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MOISTURE TRANSFER BETWEEN PLANTS THROUGH INTERTWINED ROOT SYSTEMS [1,2]

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The transfer of materials from roots to the soil has received considerable attention (1, 3, 4, 7, 8, 15), yet the transfer of materials from one root to another has received little study, despite the fact that the roots of most plants intimately grow together in soil. That material transfer between plants can occur was demonsrated by the early work of Breazeale (3) and Breazeale and Crider (4) in which wheat seedlings survived on water obtained from the roots of other plants. Recently, Kuntz and Riker (10) have shown that fungus spores, dyes, and poisons can be transported between oak trees through root grafts.

A great deal remains to be learned on the general problem of material transfer between roots. Little is known of the species capable of material transfer, the kinds of materials that move between root systems, the rate and magnitude of their transfer, the mechanisms of transfer, the environmental conditions under which transfer occurs, or the physiological importance of transferred material to the plants involved. Other questions of importance are whether transfer is primarily intra- or interspecific, whether movement of materials is polar or nonpolar when two species are involved, or whether transfer is a general phenomenon occurring in all vegetational situations or an isolated one occurring only under specific circumstances.

To make an experimental approach to the above problems a technique has been developed and several experiments on moisture transfer between plants have been completed. The purpose of these exploratory experiments was to determine whether significant moisture transfer would occur between relatively large tomato plants and to evaluate the physiological importance of the transferred water. An effort was made to assess the effect of certain environmental conditions, e.g., soil, on the success of transfer.

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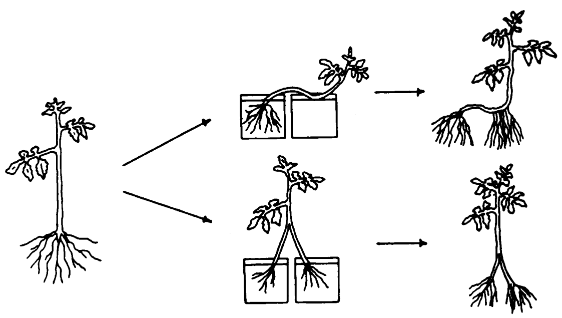
It is hoped that this will be the first of a series of experiments on material transfer between plants and that this and future work ultimately will allow an evaluation of the physiological and ecological importance of material transfer on the behavior of species and the mechanics of vegetation.

Methods and Results

General Technique: The experimental technique, based on the development of two root systems on a single plant, allows an evaluation of the transfer of material from one plant to another through adjacent intertwined root systems.

Double root systems can be developed on tomato seedlings in 7 to 10 weeks after germination in at least 3 ways. First, the exposed root system of a young seedling can be separated into two halves each of which is planted in a separate container thus allowing two discrete root systems to develop. This method was used in experiment one. Second, the stem of a seedling can be bent over, pegged to the soil surface of an adjacent container, and covered with soil and sphagnum moss at the point of contact. In about two weeks, during which both containers are kept moist, a second root system will develop (fig. 1). This method was used in all experiments but the first. In the third method, the root system and lower stem of a robust seedling are split and the halves are planted in separate containers. The exposed split, covered with moist sphagnum, soon calluses over and two discrete root systems develop (fig. 1). The latter two methods allow more flexibility in use than the first.

To permit evaluation of material transfer between plants, a donor plant with two root systems is planted with an experimental or recipient plant. One root system of the donor plant, the donor absorbing or DA system, is planted singly in a container of soil, while the other, the donor transferring or DT root system, is planted in another container along with the roots of the experimental or E plant. Following a period of adjustment during which intimate contact is established between the DT and E root systems, materials



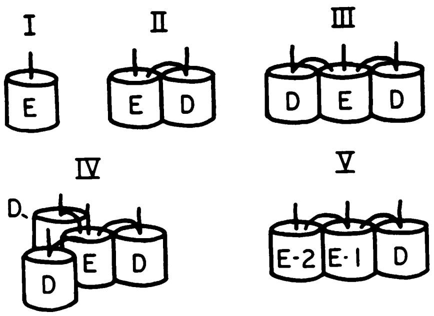


FIG. 1 (*above*). Two methods used to develop double root systems on young tomato seedlings. Above, bending and pegging; below, splitting.

FIG. 2 (*below*). Experimental groups. I represents an experimental plant with no donor; II, III, IV represent experimental plants whose roots are entwined with donor transferring roots of one, two, and three associated donor plants, respectively; V E-2 represents an experimental plant connected with a donor plant through an intervening double rooted experimental plant, V E-1.

such as water or radioactive ions are added to the container holding the DA system and withheld from the container holding the DT and E systems. After an appropriate interval of time, the E plant is checked directly or indirectly for the presence of the material. A positive result indicates that the material was absorbed by the donor plant through its DA system and transferred through its DT system to the experimental plant.

A number of variations on this basic technique are possible. More than one DT system may be planted with one experimental plant (fig 2, III, IV), or the experimental plant may be one or more times removed from the donor plant (fig 2, V). Additionally, the effect of soil on transfer may be tested by varying the media in the containers; for example, sand, loam, or clay may be used. Also, to eliminate the disturbing factor of absorption of ions by soil, the DA system may be grown in a beaker of aerated water to which test ions can be added. Environmental conditions influencing transfer, such as temperature, aeration, or light, also may be controlled.

EXPERIMENTAL WORK

During 1954 and 1955 four experiments were conducted in the Emory University greenhouse to determine the occurrence, rate, and importance of water transfer between intertwined root systems. In all experiments Marglobe wilt resistant tomatoes were used.

EXPERIMENT 1: This experiment was designed as a preliminary study of the transmission of water through adjacent root systems.

In July of 1954, fourteen pairs of plants consisting of an experimental plant and a single donor plant were prepared (fig 2, II). For each pair, two waxed one-pint ice cream containers were stapled together. The DA root system of the six-inch donor plant was planted in one container while in the other the DT system was planted along with the roots of a 6-inch experimental plant. A mixture of two-thirds loamy sand plus 1/6 manure plus 1/6 peat moss was used as a soil mixture in both containers. The paired containers were separated from one another by a layer of aluminum foil and were placed in dry flats.

After a two-week adjustment period, two groups of seven pairs each were randomly selected and subjected to drought from August 15 to 22. In the first group, 1 to 7, neither plant of a pair received any water during the drought period. In this case the "donor" plant was in reality a second experimental plant. In the second group, 8 to 14, the DA system of the donor plant was watered regularly while the containers holding the DT and E systems received no water.

During the drought period the experimental plants in both groups and the "donor" plants in the 1–7 group were scored for turgidity in accordance with the turgidity scale presented in table I. When the majority of the plants in the 1–7 group reached the severely wilted stage, on August 22, all plants were watered and recovery of turgidity was checked at hourly intervals for 6 hours.

RESULTS OF EXP'T 1: The 1–7 E group wilted most rapidly and on August 22, 86 % of the plants had reached the severely wilted stage (table II). The 1–7 " D " group followed the same trend, but showed a lesser degree of wilting with 29 % in the severely wilted category and 71 % in the wilted stage. The slightly better performance of the 1–7 "D" group might be because the "D" plants had access to two containers of soil while the E plants were restricted to one container.

TABLE I

TURGOR CATEGORIES DURING EXPERIMENTS 1, 2, AND 3

CATEGORY	TURGOR CONDITION OF PLANT
0	Fully turgid. No obvious sign of wilting.
1	Turgid. All but the lowermost leaves turgid.
2	Moderately wilted. Only the uppermost three or less leaves turgid.
3	Wilted. All leaves flaccid but not tightly curled.
4	Severely wilted. All leaves wilted and tightly curled, stem shriveled.

The 8–14 E group showed less tendency to wilt than either of the above groups, on the last day of drought only 14 % were severely wilted while 29 % were fully turgid (table II).

Recovery occurred in an inverse fashion to that of wilting. The 8–14 E group recovered most rapidly. After 4.5 hours, 86 % and 14 % were in the fully turgid and turgid categories, respectively. Groups 1–7 E and 1–7 D, after 5.5 hours, had only 29 % fully turgid, with 14 % severely wilted and 57 % in intermediate categories (table II).

These results indicate that roots of a plant not receiving water directly, but associated with roots of another plant receiving water through another root system, are able to obtain water from that plant in a sufficient quantity to delay wilting. Consequently, when water is again made directly available, recovery is speeded up. The ability of some plants in the 8–14 E group to maintain maximum turgor during an extensive drought period indicates that substantial quantities of moisture must be transferred in some instances.

Experiment 2: This experiment was designed to test the effect on moisture transfer of more than one donor plant and to determine the possibility of serial transfer through an intermediate plant. The effect of transferred water on the post-drought condition of experimental plants was also investigated.

Five different groups of plants were used in this experiment. Group I E consisted of experimental plants with no associated donor plants (fig 2, I). Groups II E and III E experimental plants had one and two associated donor plants, respectively (fig 2, II, III). Group V E-1 experimental plants, with double roots, had one system associated with a DT root system and the other associated with the roots of another experimental plant (fig 2, V E-1). Group V E-2 experimental plants were once removed from donor plants and could receive water only through intervening V E-1 plants (fig 2, V E-2). Group I E was replicated ten times, II E eight times, III E nine times, and V E-1 and V E-2 had seven replications each.

Waxed ice cream containers and the same soil used in experiment one were used here.

A drought period lasting from August 31 to September 8 was begun after the root systems in the various groups had become well established. Water was withheld from all E plants while it was added regularly to all D plants through their DA root systems. A regular watering schedule was reinstituted for all plants on September 8.

During the drought period and the first twenty-four hours of the recovery period all E plants were scored in accordance with the turgidity scale in table I. Approximately ten days after general watering was reinstituted, all experimental plants were examined and the number of dead, completely defoliated, and relatively normal plants was recorded along with the number of dead leaves on the normal plants. Growth and interdevelopment of adjacent root systems was also noted.

Results of Exp't 2: Group I E, with no donor root systems, showed the first signs of severe wilting and with the exception of one plant wilted relatively rapidly thereafter (table III). Group V E-2, whose connection with a donor plant was through an intervening experimental plant, did not show severe wilting as early as I E, but once severe wilting began this group wilted rapidly. The three remaining groups of experimental plants, all with one or more associated DT root systems, retained turgidity longer than the I E and V E-2 groups. Group V E-1 wilted more slowly than II E, perhaps because V E-1 plants ob-

Table II

Experiment 1. Percentage of Plants in Various Turgor Categories during Drought and Recovery Periods

Group	Turgor Category	Drought (August 15 to 22)						Recovery (hrs after watering)					
		15	17	18	19	20	22	0.5	1.5	2.5	3.5	4.5	5.5
II E * (1–7)	0	100	..	..	..	...	..	..	..	..	..	14	29
	1	...	..	..	..	...	..	..	..	..	..	..	14
	2	...	14	43	14	...	..	..	..	..	29	43	43
	3	...	86	57	86	100	14	29	29	71	57	29	..
	4	...	..	..	..	...	86	71	71	29	14	14	14
II D (1–7)	0	100	..	..	..	...	..	..	..	..	14	29	29
	1	...	..	43	..	...	..	..	..	14	14	14	29
	2	...	43	14	43	43	..	..	..	29	29	29	14
	3	...	57	43	57	57	71	71	71	43	29	14	14
	4	...	..	..	..	...	29	29	29	14	14	14	14
II E** (8–14)	0	100	14	14	14	29	29	29	29	29	43	86	86
	1	...	14	14	14	14	..	..	..	14	29	14	14
	2	...	43	43	43	43	14	14	14	43	14	..	..
	3	...	29	29	29	14	43	43	57	14	14	..	..
	4	...	..	..	..	...	14	14	..	..	..	..	..

* Donor plants in replications 1–7 received no water during drought period.
** Donor plants in replications 8–14 received water throughout experiment.

Table III

Experiment 2. Percentage of Plants in Various Turgor Categories during the Drought Period, September 1 to September 8

Group	Turgor Category	Date							
		1	2	3	4	5	6	7	8
	0	100	10	10	10	...	...	...	...
I E (10) *	1	...	30	..	..	...	...	...	...
	2	...	30	10	..	10	10	...	...
	3	...	30	60	30	...	...	...	...
	4	...	..	20	60	90	90	100	100
	0	100	29	14	..	...	...	...	...
V E-2 (7) *	1	...	43	29	..	...	...	...	...
	2	...	14	29	14	...	...	...	...
	3	...	14	29	71	...	...	...	...
	4	...	..	..	14	100	100	100	100
	0	100	43	14	14	...	...	...	...
V E-1 (7) *	1	...	43	71	14	...	...	...	...
	2	...	14	..	57	...	...	...	...
	3	...	..	14	14	57	57	...	...
	4	...	..	..	..	43	43	100	100
	0	100	13	13	..	...	...	...	...
II E (8) *	1	...	25	13	13	...	...	...	...
	2	...	38	13	13	...	...	...	...
	3	...	25	63	63	25	25	...	...
	4	...	..	..	13	75	75	100	100
	0	100	56	33	33	11	11	11	11
III E (9) *	1	...	..	11	..	...	...	...	...
	2	...	22	22	..	11	11	...	...
	3	...	22	33	56	22	33	11	11
	4	...	..	..	11	56	45	78	78

* Number of replications.

tained some water from V E-2 containers early in the drought period. This reaction was similar to that of the 1-7 "D" plants of experiment one. Group III E, with two donors, wilted most slowly with one plant failing to lose turgidity throughout the drought period.

Why two donor plants were more effective than one in supplying an experimental plant with moisture is puzzling. Perhaps two DT systems associated with the roots of an experimental plant increase the surface through which water exchange can take place. Another possibility is that an increased volume of soil water is indirectly available to the experimental plant. If the latter is so, a single donor with a double volume of soil might be as effective as two donors with single volumes of soil.

Recovery, based only on plants capable of recovery with dead, completely defoliated, or turgid plants excepted, proceeded in a fashion inverse to that of wilting (table IV). Group III E recovered most rapidly, 25 % reaching full turgidity within two hours, 50 % in 3 hours, and 100 % in 8 hours. Group V E-1 showed the next most rapid recovery closely followed by II E. Groups V E-2 and I E recovered most slowly. Although several plants of the I E group recovered more rapidly than plants in the V E-2 group, at the end of 24 hours all plants in the latter group had recovered full turgidity while only 60 % of those in the former group had achieved this degree of turgor.

Observations made approximately ten days after the drought treatment ended revealed striking differences between groups (table V). Four out of ten plants in the I E group were dead and a fifth was completely defoliated and only beginning to show new growth. In all other groups no dead plants were found; one defoliated plant was counted in the V E-2 group, but it was observed that the transferring root system of its E-1 partner was poorly developed. Apparently direct or indirect contact with the root system of a donor plant allowed the transmission of enough water to avert death in all instances and to avert complete defoliation in all but one instance and the validity of this instance was questionable. It seems particularly significant that plants in contact with other plants in turn in contact with donors averted the disastrous effects that befell plants with no contact, direct or indirect, with donor plants.

Even relatively normal plants showed significant aftereffects of contact with donor plants during the drought period. Experimental plants associated with two donor systems had only 0.1 dead leaves per plant, while plants in contact with one donor plant, II E and V E-1, had an average of 0.9 and 1.7 dead leaves, respectively. V E-2 plants with indirect donor contact had 2.4 dead leaves, while I E plants with no contact had an average of 3.8 dead leaves (table V).

Table IV

Experiment 2. Percentage of Plants in Various Turgor Categories during Recovery from Wilting, Sept. 8, 9 A.M., to Sept. 9, 9 A.M.

Group	Turgor Category	Hrs after watering									
		0	1	2	3	4	5	6	8	10	24
	0	...	...	...	...	..	..	20	40	60	60
I E (5) *	1	...	...	...	20	20	40	20	20	...	...
	2	...	...	...	...	40	20	20	...	...	...
	3	...	...	20	20	..	..	..	...	...	40
	4	100	100	80	60	40	40	40	40	40	...
	0	...	...	...	...	..	..	..	17	50	100
V E-2 (6) *	1	...	...	...	...	..	..	33	50	33	...
	2	...	...	...	...	17	33	33	17	17	...
	3	...	...	...	...	17	33	..	17	...	...
	4	100	100	100	100	67	33	33	...	...	...
	0	...	...	...	14	43	71	71	86	100	100
V E-1 (7) *	1	...	...	...	29	29	29	29	14	...	...
	2	...	...	14	43	29	..	..	...	...	...
	3	...	...	43	29	..	..	..	...	...	...
	4	100	100	43	...	..	..	..	...	...	...
	0	...	...	...	13	25	63	75	88	88	100
II E (8) *	1	...	...	...	13	25	25	13	...	13	...
	2	...	...	13	25	25	..	..	...	...	...
	3	...	12	25	25	13	..	13	13	...	...
	4	100	88	63	25	13	13	..	...	...	...
	0	...	...	25	50	63	75	88	100	100	100
III E (8) *,**	1	...	13	13	25	25	25	13	...	...	...
	2	...	25	13	13	13	..	..	...	...	...
	3	13	13	38	13	..	..	..	...	...	...
	4	88	50	13	...	..	..	..	...	...	...

Data based on plants with at least a few leaves capable of recovery.

* Number of plants capable of recovery.

** Does not include one plant that failed to wilt.

TABLE V

EXPERIMENT 2. CONDITION OF EXPERIMENTAL PLANTS TEN DAYS AFTER DROUGHT TREATMENT

GROUP	PLANTS PER GROUP	DEAD PLANTS	LIVING PLANTS: PLANTS WITH ALL LEAVES DEAD, NEW GROWTH ONLY	PLANTS WITH FEW DEAD LEAVES, NORMAL GROWTH	AV. NO. DEAD LEAVES PER NORMAL PLANT
I E	10	4	1	5	3.8
V E-2	7	0	1*	6	2.4**
V E-1	7	0	0	7	1.7†
II E	8	0	0	8	0.9
III E	9	0	0	9	0.1

* Transferring root system poorly developed.
** No record of dead leaves on 2 plants.
† No record of dead leaves on 1 plant.

The results of this experiment indicate that plants in direct or indirect contact with donor plants can obtain sufficient water from adjacent root systems to delay the on-set of wilting and, consequently, to speed-up recovery when water is again made directly available. Perhaps more important, this experiment indicates that for a period of time experimental plants in direct or indirect contact with donor plants can obtain quantities of water sufficient to prevent serious defoliation and death that occurs when such contact does not exist.

EXPERIMENT 3: Moisture transfer in previous experiments occurred between root systems growing in a loamy sand, peat, and manure mixture. This experiment was designed to determine the effect of another soil medium, sand, on the transfer of moisture.

A random block experimental design was employed in which each block contained three experimental plants: one with no donors, one with a single donor, and one with two donors (fig 2, I, II, III). Each block was replicated five times.

Double root systems were developed and groups were set up as in experiment two, however relatively pure medium textured sand was used as the soil medium. During the period of establishment the plants were watered with a dilute solution of Vigoro.

The drought period for the experimental plants lasted from the 10th to the 28th of September when watering of all plants was resumed. During the period of drought and recovery the turgor condition of the experimental plants was scored in accordance with the turgidity scale shown in table I.

At the conclusion of the experiment, observations were made on the number of living and dead experimental plants and the number of dead leaves per living plant. Also, an examination of associated E and DT root systems was made to determine their development, the extent of their intergrowth, and the existence of possible root grafts. This examination was facilitated by allowing the plants to wilt slightly, cutting the connection between the DT and DA systems, and allowing the DT portion to absorb a solution of eosin Y which, in turn, stained the DT system.

RESULTS OF EXP'T 3: The results, presented in table VI, are similar to those of earlier experiments. Group III E, with two donor systems, wilted most slowly and recovered most rapidly, while I E plants, with no donor system, wilted rapidly and recovered slowly. Group II E, with one donor, was intermediate in response.

Four out of five I E plants died as a result of drought, while no deaths were recorded in the other groups. The one surviving I E plant suffered greater leaf damage than the III E plants, while leaf damage to the II E group was intermediate.

The similarity between the results of this experiment using sand as a soil medium and those of previous experiments utilizing loam indicates that moisture transfer can take place under a range of soil conditions and that it is not always dependent on large amounts of colloidal matter in the soil.

Eosin uptake in most groups was considerable and examination of associated DT and E roots indicated that they were well developed and thoroughly intergrown. However, no root grafts were detected. At some points of contact between fine DT and E roots eosin *appeared* to be spreading from the DT roots over the surface of the colorless E roots.

EXPERIMENT 4: In all previous work, waxed ice cream containers with no provision for bottom drainage were used and it was thought possible that an accumulation of free water in the bottom of the DA containers might have influenced moisture transfer.

TABLE VI

EXPERIMENT 3. PERCENTAGE OF PLANTS IN VARIOUS TURGOR CATEGORIES DURING DROUGHT AND RECOVERY PERIODS

GROUP	TURGOR CATEGORY	DROUGHT (SEPTEMBER 10 TO 28) 10	16	20	24	28	RECOVERY* (HRS AFTER WATERING) 4	10	24	48
	0	100	20	...	...	...	...	...	...	100
I E**	1	...	..	...	...	...	...	...	100	...
	2	...	..	...	...	...	...	...	...	...
	3	...	20	40	...	...	...	100	...	...
	4	...	60	60	100	100	100	...	...	...
	0	100	40	...	...	...	...	...	100	100
II E	1	...	..	...	...	...	...	40	...	...
	2	...	40	20	...	...	...	60	...	...
	3	...	20	40	...	...	...	...	...	...
	4	...	..	40	100	100	100	...	...	...
	0	100	80	100	...	...	60	100	100	100
III E	1	...	20	...	20	40	40	...	...	...
	2	...	..	...	40	...	...	...	...	...
	3	...	..	...	20	60	...	...	...	...
	4	...	..	...	20	...	...	...	...	...

* All plants watered regularly beginning September 28, 8 A.M.
** Recovery data based on one living plant.

TABLE VII

EXPERIMENT 4. PERCENTAGE OF PLANTS IN VARIOUS TURGOR CATEGORIES DURING DROUGHT AND RECOVERY PERIODS

GROUP	TURGOR CATEGORY	DROUGHT (AUGUST 6 TO 12)							RECOVERY (HRS AFTER WATERING)			
		6	7	8	9	10	11	12	1	2	3	4
	1	50	25	...	50	...	...	...	...	...	...	25
I E	2	50	75	100	50	25	...	...	...	...	25	...
	3	..	..	...	...	25	25	...	...	25	...	...
	4	..	..	...	...	50	75	100	100	75	75	75
	1	25	50	...	100	...	...	...	...	...	...	100
II E	2	75	50	100	...	75	25	...	...	75	100	...
	3	..	..	...	...	25	75	50	50	25	...	...
	4	..	..	...	...	...	...	50	50	...	...	...
	1	25	25	...	25	...	...	...	...	...	25	75
III E	2	75	75	100	75	75	25	...	25	100	75	25
	3	..	..	...	...	25	50	75	75	...	...	...
	4	..	..	...	...	...	25	25	...	...	...	...
	1	25	..	...	25	...	...	...	...	75	100	100
IV E	2	75	75	100	75	100	100	75	100	25	...	...
	3	..	25	...	...	...	...	25	...	...	...	...
	4	..	..	...	...	...	...	...	...	...	...	...

To check this possibility a fourth experiment was performed during August of 1955 in which all donor and experimental plants were grown in clay pots with bottom drainage.

Four blocks, each composed of four experimental plants with zero, one, two, and three associated donor plants (fig 2, I, II, III, IV), respectively, were set up. Four-inch standard clay pots were used as containers and a loamy sand, peat, and manure mixture was used as soil. To minimize leaf area differences between experimental plants, all large leaves but the four uppermost were removed several days prior to the inauguration of the drought treatment.

Drought treatment for the experimental plants began on August 5 and ended on August 12 when all plants were thoroughly watered. Throughout the drought and recovery period the plants were scored for turgidity; however, the turgidity scale of table I did not portray accurately the various turgidity conditions. Perhaps this was because these plants, averaging sixteen inches in height, were taller and older than the experimental plants used in earlier work, and because many lower leaves had been removed.

Wilting seemed to proceed evenly over the whole plant and was scored in the following manner: 1) Fully turgid; 2) Turgid, terminal leaflets drooping; 3) Wilted, rachis arched and leaflets limp; and 4) Severely wilted, rachis arched, the angle between the petiole and the stem increased from the turgid angle, leaves rolled (particularly the uppermost) and the top of the stem drooping.

At the conclusion of the experiment, root development in several groups with intermingled E and DT systems was examined with a binocular dissecting scope and the observations were recorded.

RESULTS OF EXP'T 4: Results are presented in table VII. Plants in groups I E wilted most rapidly, and at the end of the drought period all were severely wilted. Groups II E had 50 % in the severely wilted stage at the end of the drought period, while III E and IV E had 25 and 0 %, respectively, in this stage. As in previous experiments, an increasing number of donor plants increasingly delayed wilting.

Recovery, based on all experimental plants, was quickest in IV E followed in order by III E, II E, and I E (table VII).

These results, based on donor plants in pots with adequate bottom drainage, are in agreement with those of previous experiments. This is indicative that standing water is not essential to adequate moisture transfer, and that moisture normally held in the soil can be absorbed and transferred by donor plants.

Microscopic examination indicated that E and DT root systems were well intergrown. In most instances roots tended to concentrate on the outer surface of the soil mass where many grew together in strands composed of several roots running parallel to the inner surfaces of the pot. Another experiment in which DT roots were marked with eosin indicated that the strands were composed of both E and DT roots. Some roots were found to be stuck together by a gelatinous substance which characterized their rhizospheres and which when pulled apart seemed to form a fibrous network. Apparently this same material caused soil particles to cling to roots. Root hairs were observed stretching between roots. No actual root grafts were seen, but the possibility of their existence could not be discounted.

DISCUSSION

It seems reasonably clear that the response of experimental plants was due to transferred water rather than to some other cause. Great differences in night and day temperatures might have resulted in condensation of some atmospheric moisture in E containers. If so, the importance of this moisture was probably insignificant since E plants with no donors soon wilted while those with donors tended to remain turgid. Another explanation to be ruled out is that the results were due to differences in size of plants with larger donorless experimental plants wilting more rapidly than smaller experimental plants associated with donor plants. In three experiments, differences in size of experimental plants were more or less evenly distributed throughout all groups, while, in the fouth experiment, plants with no donors were almost always smaller.

Within the bounds of the experimental conditions, moisture was transferred between roots associated in either sand or loam, or through the roots of an intervening plant which itself had access only to transferred water. It was also established that standing water as a source for donor plants is not essential to successful transfer. Water held in potted soils with adequate drainage can be absorbed and transferred by donor plants in significant amounts. The amount of water received by an experimental plant was related to its proximity to the donor plant and to the number of donor plants. An increased number of donor plants improved the ability of E plants to maintain turgor. This might have been due to increased surface contact between DT and E roots resulting from the higher ratio of DT to E roots, or to more soil moisture being indirectly available to the experimental plant.

Water obtained from donor plants, directly or through the roots of an intervening plant, was physiologically significant. It was transferred in quantities sufficient to delay, or even prevent, the onset of wilting in relatively large plants. Consequently, the plants recovered full turgidity and maximum physiological activity more quickly when water was again directly made available. Transferred water also helped to avert or lessen reaction to drought resulting in loss of leaf area. In terms of recipient plants, transferred water not only increased survival, but also allowed them to achieve a greater degree of growth following drought than would have been possible without transferred water during the drought period.

The first step in moisture transfer is loss of water from the donor plant. Although several theories have been advanced to account for loss of water through roots under various environmental conditions—loss in response to tension gradients within continuous moisture films between the roots and soil particles (3), loss by exudation (2), and loss as vapor along a vapor pressure gradient between the root and the surrounding atmosphere (5, 6, 14)—the way in which water molecules moved out of the DT roots in these experiments is uncertain.

There is some indication that transfer occurred only at higher soil moisture tensions. Double rooted E-1 plants with one root system associated with turgid DT roots (expt 2) seemed at first to withdraw available moisture from associated E-2 containers and later to supply water to the same containers. This is in agreement with observations (1, 3) that double rooted plants with one root system in water or in continuously moistened soil withdrew all moisture from a moist soil down to the wilting percentage or built up the moisture content of dry soil to the wilting percentage. This suggests that donor plants withdrew water from E containers until some critical moisture or vapor tension was achieved after which, under appropriate conditions, water was supplied to the containers.

The pathways by which water molecules move from DT root systems to E root systems are obscure. However, at least four possibilities seem to be plausible: 1) from the DT system to soil particles to the root system of the E plant; 2) movement through direct cellular contact between closely appressed roots and root hairs of DT and E systems: 3) movement between adjacent roots, not in cellular contact, through "gelatinous" material that seemed to characterize their rhizospheres; and 4) movement through fine root grafts between DT and E systems.

A plant to soil to plant transfer of moisture was advanced by Breazeale (3) and Breazeale and Crider (4) to explain the survival of small wheat seedlings whose roots were entwined with those of turgid plants in dry soil. This view is partially supported by other evidence that indicates a plant with a portion of its root system in moist soil can lose water to a dry soil through another portion of its roots (1, 3, 4, 7, 15). Breazeale and Crider (1934) suggest that an accurate measurement of water lost in this way would reveal a thin zone of relatively moist soil adjacent to the root, however, it is generally thought that the moisture content of the dry soil is raised only to approximately the wilting percentage (9). Presumably some of the water absorbed by dry soil could be absorbed by the roots of another plant.

A morphological basis for moisture transfer between adjacent roots through closely appressed rootlets or root hairs or through a "gelatinous" matrix extending between them was observed (expts 3 and 4). Examinations of E and eosin-marked DT root systems indicated that roots of both were abundant and intertwined and that many points of direct contact existed between them. The opportunity for transfer by either of the above methods seemed particularly good in instances where young roots of both systems were growing together in relatively long strands composed of 4 or 5 roots plus a common "gelatinous" matrix. These strands might have been caused by the confining nature of the pots, or possibly water deficient E roots may have grown parallel to turgid DT roots in response to the moisture available there. In many places several roots were stuck together by a "gelatinous" substance concentrated in their rhizospheres near the root apices. In single roots, this material apparently caused soil particles to cling to roots causing a soil sheath effect similar to that described by Magistad and Breazeale (13).

Perhaps, sloughed off cells of the root cap or cortex are broken down by micro-organisms to form a heterogeneous "gelatinous" matrix which in turn forms a connection between the root and surrounding soil particles. Water molecules and ions might migrate through this substance toward the root in response to gradients established by activity of the root. Under certain conditions, transfers between roots might occur when their "gelatinous" zones come into contact and a gradient is established between them.

The only evidence for transfer of moisture between roots through cellular or "gelatinous" contact was a single observation made under difficult conditions in which eosin seemed to spread from a DT root along the surface of an appressed E root (expt 3).

No actual root grafts were observed, but accurate observation was extremely difficult because of the thorough intergrowth of the E and DT root systems. It is not unreasonable to suspect grafts may have occurred between succulent tissues of adjacent roots growing under the confined conditions in the containers. Root grafting is known to occur under natural conditions, particularly in woody plants (10, 11, 12). Recently Kuntz and Riker (10) demonstrated the movement of dyes, fungus spores, and poisons between oak trees through root grafts.

The only evidence for grafting in these experiments is of an indirect nature. Several experimental plants were able to maintain almost complete turgor throughout their respective drought periods suggesting a more efficient means of moisture transfer than plant to soil to plant or contact transfer.

Root grafts as a method of transfer seem most unlikely in some instances. Since grafts between distantly related species are unlikely, moisture transfers between tomato and wheat (4) and sunflower and tomato (pilot experiment) indicate that some other means of transfer was operative in these cases. When considering the problem of material transfer in its widest context, however, grafts between species cannot be automatically dismissed since they are known to occur (11).

The evidence at hand indicates that the four methods of transfer may work individually or, perhaps, together in various combinations depending on the circumstances. The determination of the relative importance of each method will have to await further experimentation. Techniques involving the use of radioactive isotopes, large molecules like 2,4-D, biological agents such as plant viruses, and interspecific transfers show promise of resolving these problems and of helping to assay the importance of material transfer in nature.

Summary

The general problem of material transfer between plants is briefly discussed and an experimental method for its evaluation is explained. Data from four experiments on the transfer of moisture between tomato plants are reported.

Moisture was transferred between plants whose roots were associated in sand or loam, or through the roots of an intervening plant which itself had access only to transferred water. It moved in quantities sufficient to delay, or even prevent, the onset of wilting in relatively large plants.

The mechanism of transfer is discussed and it is suggested that transfer occurs only after some critical soil moisture tension is achieved. Several pathways of water movement between roots are suggested.

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