlated under normal growing conditions. Heichel and Musgrave (1969) measured the photosynthetic rates of a genetically diverse population of maize plants under field conditions and found threefold differences. However they failed to find correlations between these rates and either grain or dry matter yields. Similar findings have been reported in other crops (Nelson, Asay and Horst, 1975; Irvine, 1975).

Mauney, Fry and Guinn (1978) and Mauney et al. (1979) evaluated the relationships between photosynthetic rates and the growth and fruiting of sorghum. They determined that selecting for a high carbon exchange rate would not effectively increase yields.

There have however been some studies which have correlated photosynthetic rates with yield (Simpson, 1967). Shimshi and Ephrat (1975) working with irrigated spring wheat genotypes found photosynthetic activity to be positively correlated with both crop growth rate during grain filling and with yield. Fisher et al. (1981) also found that photosynthesis was "...positively correlated with crop growth rate during grain filling ($r = 0.46$, significant at the 0.01 level) and with yield ($r = 0.45$, significant at the 0.01 level)." However they "...conclude that this relationship reflected correlated responses to variation in days to anthesis, and probably sink strength during grain filling, rather than implying that increased photosynthetic activity was a primary cause of increased yield."

The observation that photosynthetic rates are poorly correlated with dry matter production seems to be valid at least under moderate environments. However Sullivan and Ross (1979) emphasize that "...when stress is involved, ability of plants to continue a relatively high rate of photosynthetic activity may well contribute to yield."

The influence of water stress on photosynthesis has been extensively reviewed (Dastur, 1925; Slavik, 1963, 1965; El Sharkawy and Hesketh, 1964; Jones, 1973; Turner et al., 1978; Berry and Bjorkman, 1980; Boyer, 1970, 1976). These studies conclude that photosynthesis is very sensitive to reductions in leaf water potential.

Kaul (1974) and Kaul and Crowle (1974) found differing degrees of photosynthetic tolerance to desiccation tolerance in drought stressed wheat cultivars. They "...proposed that single P_N-measured on slowly stressed plants could serve as a technique for selecting the highest yielding cultivars."

Wilson, van Bavel and McCree (1980) determined that water deficient sorghum plants had reduced rates of substrate production by way of photosynthesis. Substrate production per unit leaf area was reduced approximately 36% when leaf water potential was decreased from -1 to -24 bars.

The ability of sorghum to persist under moisture stress was observed by Shearman et al. (1972). They found that carbon dioxide uptake decreased to nearly the compensation point at leaf water potentials of -25 atmospheres. At this point leaf resistances were extremely high. They determined that the activity of phosphoecol pyruvic carboxylase remained comparatively high with increased water stress and concluded "...leaf resistance appears to be more limiting to CO_2 uptake with increasing water stress than does enzyme activity."

As mentioned previously, some developmental stages are more sensitive to moisture stress. There appears to be critical periods when reduced photosynthesis can more dramatically affect yield. Thorne (1965) found that in most cereal grains the photosynthate produced prior to anthesis contributes only a small proportion to the grain filling process. In sorghum, Fischer and Wilson (1971a) determined that only 12% of the carbon assimilated in the pre-anthesis period could have gone to grain production.

Fischer and Wilson (1971b) also found that during sorghum grain filling, 93% of the photosynthate needed was produced in the head and upper four leaves. The head contributed only 18%. The flag leaf was the most important contributor of photosynthate of the four upper leaves.

The relative importance of photosynthesis by sorghum heads (Easton and Sullivan, 1969; Pasternak and Wilson, 1976) can be greatly increased with severe stress. Pasternak and Wilson (1976) determined that "the photosynthetic activity of heads increased from about 12% of the total in a well watered plant to about 88% for a plant at high moisture deficit."

Simply maintaining a high level of photosynthesis under stress will not insure increased productivity. Watson (1952) reasoned that an adequate rate of carbon assimilation must be coupled with an efficient partitioning. As summarized by Lawes and Treharne (1971) "...varieties may have a high potential photosynthetic activity per unit area of leaf and yet not produce a high dry matter yield because other factors, either genetic or environmental, limit the utilization of this potential."

Under conditions of water stress it has been well documented that the proportion of photosynthate diverted to root development is increased (Larchner, 1975; Caldwell, 1976; Fischer and Turner, 1978; Mayaki, Stone and Teare, 1976; Teare et al., 1973) and that the root to shoot dry weight ratio is also increased. This increase in the root to shoot dry weight ratio in response to stress has been observed in sorghum and the magnitude of this increase appears to be correlated with the relative drought resistance of sorghum genotypes (Bhan, Singh and Singh, 1973; Kaigama et al., 1977; Nour and Weibel, 1978). Jordan, Miller and Morris (1979) concluded "...that sufficient variability exists in shoot to root growth characteristics to warrant further study on the problem of systematic improvement of sorghum root systems which may allow superior crop performance in specific environments."

This morphological response to stress does not cause a change in photosynthetic rate, but the price of producing more roots is paid by a corresponding reduction in new photosynthetic leaf development (Fischer and Turner, 1978). Both total leaf area and leaf area expansion rates are important in determining final yield (Yoshida, 1972; Krishnamurthy et al., 1973; Wilson et al., 1980).

Potter and Jones (1977) stress that the rate of "...partitioning of photosynthate into new leaf area is an important component on growth." They determined that this leaf area partitioning is much better correlated to growth than the net assimilation ratio. They conclude that "it seems reasonable that the relative growth rate of a species could be enhanced if traits for high photosynthesis were combined with traits for high leaf area partitioning."

The literature supports the concept that photosynthetic rates alone may not be limiting to crop yields. Under conditions of moisture stress however, superior rates coupled with efficient photosynthetic partitioning may have considerable importance.

If more drought resistant sorghum genotypes are to be developed, the genetic variability which has been observed must be manipulated. Fortunately significant heterosis is expressed by most sorghum hybrids (Argikar and Chavan, 1957; Arnon and Blum, 1962; Beil and Atkins, 1967; Kambal and Webster, 1965, 1966; Niehaus and Pickett, 1966; Quinby, 1963; Patanothai and Atkins, 1971; Arkin and Monk, 1979).

Superior yields have been reported for sorghum in single cross hybrids grown under adequate soil moisture conditions (Walsh and Atkins, 1973; Blum, 1973; Patanothai and Atkins, 1974). Quinby (1963) reported yield increases of 100% in hybrids as compared to either parent. He attributes faster cell division to be the basis of heterosis in sorghum. He later (Quinby, 1970) stated "the important difference between parents and hybrids appeared to be a difference in growth rate in favor of the hybrid that began in the embryo and finally resulted in larger panicles in the hybrids."

This growth rate advantage was emphasized by Gibson and Schertz (1977). They found the growth rate of the hybrid was greater than that of either parent from emergence to panicle initiation. Kirby and Atkins (1968) found that average grain yields for 24 F_1 hybrids were "...122% of the mid-parent values, with a range of 106 to 147% among individual hybrids." They also found more grains per head in the hybrids.

Significant heterosis has been found in sorghum hybrids for length of seminal root, growth rate of adventitious roots and root volume (Blum, Jordan and Atkins, 1977). Heterosis has also been observed under limited soil moisture conditions. Arnon and Blum (1962) found a 20 to 28% increase in yield of the best hybrids over the best self-pollinated variety. In the plots which received only partial irrigation, a 67% advantage in yield was measured.

The USDA (1977) demonstrated that drought tolerance could be inherited in sorghum. They also found that genotypes selected for drought tolerance "...did not produce the highest yields in a season when there was little drought stress."

To take full advantage of the potential benefits of hybrids, new selection and breeding techniques are required. Hanson and Nelson (1980) suggest that we can no longer rely on the continued availability of cheap fossil fuel energy to modify the crop environment and that we need "...research and development aimed at fitting crop plants to fluctuating drought-prone environments." They emphasize that research must focus on both drought resistant and drought sensitive genotypes to determine underlying physiological processes.

The physiological response may also be modified by the degree of stress imposed. Hanson (1980) using data collected by the sorghum breeding program at the International Crops Research Institute for the Tropics (1977) evaluated a number of sorghum entries which had been subjected to severe, mild or no drought stress treatments. The mild stress reduced yields of all genotypes by about 20% and a very high correlation ($r = 0.94^{***}$) remained between the mild and no stress treatments. Severe stress yields however failed to correlate closely with the no stress yields ($r = 0.555^{***}$). The author suggest that there are different mechanisms for adaptation to mild versus severe drought stress.

A crop suited to fluctuating environments has the ability to give better than average yields over a wide range of conditions (Reich and Atkins, 1970). Finlay and Wilkinson (1963) developed a regression analysis technique to measure "...the ability of some crop plants to perform well over a wide range of environments. Their technique can be used to evaluate a genetically diverse group of plants grown at numerous locations with dissimilar environments. Individual variety yields are regressed on the overall means at the individual location. The regression coefficient and mean variety yield across all environments are used to identify the adapted and stable genotypes.

Eberhart and Russell (1966) improved upon the regression approach by regarding deviation from the regression line as an important aspect of phenotypic stability. They use the slope and r^2 values as stability indices. If two varieties have equal slopes, the one with the lower r^2 is considered less stable.

The Finlay and Wilkinson technique has been used to measure "...progress in developing wheat varieties with both improved stability of performance and high yield potential" (Johnson, Shafer and Schmidt, 1968). Keim and Kronstad (1979) studied dryland adapted winter wheat and found "the degree of association of drought resistance and wide adaptation have implications in breeding to combine both traits in a single cultivar." Additional research has used the regression technique to analyze genotypic adaptation (Joppa, Lebsock and Busch, 1971; Busch, Hammond and Frohberg, 1976; Knight, 1970; Hardwick, 1981; Campbell and LaFever, 1977). It has been used to measure stability in sorghum (Jowett, 1972; Jika, St. Pierre, and Denis, 1980).

The purpose of the present study was to further evaluate the effects of moisture stress on sorghum photosynthesis, transpiration, diffusive resistance, leaf temperature and dry weight partitioning. Physiological responses were evaluated on six hybrids and their parents over two growing seasons. Analyzing responses under both stressed and non-stressed moisture conditions gives a better understanding of stress physiology in sorghum.

MATERIALS AND METHODS

Field research involving the physiological response of sorghum hybrids and their parents to moisture stress was conducted during 1980 and 1981 at the U.S.D.A. Soil Conservation Service Plant Materials Center in Tucson, Arizona. The soil was a Comoro sandy loam (course-loamy, mixed calcarious, thermic, Typic Torrifluvent) which had been fertilized with 60 kg ammonium phosphate/ha.

Seed was obtained from Dr. Bruce M aunder of the DeKalb Seed Company in Lubbock, Texas. Four hybrids and their respective parents were evaluated in 1980. The two superior hybrids from 1980 and two new hybrids were planted along with their respective parents in 1981.

The experimental design was a split plot with three replications. Germplasm entries were assigned to subplots. Subplots were five rows with 50 cm spacing. The subplots were 7.6 meters in length. All evaluations were taken from the center three rows allowing the outer rows to serve as buffers between subplots. Irrigation treatments were imposed on the main plots. Dikes were formed around main plots to allow for differential flood irrigation.

Plantings were made on 5/12, 1980 and 5/14, 1981 in moist soil which had been irrigated to field capacity. The field was planted with a two row precision cone planter at a rate of 100 seed per 7.6 m. All plots were flood irrigated immediately after planting.

After emergence the field was thinned to a uniform stand (approximately 10 cm between plants). During stand establishment, the entire field was flood irrigated when 50% of the available soil moisture was depleted. After reaching the five leaf stage (Vanderlip, 1972; Vanderlip and Reeves, 1972) the low moisture main plots received no further irrigation. The irrigated main plots subsequently had water supplied through a 10 cm aluminum pipe. Moisture depletion was evaluated with a Campbell Pacific Nuclear Corporation Model 503 neutron probe. In 1980 all plots received 306 mm of water from the time of planting until the five leaf stage. In addition to the preplant irrigation, total moisture received by the irrigated and non-irrigated plots over the growing season was 1543 and 476 mm, respectively. In 1981, 612 mm of water were applied to all plots through the five leaf stage of development. In addition to the preplant irrigation, total moisture received by the irrigated and non-irrigated plots over the growing season was 1558 and 694 mm, respectively.

At the two leaf stage, atrazine (2-chloro-4-(ethylamino)-6-ispropylamino-s-triazine) was applied for weed control at 0.8 kg ha^{-1} active ingredient (Heathman, 1972). Insects were controlled with granular diazonon (0,0-diethyl 0-(2-Isopropyl-4-methyl-6-pyrimidyl) phosphorothioate) spread at a rate of 1.0 kg ha^{-1}. After the five leaf stage when the irrigation treatments were established, physiological measurements were made at weekly intervals. The repeated measurements included determinations of apparent photosynthesis, transpiration, diffusive resistance, leaf temperature and ambient temperature. All physiological measurements were made simultaneously.

Apparent photosynthetic rates ($mgCO^2$ dm^{-2} hr^{-1}) were determined using the methods of Clegg and Sullivan (1975) and Sullivan, Clegg and

Bennett (1976). These measurements were made between 10:00 a.m. and 2:00 p.m. except for one day each year when early morning and late afternoon measurements were performed. A small plexiglass chamber (2.2 ℓ) was sealed around the central portion of the upper most fully expanded leaf blade. A small battery driven fan inside the chamber insured adequate circulation. Two rubber septa mounted on the side of the chamber allowed gas to be sampled with 6 ml syringes. After the chamber was sealed on the leaf and the gasses allowed to circulate for several seconds, a gas sample was taken with the first syringe. The second syringe was pulled 30 or 60 seconds later. The two coded syringes from each plant sampled were returned to the laboratory for analysis. The leaf area within the chamber was estimated by measuring the width of the blade on either side of the chamber and multiplying the average of these measurements times the inside length of the chamber.

The CO_2 concentration differences in the two syringes taken from each plant were measured using a Beckman model 865 infrared gas analyzer as described by Clegg, Sullivan and Eastin (1978). Five millileters of the gas from the photosynthetic chamber was injected from the syringe into a nitrogen carrier gas flowing (1 ml min^{-1}) through the analyzer (Fig. 1). The peak output was measured with a Heath-Schlumberger model SR-205 strip chart recorder. The system was calibrated with standard gases of known CO_2 concentrations. The differences in CO_2 concentrations between the first and second syringe taken from each leaf was a measure of CO_2 uptake.

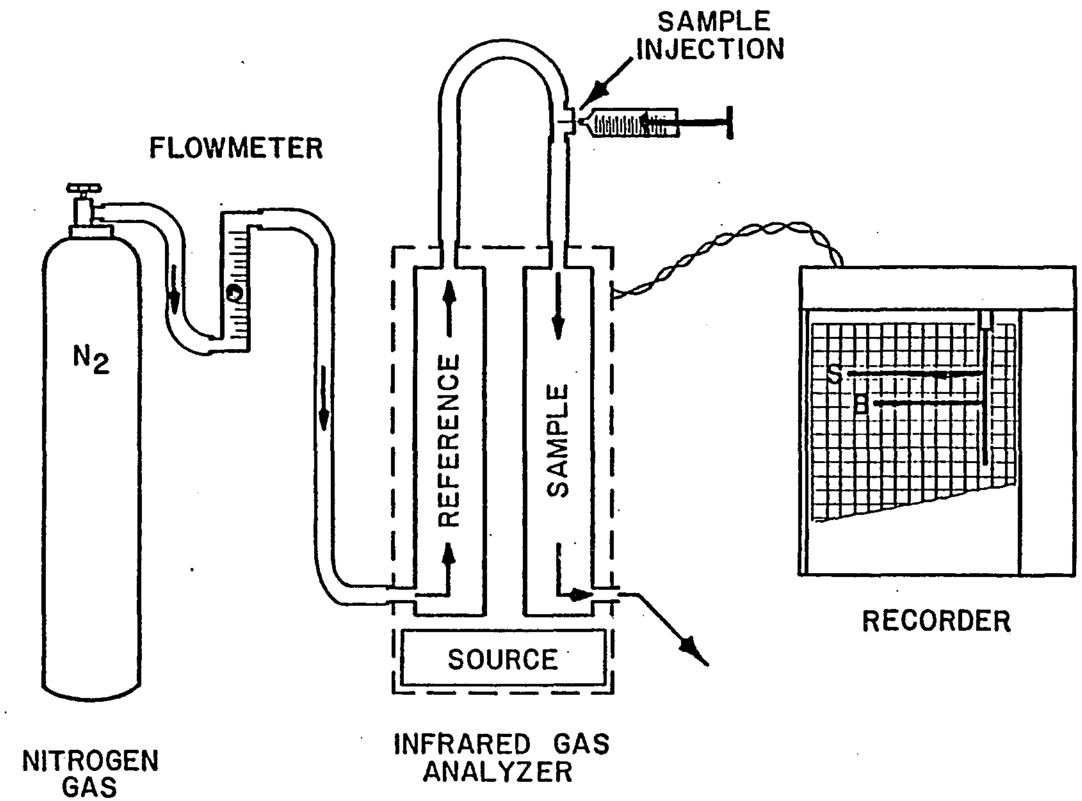

Fig. 1. Diagram of the carbon dioxide measurement system using the syringe technique described by Clegg, Sullivan and Eastin (1978).

A modification to the system was made during the second season. A Fluke model 8024A digital multimeter with a peak hold function was wired in parallel with the strip recorder. The peak hold function provides a short term memory which stores the maximum voltage output from the analyzer. Use of the digital multimeter simplified the collection of data. Once the CO_2 concentrations had been determined, apparent photosynthesis on a leaf area basis was calculated using the method described by Musgrave and Moss (1961).

A LiCor model LI-1600 steady state porometer was used to measure transpiration ($\mu g\ cm^{-2}\ s^{-1}$), diffusive resistance ($s\ cm^{-1}$), leaf temperature (C) and ambient temperature (C). This instrument was first described by Beardsell, Jarvis and Davidson (1972). The porometer measurements were made concurrently with the measurements of apparent photosynthesis.

Stomate densities of leaves from plants grown under adequate moisture were determined in 1980 and 1981 using impressions made with cellulose acetate. The stomata in three separate fields were counted using a magnification of 450 X.

Dry weight distribution into roots, stems and leaves during the first five weeks of growth was evaluated in 1981. In a border adjacent to the main experiment, three single row replicates of each entry were planted. Plots were 10 meters in length with 50 cm spacing arranged in a randomized complete block design. Irrigation water was supplied when approximately 50% of the available soil moisture was depleted. One week after planting and the four subsequent weeks, 10 plants were dug from each plot. Care was taken to obtain as much root tissue as possible. The plants were separated into leaves, stems, and roots. After the leaf area had been measured, all three components were dried and then weighed. Leaf area partitioning was evaluated using the methods of Potter and Jones (1977).

Due to severe problems with birds eating the grain, it was necessary to bag inflorescences at anthesis to obtain estimates of yield (Broadhead, 1979). Approximately 20 bagged heads were collected from each plot and thrashed. Grain weights from these heads were used to provide an approximation of actual yields.

The analysis of the data for photosynthesis, transpiration diffusive resistance and temperature differential (ambient temperature - leaf temperature) required a method which would effectively measure the genotype - environment interactions. The regression analysis technique of Finlay and Wilkinson (1963) was found to be effective. The response of an individual entry to the response of a larger population is compared. The regression coefficient (b) and the seasonal mean ($\bar{x}$) response of each entry were used to characterize the genotype - environment interactions and to identify those with superior response over a wide range of conditions.

By definition the average phenotypic stability for a group of entries is b = 1.0. Deviations from the mean response are interpreted as an indication of reduced stability. If two entries have similar regression coefficients, the one with the higher mean response is considered superior.

Eberhart and Russell (1966) included the unexplained deviations from the regression line (r) as a second index of stability. If two entries have equal regression coefficients (b), the one with the higher r value would be more stable.

In this study the regression analysis technique was employed to make numerous comparisons. Thirteen measurements in 1980 and fourteen measurements in 1981 at the two moisture levels, resulted in 26 and 28 data points per regression line for the two years, respectively. The individual hybrids and their parents were analyzed independently. The four hybrids in 1980 and the four hybrids in 1981 were evaluated against their mean responses. The two hybrids which had been included in both years of this study were evaluated with their parental lines over a two year period. The results were plotted on the University Computer Centers Calcomp plotter.

RESULTS AND DISCUSSION

Mean responses from the 1980 and 1981 seasons for the temperature differential (ambient temperature minus leaf temperature), leaf temperature, diffusive resistance, transpiration, and apparent photosynthesis for the hybrids and their respective parents under both irrigation treatments show superior responses from the hybrids in many cases (Fis. 2, 3). The range of response for apparent photosynthesis is consistent with those reported for sorghum by Beadle et al. (1973). Under conditions of high leaf water potential and high light intensity, the authors measured rates of over 50 $mgCO_2\ dm^{-2}\ hr^{-1}$. Beadle et al. (1973) also measured transpiration rates in sorghum very similar to those presented here. Their highest rate was about 25.5 $\mu g\ cm^{-2}\ s^{-1}$ as compared to the 26.0 $\mu g\ cm^{-2}\ s^{-1}$ reported here. Brun et al. (1972) reported that over a growing season, diffusive resistances in sorghum ranged from 1.25 to 5.60 $s\ cm^{-1}$. Teare et al. (1972) found a range for leaf diffusive resistance of 1.0 to 7.0 $s\ cm^{-1}$. The mean response reported in this study ranged from 1.16 to 4.81 $s\ cm^{-1}$ which is consistent with earlier findings.

Relatively consistent hybrid vigor is evident in 1980 for most of the physiological measurements made on the four hybrids and their respective parents under both the dry and wet irrigation treatments (Fig. 2). Hybrid 4 exhibited heterosis for all five physiological responses under both irrigation levels. It had higher rates of

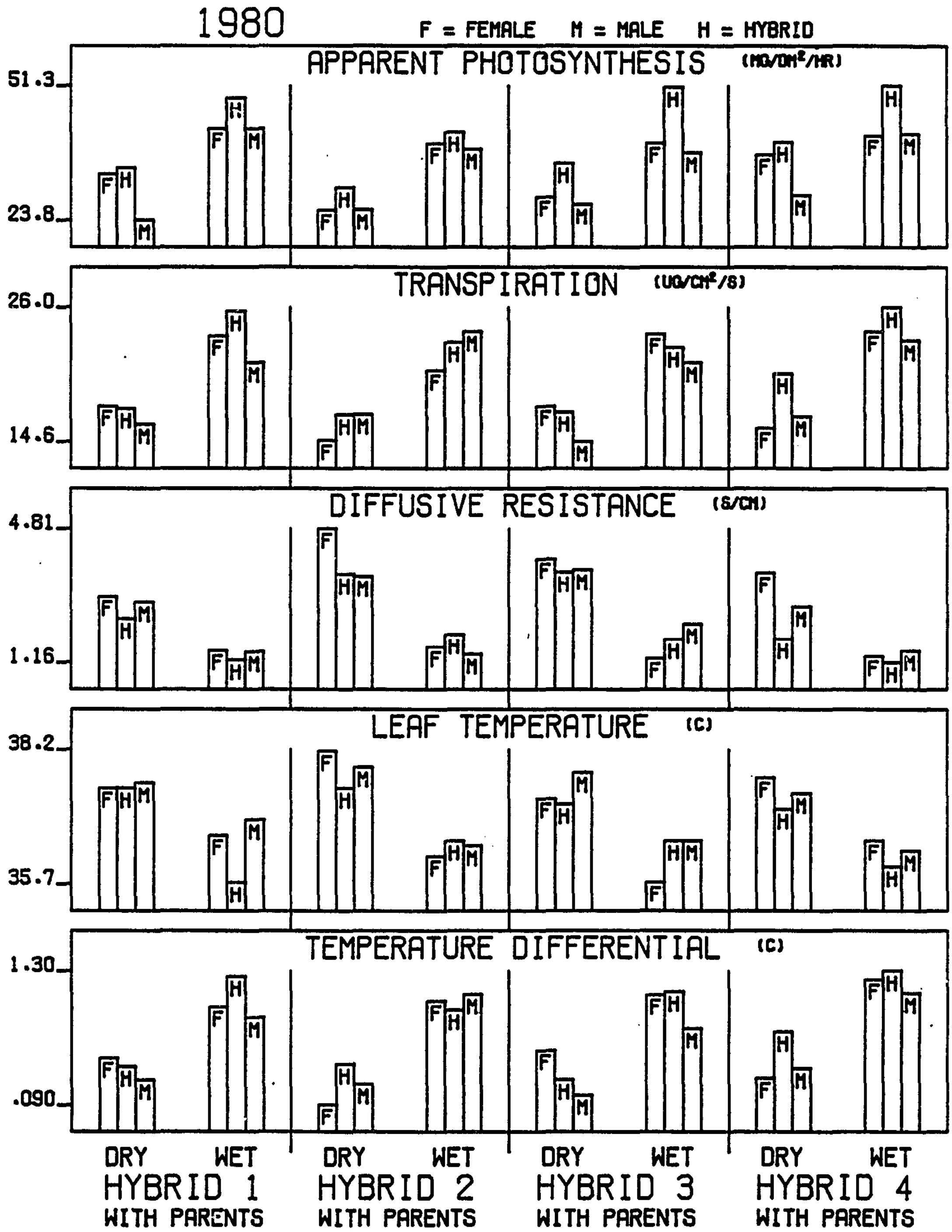

Fig. 2. Seasonal mean responses for apparent photosynthesis, transpiration, diffusive resistance, leaf temperature, and temperature differential for four hybrids and their respective parents grown under dry and wet soil moisture conditions in 1980.

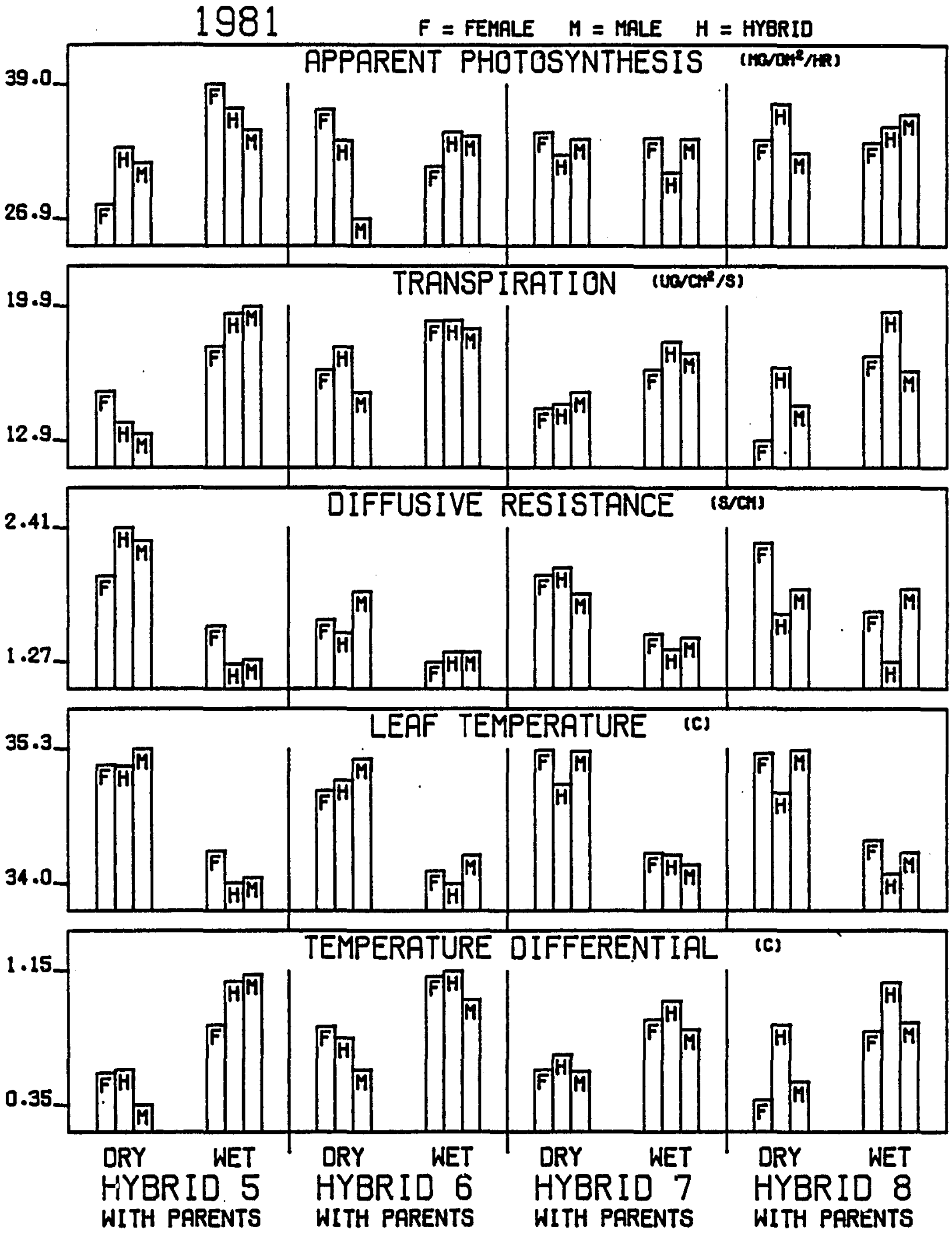

Fig. 3. Seasonal mean responses for apparent photosynthesis, transpiration, diffusive resistance, leaf temperature, and temperature differential for four hybrids and their respective parents grown under dry and wet soil moisture conditions in 1981.

apparent photosynthesis and transpiration and a greater temperature differential. Both diffusive resistance and leaf temperature were lower in hybrid 4 compared to either of its parents.

Hybrid 1 showed heterosis under adequate moisture conditions for all five physiological characteristics. In the stressed plots; however, responses were more inconsistent. Hybrids 2 and 3 displayed extremely variable results regardless of irrigation treatments with the exception of apparent photosynthesis. Both of these hybrids had superior apparent photosynthetic rates under both irrigation levels. All four hybrids displayed heterosis for apparent photosynthesis at both irrigation levels. No other consistent physiological responses for all of the hybrids were observed.

Due to their superior responses in 1980, hybrids 1 and 4 were evaluated with their respective parents in 1981. Hybrids 1 and 4 were assigned the codes 5 and 8 respectively in 1981. Hybrids 6 and 7 and their respective parents were two new germplasm sources. Seasonal mean responses in 1981 reveal fewer heterotic responses (Fig. 3).

The consistant heterosis observed for apparent photosynthesis in 1980 was not evident in 1981. Hybrids 5 and 8 did display superior rates under the dry moisture conditions. There was a much narrower range of mean apparent photosynthetic rates in 1981 (26.9 to 39.0 mg $dm^{-2}hr^{-1}$) as compared to 1980 (23.8 to 51.3 mg $dm^{-2}hr^{-1}$). This may be explained in part by the lower leaf temperatures in 1981. The maximum mean leaf temperature in 1981 (35.3 C) was less than the minimum temperature in 1980 (35.7 C).

Hybrid 8 (hybrid 4 in 1980) again showed heterosis for transpiration, diffusive resistance, leaf temperature, and temperature differential under both irrigation treatments. Hybrids 5, 6, and 7 failed to display consistant hybrid vigor.

The effects of available soil moisture had a pronounced effect on physiological characteristics during both years of this study (Figs. 2, 3). For each of the germplasm sources grown under low soil moisture conditions, transpiration and temperature differential were reduced while diffusive resistance and leaf temperature were increased. Apparent photosynthetic rates were consistantly lowered by soil moisture stress in 1980 and for hybrid 5 and its parents in 1981.

These comparisons of seasonal mean responses from the hybrids and their respective parents provide useful information on the average responses for the individual genotypes. Comparing mean responses from the two irrigation treatments gives some indication of genotypic stability but fails to adequately resolve response characteristics across a wide range of environmental conditions. The regression analysis technique developed by Finlay and Wilkinson (1963) is a better approach for the identification of genotypes which are adapted to a wide range of environmental conditions. In this study, numerous comparisons were made using this method (Figs. 4 to 27). Each of these individual regression lines compares the response of the individual genotypes, as indicated by the legend, against the mean response of all the genotypes being compared. By combining the physiological responses from each of the weekly measurements along with the results

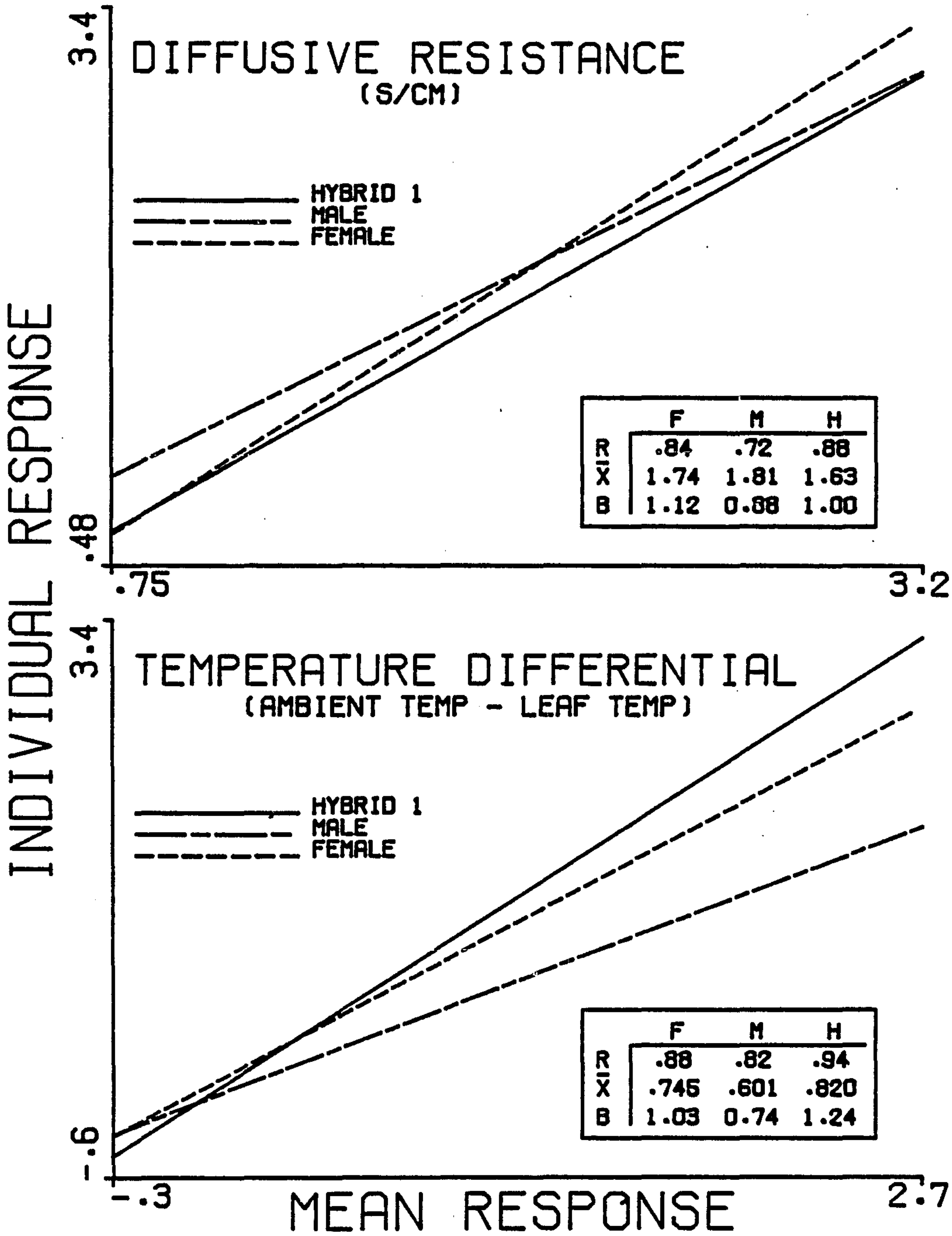

Fig. 4. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 1 (H) and its male (M) and female (F) parents.

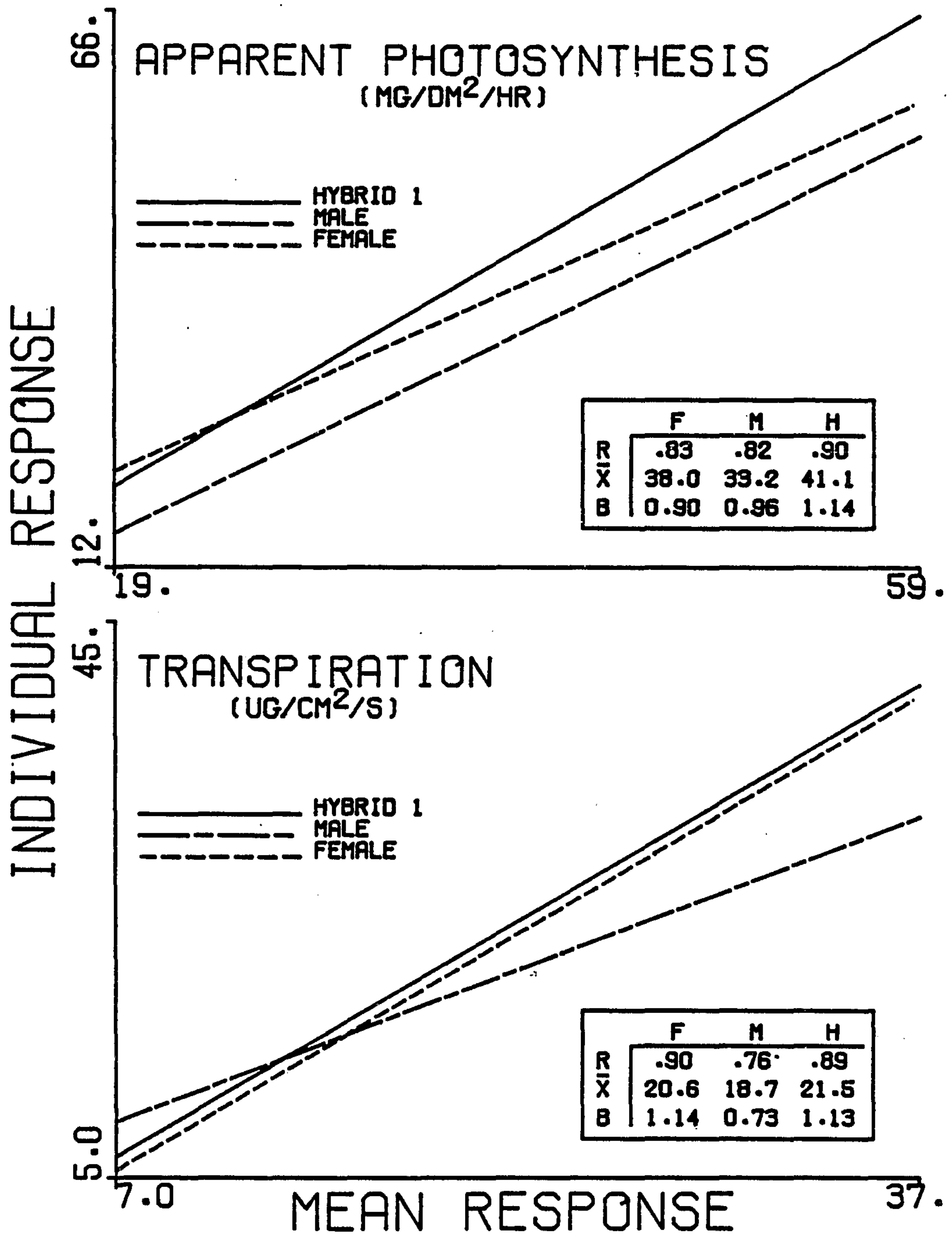

Fig. 5. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 1 (H), and its male (M) and female (F) parents.

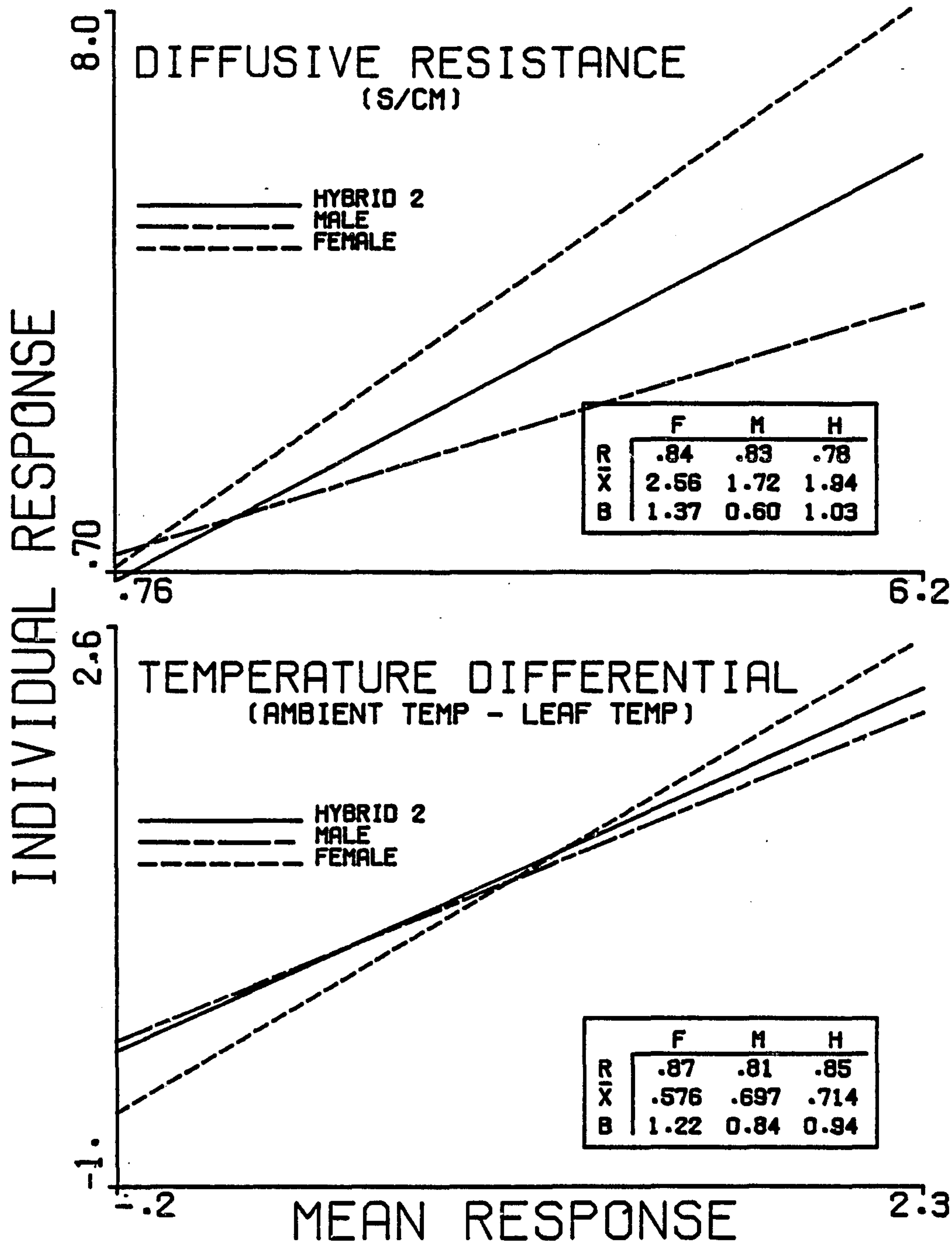

Fig. 6. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 2 (H) and its male (M) and female (F) parents.

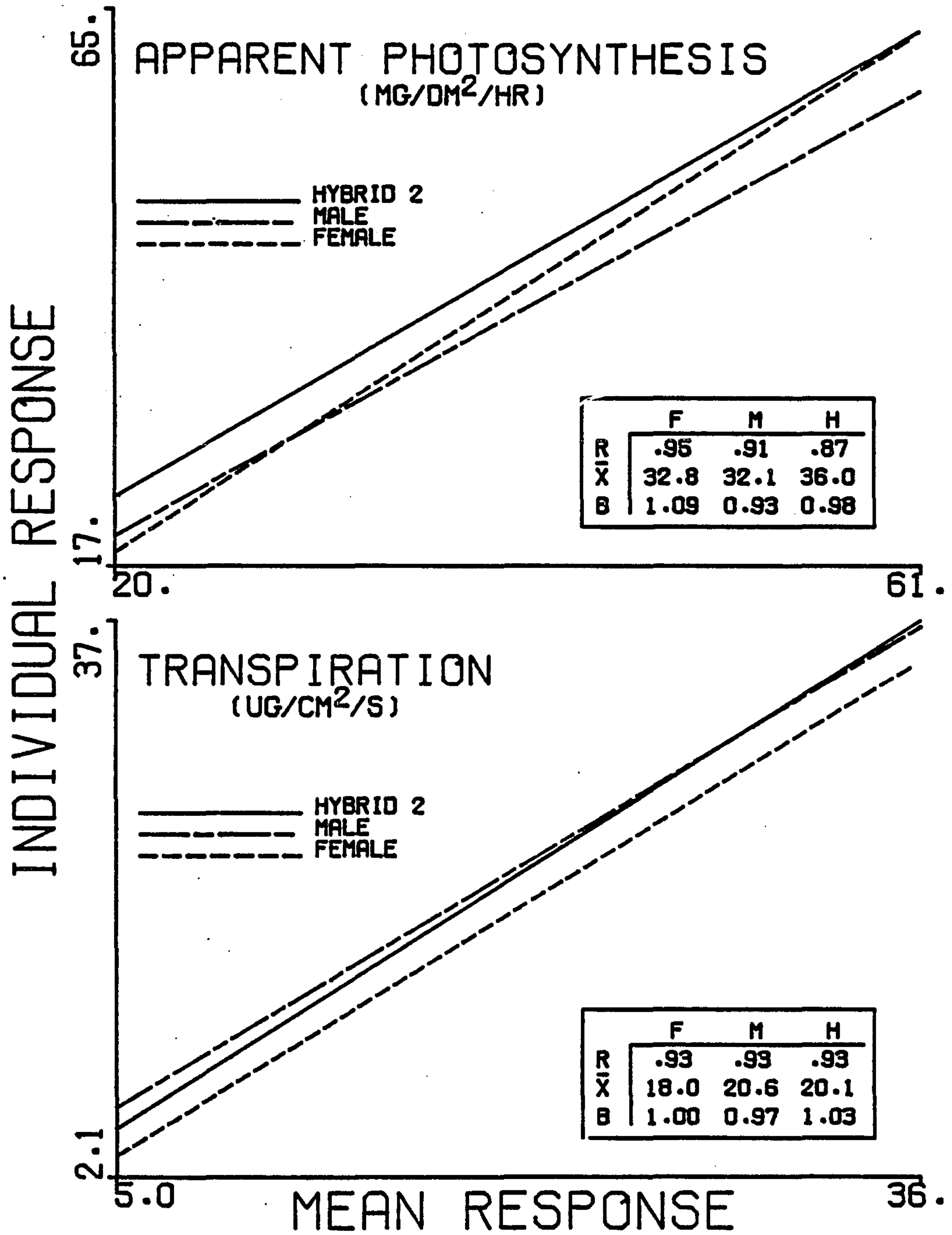

Fig. 7. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 2 (H), and its male (M) and female (F) parents.

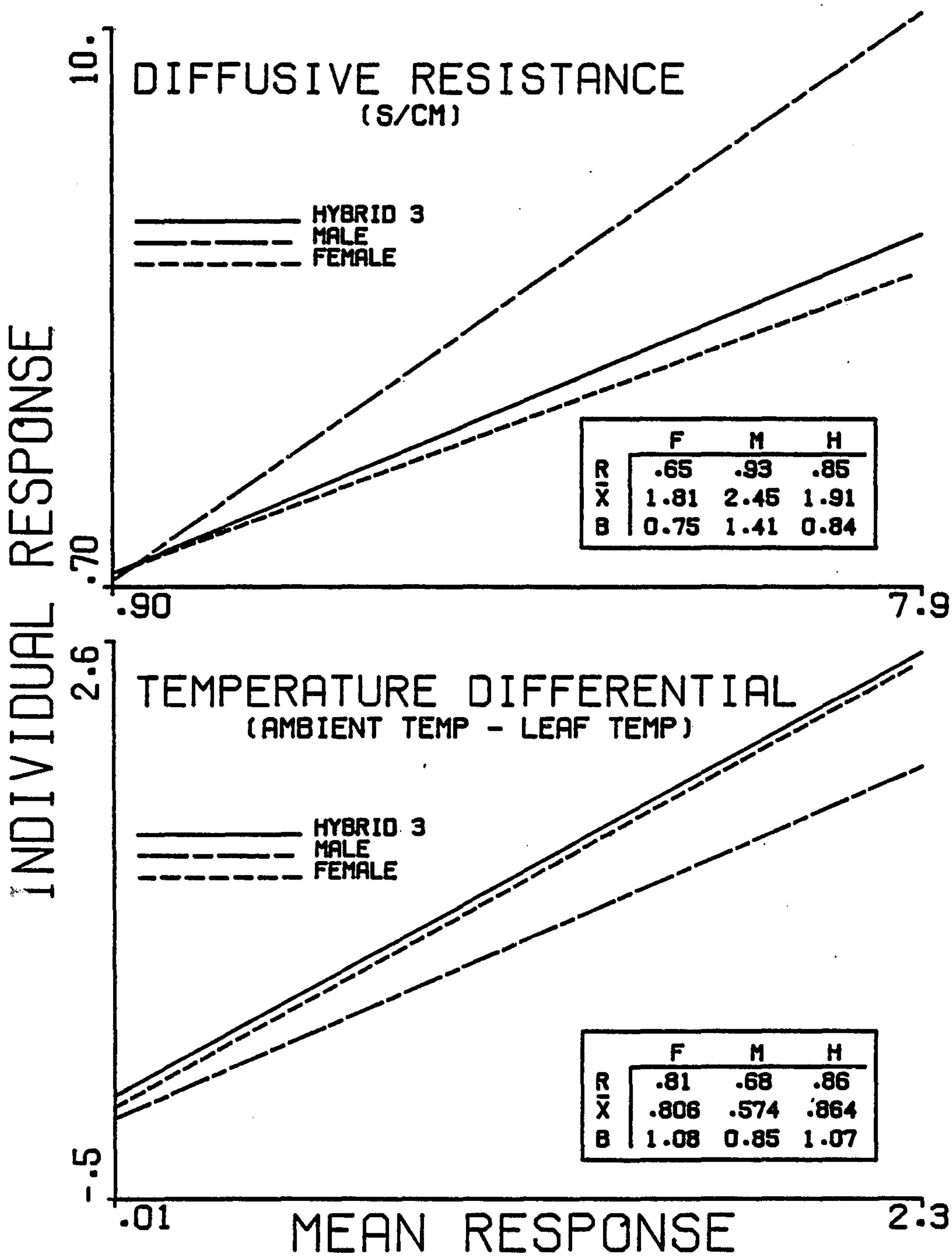

Fig. 8. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 3 (H) and its male (M) and female (F) parents.

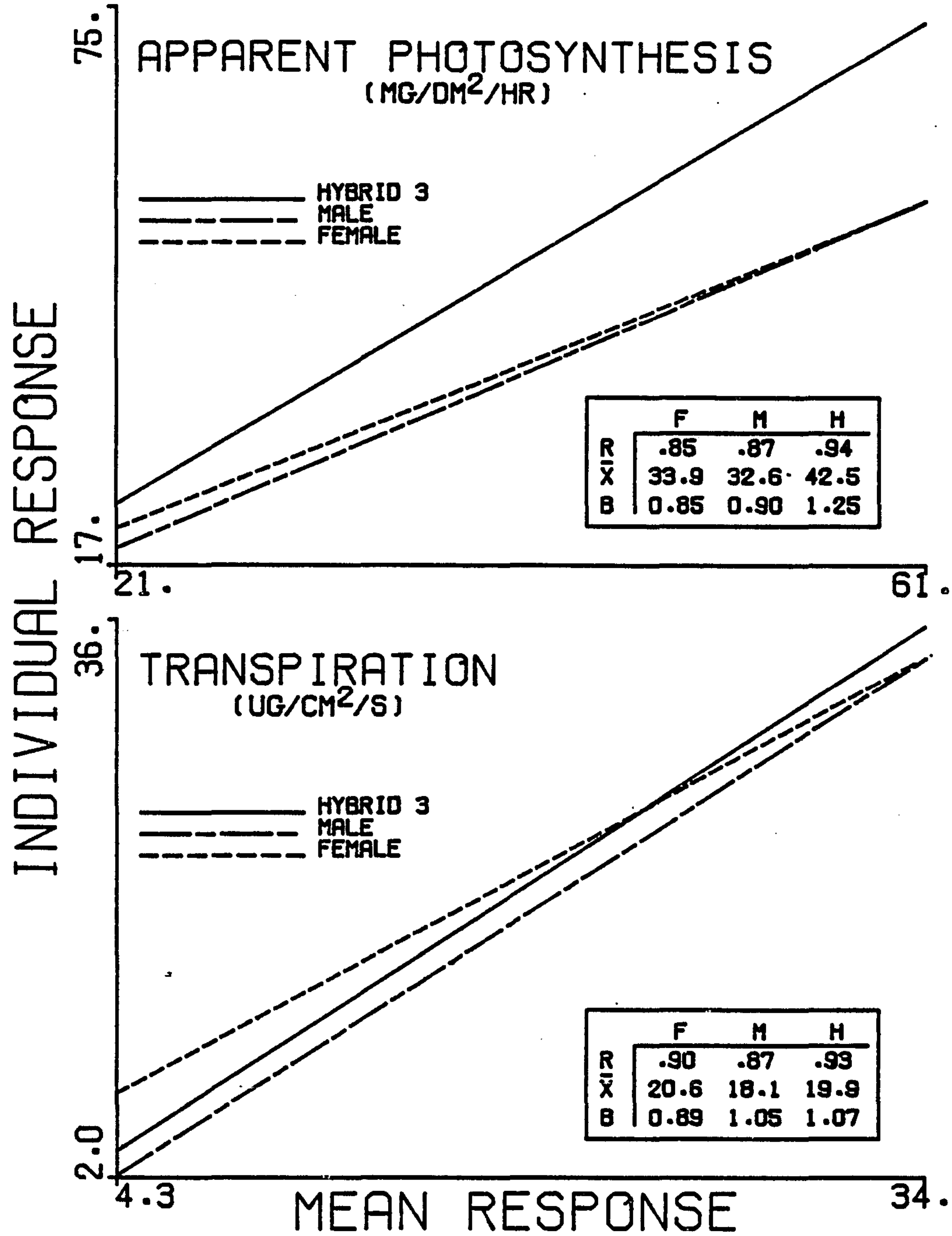

Fig. 9. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 3 (H), and its male (M) and female (F) parents.

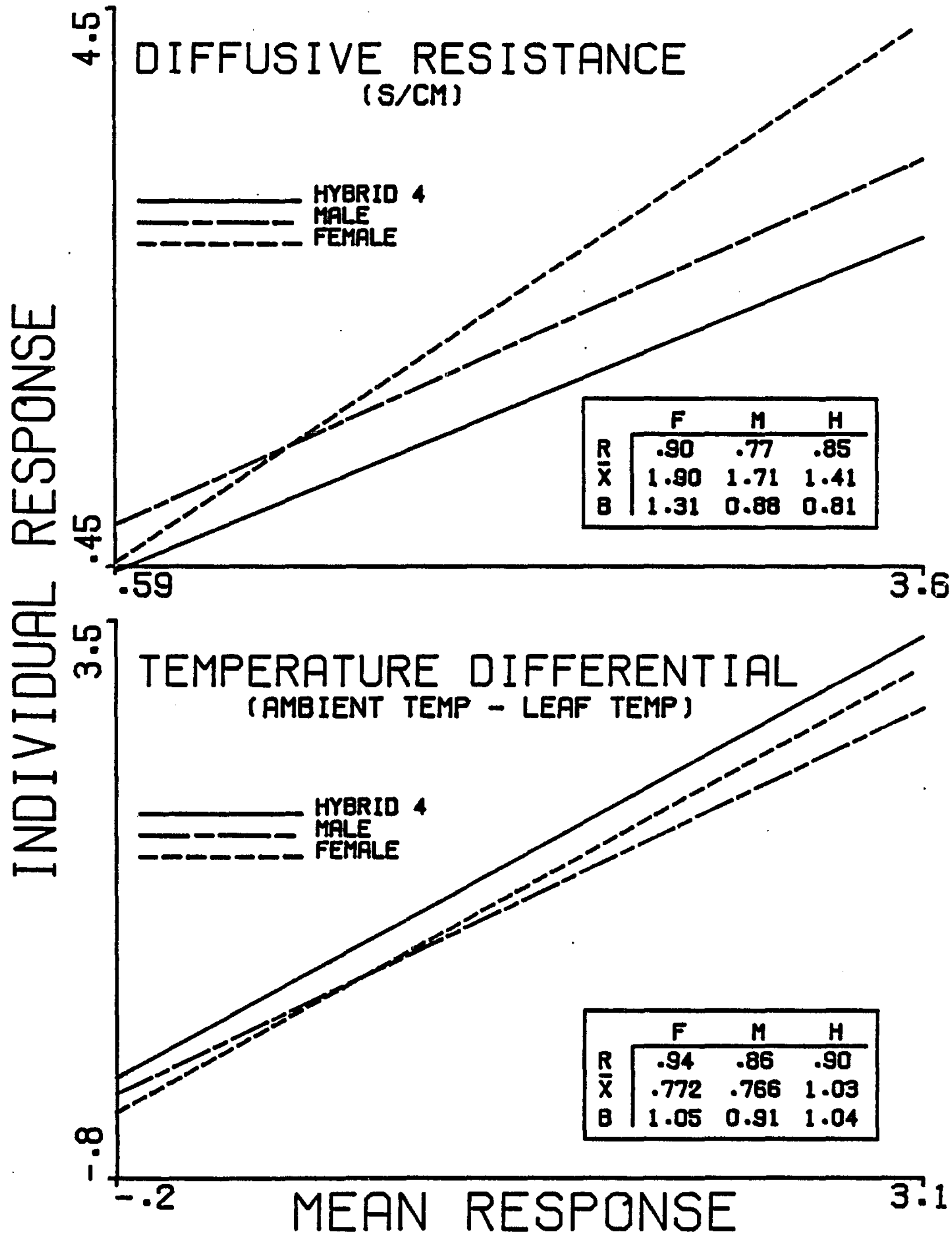

Fig. 10. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 4 (H) and its male (M) and female (F) parents.

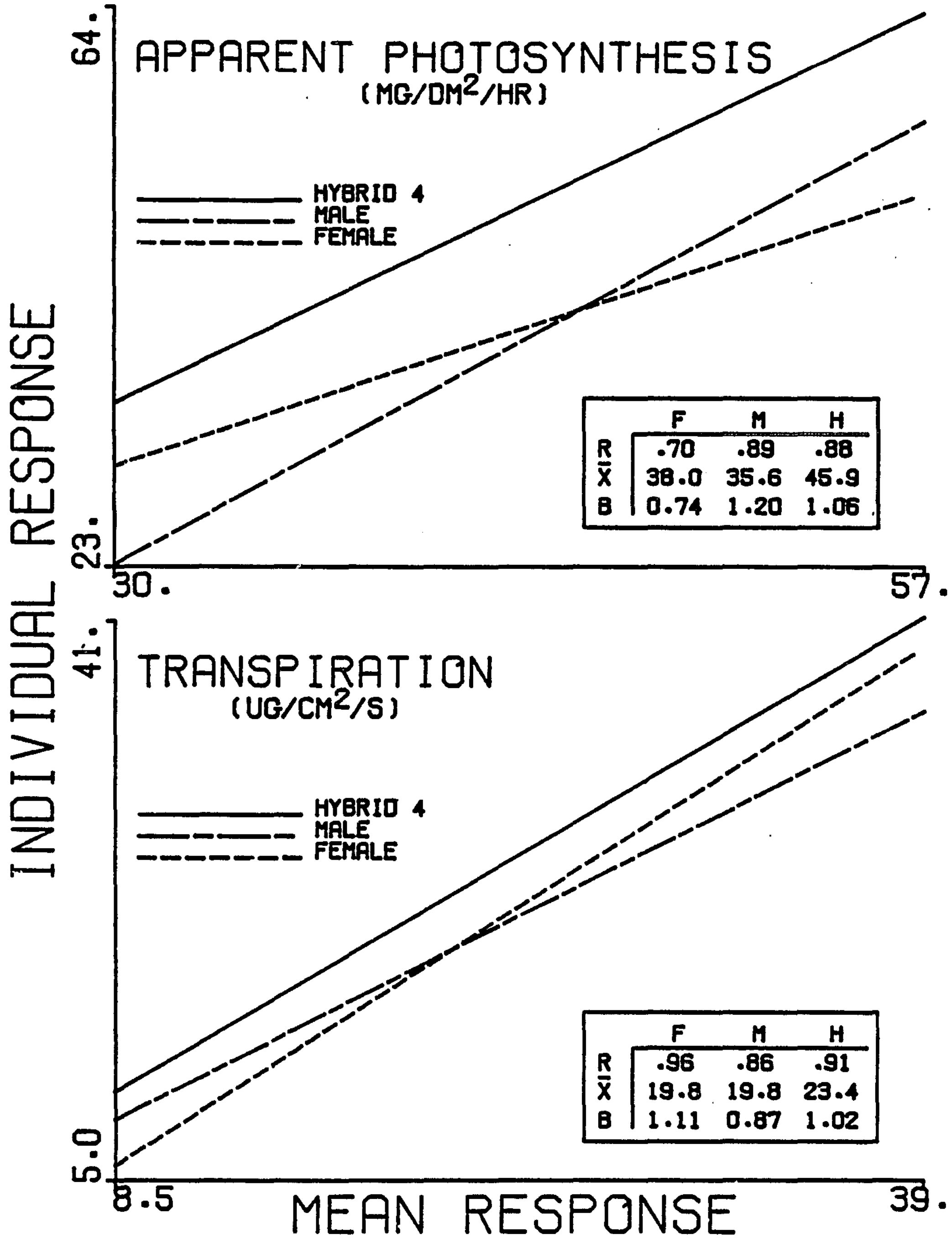

Fig. 11. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 4 (H), and its male (M) and female (F) parents.

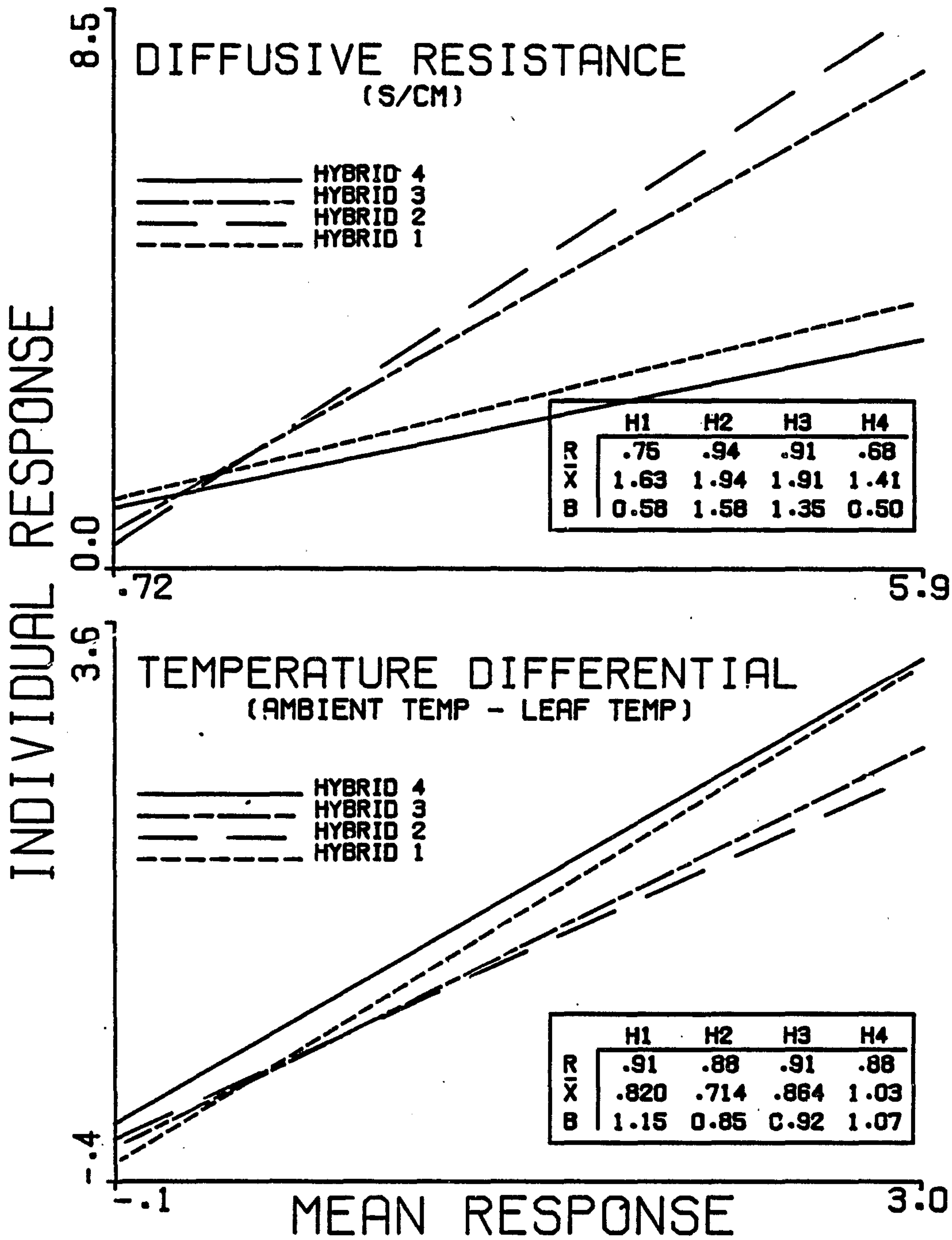

Fig. 12. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 1 (H1), hybrid 2 (H2), hybrid 3 (H3), and hybrid 4 (H4).

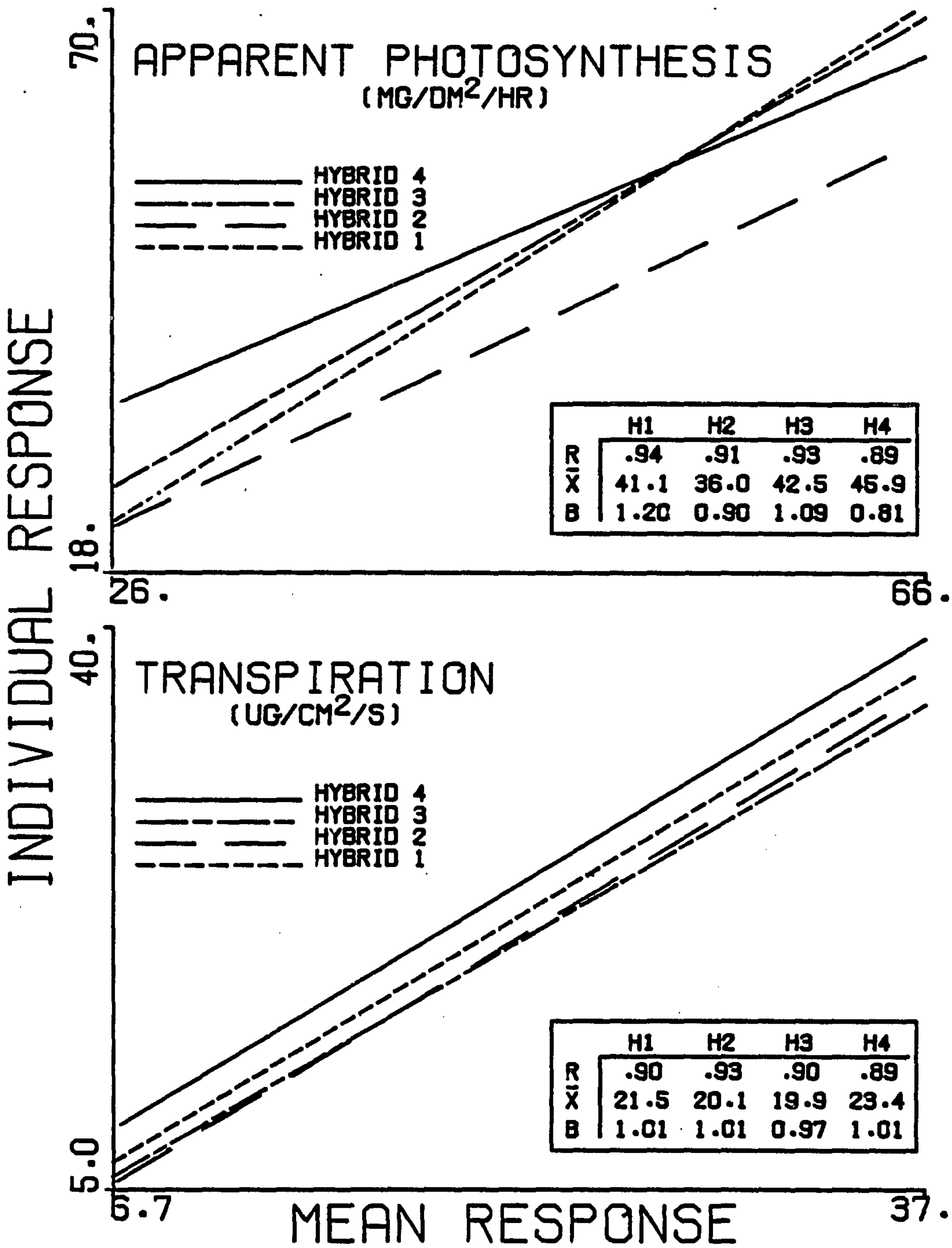

Fig. 13. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 1 (H1), hybrid 2 (H2), hybrid 3 (H3), and hybrid 4 (H4).

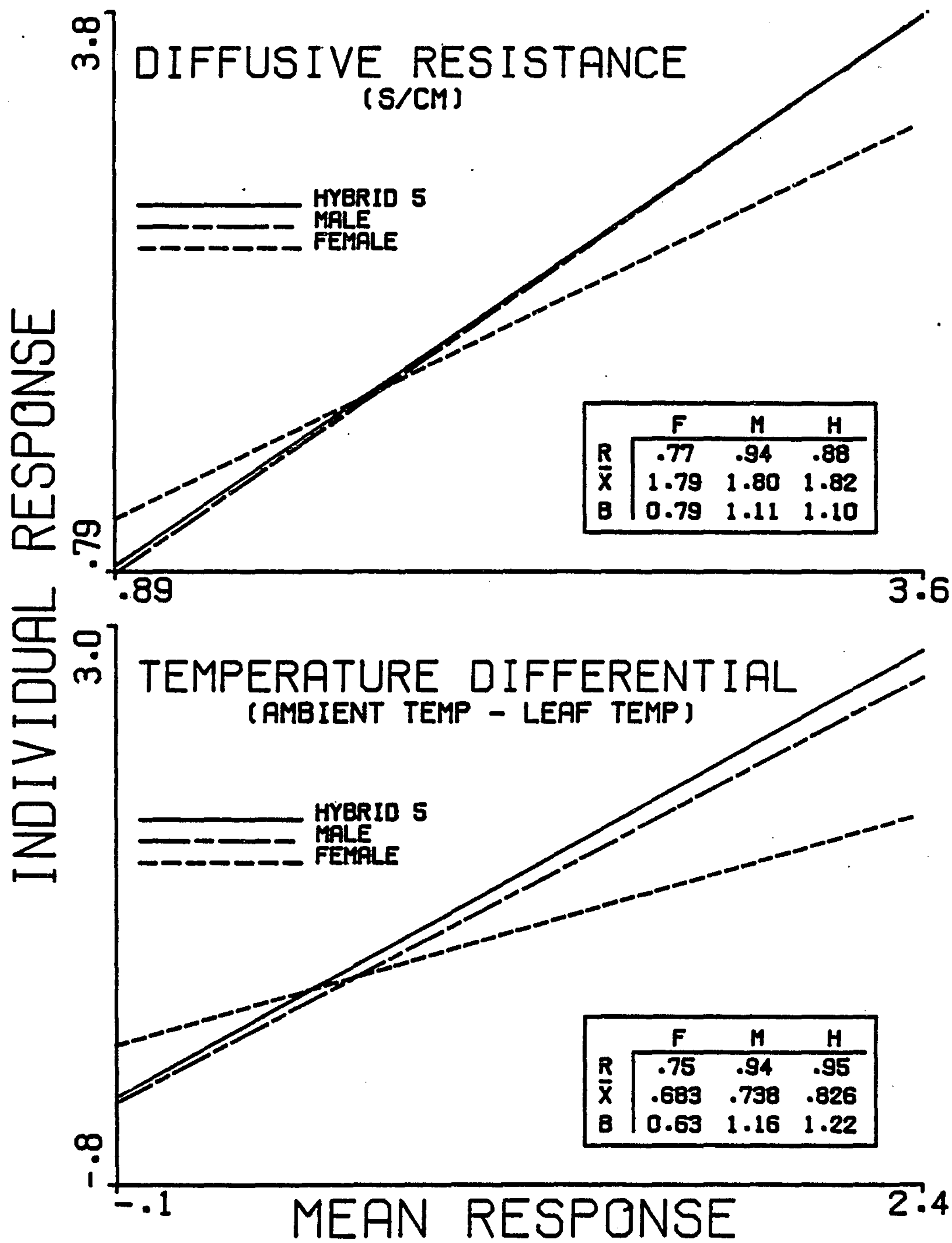

Fig. 14. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 5 (H) and its male (M) and female (F) parents.

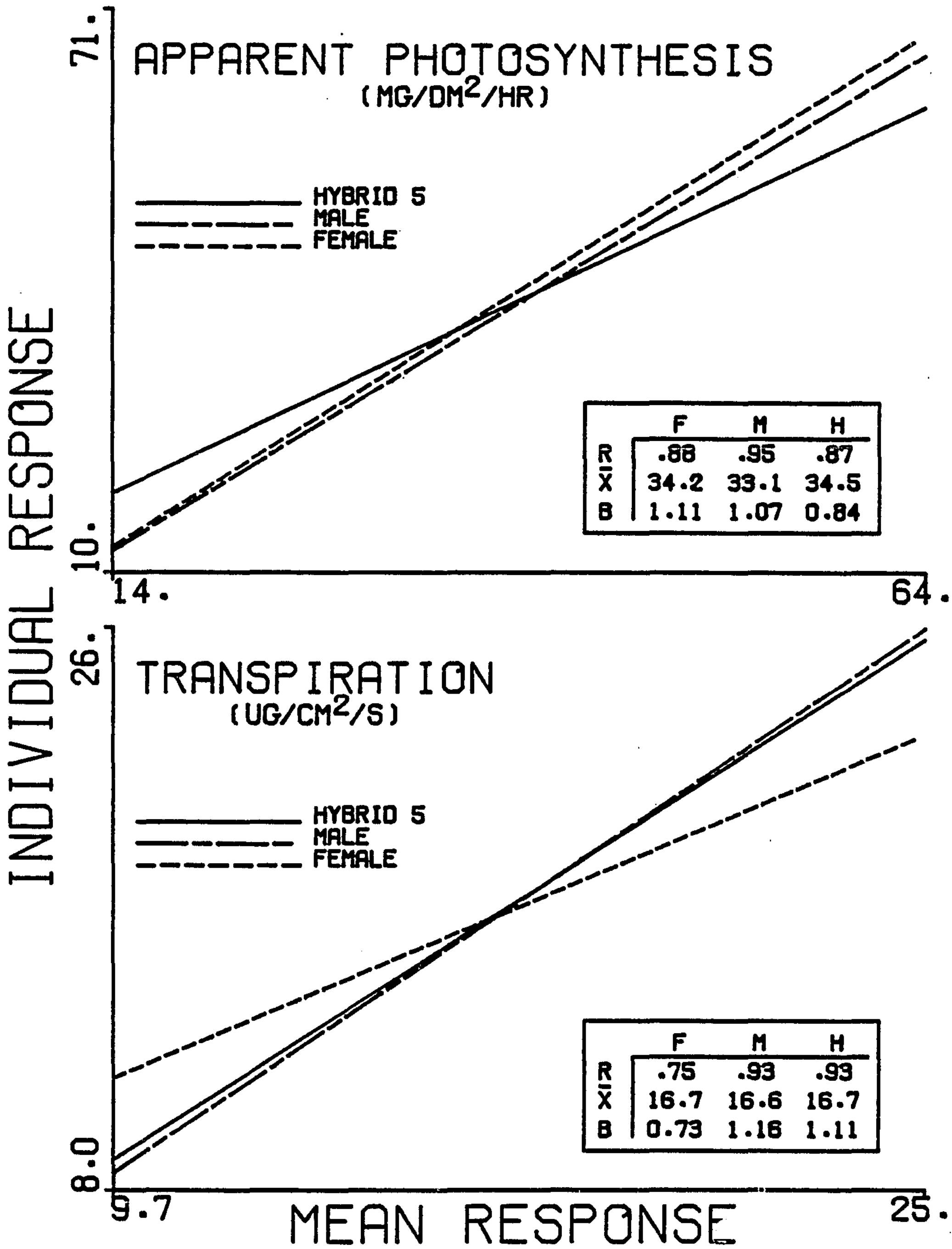

Fig. 15. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 5 (H), and its male (M) and female (F) parents.

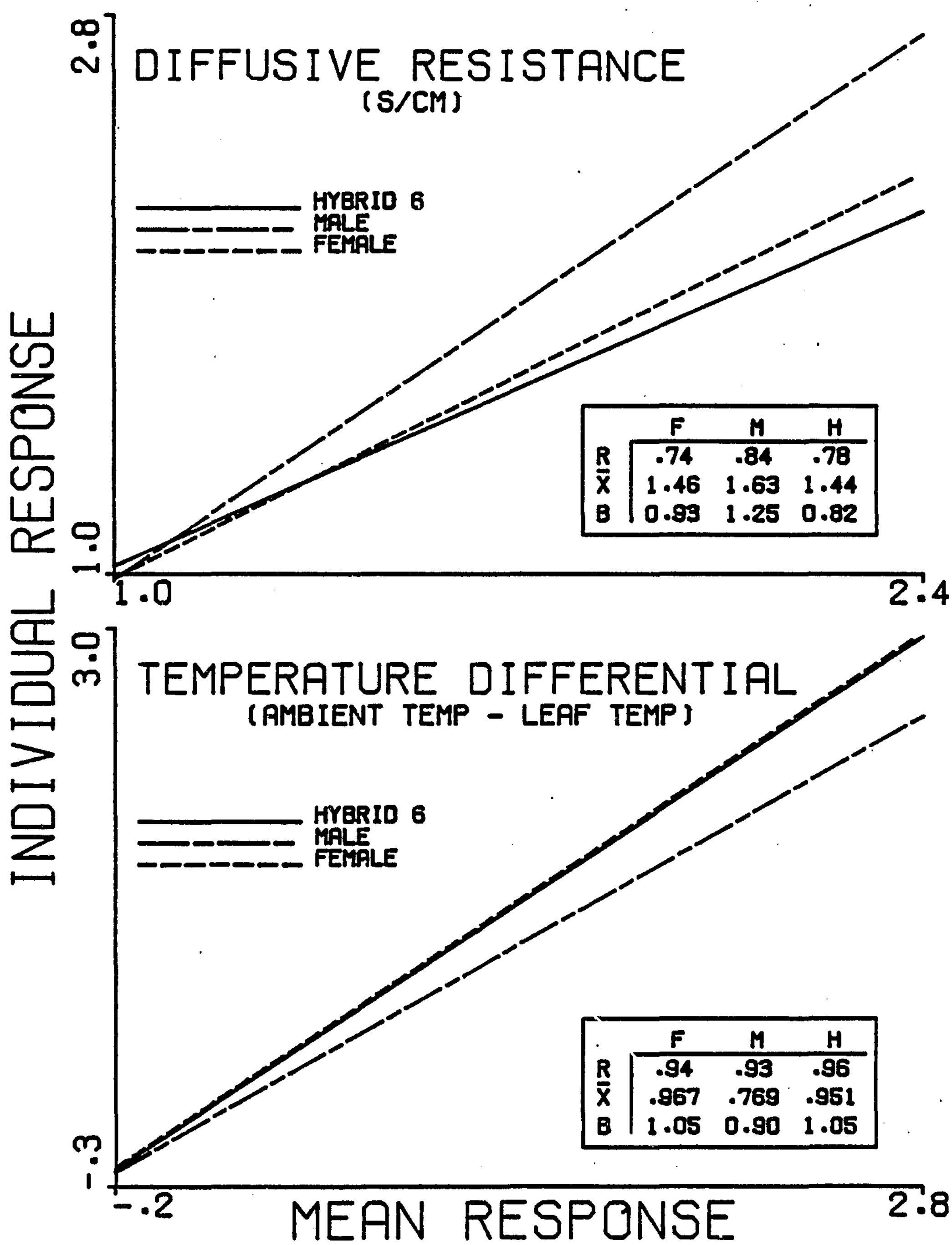

Fig. 16. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 6 (H) and its male (M) and female (F) parents.

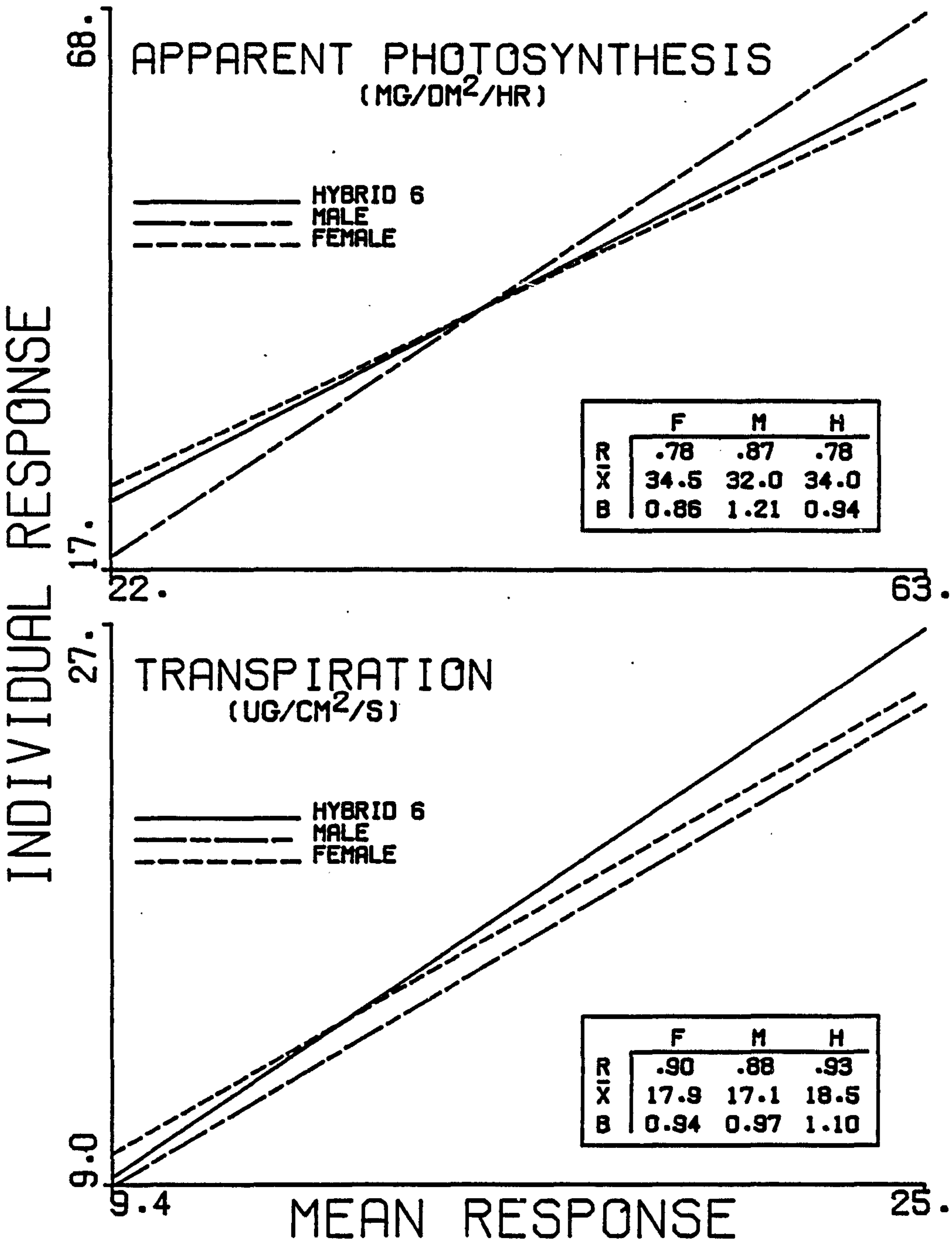

Fig. 17. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 6 (H), and its male (M) and female (F) parents.

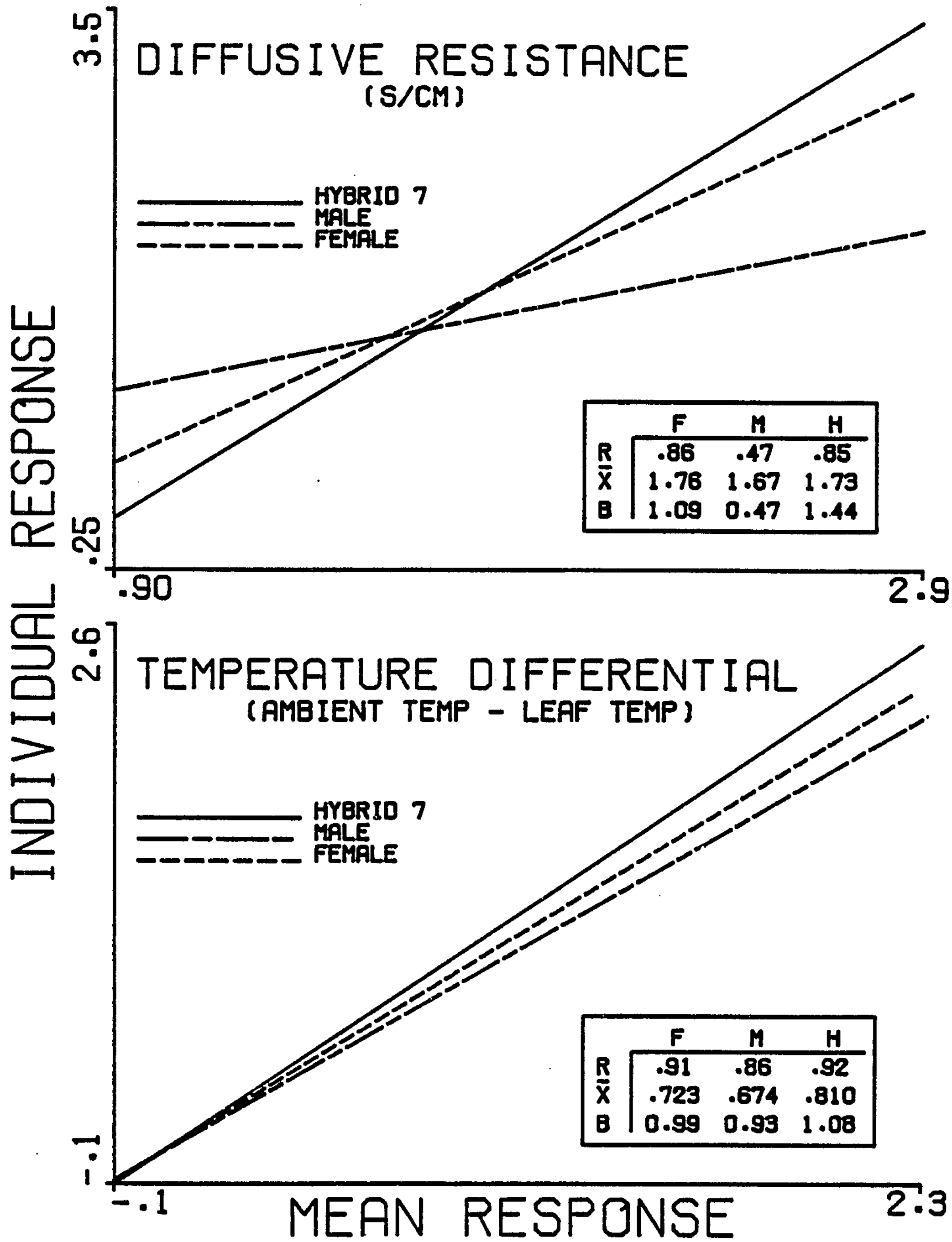

Fig. 18. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 7 (H) and its male (M) and female (F) parents.

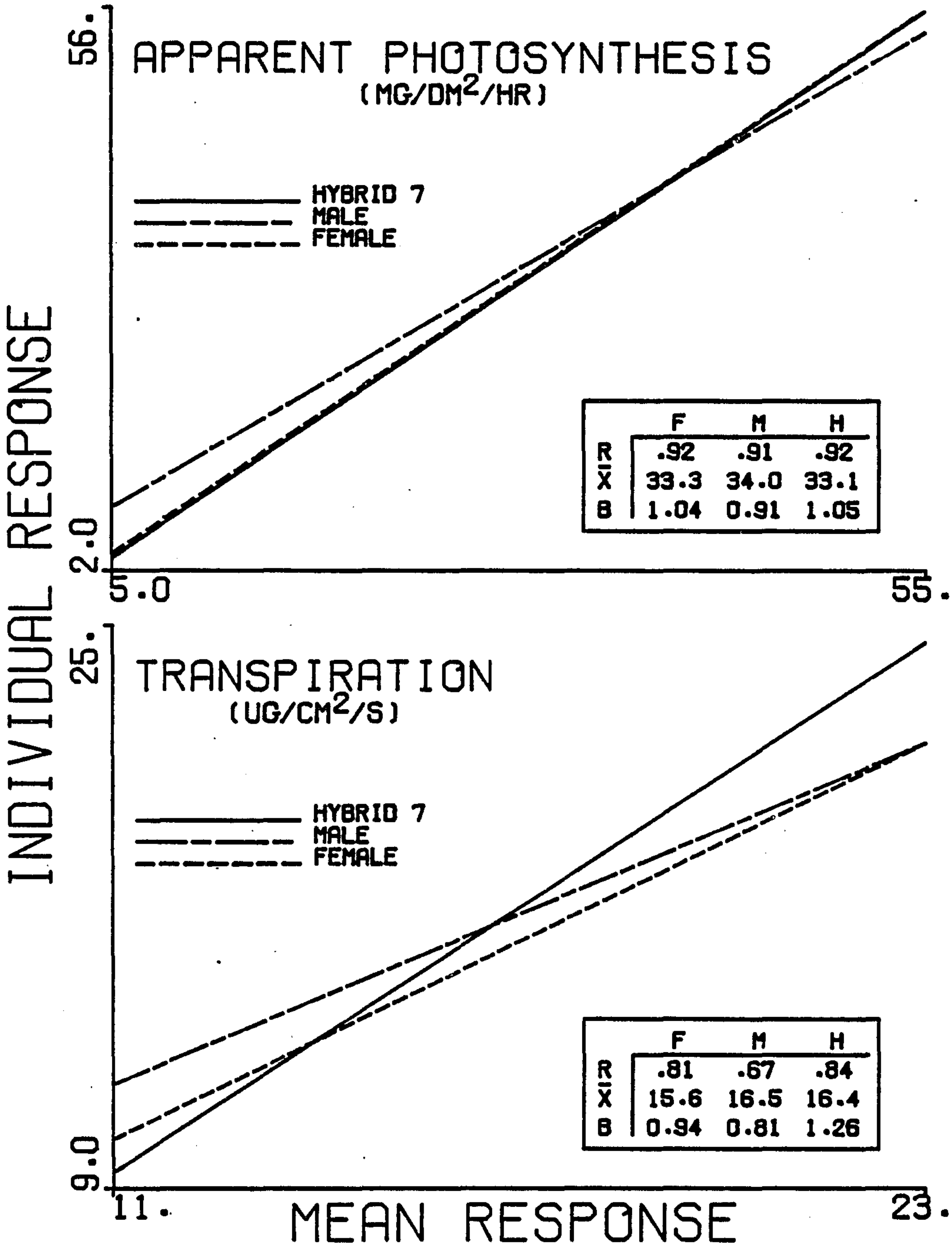

Fig. 19. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 7 (H), and its male (M) and female (F) parents.

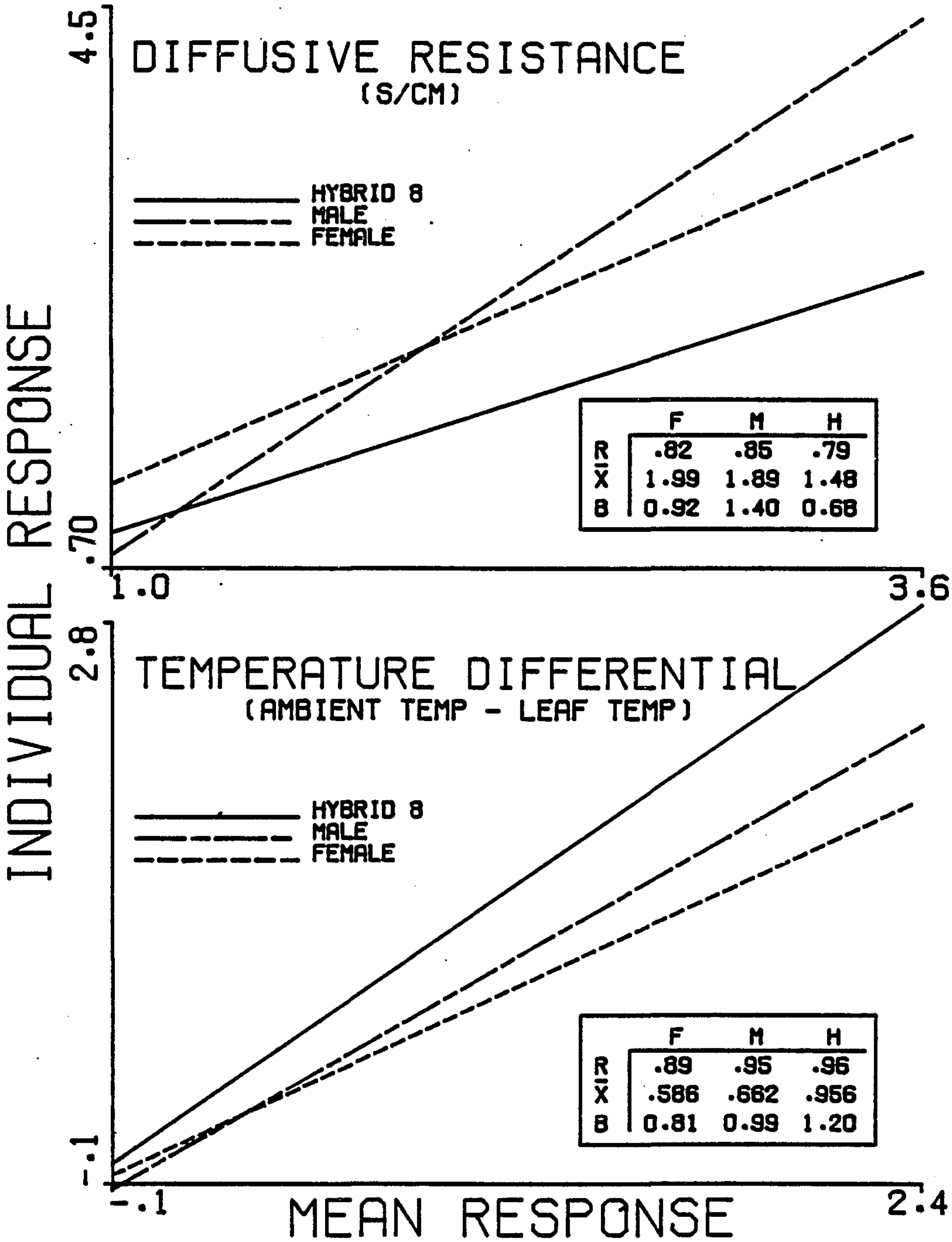

Fig. 20. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 8 (H) and its male (M) and female (F) parents.

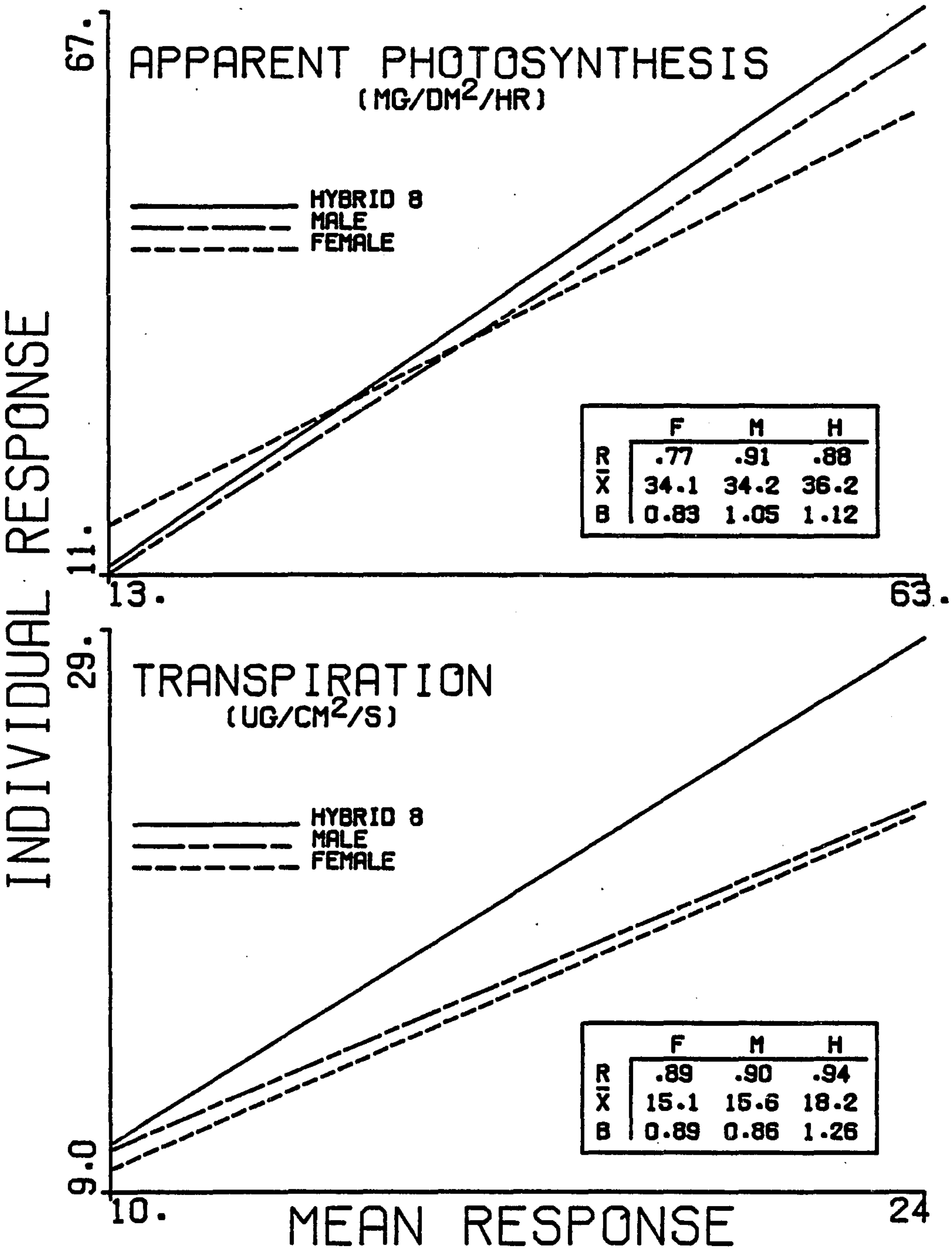

Fig. 21. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 8 (H), and its male (M) and female (F) parents.

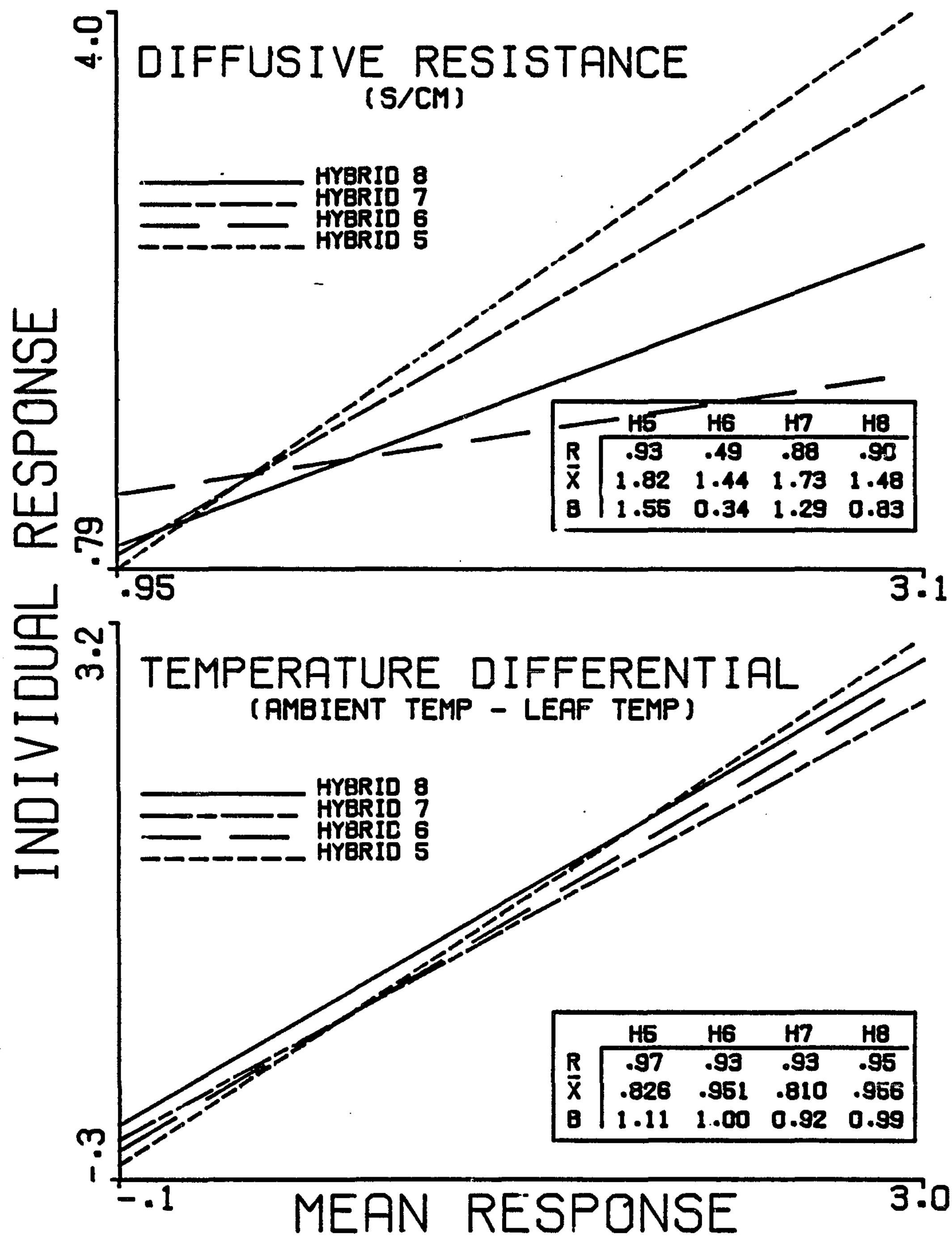

Fig. 22. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for hybrid 5 (H5), hybrid 6 (H6), hybrid 7 (H7), and hybrid 8 (H8).

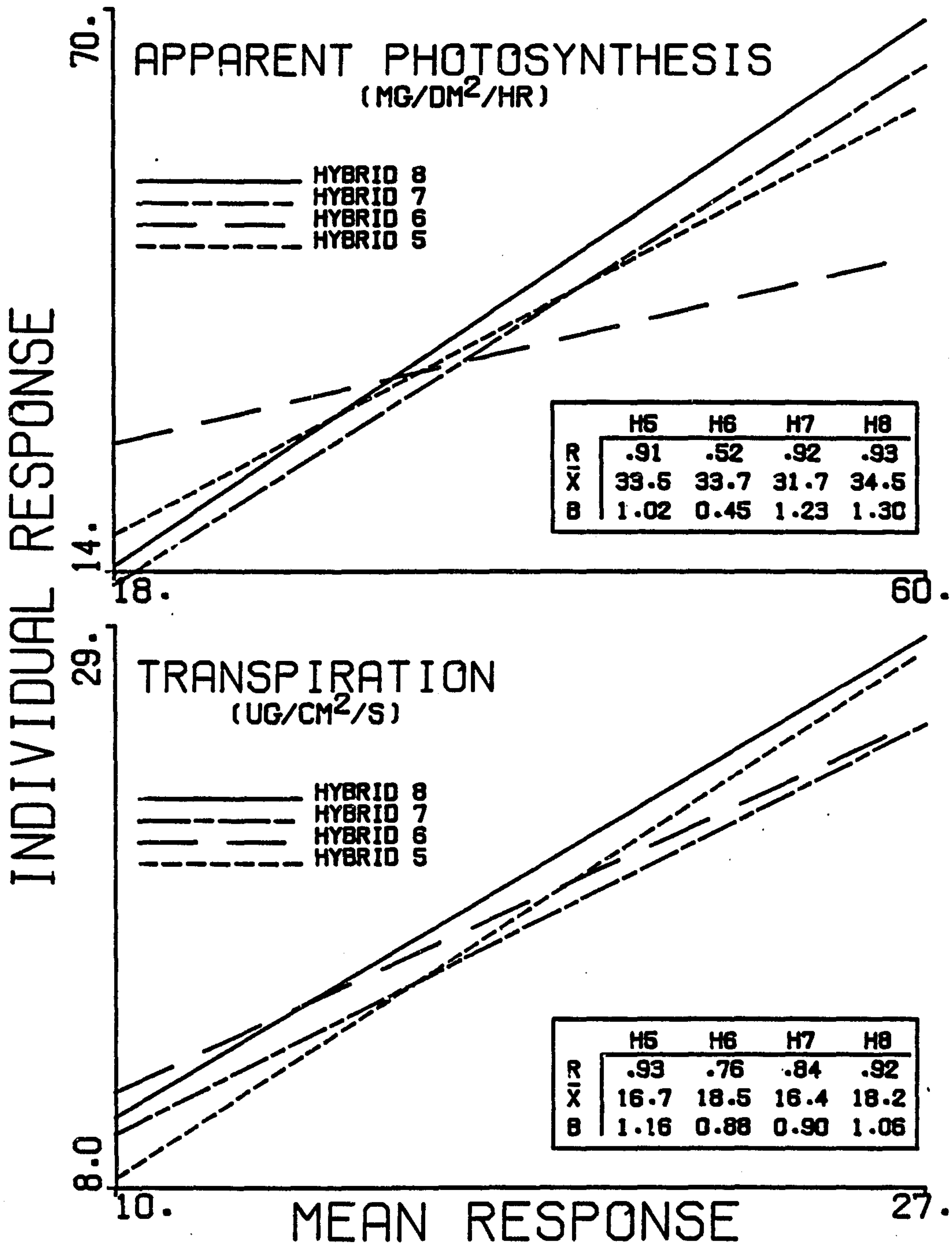

Fig. 23. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for hybrid 5 (H5), hybrid 6 (H6), hybrid 7 (H7), and hybrid 8 (H8).

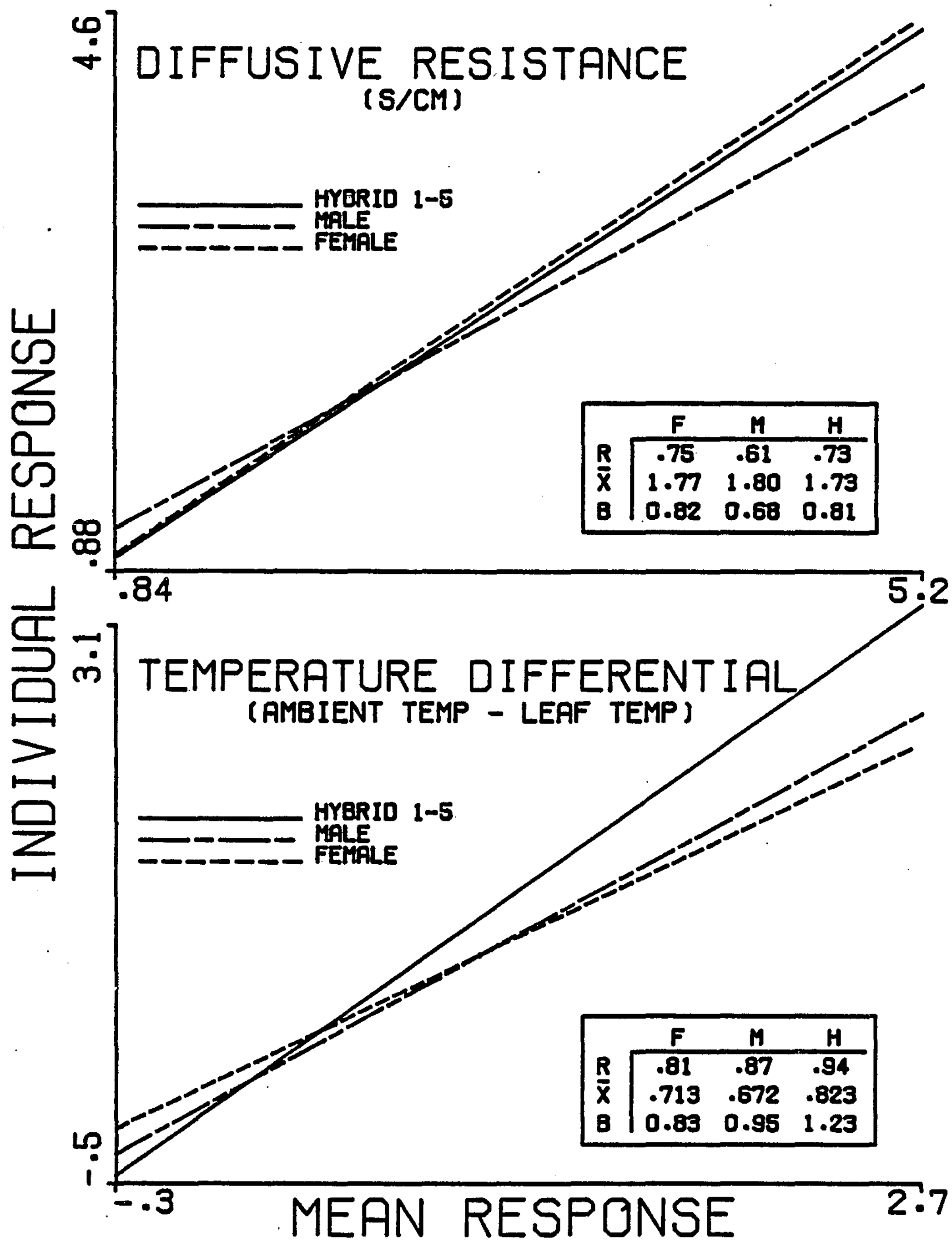

Fig. 24. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for the two year response of hybrid 1-5 (H) and its male (M) and female (F) parents.

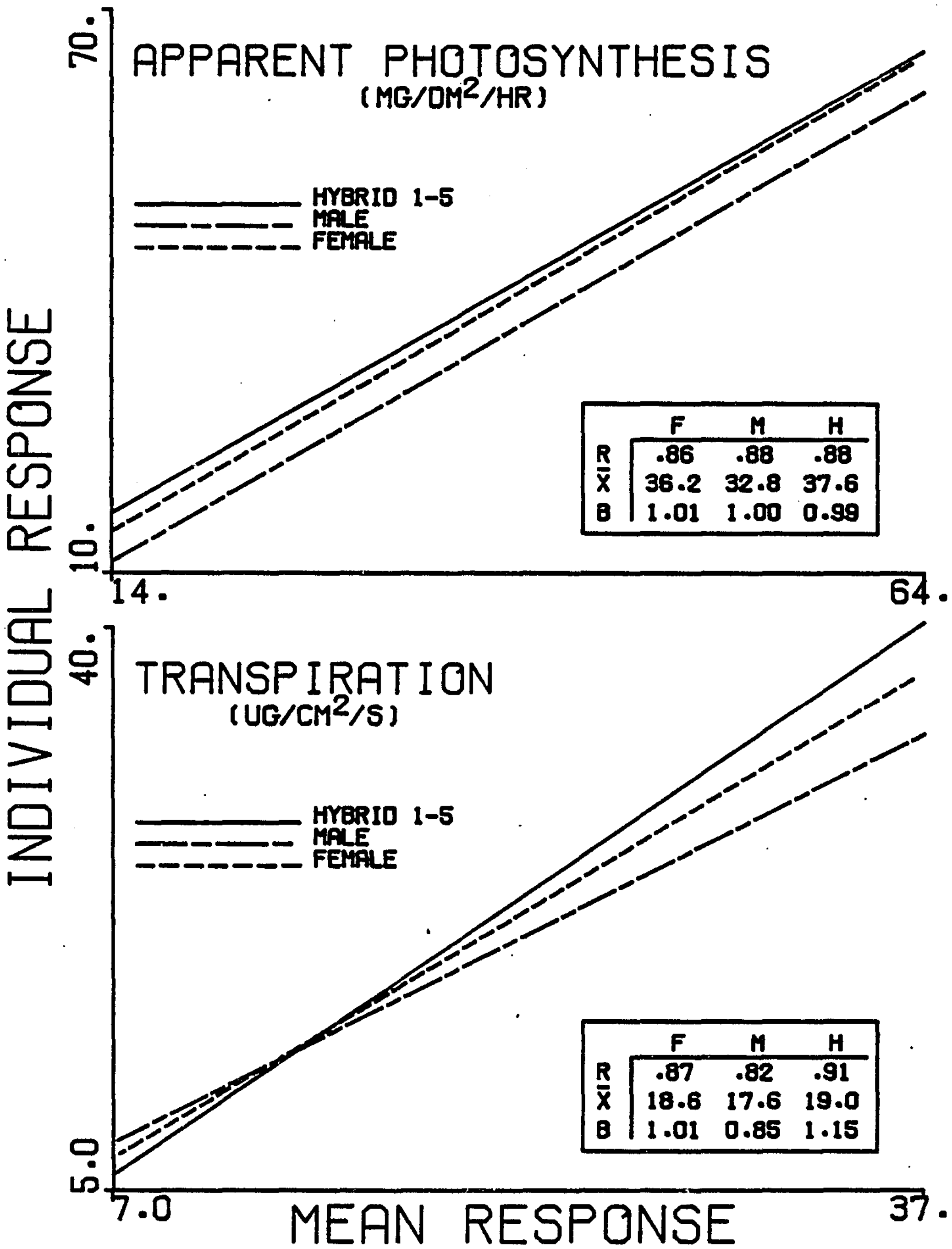

Fig. 25. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for the two year response of hybrid 1-5 (H) and its male (M) and female (F) parents.

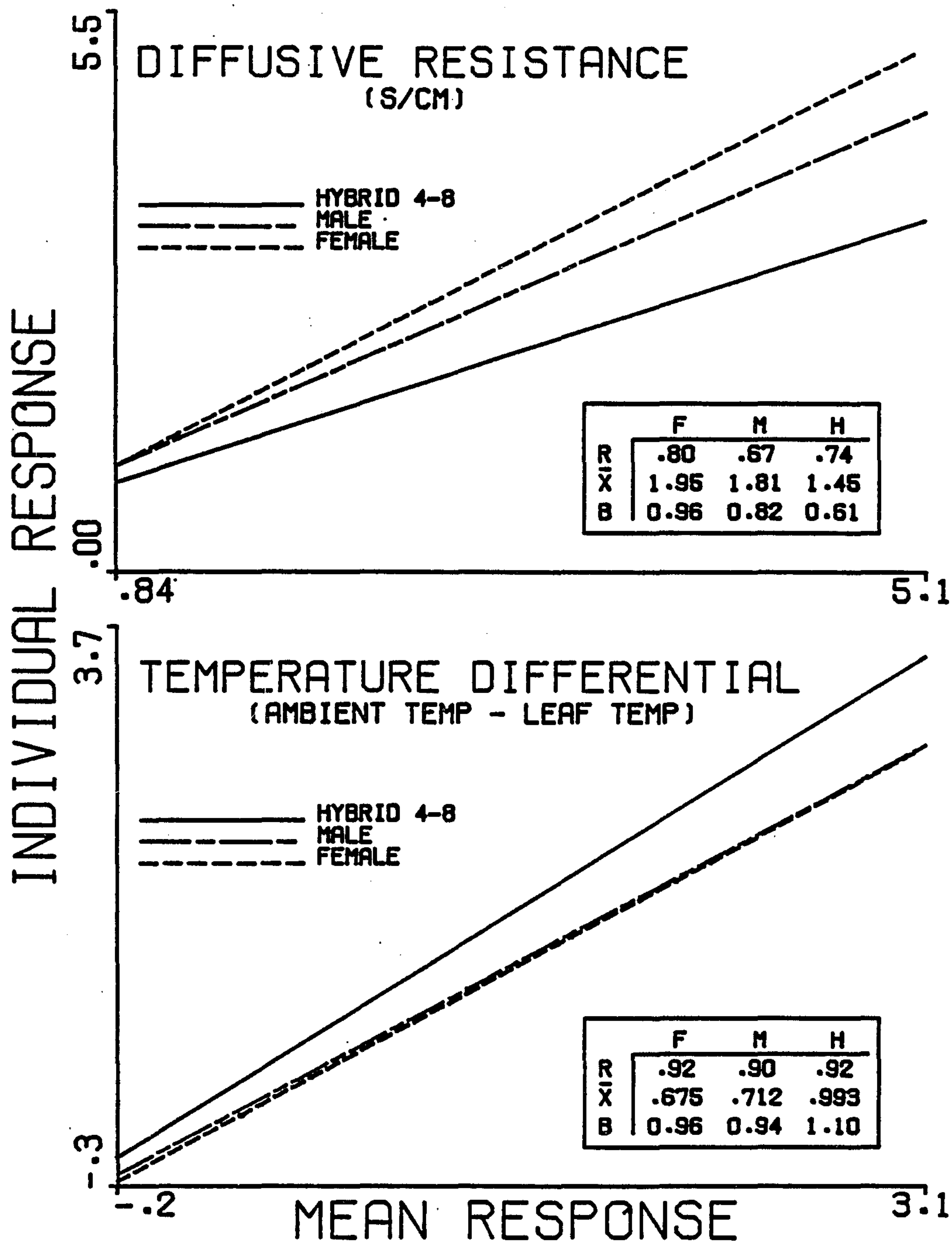

Fig. 26. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for diffusive resistance and temperature differential for the two year response of hybrid 4-8 (H) and its male (M) and female (F) parents.

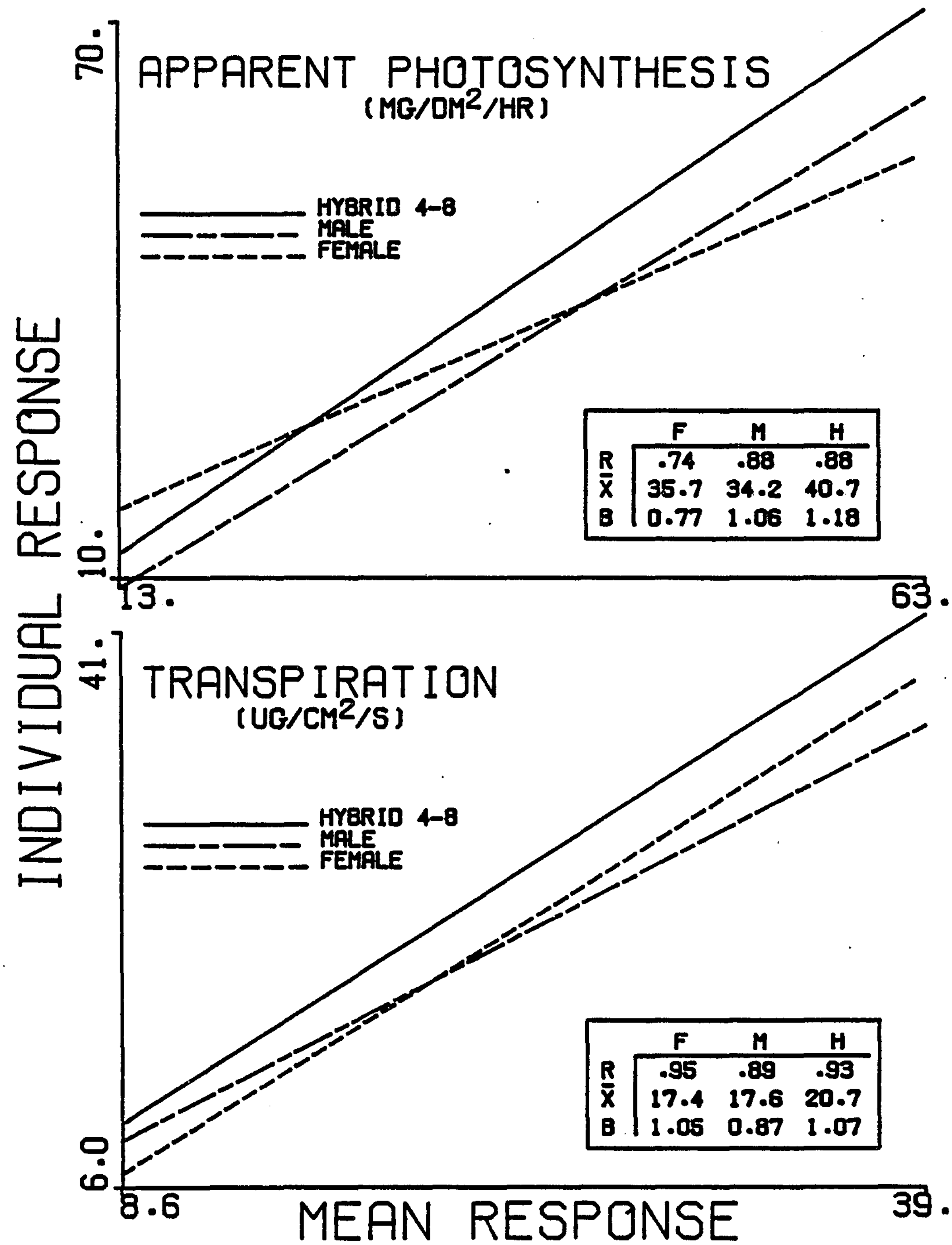

Fig. 27. Finlay and Wilkinson regressions with correlation coefficient (R), mean ($\bar{X}$), and slope (B) for apparent photosynthesis and transpiration for the two year response of hybrid 4-8 (H) and its male (M) and female (F) parents.

from both of the water levels, it is possible to evaluate genotypic responses across a diverse spectrum of environmental conditions.

Finlay and Wilkinson interpret the regressions in terms of the regression coefficient (b) and mean genotypic response. If two genotypes have similar mean responses, the one with the lower regression coefficient would be considered more stable and better suited to a wide range of environmental conditions. The transpiration responses observed for hybrid 5 and its parents (Fig. 15) is an example of three genotypes with similar mean responses but the female parent would be considered more stable because of its relatively low regression coefficient. This female entry showed relatively consistant transpiration rates over all of the environmental conditions. A germplasm source with this stability would be suited to unpredictable growing conditions, but probably would be unable to fully exploit more favorable growing conditions.

The regressions are often well defined and the superiority of an individual entry is clear. Hybrid 4 in 1980 showed heterosis for all four physiological characteristics across all environmental conditions (Figs. 10, 11). This hybrid had consistantly higher temperature differential, transpiration, and apparent photosynthesis. Hybrid 4 had lower diffusive resistances than either parent under all conditions observed.

The superior rates of apparent photosynthesis found in the hybrids in 1980 are substantiated by these regressions (Figs. 5, 7, 9, 11). All had higher rates across all environments except hybrid 1 which was surpassed by its female parent under conditions unfavorable for higher rates of carbon uptake. A consistantly higher temperature differential was displayed by hybrid 3 (Fig. 8), but consistant responses were not evident for hybrids 1 or 2 (Figs. 4, 6). Hybrid 1 had lower diffusive resistances (Fig. 4) than either of its parents, while hybrids 2 and 3 were intermediate (Figs. 6, 8). The transpiration rates from hybrids 1, 2, and 3 were not consistantly superior to their respective parents (Figs. 5, 7, 9).

When the four hybrids from 1980 are compared with each other, the stability and superiority of hybrid 4 becomes evident (Figs. 12, 13). This hybrid exhibited consistantly higher temperature differential and transpiration. The mean diffusive resistance (1.41 s cm^{-1}) and low regression coefficient ($b = 0.50$) indicate that hybrid 4 is the most stable hybrid for this characteristic. The same analysis holds for apparent photosynthesis where hybrid 4 has the highest mean rate and is the most stable across environments. Due to their superior responses, hybrids 1 and 4 were included in the 1981 field trials and coded and hybrids 5 and 8, respectively.

In 1981, hybrid 8 consistantly expressed heterosis for temperature differential and transpiration (Figs. 20, 21). This hybrid had lower diffusive resistance than either of its parents under all but the most favorable conditions (Fig. 20). Hybrid 8 had higher rates of apparent photosynthesis than its male parent but was surpassed by its female parent under environmental conditions which were more conducive to low apparent photosynthetic rates.

Hybrid 6 displayed generally superior responses for diffusive resistance but behaved much like its female parent for temperature differential, transpiration, and apparent photosynthesis (Figs. 16, 17). Hybrid 5 and its male parent had very similar responses for diffusive resistance, temperature differential, and transpiration. This hybrid was superior to either parent for apparent photosynthesis. Physiological responses of hybrid 7 were erratic (Figs. 18, 19). It had superior temperature differential but did not express heterosis or stability for diffusive resistance, transpiration, or apparent photosynthesis.

A comparison of the four hybrids from 1981 indicates that hybrids 6 and 8 are better adapted to a wide range of environmental conditions (Figs. 22, 23). Hybrid 6 appears to be the most stable in terms of diffusive resistance, transpiration, and apparent photosynthesis. Hybrid 8 showed a slight advantage in temperature differential. A potential disadvantage which surfaces in evaluating hybrid 6 is its relatively low correlation coefficients (r). Eberhart and Russell (1966) consider this to be an indication of low stability. A low correlation coefficient reflects erratic responses across all conditions.

The results obtained for the two hybrids which were evaluated both years were combined and evaluations made (Figs. 24, 25, 26, 27). Hybrid 4 (hybrid 8 in 1981) displayed heterosis across all environments for diffusive resistance, temperature differential, and transpiration (Figs. 26, 27). Hybrid 4 was superior to its male parent for apparent photosynthesis, but was surpassed by its female parent in environments conducive to low rates of apparent photosynthesis (Fig. 27). Hybrid 1 (hybrid 5 in 1981) displayed consistant heterosis only for apparent photosynthesis (Figs. 25). The transpiration and temperature differential of hybrid 1 were superior to both parents at the higher ranges but was surpassed by both parents in more stressful environments (Figs. 24, 25). The diffusive resistance of hybrid 1 showed no clear advantage over either parent (Fig. 24).

The regression analysis supports research by Jowett (1972) that sorghum hybrids can be more stable than open pollenated lines. The Finlay and Wilkinson regression analysis is an effective method for identifying sorghum hybrids and lines with superior physiological characteristics under a wide range of environmental conditions. The technique is a valuable tool for studying the relative contribution of an individual parent of a hybrid cross and can also aid in the identification of stable and superior hybrids.

Dry Weight Partitioning

The results from the 1981 seedling dry weight partitioning study do not reveal any differences in the proportion of total dry weight which is dispersed among the leaf, stem, and root components of the 12 germplasm sources (Fig. 28). Seven days after planting, the roots of all entries represented 60 to 75% of the total dry weight. Leaves were the next largest component representing 20 to 30% of the dry weight. Stem tissue accounted for only 10 to 20% of the total dry matter.

The percent dry weight distribution favored the leaves and stems 35 days after planting. The percent of total dry matter in the leaves represented approximately 50 to 55%. The stems were

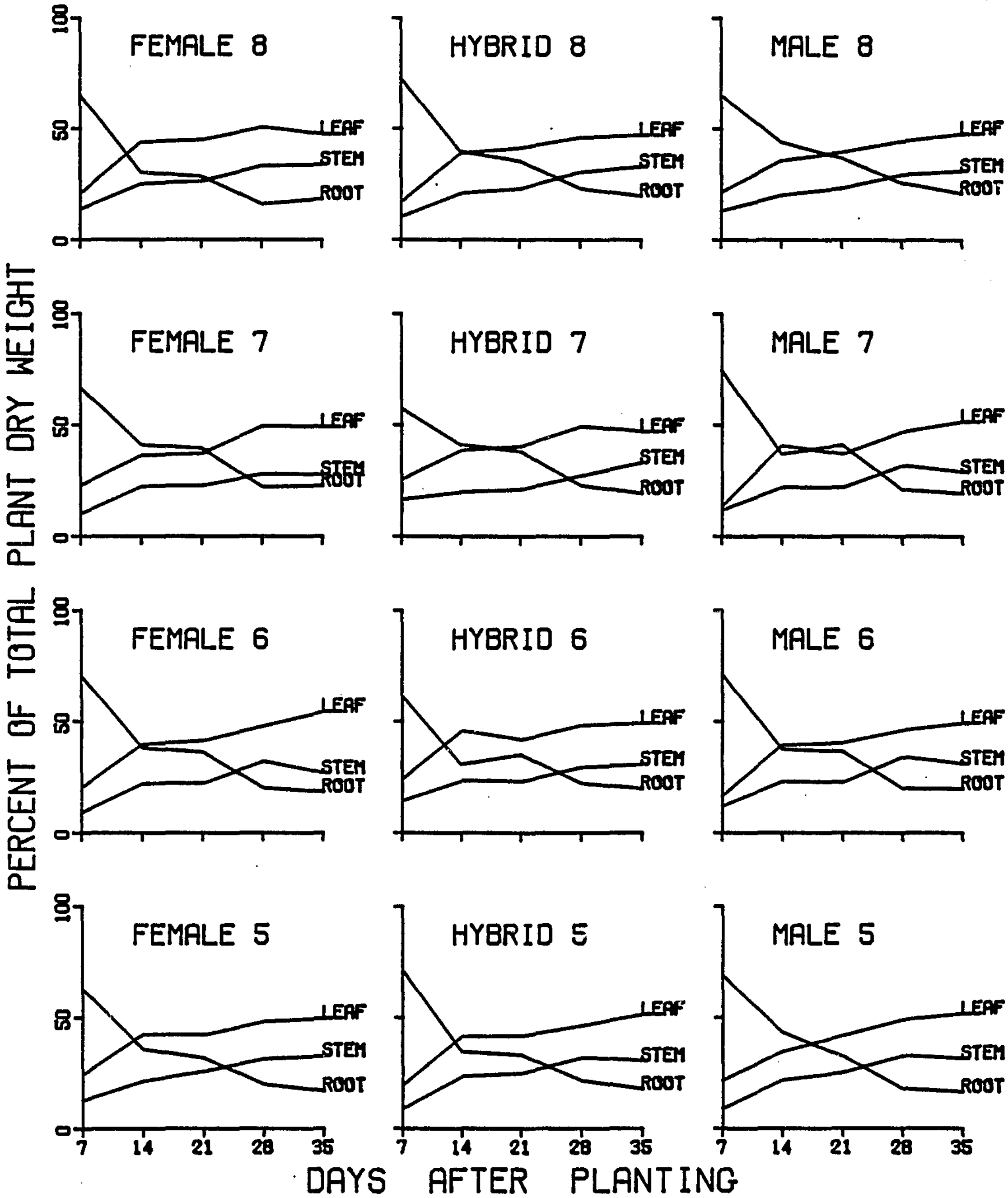

Fig. 28. Percent dry weight partitioning into leaf, stem, and root tissue for four hybrids and their respective parents during the first 35 days after planting.

consistantly the next heaviest component with 25 to 35% of the total plant dry weight followed by the roots with 15 to 25 percent.

While the percent dry matter partitioned to the leaves, stems, and roots failed to reveal any differences among the 12 entries, the actual dry weights of each component were different among germplasm sources (Fig. 29). Hybrid 8 had the highest dry weights for all three components 35 days after planting. Only hybrids 7 and 8 showed heterosis for the dry weights of leaves, stems, and roots 35 days after planting. Hybrids 5 and 6 displayed responses intermediate to their parents at the 35 day point.

Potter and Jones (1977) suggested that the partitioning of photosynthate into new leaf area is an important component of plant growth rates. They found that leaf area partitioning (LAP) and the relative leaf area expansion rates (K_a) were closely correlated with plant growth rates. Leaf area partitioning (LAP) and K_a values for the 12 sorghum entries were calculated in 1981. Potter and Jones assume that during exponential growth, relative growth rates are constant. This assumption may be true under the controlled conditions of their study with plants evaluated every two days, but not under field conditions. Therefore mean values were used for these two values.

The LAP values obtained (Table 1) were not consistantly related to growth under field conditions. Hybrid 8 which had the highest dry weight at 35 days (Fig. 29) also had the highest relative leaf area expansion rate, but only an intermediate value for leaf area partitioning. Hybrids 6 and 8 had essentially the same LAP values, yet they

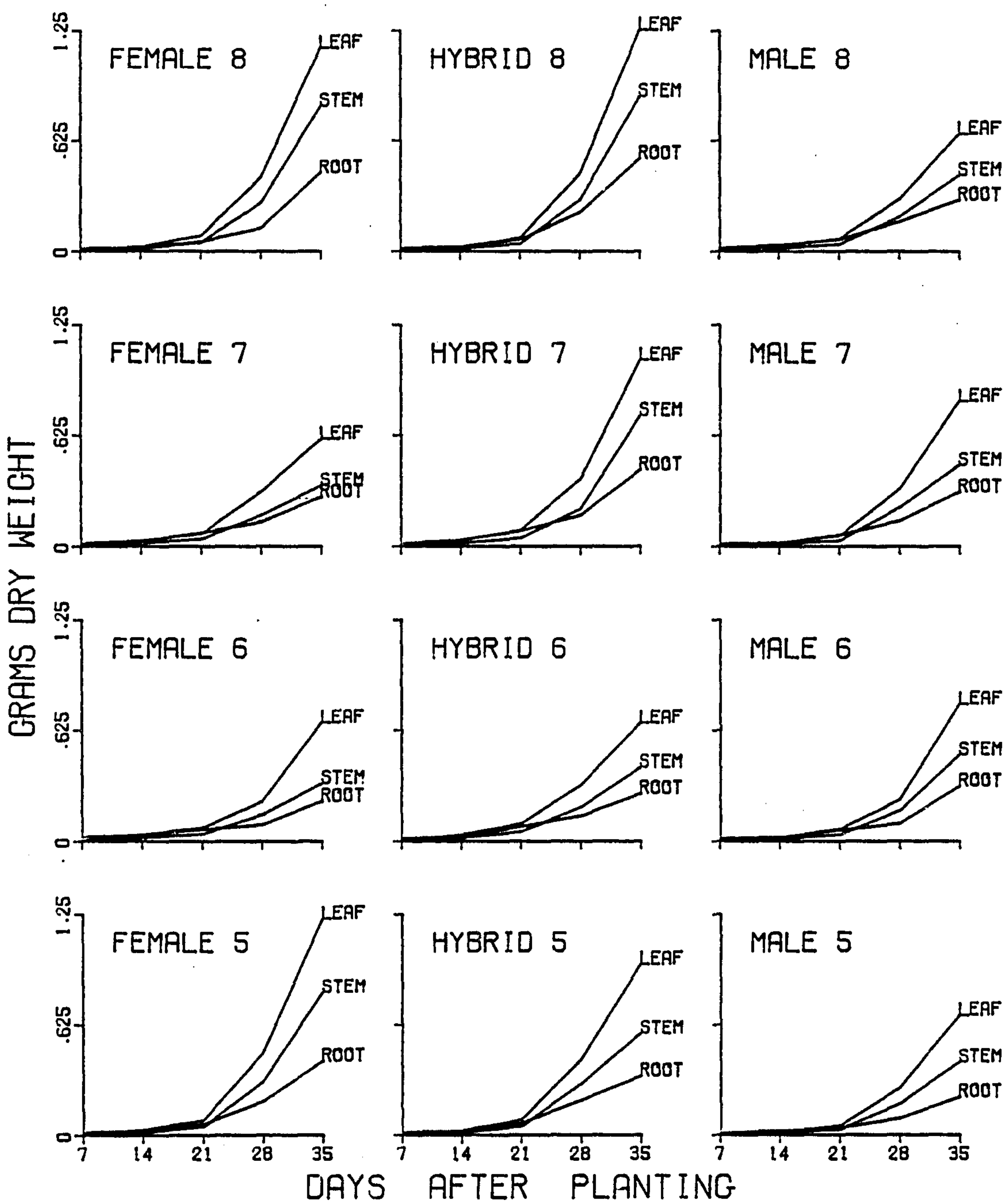

Fig. 29. Dry weight partitioning into leaf, stem, and root tissue for four hybrids and their respective parents during the first 35 days after planting.

Table 1. Calculated values for leaf area partitioning (LAP), leaf area (dm^2), relative leaf area expansion rate (k_a), dry weight (Wm), and relative growth rate (k_w) at 17.5 days after planting for the four hybrids (H) and their respective female (F) and male (M) parents in 1981.

Entry	Am (dm^2)	k_a ($dm^2 dm^{-2} day$)	Wm (mg)	k_w ($mgmg^{-1} day^{-1}$)	LAP $\frac{dm^2 day^{-1}}{g\ day^{-1}}$
F5	.16	.171	81.45	.191	1.73
M5	.11	.169	49.40	.188	2.05
H5	.16	.166	66.69	.190	2.05
F6	.13	.147	71.16	.162	1.65
M6	.11	.171	54.60	.188	1.85
H6	.17	.144	81.45	.161	1.83
F7	.12	.152	66.69	.168	1.61
M7	.12	.163	51.94	.194	1.89
H7	.16	.161	85.63	.177	1.72
F8	.14	.171	73.70	.195	1.67
M8	.12	.143	66.69	.169	1.51
H8	.14	.176	66.69	.204	1.84

$$LAP = \frac{Am\ k_a}{Wm\ k_w}$$

represented the lower and upper dry weight extremes for the hybrids. Hybrid 6 had the lowest leaf area expansion rate of the four hybrids.

The partitioning of photosynthate into new leaf area should be an important component of growth, but calculating leaf area partitioning for plants grown under field conditions is difficult. The relative growth rate and relative leaf area expansion rate are now constant, so mean responses must be used. If this technique is to have application outside the growth chamber, better methods need to be employed. Sampling more plants at shorter intervals would help reduce the problems associated with environmental variability in the field.

Stomate Densities

Stomate densities were significantly different among the 12 germplasm sources in 1980 and 1981 (Tables 1, 2). In 1981 hybrid 4 had a significantly higher density (333.3 stomata mm^{-2}) than both hybrids 1 (267.4 stomata mm^{-2}) and hybrid 2 (280.0 stomata mm^{-2}). Hybrid 3 had the second highest density (303.0 stomata mm^{-2}). None of the hybrids were significantly different in 1981. They ranged from 249.4 stomata mm^{-2} for hybrid 6 to 297.6 stomata mm^{-2} for hybrid 5. None of the hybrids in either 1980 or 1981 had higher stomate densities than both of their parents. Electron microscope photographs of stomates on the adaxial surface of hybrid 4 appear in Fig. 30.

Yields

Yield estimates were made on the hybrids and males in 1980 and 1981 with the hybrids showing a superior response (Tables 4, 5). Only hybrid 3 in 1980 failed to out yield a male line (Table 4). Hybrid 4

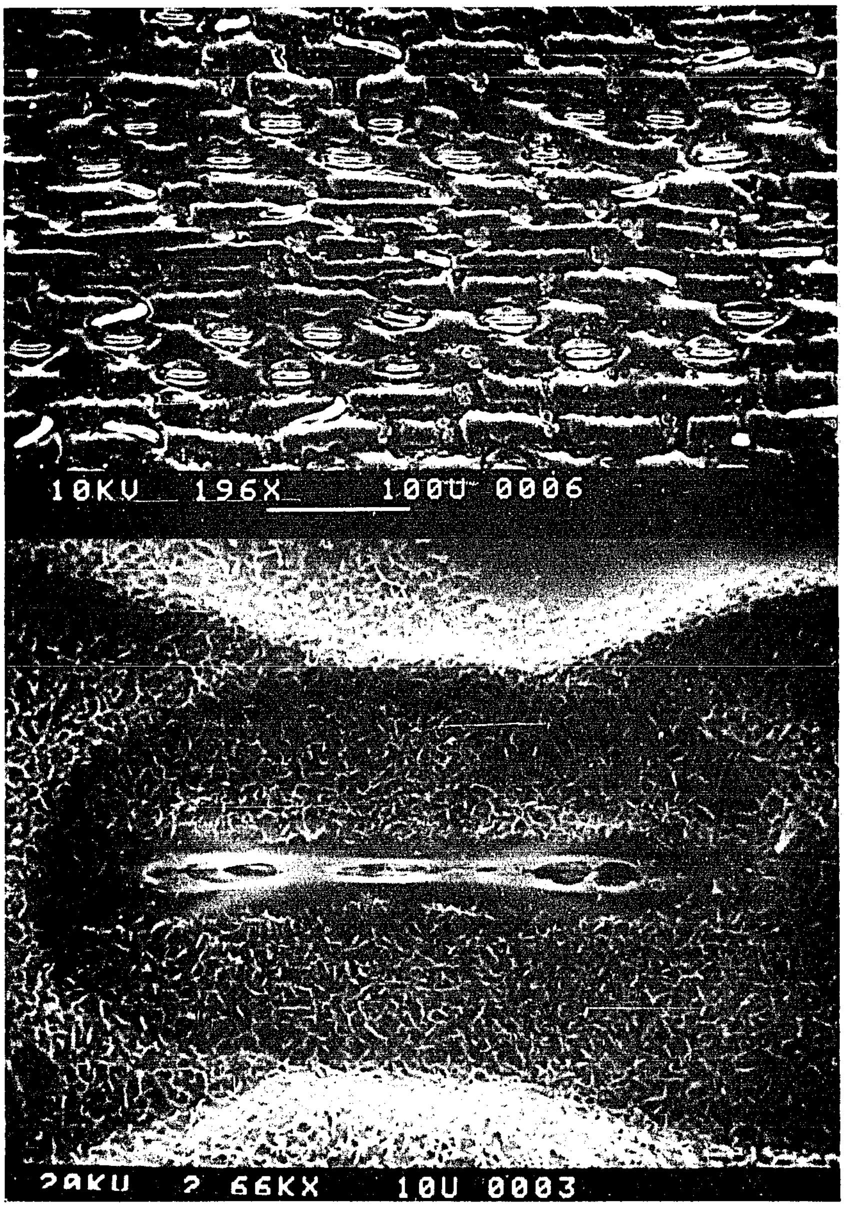

Fig. 30. Electron microscope photographs taken at two magnifications on the adaxial surface of hybrid 4.

Table 2. Stomatal densities for the abaxial, adaxial, and total leaf surfaces for the 12 germplasm sources grown in 1980.

Abaxial Surface		Adaxial Surface		Total	
Entry	(stomata mm^{-2})	Entry	(Stomata mm^{-2})	Entry	(Stomata mm^{-2})
F4	243.9 a[1]	F4	148.5 a	F4	392.4 a
M1	238.6 a	H4	134.1 ab	M1	356.1 b
F3	228.8 ab	F1	127.3 abc	F3	350.0 b
F1	215.2 abc	M2	122.0 bc	F1	342.4 bc
M4	203.8 bcd	F3	121.2 bc	H4	333.3 bc
H4	199.2 cde	M4	120.5 bc	M4	324.2 bcd
H3	193.2 cdef	M1	117.4 bc	H3	303.0 cde
M2	181.1 def	H2	115.9 bc	M2	303.0 cde
M3	176.5 def	M3	112.1 bc	M3	288.6 de
H1	169.7 efg	H3	109.8 bc	H2	280.0 e
H2	164.4 fg	H1	97.7 cd	H1	267.4 e
F2	147.0 g	F2	84.8 d	F2	231.8 f

1. Values followed by the same letter within a column are not significantly different at the 0.05 level according to the Student-Newman-Keul test.

Table 3. Stomatal densities for the abaxial, adaxial, and total leaf surfaces for the 12 germplasm sources grown in 1981.

	Abaxial Surface		Adaxial Surface		Total
Entry	(Stomata mm^{-2})	Entry	(Stomata mm^{-2})	Entry	(Stomata mm^{-2})
M7	205.2 a[1]	M7	143.8 a	M7	349.0 a
H5	192.3 a	F8	124.1 ab	M5	314.8 ab
M5	190.9 a	M5	123.9 ab	F5	302.4 ab
F5	185.8 ab	H7	117.3 abc	F8	301.6 ab
F8	177.5 abc	F5	116.5 abc	H5	297.6 ab
H7	176.4 abc	M8	114.1 abc	H7	293.6 ab
H8	170.3 abc	H8	113.3 abc	H8	283.6 ab
H6	153.7 bcd	F6	109.7 bc	M8	255.6 ab
M6	143.8 cd	H5	105.3 bc	H6	249.4 ab
M8	141.4 cd	H6	95.6 bc	F6	241.8 ab
F6	132.2 d	M6	94.6 bc	M6	238.4 ab
F7	129.7 d	F7	84.7 c	F7	214.4 b

1. Values followed by the same letter within a column are not significantly different at the 0.05 level according to the Student-Newman-Keul test.

Table 4. Grain weight per head for the male (M) and hybrid (H) germplasm sources grown in 1980 under low and high moisture conditions.

Irrigation Treatment					
Low		High		Mean	
Entry	(g $head^{-1}$)	Entry	(g $head^{-1}$)	Entry	(g $head^{-1}$)
H4	52.1 a[1]	H4	59.9 a	H4	56.0 a
H1	50.4 a	H2	51.3 b	H1	49.4 ab
H2	43.8 a	H1	48.4 b	H2	47.5 ab
H3	37.6 ab	M4	46.6 bc	M4	40.2 bc
M4	33.8 abc	H3	41.3 bc	H3	39.5 bc
M2	20.0 bc	M2	40.1 bc	M2	30.0 c
M1	17.5 c	M1	36.3 c	M1	26.9 c
M3	15.0 c	M3	17.0 d	M3	16.0 d

1. Values followed by the same letter within a column are not significantly different at the 0.05 level according to the Student-Newman-Keul test.

Table 5. Grain weight per head for the male (M) and hybrid (H) germplasm sources grown in 1981 under low and high soil moisture conditions.

Irrigation Treatment					
Low		High		Mean	
Entry	(g $head^{-1}$)	Entry	(g $head^{-1}$)	Entry	(g $head^{-1}$)
H7	45.4 a[1]	H7	54.6 a	H7	50.0 a
H8	44.1 a	H6	54.2 a	H6	45.2 ab
M8	38.9 ab	H5	52.2 a	H8	45.0 ab
H6	36.2 ab	H8	45.9 ab	H5	43.0 ab
H5	33.8 ab	M8	45.5 ab	M8	42.2 ab
M7	31.9 ab	M5	43.1 ab	M7	36.5 ab
M6	23.6 b	M7	41.1 ab	M5	32.7 b
M5	22.4 b	M6	34.4 b	M6	30.0 b

1. Values followed by the same letter within a column are not significantly different at the 0.05 level according to the Student-Newman-Keul test.

had the highest yields under both the stressed and irrigated conditions and it was statistically superior under the high soil moisture conditions.

Hybrid 4 also displayed consistantly the highest transpiration rates in 1980 (Fig. 13). This supports DeWit's (1958) premise that there is a direct relationship between dry matter production and transpiration rates. Hybrid 1 had the second highest yield and also ranked second in transpiration rates.

There were no significant differences in yield for the four hybrids in 1981. Hybrid 7 had the highest yield in both irrigation treatments. There was an overall range in yield of only 14% between the four hybrids in 1981.

SUMMARY

Six sorghum hybrids and their respective male and female parents were evaluated over a two year period for physiological responses under high and low soil moisture conditions. These data suggest that sorghum hybrids better adapted to moisture stress and more stable over a wide range of environmental conditions can be identified using the Finlay and Wilkinson (1963) regression analysis. Hybrid 4 in 1980 was superior to both of its parental lines across all environments for temperature differential, diffusive resistance, transpiration, and apparent photosynthesis. When compared with the three other hybrids evaluated in 1980, hybrid 4 was consistantly superior in temperature differential and transpiration, possessing the highest mean apparent photosynthesis and the lowest mean diffusive resistance. The other hybrids surpassed hybrid 4 under extreme environments. Hybrid 4 had the highest yields under both irrigation treatments in 1980. This same germplasm in 1981 (hybrid 8) was generally superior to its parental lines, but displayed no clear advantage over the other hybrids.

No differences were observed in 1981 for the percent dry weight distributed to the leaf, stem, and root tissue in the four hybrids and their respective parents over the first 35 days after planting. There were differences in the grams of dry weight produced by the individual germplasm sources. Hybrid 8 (hybrid 4 in 1980) had the highest dry weight in leaf, stem, and root tissue at 35 days after planting. Hybrid

8 also had the fastest relative leaf area expansion rate and relative growth rate.

Significant differences in stomatal densities were observed in 1980 and 1981. In 1980, hybrid 4 had the highest density of the four hybrids evaluated. Hybrid 4 surpassed in stomatal density by its own female parent. There was no consistant heterosis for stomatal densities in either year of this study.

Yields in both 1980 and 1981 confirmed the superiority of the hybrids. All six hybrids were superior to their respective male parents under both irrigation treatments. The male parent of hybrid 4 (hybrid 8 in 1981) was consistantly the highest yielding male line. Male 4 outyielded hybrid 3 in 1980 under both soil moisture conditions and hybrids 5 and 6 under low soil moisture conditions in 1981.

Evaluations of physiological responses in sorghum germplasm across diverse environments would help in the identification of stable and drought resistant material. This information could prove invaluable to the plant scientist in the development of superior cultivars.

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