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Water use efficiency in *Flaveria* and *Moricandia* species

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Abstract

The water use efficiency (WUE) of the C_3-C_4 intermediate species *Flaveria anomala* and *F. pubescens* was similar to that found in *F. cronquistii* (C_3). Compared to this values, the value in *F. brownii* (C_4-like) was significantly increased and was doubled in *F. trinervia* (C_4). *Moricandia arvensis*, a species with an enhanced CO_2 reassimilation potential has a very similar water use efficiency as *M. moricandioides* (C_3) but a lower transpiration rate.

Introduction

Adaption to constant or temporary drought conditions by a more economical use of available water is assumed to be a major driving force during the evolution of C_4 species from C_3 ancestors (Edwards and Walker 1983, Raghavendra and Rama Das 1993). Thus, considerations on the evolution of the C_4 pathway of photosynthesis are usually associated with the better water use efficiency (WUE) of C_4 plants. In addition to drought tolerance adaptation to other stress conditions such as salinity, nitrogen deficiency or low atmospheric CO_2 content perhaps were also evolutionarily important mechanisms (Osmond *et al.* 1980, Ehleringer *et al.* 1991). However, the recent distribution of C_4 species, their dominance in semiaride habitats, indicates that an improved WUE was of primary importance. The evolution of the highly complex C_4 syndrome probably has been a stepwise process via C_3-C_4 intermediate species. In fact, in several recent genera such intermediates occur (Raghavendra and Rama Das 1993). In the present paper, WUE of such intermediates in relation to C_3 and C_4 species was investigated in order to obtain insight into evolutionary mechanisms leading to C_4 photosynthesis.

Materials and methods

The following species were grown from seeds: *Hordeum vulgare* L., *Flaveria anomala* B.L. Robinson, *Flaveria trinervia* (Spreng.) C. Mohr, *Moricandia arvensis*

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(L.) DC., *Moricandia moricandioides* (Boiss.) Heywood and *Zea mays* L. Plants of *Flaveria cronquistii* A.M. Powell, *Flaveria brownii* A.M. Powell and *Flaveria pubescens* Rydb. were propagated by rooted cuttings. The plants grew in plastic pots (2 000 cm^3) in a mixture of compost and sand in air-conditioned chamber (irradiance 450 $\mu mol\ m^{-2}\ s^{-1}$ (PAR), photoperiod 16/8 h, relative humidity of 70 % and day/night temperature of 21/16 °C). Water content of the soil was 70 % of the water holding capacity and was held constant by daily weighing and watering. Evaporation by the soil surface was determined from pots without plants. Each experiment was run with 5 replicates for 28 d.

Results and discussion

Traditionally water use efficiency is expressed as the ratio of dry matter of plants formed during a given growth period and the amount of water transpired during that time. With the establishment of gas exchange measurements the ratio of CO_2 uptake rate and transpiration rate is often used as a measure of water use efficiency. Ecologically aimed investigations should prefer the more time consuming growth experiments because losses by dark respiration, diurnal changes in the CO_2/H_2O ratio *etc.* are not considered in the short term gas exchange measurements. Species of *Flaveria* are frequently used for investigations with regard to the evolution of the C_4 pathway of photosynthesis (Powell 1978, Apel and Maass 1981, Brown and Bouton 1993) because the genus contains C_3, C_4 and C_3-C_4 intermediate species.

Flaveria trinervia (C_4), an annual weedy species in a variety of usually saline habitats, exhibited the highest WUE, more than twice in comparison with that of the C_3 species *F. cronquistii* (Table 1). *F. cronquistii* is a perennial shrub, naturally occurring in rocky limestone areas. *F. brownii*, a perennial herbaceous species, inhabits saline, sandy, and marshy areas and was earlier classified as C_4 (Powell 1978). In more recent investigations, it was shown that, in contrast to true C_4 species, *F. brownii* contains Rubisco also in mesophyll cells (Bauwe 1984, Reed and Chollet 1985). Further, gas-exchange results and biochemical investigations suggest that *F. brownii* is an advanced, C_4-like C_3-C_4 intermediate (Monson *at al.* 1987). Therefore, *F. brownii* is evaluated as a borderline case of C_4 and denominated as "C_4-like". Both intermediate species, *F. pubescens* (perennial) and *F. anomala* (annual) exhibit WUE close to the C_3 species, *F. cronquistii.* Under well watered conditions, like in these experiments, the C_3-C_4-intermediate species do not exhibit improved WUE as it could be expected from their higher CO_2 uptake rates in comparison to the C_3 species (Apel and Maass 1981). The relatively high absolute values for WUE in all species can be explained by the fact that the plants were in the vegetative stage of exponential growth without visible indications of senescence (Edwards and Walker 1983, Slavík 1974).

The rate of transpiration per leaf area unit was determined from the mean of water use during the last three days and leaf area at harvest. The transpiration rate of *F. cronquistii* is more than twice the tranpiration rate of *F. trinervia*; this corresponds

to WUE of both species. The values of the C_4-like *F. brownii* and both C_3-C_4 intermediates are intermediate with regard to the C_3 and C_4 species.

Table 1. Water use efficiency (WUE), transpiration rate (E), specific leaf mass (SLM) and the ratio between shoot and root dry mass (S/R) in different plant species. Mean ± standard error.

Species	WUE [mg(d.m.) $g^{-1}(H_2O)$]	E [mg(H_2O) cm^{-2} d^{-1}]	SLM [mg(d.m.) cm^{-2}]	S/R
Fraveria cronquistii	16.15 ± 3.25	122.6 ± 6.63	8.03 ± 0.53	2.05 ± 0.41
Flaveria pubescens	12.21 ± 1.02	83.5 ± 2.07	4.80 ± 0.27	2.60 ± 0.11
Flaveria anomala	15.86 ± 1.09	105.2 ± 7.56	7.10 ± 0.29	2.73 ± 0.45
Flaveria brownii	21.64 ± 0.95	77.1 ± 3.66	6.04 ± 0.08	2.77 ± 0.15
Flaveria trinervia	35.75 ± 1.73	56.2 ± 4.57	7.94 ± 0.13	2.49 ± 0.08
Moricandia moricandoides	11.62 ± 0.68	113.9 ± 3.90	7.68 ± 0.92	2.32 ± 0.30
Moricandia arvensis	11.55 ± 0.79	86.5 ± 5.04	5.74 ± 0.14	3.00 ± 0.08
Hordeum vulgare cv. Salome	10.64 ± 0.36	139.0 ± 3.58	4.51 ± 0.08	1.41 ± 0.09
Hordeum vulgare cv. Salome	14.44 ± 0.80*	112.2 ± 4.11	4.61 ± 0.13	1.47 ± 0.14
Hordeum vulgare cv. Tamina	8.78 ± 0.33	124.7 ± 1.63	4.56 ± 0.21	1.54 ± 0.09
Zea mays cv. Bema	18.21 ± 1.30	48.9 ± 2.79	3.52 ± 0.03	1.61 ± 0.21

* - experiment at ambient CO_2 concentration 500 cm^3 m^{-3}

Root/shoot ratio and specific leaf mass do not correspond to the type of photosynthesis.

Moricandia arvensis was earlier classified as C_3-C_4-intermediate because of the low CO_2 compensation concentration (Krenzer *et al.* 1975, Apel and Ohle 1979, Apel and Peisker 1979, Apel 1980, 1985). However, a significant PEP carboxylation is lacking (Bauwe and Apel 1979). The explantation for the low value of the CO_2 compensation concentration was found in a special compartmentation of photorespiratory enzymes between bundle sheath and mesophyll cells (Rawsthorne *et al.* 1988). Therefore, the species is now classified as a C_3 species with enhanced CO_2 reassimilation potential. *Moricandia moricandioides* is a true C_3 species (Apel 1980); there is no difference in WUE between *M. arvensis* and *M. moricandioides*. The transpiration rate in *M. arvensis* is 24 % lower and shoot/root ratio 29 % higher compared to the C_3 species (Table 1).

Corresponding values in maize and barley (grown at 340 and 500 $cm^3(CO_2)$ m^{-3}) are given for evaluation of the method. As it can be expected, WUE of the C_4 species maize is about twice the value as in barley (C_3) at normal atmospheric CO_2 concentration. An increase in CO_2 up to 500 cm^3 m^{-3} increased WUE with barley cv. Salome significantly, mainly by a decreased transpiration rate due to partial stomatal closure.

From the results it can be concluded that under well watered conditions C_3-C_4 type of CO_2 fixation in *Flaveria* is not connected with an improved WUE in comparison to a C_3 species. The enhanced CO_2 reassimilation potential in *Moricandia arvensis* also does not improve WUE. Preliminary results from

experiments of the same type but under saline- and water stress conditions indicate a higher flexibility of C_4 and C_3-C_4 intermediate species.

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