

Stable Carbon Isotope Composition ($\delta^{13}\text{C}$), Water Use Efficiency, and Biomass Productivity of *Lycopersicon esculentum*, *Lycopersicon pennellii*, and the F₁ Hybrid

Received for publication December 21, 1987 and in revised form March 30, 1988

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ABSTRACT

Three tomatoes, *Lycopersicon esculentum* Mill. cv UC82B, a drought-tolerant wild related species, *Lycopersicon pennellii* (Cor.) D'Arcy, and their F₁ hybrid, were grown in containers maintained at three levels of soil moisture. Season-long water use was obtained by summing over the season daily weight losses of each container corrected for soil evaporation. Plant biomass was determined by harvesting and weighing entire dried plants. Season-long water use efficiency (gram dry weight/kilogram H₂O) was calculated by dividing the dry biomass by the season-long water use. The season-long water use efficiency was greatest in the wild parent, poorest in the domestic parent, and intermediate (but closer to the wild parent) in the F₁ hybrid. Instantaneous water-use efficiency (micromole CO₂/millimole H₂O) determined by gas exchange measurements on individual leaves was poorly correlated with season-long water use efficiency. However, the relative abundance of stable carbon isotopes of leaf tissue samples was strongly correlated with the season-long water use efficiency. Also, the isotopic composition and the season-long water use efficiency of each genotype alone were strongly negatively correlated with plant dry weight when the dry weight varied as a function of soil moisture.

Efficient water use confers drought tolerance to plants by maintaining the soil moisture longer. Thus, plants avoid drought stress and the growing season is extended. These are ecologically important factors influencing adaptation of plants to dry habitats. Also, in agriculture efficient water use is desirable because it is, perhaps, the most important of all yield components.

Few traits are as difficult to measure as season-long water use efficiency, WUE_{sl}¹ since the measurements, at least in the agricultural field, must be based on water used by, rather than applied to, a plant for the measurement to be meaningful. Otherwise, a high-yielding individual may have been a luxuriant user of soil water, leaving little moisture for its neighbors. Such a high yielder would be of low WUE_{sl} and would not fare well in a homogeneous population of equals.

WUE_{sl} can be measured in container-grown plants as described by Farquhar and Richards (17). However, only small numbers of plants can be handled this way, and there is concern that such plants are not fully representative of field-grown plants.

¹ Abbreviations: WUE_{sl}, season-long water use efficiency (g dry weight/kg H₂O); WUE_i, instantaneous water use efficiency ($\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$); $\delta^{13}\text{C}$, ratio of $^{13}\text{C}/^{12}\text{C}$ relative to the Pee Dee belemnite standard; C_i, intercellular CO₂ concentration; Rubisco, ribulose-1,5-bisphosphate carboxylase/oxygenase; P_n, rate of net photosynthesis; Tr, rate of transpiration; PPFD, photosynthetic photon flux density (400–700 nm).

Indirect means to evaluate WUE_{sl} accurately in field-grown plants are needed to improve our understanding of water relations and adaptation in native plants and to serve as selection criteria in crop improvement programs. Light-weight portable equipment for measuring rates of photosynthesis and transpiration of individual leaves or canopies are becoming commonplace. Such a measurement (4, 8, 13, 31) yields the WUE_i of the plant part under measurement, and it represents the performance of that plant part at a specific time only. The relationship between such a point measurement and long-term plant performance is uncertain. Micrometeorological approaches to determine the water use efficiency (1) have been partially successful. They give season-long integrated measures, but they are feasible with large, uniform fields only.

Clearly, new, reliable methods to identify individual plants of great WUE_{sl} are needed. The relative ratio of $^{13}\text{C}/^{12}\text{C}$ (typically expressed relative to the PDB standard as $\delta^{13}\text{C}$) in plant tissue samples has been shown to reflect WUE_{sl} in native species (11, 12, 26), and recently the correlation was shown to be strong also in several crop species (5, 15, 17, 19) demonstrating the usefulness of $\delta^{13}\text{C}$ analysis in plant breeding to improve WUE_{sl}. The reason for the correlation between WUE_{sl} and $\delta^{13}\text{C}$ is presently quite well understood (17, 18). Reduced stomatal aperture causes increased WUE_i because the rate of photosynthesis is reduced proportionally less than the rate of transpiration (2, 3, 6, 7, 20), except perhaps under very rare field conditions of extremely stagnant air (large boundary layer resistance) (1, 3, 6, 7, 31). Reduced stomatal aperture also simultaneously decreases the concentration of CO₂ in the intercellular air spaces, C_i. The isotopic discrimination at any moment in time against $^{13}\text{CO}_2$ as a substrate is inherent with the primary carboxylating enzyme of C₃ photosynthesis, Rubisco. It is great when C_i is high, and the discrimination is reduced with decreasing C_i (2, 16, 21, 22, 29). Thus, $\delta^{13}\text{C}$ of a plant or plant part will reflect the integral of C_i over the time of tissue formation as well as the water use efficiency averaged over the growth period, WUE_{sl}.

The enzymic discrimination against ^{13}C is the major cause for the difference in plant $\delta^{13}\text{C}$ and $\delta^{13}\text{C}$ of CO₂ in the air, although minor isotopic fractionation occurs due to different diffusivities and solubilities of $^{13}\text{CO}_2$ and $^{12}\text{CO}_2$ (14, 16, 21). Note also that the relationship between $\delta^{13}\text{C}$ and WUE_{sl} would be similar also if these two parameters were affected by photosynthetic perturbations of the mesophyll (photochemistry, biochemistry), rather than by stomatal behavior, as the theoretical relationships worked out by Farquhar and Richards (17) and Francey and Farquhar (18) show.

The variability in $\delta^{13}\text{C}$ around the mean of a given C₃ species is just a few parts per thousand. Yet, Farquhar and Richards (17) were able to show a strong correlation between $\delta^{13}\text{C}$ and WUE_{sl} in a study on four dwarf wheat varieties, as were Hubick *et al.*

(19) working with diverse peanut germplasm, and Farquhar et al. (14) in a study on several barley cultivars.

This study was undertaken to evaluate new methods that can be used to identify WUE_{st} of field-grown plants. The objectives were (a) to determine the relationship between WUE_i and WUE_{st} , (b) to determine the relationship between $\delta^{13}C$, WUE_{st} , and biomass productivity.

MATERIALS AND METHODS

Plant Material. The following three tomato genotypes were used: (a) *Lycopersicon esculentum* Mill. cv UC82B, a common processing tomato cultivar; (b) *Lycopersicon pennellii* (Cor.) D'Arcy, a wild tomato species native to the deserts of Peru; and (c) the F_1 generation obtained by crossing the two *Lycopersicon* species, using the domestic tomato as the maternal parent (23).

Twenty-seven 5-cm high plantlets (nine of each genotype) were transplanted into separate containers without drainage outlets. Each container held 7.5 L of a standard greenhouse soil mix. A 3-cm thick layer of white crushed rock was put on top of the soil to minimize evaporation from the soil surface. The containers were placed outside in a field on the east side of the Salt Lake Valley, Utah, on June 2, 1986. Nine containers (three replicates of each genotype) were watered to a weight corresponding to 100% of field capacity of the soil. Another nine containers were watered to weights comparable to 50% of field capacity, while the last nine containers were watered to weights comparable to 25% of field capacity. Eight containers without plants, ranging in soil moisture from 10% to 100% of field capacity, were also included to enable estimation of evaporation from the soil surface. Early in the season each container was weighed and watered to the original weight once every day. Later in the season, when the plants grew bigger and drained the soil moisture more rapidly, this procedure was repeated twice every day.

Season-Long Water Use. Season-long water use of each plant was obtained by summing the daily additions of water over the entire season, and by correcting for soil evaporation estimated from the weight losses of the plantless containers.

Plant Biomass. The experiment was terminated by harvesting each plant on August 1, 1986. The tops of the plants were separated from the roots. The root-soil clumps were first shaken free of loose soil and soaked in water in separate containers over night. The remaining soil was then removed by gentle rinsing in a jet of water. The root and the top of each plant were separately dried to constant weight in an oven set at 70°C.

WUE_{st} . WUE_{st} was calculated by dividing the total plant dry weight (top plus root) by the season-long water use. Thus, WUE_{st} represents the amount of dry biomass accumulated over the season for each unit of water spent by the plant (g dry weight/kg H_2O).

WUE_i . Measurements of the rates of net photosynthesis, P_n , and transpiration, Tr , were made every 90 min from sunrise to sunset on July 2, 1986, and again on July 21, 1986. Individual leaves in outer, exposed positions of the canopies were measured with a Portable Leaf Chamber Analyzer System (ADC, Hoddesdon, England). Although P_n and Tr varied dramatically over the light part of the day, WUE_i (P_n/Tr) remained surprisingly constant. The WUE_i values presented in this paper are averages of eight to twelve measurements performed at above 1200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ PPFD over the 2 d of measurement. WUE_i was calculated as the amount of CO_2 fixed per unit of water lost ($\mu\text{mol } CO_2/\text{mmol } H_2O$).

Composition of Stable Carbon Isotopes, $\delta^{13}C$. At the termination of the experiment, 10 leaflets from outer, exposed positions of the canopy were randomly collected and pooled for each plant. The leaves were dried in an oven at 70°C and then ground to a fine powder. Subsamples of the powder were combusted, and the resulting CO_2 was analyzed for the relative abundance of ^{13}C

and ^{12}C as described by Tieszen *et al.* (27). The ratios of $^{13}C/^{12}C$ of the samples were expressed as $\delta^{13}C$ (per mil) relative to the isotopic composition of the belemnite carbonate standard from the Pee Dee formation of South Carolina (9).

RESULTS

The dry weight accumulation over the season of plants grown in containers outside in the field was greater for the domestic tomato species, *L. esculentum* than it was for the South American wild related species, *L. pennellii* (Table I). The size disadvantage of the wild species relative to the domestic tomato remained at about 40% independently of the soil moisture level. The F_1 hybrid grew with exceptional heterotic vigor. The growth advantage of the F_1 generation relative to both its parents was maintained also under greatly reduced soil moisture conditions. However, the size advantage of the F_1 hybrid relative to the domestic tomato cultivar was maximal (about 60%) at the intermediate soil moisture level, and slightly lower (40–50%) at the high and the low moisture levels. The shoot/root ratio (shoot includes stems, leaves and fruits), calculated from dry weight determinations of the plant parts, was very much larger for *L. pennellii* (the means at the three soil moisture levels varied between 27 and 36) than it was for the F_1 generation (10 and 12) and for *L. esculentum* (6 and 10). The shoot/root ratio of each genotype was unexpectedly constant over the great range of soil moisture conditions.

The F_1 generation used the most water over the growing season, *L. pennellii* used the least, while *L. esculentum* was intermediate in its season-long water use (Table I). Although the order of ranking of the three tomato genotypes according to the dry weight accumulation was identical to the order of ranking according to the season-long water use, the order of ranking according to dry weight/water use, *i.e.* WUE_{st} , did not conform to this pattern. Rather, WUE_{st} was greater at all soil moisture levels for the F_1 hybrid than for the domestic tomato cultivar, and WUE_{st} of *L. pennellii* was always greater than for any of the other two genotypes. WUE_{st} increased with conditions of decreasing soil moisture. The relative change was the greatest for *L. pennellii* and the smallest for *L. esculentum*. The advantage in WUE_{st} of *L. pennellii* over *L. esculentum* was 15% at the high soil moisture level. From there it increased to 22% at the intermediate moisture level and to 29% at the low moisture level. The advantage over the domestic tomato of the F_1 hybrid reached 21% at the intermediate soil moisture level and was somewhat lower, but still present, under both the higher and the lower moisture conditions.

WUE_i was determined for each plant with portable gas exchange measurement equipment every 90 min throughout 2 d during the growing season. These measurements were made by clamping the assimilation chamber on leaves in outer, exposed positions of the canopy. Means of WUE_i for each tomato genotype at each soil moisture level are given in Table I. Only measurements made when PPFD exceeded 1200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ were used in the table.

At the end of the experiment, leaf samples were collected from each plant and subsequently analyzed for the composition of stable carbon isotopes, $\delta^{13}C$ (Table I). *L. pennellii* had higher $\delta^{13}C$ values than *L. esculentum* at all soil moisture levels, and the $\delta^{13}C$ values for each genotype increased with decreasing soil moisture. The F_1 hybrid was generally quite close to the wild parent, *L. pennellii*.

Figure 1 shows WUE_i of the 27 plants plotted against their WUE_{st} values. The three panels represent plants grown under the three levels of soil moisture. Although there may appear to be an increase in WUE_i with increasing WUE_{st} , the correlation was not in any case significant at the $P < 0.05$ level. Thus, WUE_i was not an efficient indicator of WUE_{st} .

Figure 2 shows $\delta^{13}C$ of each plant plotted against WUE_{st} . The

Table I. *Experimental Results*

Mean \pm SE of plant water-use; weight of dry biomass in whole plants, shoots, and roots; shoot/root ratio; WUE_{sl} , WUE_i ; and $\delta^{13}\text{C}$ of *L. esculentum*, *L. pennellii*, and the F_1 generation grown at soil moisture levels of 100%, 50% and 25% of field capacity. $n = 3$, except for WUE_i , $n = 9$ to 12.

Genotype	Soil Moisture	Water Use	Dry Weight			Shoot/Root Ratio	WUE_{sl}	WUE_i	$\delta^{13}\text{C}$
			Total	Shoot	Root				
	%	kg	g	g	g	g/g	g/kg	$\mu\text{mol}/\text{mmol}$	per mil
<i>L. esculentum</i>	100	63.5 \pm 2.4	153.4 \pm 10.9	134.4 \pm 8.5	19.0 \pm 3.8	7.2 \pm 1.1	2.41 \pm 0.11	0.95 \pm 0.14	-27.9 \pm 0.2
F_1	100	82.2 \pm 2.9	214.8 \pm 5.0	197.0 \pm 3.1	17.8 \pm 2.0	11.2 \pm 1.1	2.61 \pm 0.06	0.93 \pm 0.34	-26.6 \pm 0.4
<i>L. pennellii</i>	100	33.3 \pm 6.3	92.0 \pm 16.4	89.4 \pm 15.7	2.6 \pm 0.7	35.6 \pm 3.3	2.77 \pm 0.18	1.23 \pm 0.16	-26.1 \pm 0.1
<i>L. esculentum</i>	50	28.3 \pm 1.5	66.9 \pm 6.8	56.7 \pm 5.4	10.2 \pm 1.7	5.6 \pm 0.6	2.37 \pm 0.13	0.84 \pm 0.28	-26.4 \pm 0.2
F_1	50	37.8 \pm 1.9	108.5 \pm 6.0	89.6 \pm 4.5	10.0 \pm 1.5	10.0 \pm 1.1	2.87 \pm 0.09	0.83 \pm 0.29	-25.4 \pm 0.4
<i>L. pennellii</i>	50	13.8 \pm 1.8	39.9 \pm 5.9	38.7 \pm 5.8	1.2 \pm 0.3	32.7 \pm 6.7	2.89 \pm 0.24	1.37 \pm 0.12	-25.0 \pm 0.2
<i>L. esculentum</i>	25	10.3 \pm 0.5	27.7 \pm 0.2	25.1 \pm 0.4	2.6 \pm 0.2	9.8 \pm 0.9	2.68 \pm 0.12	0.81 \pm 0.40	-25.1 \pm 0.1
F_1	25	13.6 \pm 0.7	40.6 \pm 3.2	37.5 \pm 2.7	3.1 \pm 0.5	12.2 \pm 1.3	2.97 \pm 0.09	0.95 \pm 0.06	-24.5 \pm 0.2
<i>L. pennellii</i>	25	4.6 \pm 0.9	16.0 \pm 4.0	15.4 \pm 3.8	0.6 \pm 0.2	27.0 \pm 5.9	3.47 \pm 0.21	1.09 \pm 0.14	-24.7 \pm 0.7

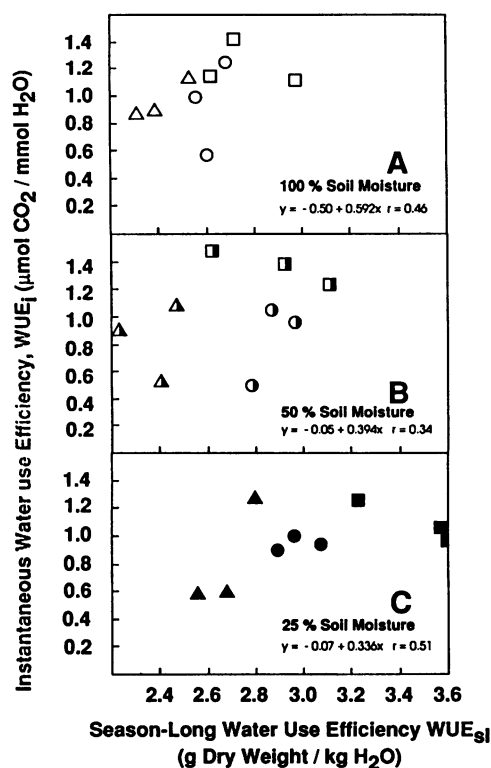


FIG. 1. Relationship between WUE_i and WUE_{sl} . Panels A, B, and C are for plants grown at 100% (open symbols), 50% (half closed symbols), and 25% (closed symbols) of soil field capacity, respectively. Triangles, *L. esculentum*; squares, *L. pennellii*; circles, F_1 hybrid. None of the correlations are significant at the $P < 0.05$ level.

correlation between $\delta^{13}\text{C}$ and WUE_{sl} was much improved over that found between WUE_i and WUE_{sl} in Figure 1. In fact, the correlation between $\delta^{13}\text{C}$ and WUE_{sl} (Fig. 2) was statistically significant at the $P < 0.01$ level at the high moisture level, and significant at the $P < 0.05$ level at the intermediate moisture level. The correlation was not significant at the $P < 0.05$ level at the lowest moisture level, however. The three replicate measurements at each soil moisture level clustered together quite tightly and much better than in Figure 1.

In Figure 3, $\delta^{13}\text{C}$ is plotted and in Figure 4 WUE_{sl} against total plant dry weight for each tomato genotype separately. Both $\delta^{13}\text{C}$ and WUE_{sl} increased when the plant size was reduced by reduc-

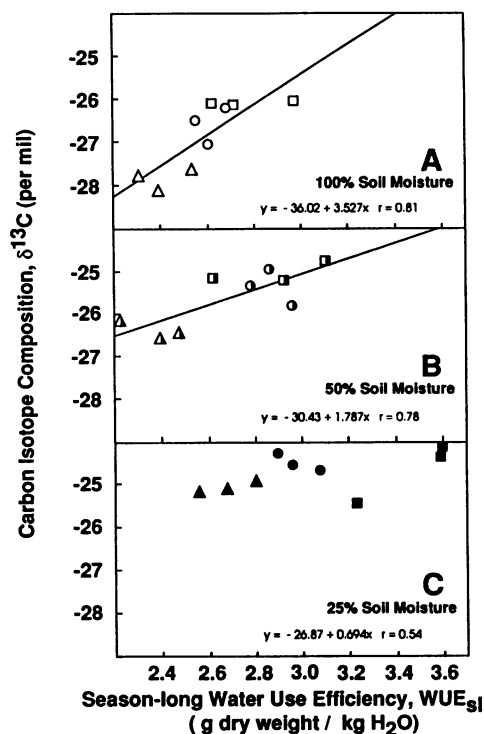


FIG. 2. Relationship between the relative abundance of stable carbon isotopes ($\delta^{13}\text{C}$) of leaf tissue and the WUE_{sl} . Symbols and panel composition are as defined in the legend of Figure 1. The correlations in panels A and B are significant at the $P < 0.01$ and $P < 0.05$ levels, respectively.

ing the soil moisture. Careful comparison reveals, however, that the regression lines of the different genotypes did not follow identical paths. The F_1 hybrid had less negative $\delta^{13}\text{C}$ than any of the parents at any given weight (Fig. 3). WUE_{sl} was also greater in the F_1 hybrid than in *L. pennellii* at comparable plant weights, except when the plants were extremely dwarfed (< 50 g dry weight) by lack of soil moisture (Fig. 4). The negative correlation between $\delta^{13}\text{C}$ and dry weight was statistically significant at the $P < 0.01$ level for all three genotypes (Fig. 3). The correlation between WUE_{sl} and dry weight was significant at the $P < 0.01$ level for the F_1 hybrid, and at the $P < 0.05$ level for *L. pennellii*, but not significant at the $P < 0.05$ level for *L. esculentum* (Fig. 4). WUE_{sl} and $\delta^{13}\text{C}$ were not correlated at the $P < 0.05$ level with the dry weight when the three genotypes were compared at each moisture level separately. The correlation coefficients, r ,

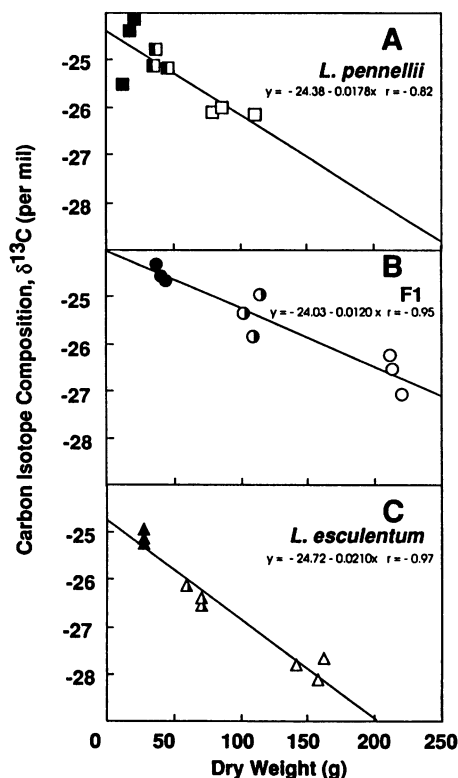


FIG. 3. Relationship between the relative abundance of stable carbon isotopes ($\delta^{13}\text{C}$) of leaf tissue and the total plant dry weight. Panels A, B, and C are for *L. esculentum*, *L. pennellii*, and the F_1 hybrid, respectively. Symbols are as defined in the legend of Figure 1. The correlation in each panel is significant at the $P < 0.01$ level.

were only -0.27 , -0.13 , and 0.26 for $\delta^{13}\text{C}$ versus dry weight at the high, the intermediate, and the low soil moisture level, respectively. The correlation coefficients, r , were -0.33 , 0.13 , and -0.48 for WUE_{sl} versus dry weight at the same three soil moisture levels.

DISCUSSION

The dry matter accumulation was greater for the domestic tomato than for the wild species, while the F_1 hybrid grew bigger than both parents at all three levels of soil moisture (Table I). In greenhouse experiments, Yu (30) observed that the F_1 hybrid grew to about the same extent as did the domestic parent, *L. esculentum*. The lack of heterosis in his study may have resulted from the use of a different cultivar of *L. esculentum* and a different ecotype of *L. pennellii*. It could also have resulted from the particular environmental conditions of the greenhouse, or from the much shorter growth period (3 weeks) than in our experiment. The dry matter accumulation presented by Yu (30) was only a few percent of what was observed in our study.

L. pennellii possesses a great degree of drought tolerance, as reported by Rick (24, 25). In light of the root data presented in Table I, it appears that the drought tolerance is not the result of a large, penetrating root, but that other physiological or morphological/anatomical characteristics must be the basis for this trait. (Unpublished data from our laboratory show that the wild tomato restricts water loss from the leaves much more efficiently than does the domestic tomato, and that this trait is inherited by the F_1 hybrid.)

In breeding for greater yield under water-limited conditions it is important to maximize the yield for each unit of water used by the plant, *i.e.* to optimize WUE_{sl} . Since it is not possible to

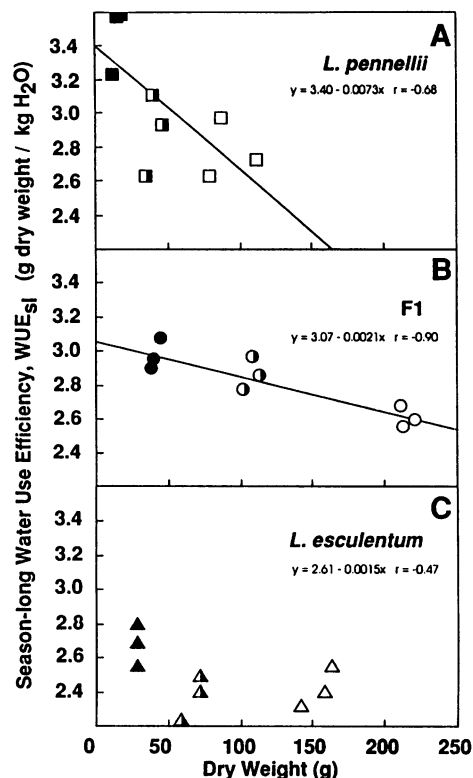


FIG. 4. Relationship between the WUE_{sl} and the total plant dry weight. Symbols are as defined in the legend of Figure 1, and panel composition as in the legend of Figure 3. The correlations in panels A and B are significant at the $P < 0.05$ and $P < 0.01$ levels, respectively.

make direct measurements of WUE_{sl} on large numbers of field-grown plants, tools to indirectly estimate WUE_{sl} are needed. It is then unfortunate, but not unexpected, that WUE_i was a poor indicator of WUE_{sl} (Fig. 1). Another potentially useful tool, which has recently been suggested by Farquhar and coworkers (17, 19) is based on the determination of the relative abundance of stable carbon isotopes, $\delta^{13}\text{C}$, of leaf tissue samples.

Analyses of $\delta^{13}\text{C}$ made it clear that there were large genotypic differences (Table I). *L. esculentum* had more negative $\delta^{13}\text{C}$ values than *L. pennellii*, and the F_1 hybrid fell in between but closer to the wild parent. Figure 2 shows that the slopes of the regression lines correlating $\delta^{13}\text{C}$ with WUE_{sl} were positive at all moisture levels, but that the magnitudes of the slopes were slightly different. In fact, a given change in $\delta^{13}\text{C}$ represented a greater change in WUE_{sl} the lower the soil moisture level was. Therefore, knowledge of the soil moisture conditions is required if any quantitative information on gain in WUE_{sl} is desired from $\delta^{13}\text{C}$ determinations. Other environmental factors that were not investigated in this study will also affect the quantitative relationship between $\delta^{13}\text{C}$ and WUE_{sl} . Among such factors are temperature (10, 28), humidity (4, 13), degree of exposure to sun and wind, and probably many others (12, 14, 20).

Although $\delta^{13}\text{C}$ versus WUE_{sl} of each genotype alone analyzed at the three moisture levels of the soil behaved qualitatively similarly, there were quantitative differences. (Data of these plots are not presented but they can easily be derived from Fig. 2.) The equations for the regression lines and the correlation coefficients were: *L. esculentum*, $y = 4.111x - 36.68$, $r = 0.61$; *L. pennellii*, $y = 1.571x - 30.04$, $r = 0.77$ ($P < 0.05$); F_1 , $y = 4.464x - 38.07$, $r = 0.82$ ($P < 0.01$). Thus the slope was steeper, but the correlation between $\delta^{13}\text{C}$ and WUE_{sl} was less strong, for the domestic parent than for the wild parent, while the slope of the

F₁ hybrid was the steepest and the fit of the regression line the tightest of all genotypes.

Figures 3 and 4 show that $\delta^{13}\text{C}$ as well as WUE_{sl} increased as plant size was kept smaller by reducing the availability of soil moisture. This is a topic which may be of some practical importance. Nevertheless, it should be kept in mind that increased WUE_{sl} means increased total yield per given area of land if the water availability is limiting for growth. Decreased plant size only becomes a disadvantage if the cost of seed is significant, or if the plant size is so dwarfed that available equipment or standard farming practices cannot be used. Since plants exposed to drought stress normally reduce the stomatal aperture to reduce the rate of canopy water loss, C_i is expected to go down and, therefore, $\delta^{13}\text{C}$ up. Concomitantly, the rate of P_n should be reduced by the proportionally more closed stomata. Thus, it was not surprising to find that the negative correlation between $\delta^{13}\text{C}$ and dry weight was significant at the $P < 0.01$ level at all soil moisture levels, or that the negative correlation between WUE_{sl} and dry weight was significant at the $P < 0.05$ level or better at the high or the intermediate soil moisture. Tighter correlation between $\delta^{13}\text{C}$ and dry weight (Fig. 3) than between WUE_{sl} and dry weight (Fig. 4), we believe, is an indication that the error in measuring WUE_{sl} is bigger than the error in determining $\delta^{13}\text{C}$, which, if the assumption is correct, would strengthen the use of the $\delta^{13}\text{C}$ technology as a research and breeder's selection tool.

Strong negative correlations are presented in Figures 3 and 4 for each genotype plotted separately but grown under different levels of soil moisture. More appropriate to the situation in the field, however, is consideration of genotypic differences within each soil moisture level. When that was done, no significant correlations between dry weight and $\delta^{13}\text{C}$ or dry weight and WUE_{sl} were found. (Data are not presented but can easily be generated by replotting data from Figures 3 and 4.) The correlation coefficients for $\delta^{13}\text{C}$ versus dry weight were $r = -0.27$, -0.13 , and 0.26 at 100%, 50%, and 25% of soil field capacity, respectively; for WUE_{sl} versus dry weight the corresponding correlation coefficients were $r = -0.33$, 0.13 , and -0.48 . (Unpublished data from our laboratory showing lack of correlation between aboveground fresh weight and $\delta^{13}\text{C}$ of about 50 F₃ and BC₁S₁ field-grown seed families are consistent with the more detailed study on the smaller population presented here.) In a study on a large number of wheat varieties, Condon *et al.* (5) found that weight correlated well with $\delta^{13}\text{C}$ and Hubick *et al.* (19) reported that dry weight correlated well with $\delta^{13}\text{C}$ when diverse peanut germplasm was grown under moisture stress, but not when grown under well watered conditions. The tomato genotypes of our study are further apart taxonomically, and they differ more in growth type than those wheat and peanut varieties, which may explain the differences in behavior between tomato and wheat or peanut.

The result of this research strongly supports the conclusion of Farquhar *et al.* (16) and Farquhar and Richards (17) that the $\delta^{13}\text{C}$ technology may be developed into an efficient tool by which to select for water use efficiency in C₃ plants.

Acknowledgments—We thank Dr. J. Nienhuis for making his seed material available to us, and Dr. J. R. Ehleringer for helpful comments on the manuscript and for performing the $\delta^{13}\text{C}$ analyses.

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