Apparent Sap Velocity in Peanut Genotypes Under Control and Stress Conditions[1]

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ABSTRACT

In order to sustain plant growth and hydration, water must be continuously supplied to the leaf as it is lost by transpiration. This becomes especially difficult under low soil moisture conditions. The objective of this investigation was to compare peanut (*Arachis hypogaea* L.) genotypes for their ability to maintain water supply to leaves by measuring apparent sap velocity (V_a) under water stress conditions. V_a was determined by the thermoelectric heat pulse method. Three genotypes (Chico, Florunner, and PI 355993) that differed in rooting traits were studied in the greenhouse. Plants were grown in fritted clay in PVC tubes (10.2 cm inside diameter and 76.2 cm in length). Six genotypes, including Chico and PI 355993, were studied in the field. Soil type was Teller sandy loam (fine, mixed, thermic, Udic Argiustoll). Under control conditions in the greenhouse and irrigated conditions in the field, V_a ranged from about 0.8 to 1.1 cm/min for all genotypes. As water was withheld, V_a declined with time in the greenhouse and was significantly lower under rainfed (-0.25 MPa soil potential) than irrigated (-0.10 MPa soil potential) conditions in the field. Significant genotypic differences were found in both greenhouse and field experiments. Chico maintained the highest V_a ratio (stress V_a/control V_a) in the greenhouse. PI 404021, Chico, and PI 355993 showed the least reduction (20, 26, and 29%, respectively) in V_a under rainfed conditions in the field. Thus, the data are indicative of differences among peanut genotypes in maintaining V_a under stress conditions. Knowledge of V_a could be useful in determining relationships between root activity, soil water content, and water uptake and in selecting genotypes for inclusion in breeding programs to develop cultivars that avoid drought stress.

Key Words: *Arachis hypogaea* L. , groundnut, water stress, transpiration, water flow, water potential, root resistance, thermoelectric heat pulse, drought tolerance.

Water must be moved to cells of plant leaves almost continuously to replace water lost by transpiration. Maintenance of hydration sufficient to sustain growth becomes very difficult under low soil moisture conditions. There are two components of water flow in intact plants under high soil moisture conditions: one for growth and one for transpiration (9). Two concepts are expressed in the literature concerning the driving force for transpiration water flow: One considers the water potential difference between the root

and leaf as the primary force (9, 10, 22), while the other considers hydrostatic and osmotic pressure differences as the factors determining water flow (25, 26, 31). In either case, water flow is opposed by transport resistances within the root, xylem, and leaf. Roots have a low conductance for water and represent an important rate-limiting barrier to water movement in the plant (9, 20). The intracellular path occurs during growth of plant tissues when water must be transported from cell to cell and offers a high resistance to water transport (8, 9). Compared to cell-to-cell transport, water evaporation from inside the leaf passing through the stomata as vapor is a low-resistance path (8). However, compared to the liquid phase transport in the xylem, the vapor phase flow is a high-resistance path.

Thus, water transport in the intact plant is a complex phenomenon governed by both internal plant factors and also by external environmental conditions. If water flows primarily for transpiration, roots are the rate-limiting resistance (8, 9, 20). The major water flux consists primarily of transpiration. Several methods have been developed for measuring water flow in intact plants (1, 4, 7, 27, 28). Two thermoelectric approaches (the heat pulse and the steady-state heat flow methods) have been used to study water flow in plants (4, 27).

Saddler and Pitman (27) described a steady-state heat-flow method for measuring sap flow in intact plants. However, their apparatus proved useful only under laboratory conditions and could not be successfully calibrated in the field. Further development of this method by Sakuratani (28, 29) has resulted in a cylindrical heat flow sensor that quantitatively evaluates water flow rate in intact plants. Water flow rates measured by the sensor were in good agreement with transpiration rates determined gravimetrically (29). Additional improvement in the design of the heat flow sensor by Baker and van Bavel (1) confirmed Sakuratani's results and indicated that the heat balance method of measuring sap flow is sufficiently accurate to be useful in many agronomic and physiologic applications.

Bloodworth *et al.* (4, 5) developed a heat pulse method to study water flow in cotton (*Gossypium* sp.) plant stems. Both atmospheric (temperature, humidity, and wind velocity) and soil (soil moisture and salinity) variables affected the rate of water flow, but not the amount and duration of the heat pulse. An increase in soil moisture tension decreased the rate of water flow. Marshall (23) studied sap flow in conifers by heat transport and did a thorough theoretical analysis of the method. The experimental method gave a measure of both heat conduction and convection (heat-

pulse velocity) which was determined to be an accurate measure of "relative sap flow rates." Closs (11), using a theoretical approach similar to Marshall (23) with two points of reference (one below and one above the point of heat application) along the stem, measured the time required for the temperature difference between these points to return to zero as an estimate of water (sap) flow for small plants. The lower sensor measured heat transfer by conduction, while the upper sensor measured heat transfer by both conduction and convection in the sap stream. The difference between the measurements gave the "relative sap flow rate." Closs (11) concluded that this method gave a satisfactory estimate of sap flow in an intact plant and has the advantage of not needing to know the conductivity of the material through which the sap is flowing. This technique also was used by Wendt et al.(35) to estimate relative sap flow rates in monocotyledons. Recent innovations in the heat-pulse method are described by Stone and Shirazi (32) and Gray et al.(17). The improved thermoelectric probe (17) for measurements of "apparent sap velocity" or "relative sap flow," designated V_a below, was used to further study this phenomenon in intact peanut (Arachis hypogaea L.) plants. The objective was to compare V_a of different peanut genotypes and study their ability to maintain water supply to leaves during induced water stress.

Materials and Methods

Three peanut genotypes (Florunner, Chico, and PI 355993), found by Ketring (18, 19) to differ in rooting traits, were grown in two experiments in a fiberglass greenhouse. The genotypes were chosen because of their genetic diversity in rooting characteristics (Table 1). Chico is smaller in all traits than Florunner and PI 355993, while Florunner had more lateral roots at 1-meter dept, and PI 355993 had the largest volume of roots. Our interest was in determining which of these rooting traits would be most beneficial in maintaining water supply to leaves under stress. Plants were grown in PVC tubes of 10.2 cm inside diameter and 76.2 cm length. The tubes contained fritted clay described by van Bavel et al. (34). Fine particles were removed using a 14-mesh stainless steel screen. The fritted clay was found to be a suitable medium for growing plants and easily washed away from roots. Plants were fertilized twice weekly with 200 mL of modified Hoagland solution containing additional Ca^{++} (10 mM) and NO_3^- (25 mM) and were watered twice daily until water was withheld for the stress treatment. Each tube contained one plant. Experiments No. 1 and No. 2 in the greenhouse (designated EXPT-1 and EXPT-2 in the figures) were planted 1 February and 18 April 1984, respectively. Stress was initiated by withholding water, beginning 23 March and 18 May, 51 and 30 days after planting (DAP) for EXPT-1 and EXPT-2, respectively. Phenological stages of the plants progressed from vegetative (30 DAP) to early reproductive development (flowering to early fruiting, 71 DAP) during the experiments. These times are inclusive of when rooting traits were determined (18, 19). The results indicate that stage of development did not change the comparative V_a ranking between genotypes under stress. The experiments were terminated to obtain shoot and root growth measurements (18, 19). Stress in EXPT-2 was initiated earlier to determine the effect of plant age on apparent sap velocity (V_a). In greenhouse experiments, because the plants did not have sufficient lateral branch length at early growth stages, the thermoelectric probe (17) was attached to the petiole of the uppermost fully expanded leaf on the main stem (usually the 2nd node below the main stem apex). V_a was measured five times following stress initiation in EXPT-1 and four times in EXPT-2 (DAP for each measurement time is given in the figures). Measurements were made from 1030 to 1330 and 0930 to 1230 hours solar time under full sun for EXPT-1 and EXPT-2, respectively. The requirement for full sun to maximize the stress limited the number of times measurements could be made. Plants were harvested 71 and 56 DAP for EXPT-1 and EXPT-2, respectively. Shoots and roots were separated, air dried in the greenhouse for about 2 weeks, and weighed. EXPT-1 was a randomized block with three replications, and EXPT-2 was a 6 x 6 Latin square design.

A field test with six genotypes (UF 77318, PI 404021, PI 405915, OK-FH15, PI 355993, and Chico) also was conducted. The breeding line OK-

FH15 is a selection from Comet X Florunner with the same virginia-runner growth habit as Florunner, but was found to be more drought tolerant than Florunner (14). For this reason, OK-FH15 was substituted for Florunner in the field test. The other genotypes were chosen because of their previous inclusion in root growth studies (18) and their purported drought tolerance. The field test was conducted at the Agronomy Research Station, Perkins, OK. Soil type was a Teller sandy loam (fine, mixed, thermic, Udic Argiustoll). Two-row plots (0.91 m wide by 6.1 m long) with two-row borders were planted with a two-row cone planter on 31 May 1984 in a randomized block design with two replications and two water treatments (irrigated and rainfed). One hundred seeds were planted per each 6.1 m of row length. About 5 cm of water was applied weekly to the irrigated plots with a solid-set impact type irrigation system (14). Only two replications were used because the automated heat pulse application and measuring equipment would accommodate just 12 sensors for sequential heat pulse application (6 genotypes X 2 replications), and the sensors must be moved manually between replications. This provided the minimum time between successive measurements in order to have similar environmental conditions during the measurements. All replications were measured sequentially on the same day. Measurement of V_a in the field was between 1130 and 1430 hours solar time at 77 DAP. The plants were at growth stages comparable to the greenhouse-grown plants at 71 DAP in EXPT-1. The thermoelectric probe was attached to a lateral branch in the field test. The equipment used to determine V_a is described by Stone and Shirazi (32), and the method for measuring V_a follows their procedure with the improved thermoelectric probe described by Gray et al. (17). The time required for the peak of the heat pulse to move from the heater wire to the thermistor was determined. Also, since water uptake and V_a measured simultaneously have similar patterns (15, 32), V_a can provide a relative measure of sap velocity for comparisons between peanut genotypes and between water treatments.

Results and Discussion

The control plants maintained V_a between 0.8 to 1.0 cm/min (Fig. 1A). Chico had the lowest control V_a (0.8 to 0.9 cm/min.) from 50 to 63 DAP, but was equal to the other genotypes at 65 and 70 DAP. Plants previously selected in the randomization to be stressed also had V_a's of 0.8 to 1.0 cm/min except Chico on the day stress began (Fig. 1B). However, all genotypes had similar V_a at 54 DAP, three days after stress was initiated by withholding water at 51 DAP. In the stress treatment at 59, 65, and 71 DAP, Florunner had significantly (P< 0.05) less V_a than both Chico and PI 355993, and at 63 DAP was less than Chico (Fig. 1B). Although the genotypes maintained similar control V_a, there were significant differences under stress (Fig 1A and 1B). A relative comparison (stress/control V_a ratio) shows that after stress began Chico maintained a V_a ratio of 1.0 from 54 to 63 DAP while the V_a ratio of Florunner and PI 355993 declined (Fig. 2). By the end of the experiment Florunner had the lowest V_a ratio. The ability to maintain V_a under drying soil conditions may be a means to escape or tolerate drought (maintain water supply to leaves). However, based on rooting traits shown in Table 1, it was not expected that Chico would maintain V_a better than the other genotypes. Florunner with more lateral roots or PI 355993 with larger root volume would be expected to maintain V_a better than Chico unless: 1) larger plants depleted the water supply faster than smaller plants, 2) root resistance to water flow was higher in Florunner and PI 355993 than in Chico, or 3) roots of Florunner and PI 355993 "sensed" the drying soil sooner than Chico and consequently V_a declined earlier than for Chico. Under drying soil conditions, a change in growth partitioning can occur which results in more root growth and higher root/shoot ratios. Pandey et al. (24) showed that peanut had more root length density deeper in the soil than three other legumes and adjusted shoot growth (reduced

leaf area and slower growth) in response to drought. These changes in growth were considered a means of drought avoidance. Under well-watered conditions, root and shoot growth of peanut genotypes is highly correlated (18, 19). Under stress conditions in studies here both shoot and root growth were reduced except for PI 355993, which showed a slight but not significant increase in both shoot and root dry weight (Table 2). The root/shoot ratio increased under stress, but was not significantly different among the genotypes (Table 2). The linear correlation coefficient (r) between root and shoot dry weight was 0.97 (P < 0.01), which agrees with previous findings (18, 19). Thus, for plants of this age it apparently was not a genetic difference in growth partitioning to more root growth or a specific rooting trait (Table 1) that resulted in higher V_a and V_a ratio for Chico and PI 355993 than for Florunner.

In studies designed to manipulate root/shoot ratios, Eavis and Taylor (13) found no consistent relation between transpiration rate and root/shoot ratio of soybean (*Glycine max* L.). The relation they found was between transpiration rate and soil water content. In view of recent evidence (2, 3), the conclusion to be drawn is that shoots can be controlled by signals from the roots (26). Bates and Hall (2) hypothesized that in treatments that differed in leaf conductance but were
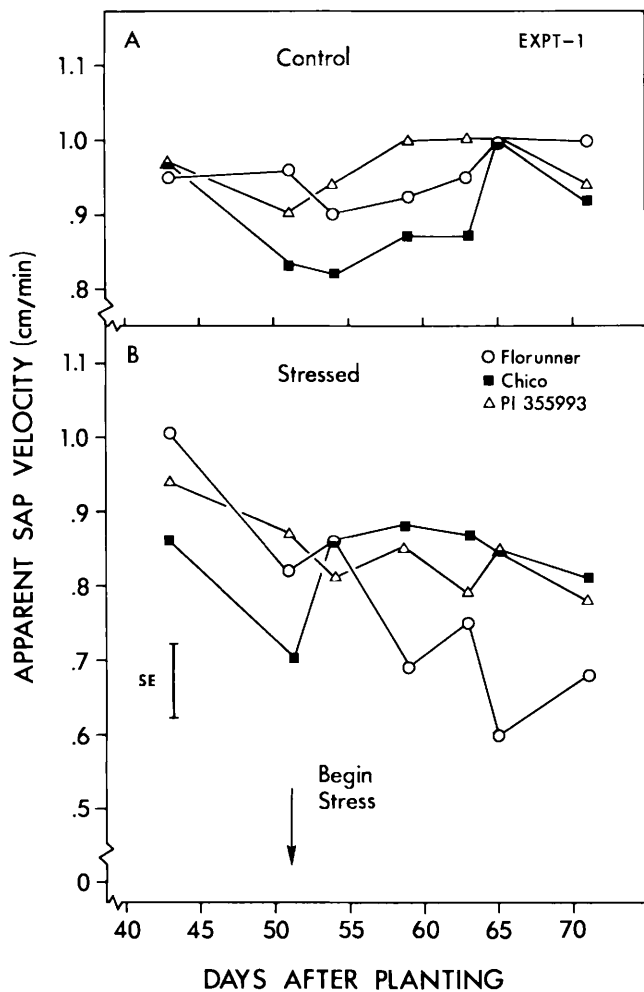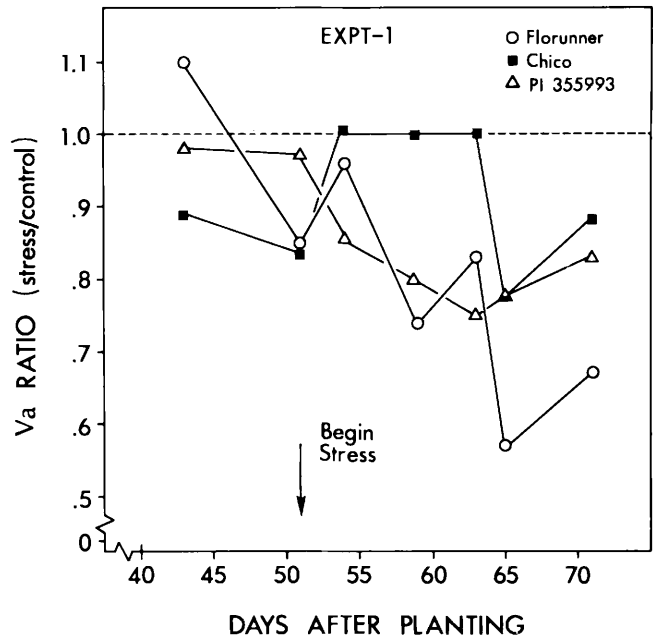

Fig. 2. EXPT-1 V_a ratio (stress/control) of peanut genotypes.

Table 1. Root characteristics of peanut genotypes used for apparent sap velocity measurements.

Genotype[1]	Tap root length[3]	Roots at 1-m depth[3]	Root volume	Root dry wt
	cm	no.	mL	g
Chico	154	1.2	20.6	1.55
Florunner	193	4.9	23.5[2]	2.30[2]
PI 355993	194[2]	3.0	32.4	2.62

[1] Botanical types are spanish, virginia-runner, and valencia for Chico, Florunner, and PI 355993, respectively.

[2] Values normalized to the standard cultivar Tamnut 74 which was grown in all experiments. This is necessary to compensate for different environmental effects on growth if comparisons of genotypes between experiments are made. Data from references 18 and 19.

[3] Tap root length and strong, downward-growing lateral roots were from a previous study (19).

similar in leaf water potential, soil water depletion induced changes in root water status that mediated leaf conductance by effects on the flow of information from root to shoot. A continuous supply of cytokinin from the roots may be necessary to maintain maximal stomatal opening in maize (*Zea mays* L.) when soil drying affects root activity (3). It may be that differences in transpiration of the peanut genotypes due to declining soil water could be related to information (possibly phytohormones) supplied by the roots and these hormones also function in the correlative growth response of the plants.

EXPT-2 conducted with younger plants gave the same results. Control plants had V_a of about 0.8 to 1.1 cm/min. (Fig. 3A). There apparently was a transient decline in V_a of the genotypes in both control and stress treatments prior to

Fig. 1. Experiment 1 (EXPT-1). Apparent sap velocity (V_a) of peanut genotypes under well-watered (A) and stressed (B) conditions in the greenhouse.

Table 2. Root and shoot growth of peanut genotypes tested for apparent sap velocity in the greenhouse, Experiment 1.

Genotype and treatment		Root dry wt	Shoot dry wt	Root/shoot ratio
		g	g	
Florunner	Control	4.14a[1]	12.57a	0.33a
	Stress	3.00b	7.37b	0.41b
PI 355993	Control	1.32c	4.33bc	0.32a
	Stress	1.95bc	4.85bc	0.41b
Chico	Control	1.93bc	5.91bc	0.36a
	Stress	1.16c	2.47c	0.45b

[1] Mean values within columns followed by the same letter were not significantly different (P < 0.05) according to Duncan's multiple range test. Stress began 51 DAP, and harvest was at 71 DAP.

stress initiation (Fig. 3A and 3B, cause is unknown), but stress V_a remained at least equal to minimum control V_a until a substantial decline occurred at 41 DAP, 11 days after stress initiation. At 5 days after stress initiation (35 DAP) there was only a slight decline in V_a of Florunner and PI 355993, while V_a of Chico actually increased (Fig. 3B). Thereafter, V_a declined steadily for all genotypes. Again, although the genotypes maintained similar control V_a, there were significant differences (P < 0.05) between genotypes under stress. This was evident at 41 and 54 DAP (Fig. 3B). A relative comparison (stress/control V_a ratio) shows that from the time a noticeable stress effect occurred (35 DAP) until the end of the experiment, Chico had the highest V_a ratio followed by PI 355993 and then Florunner (Fig. 4). Growth of the plants under stress in EXPT-2 resulted in higher root/shoot ratios, primarily due to greater reduction in shoot than root dry weight (Table 3). Due to this differential growth response by the younger plants under stress, the r value for the relationship of roots to shoots (0.71, P < 0.01) was less than the older plants in EXPT-1. This reduction in shoot growth relative to root growth agrees with the data of Pandey et al. (24). Their and our measurements were made at 55 and 56 DAP, respectively. Apparently the younger plants were able to adapt more readily to the stress condition than the older plants. Both Chico and PI 355993 had significantly higher root/shoot ratios than Florunner (Table 3). This could be a factor in maintenance of comparatively high V_a under drying soil conditions (Fig. 4) which could be a drought avoidance mechanism. A disadvantage could be too rapid a depletion of soil water so that insufficient water is available during fruit development.

A field test was conducted to determine if V_a differed among genotypes under drying soil conditions. Limitations due to container size would not likely be a factor in the field. Table 4 shows the soil moisture conditions early in the season (32 DAP) compared to later in the season (77 DAP) when the V_a measurements were made. Although the irrigated plots had declined somewhat in soil moisture, there was less soil moisture under rainfed (RF) than irrigated (IRR) conditions. Irrigated plots had V_a's of similar (0.8 to 1.1 cm/min) magnitude as those for the control plants in the greenhouse. Under RF conditions, V_a was reduced for all
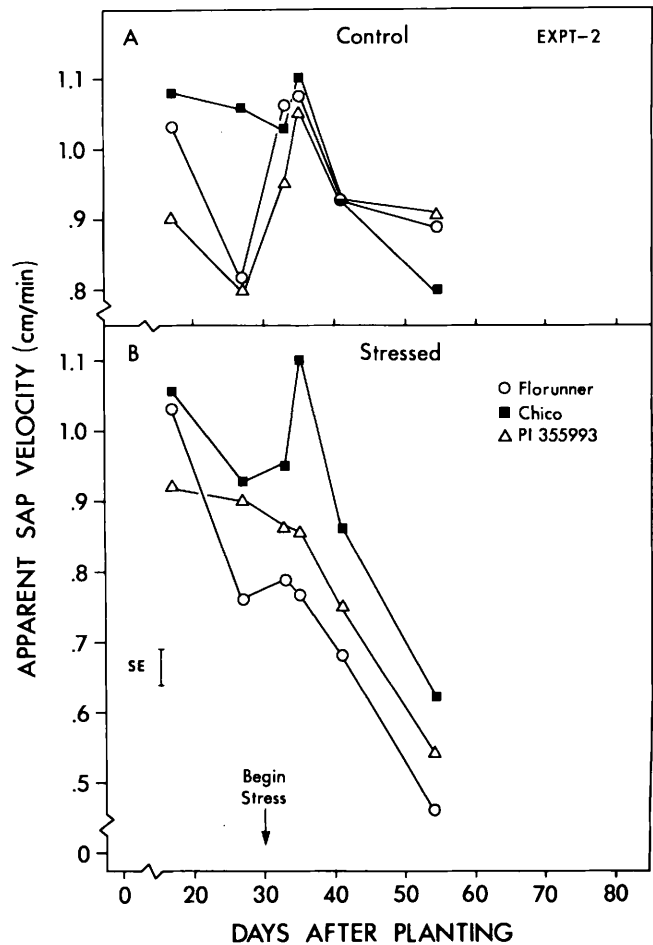

Fig. 3. Experiment 2 (EXPT-2). Apparent sap velocity (V_a) of peanut genotypes under well-watered (A) and stressed (B) conditions in the greenhouse.

genotypes. However, Figure 5 shows a significant differential response of the genotypes under stress, which is the important finding for these studies. The percentage of V_a reduction
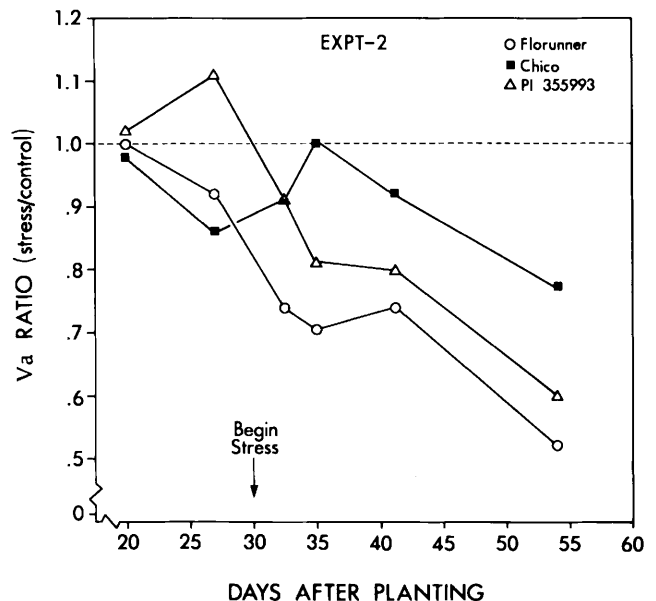

Fig. 4. EXPT-2 V_a ratio (stress/control) of peanut genotypes.

Table 3. Root and shoot growth of peanut genotypes tested for apparent sap velocity in the greenhouse, experiment 2.

Genotype and treatment		Root dry wt	Shoot dry wt	Root/shoot ratio
		g	g	
Florunner	Control	4.09a[1]	8.34a	0.49a
	Stress	3.16b	4.44bc	0.71c
PI 355993	Control	3.08b	6.14b	0.50a
	Stress	2.99b	2.92c	1.02b
Chico	Control	2.18c	4.12c	0.53a
	Stress	2.97b	3.03c	0.98b

[1] Mean values within columns followed by the same letter were not significantly different (P < 0.05) according to Duncan's multiple range test. Stress began 30 DAP, and harvest was at 56 DAP.

Table 4. Soil water relations of Teller loam soil during apparent sap velocity measurements.

DAP	Irrigated		Rainfed	
	Total soil water[3]	Soil water potential	Total soil water[3]	Soil water potential
	cm	MPa	cm	MPa
32[1]	33.1±1.3[2]	-0.02	32.2±0.8	-0.02
77	27.0±2.0	-0.10	22.1±1.2	-0.25

[1] Dates were 2 July 1984 and 15 August 1984.

[2] Mean values ±SD of twelve sites, from a randomized block design with two replications, six neutron tubes per replication.

[3] Total soil water for 120-cm depth.

significantly differed among the genotypes as indicated on the bars for each genotype in Fig. 5. Chico had less percentage reduction in V_a under RF than did PI 355993, but it was not significantly different under field conditions. This is in agreement with the higher stress V_a/control V_a ratio (less reduction of V_a under stress for Chico than PI 355993) during most of the stress treatment in EXPT-1 and -2 (Figs. 2 and 4). V_a reduction of OK-FH15 was greater than but not significantly different from Chico and PI 355993. This could indicate a genetic contribution from the more drought-tolerant spanish parent, Comet. OK-FH15 was intermediate between the Comet and Florunner parents in the apoplastic water fraction through which the major transpirational water flow occurs (14). PI 404021 had the least and PI 405915 the greatest percentage reduction in V_a (Fig. 5). It is interesting that both PI's introduced from Senegal, West Africa, and purported to have drought tolerance, differ in V_a response in drying soil. Maintenance of V_a under drying soil conditions could be a means of drought avoidance for PI 404021 but apparently not for PI 405915. In the same greenhouse test, PI 404021 and PI 405915 had root/shoot ratios of 0.83 and 0.66, respectively (18). Similarly, Chico and UF 77318 had root/shoot ratios of 0.63 and 0.62, respectively (18), but differed significantly in V_a (Fig. 5) under drying soil conditions, as did PI 404021 and PI 405915. Thus, correlative growth response of root and shoot does not entirely explain the genotypic differences in V_a.

Kramer (21), in studying the lag of water uptake behind transpiration, found that roots offered considerable resistance to water flow and that root resistance was much greater than stem resistance. Recently, dynamic changes in the transpiration stream induced by light treatments applied to cucumber (Cucumis sativus L.) leaves were interpreted as predominantly due to lag of root water absorption (20). Bloodworth et al. (4, 5) demonstrated that an increase in soil moisture tension decreased the rate of water flow, as we also found here. The heat pulse method used here was previously found to provide high correlation between V_a and transpiration in a system where water flow was reduced biologically by Verticillium wilt disease (15). Boyer (6) showed that resistances to water transport in intact plants
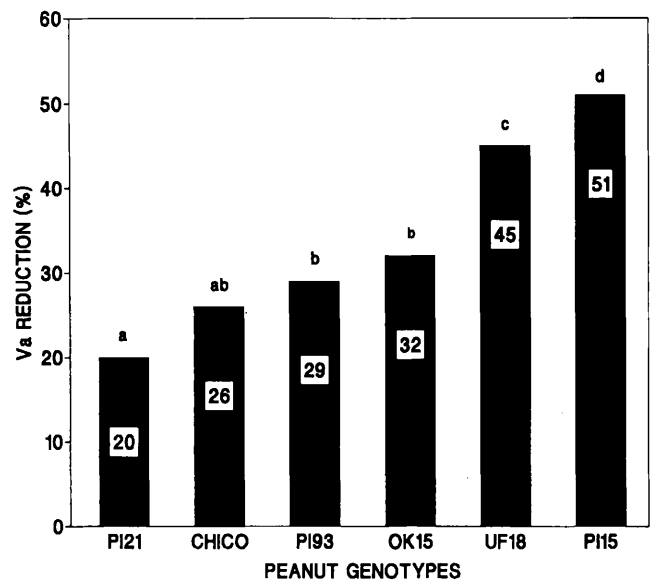

Fig. 5. Percentage V_a reduction of peanut genotypes grown in the field under rainfed conditions. Numbers on bar for each genotype indicate the percentage reduction in V_a from irrigated to rainfed conditions. Different letters above bars indicate significant differences (P<0.05) according to Duncan's multiple range test. Abbreviations: PI 404021, PI21, Chico; PI 355993, PI93; OK-FH15, OK15; UF 77318, UF18; PI 405915, PI15.

differed among species. Others (33) also have found that hydraulic resistance of roots differs between species. Soybean (Glycine max L.) had twice the resistance to water flow as sunflower (Helianthus annus L.) and bean (Phaseolus vulgaris L.) (6). Root resistance was much higher in soybean than in the other species and was located in tissues external to the vascular tissue. A site for radial resistance to flow of water in roots could be the endodermis (30). It was indicated that leaf water potential in soybean would have to decrease about twice as much as in sunflower or bean to supply water to the leaf at the same rate per unit area. Since in EXPT-1 and -2 the plants were under sufficient stress to reduce growth (Tables 1 and 2), the water flow was primarily transpirational flow. Under these conditions, roots are the rate-limiting resistance (8, 9). Our data suggest that one hypothesis to explain differences in V_a among peanut genotypes could be

differences in root resistance. Based on the degree of V_a reduction under stress, PI 404021, Chico, and PI 355993 had lower resistances to sap flow than UF 77318, OK-FH15, and Florunner. PI 405915 had the largest resistance to sap flow under stress. An alternative hypothesis is that roots of peanut genotypes differ in sensitivity to soil water depletion. As a consequence, information (possibly phytohormones) from the roots to the shoots is changed (2, 3). For the peanut genotypes, sensitivity to soil water depletion would be in the opposite order as for resistance.

In addition, transpirational water flux in the plant is dependent on pressure potential gradients that develop between the root xylem and external solution (12). Where root resistance differed (changed by the area of roots present), volume of water flux was much greater at low root resistance at the same pressure difference (12). In intact plants the driving force for water flow is interpreted as the leaf water potential difference between root and shoot by some investigators (9, 10, 22), while others consider the pressure potential gradient as the determining factor (25, 26, 31). Fiscus et al. (16) have proposed a model that takes into account a root transport function, xylem tension, and leaf water potential in an overall water flow system. Their model predictions are in good agreement with the data of Boyer (7,8). However, increasing evidence indicates the importance of plant roots in "sensing" soil water deficits (2, 3, 26, 33).

The heat pulse method used to measure V_a in these studies provided an estimate of sap velocity of intact plants under well-watered and drying soil conditions. Comparisons among the genotypes tested suggest that differences in V_a can occur when the plants are under drying soil conditions. Young plants, 30 to 56 DAP (Table 3), probably adapted by correlative changes in shoot and root growth such that plants with larger root/shoot ratios (less transpiring surface) depleted the soil water at a slower rate, and V_a was sustained at a higher rate (Table 3, Fig. 3). The correlative growth changes could occur by changes in phytohormone synthesis of the roots induced by the drying soil (2, 3, 26). For older plants, 51 to 71 DAP (Table 2) or field plants, a correlative growth response due to drying soil conditions was not evident, but phytohormones could still be involved through alteration of stomatal resistances (2, 3). Differences in root resistance (6, 8, 9, 20, 21, 30, 33) also have been interpreted as causing differences in water flow in plants. Alternatively, without any differential adaptive responses or genetic differences in plant resistances, the peanut genotypes with larger shoots (more transpiring surface) merely used water at a faster rate, and V_a concomitantly declined. This seems unlikely in view of the diversity of germplasm used in the studies and the differences in V_a that were found.

The differences found here among peanut genotypes in ability to maintain sap flow rates to leaves under stress requires further research to establish the contribution of each component (root, xylem, leaf) of the system. With additional information, the heat pulse or other water flow measuring method could be a valuable aid for selecting genotypes with the ability to maintain V_a under stress. Knowledge of V_a could be useful in determining relationships between root activity, soil water content, and water uptake, and perhaps in selecting genotypes for inclusion in breeding programs to develop cultivars that avoid drought stress.

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