Gypsophyles use water from deeper soil layers than gypsovags during drought in a semiarid gypsum shrubland community: is deep rooting a key functional trait of gypsum specialists?

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Hypothesis 1: "True" gypsum specialists (gysophiles) are capable of reaching deeper soil layers than their gypsovag neighbours, thanks to the greater ability of their roots to penetrate through hard subsoil gypsum layers and to tolerate the extremely high S and Ca concentrations of these "pure" gypsum layers (specialized root mechanical and biochemical traits).

Hypothesis 2: Greater root access to deeper, wetter soil layers enables gypsophiles to maintain higher cumulative stomatal conductance and transpiration rates over the entire growing season than their gypsovag neighbours, especially during dry periods.

Hypothesis 3: High accumulation of S and Ca in the leaves of gypsophiles may be (in part) the consequence of both deep rooting and high cumulative transpiration (given that water in subsoil pure gypsum layers is highly saturated with S, Ca).

METHODS: We measured the stable isotope composition and elemental composition (C, N, P, K, Ca, S, Mg, etc) of leaves and the stable isotope composition of stem water in 12 common plant species (4 gypsophiles + 8 gypsovags) growing on gypsum soils at three different study sites located in the southeastern Iberian Peninsula (Novelda, Sax, Petrer) in summer (July).

The oxygen and hydrogen isotopic composition of water extracted from plant woody tissue (Stem water $\delta 18O$ and $\delta 2H$, respectively) reflects the isotopic composition of the water sources used by the plant.

The isotopic composition of soil water (0-20 cm depth) and gypsum crystallization water were also measured at the same time.

The carbon isotope composition of leaf dry matter (Leaf $\delta 13C$) provides a time-integrated proxy measure of intrinsic water use efficiency (the ratio photosynthetic rate/stomatal conductance) throughout the lifespan of the leaf.

The oxygen isotope composition of leaf dry matter (Leaf $\delta 18O$) provides a time-integrated proxy measure of cumulative stomatal conductance and transpiration rate throughout the leaf lifespan. It is also influenced by the $\delta 18O$ of the source water used by the plant.


Teucrium libanitis
Serra de Crevillent (262 m) - (A)
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Teucrium libanitis Schreb.
Cabezo de la Sal, Pinoso (Alicante)
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Herniaria fruticosa
Sierra de Crevillente (A)

Ononis tridentata L.
Villena (Alicante)


© José Quiles


Thymus moroderi Pau ex Martínez
Mutxamel (Alicante)
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Thymus vulgaris L. *subsp. vulgaris*
San Isidro (Alicante)


Stipa tenacissima L.
Montnegre, Xixona (Alicante)
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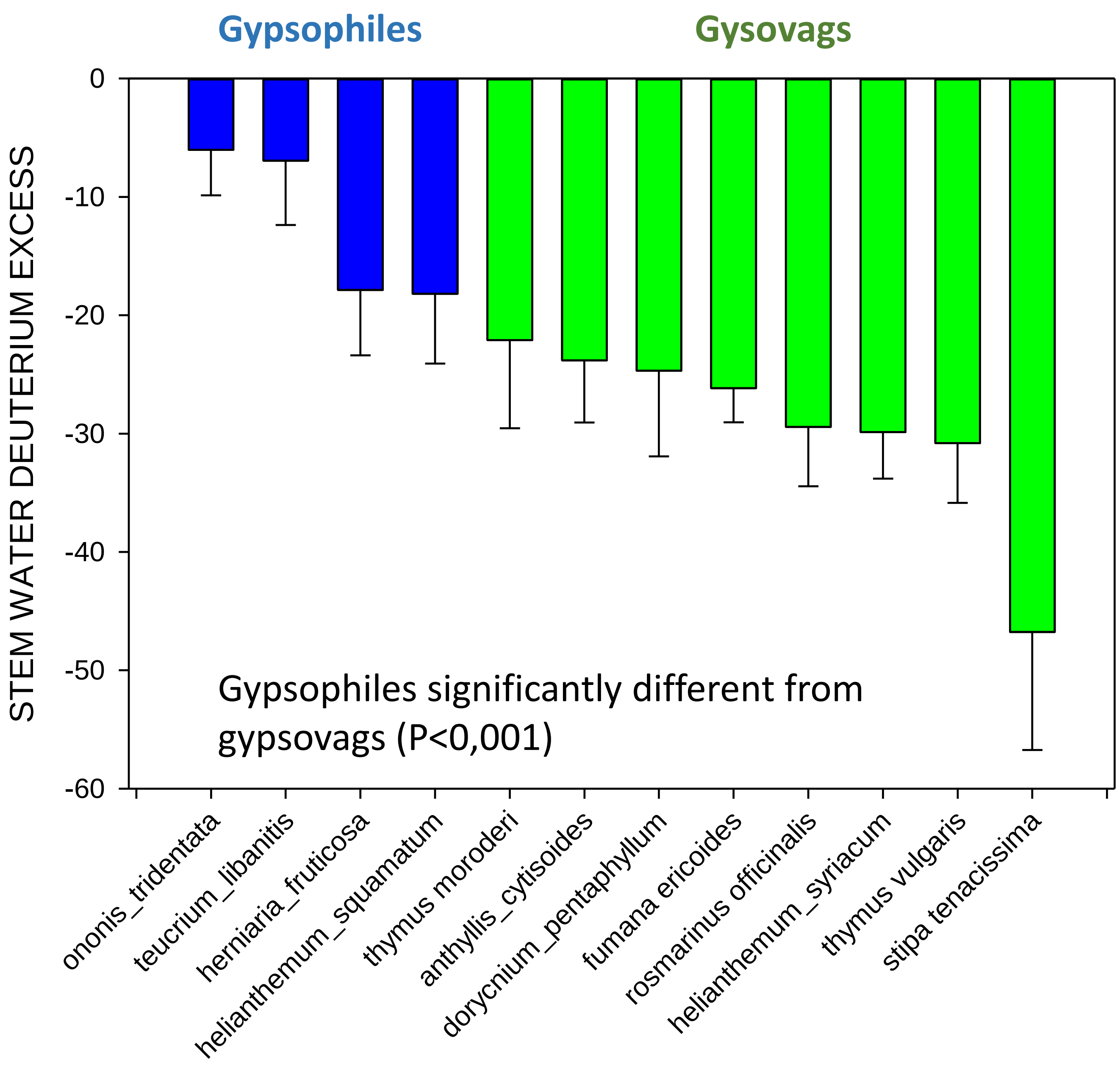
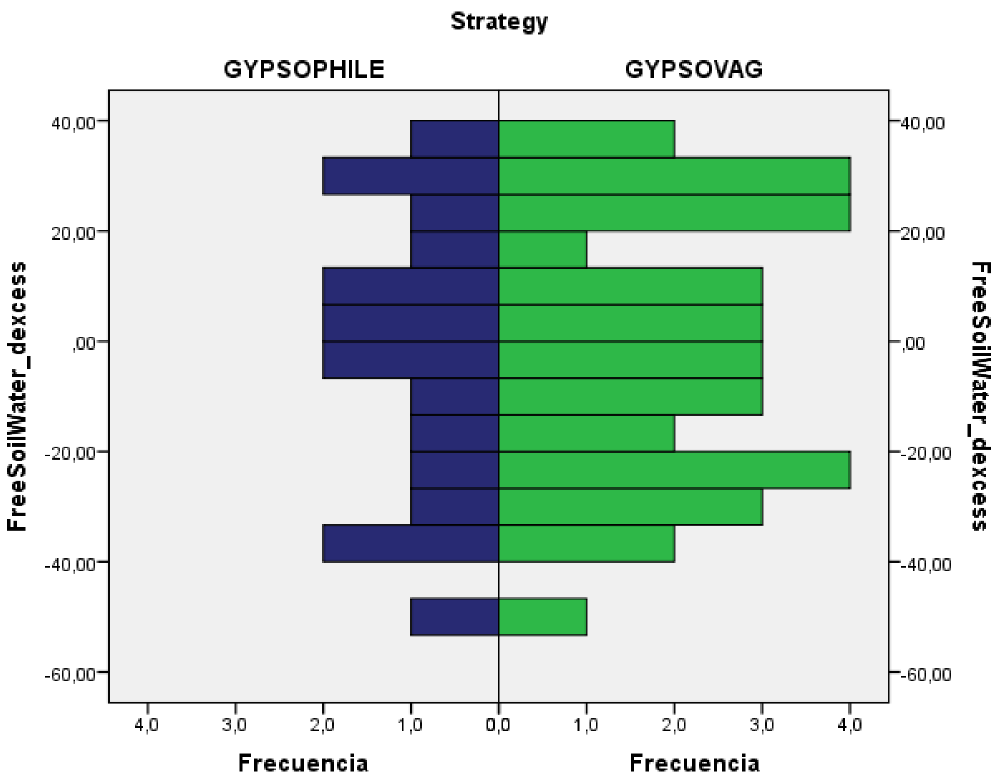
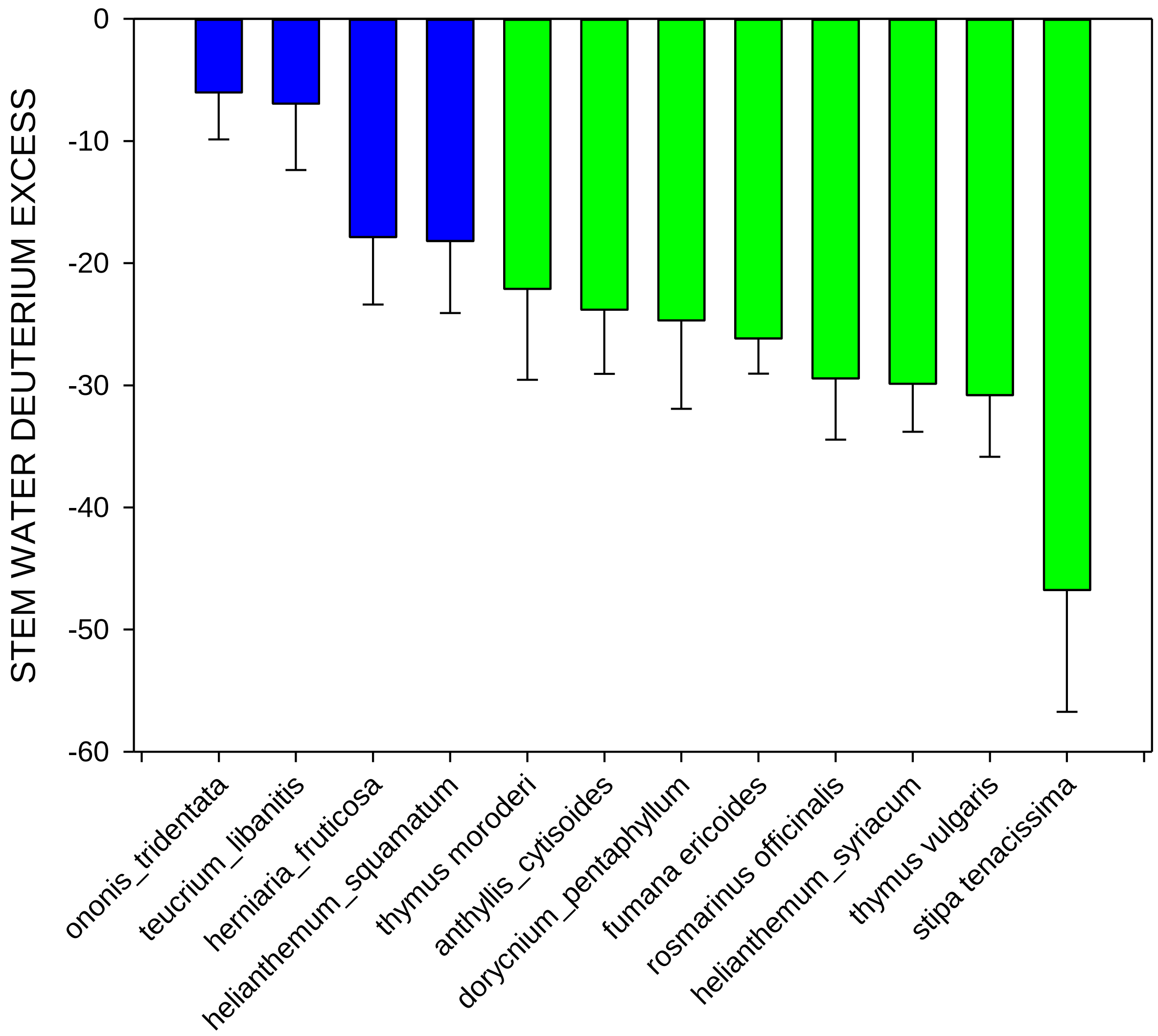
Gypsophiles tend to use non-evaporated or slightly evaporated water extracted from deep soil layers during the summer drought



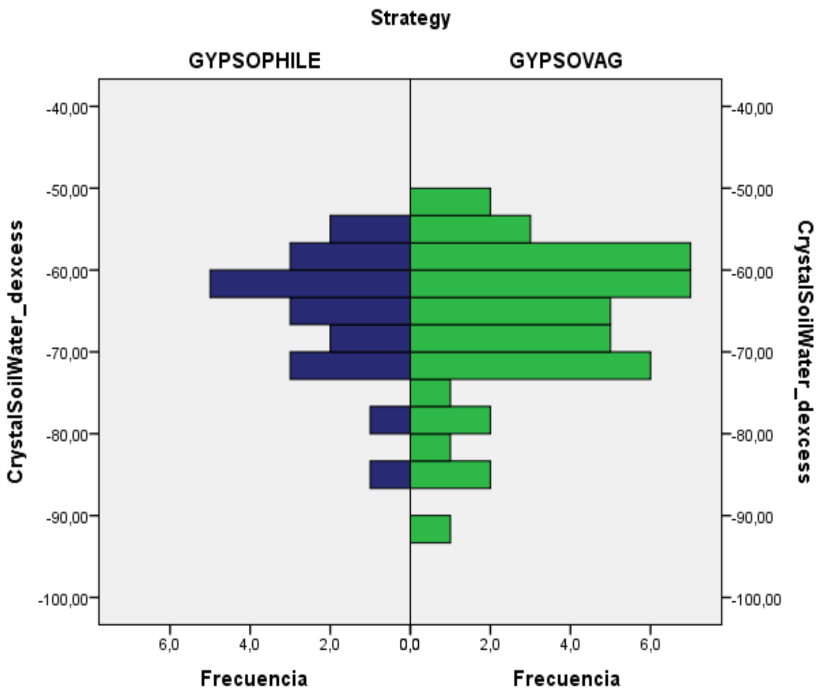
Gypsovags tend to use strongly evaporated water extracted from shallower soil layers during the summer drought

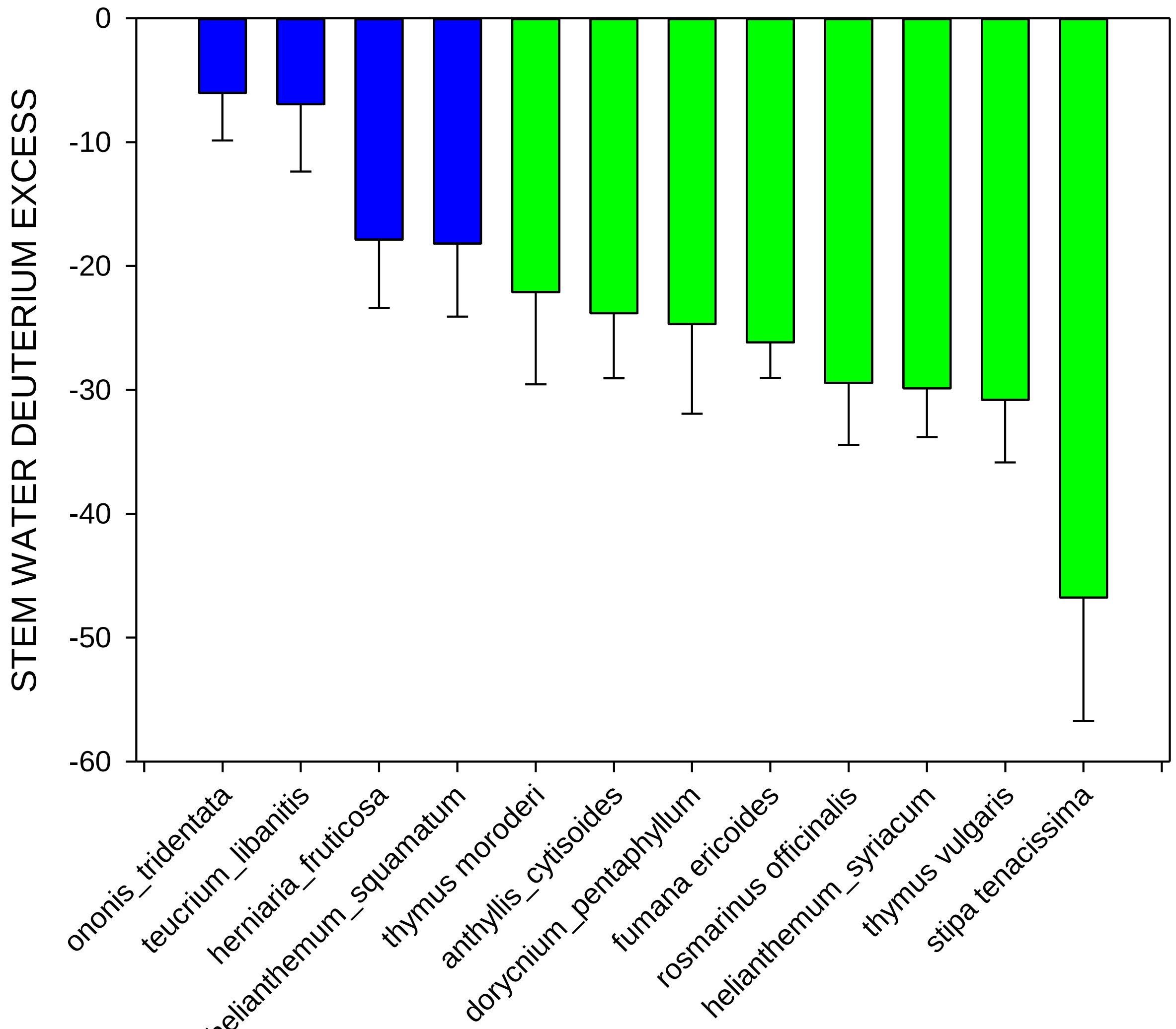
The isotopic composition of stem water in gypsophiles and gypsovags is within the range of isotopic values found in free soil water (measured only at 0-20 cm depth)

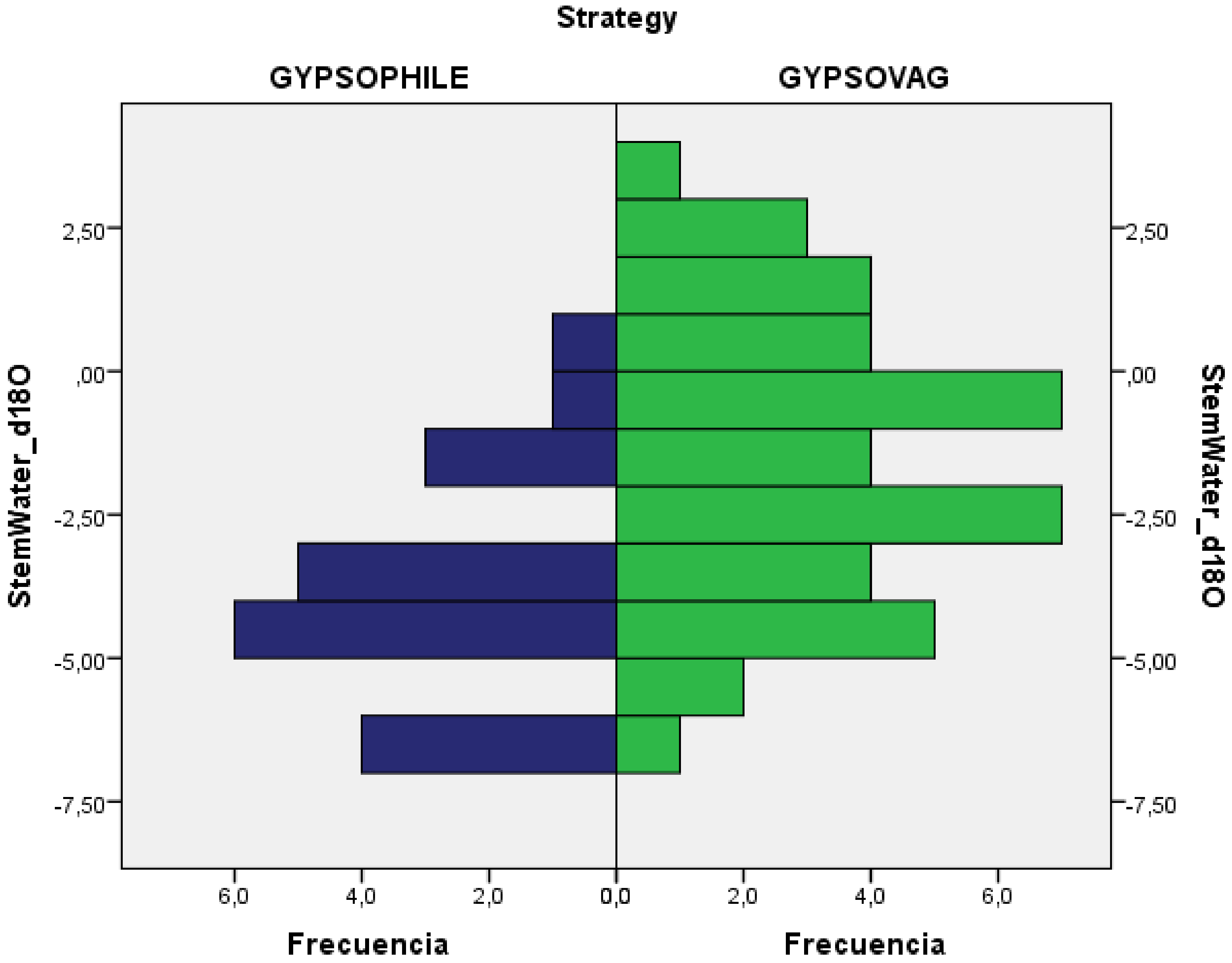




The isotopic composition of stem water is different from the isotopic composition of gypsum crystallization water in both gypsophiles and gypsovags

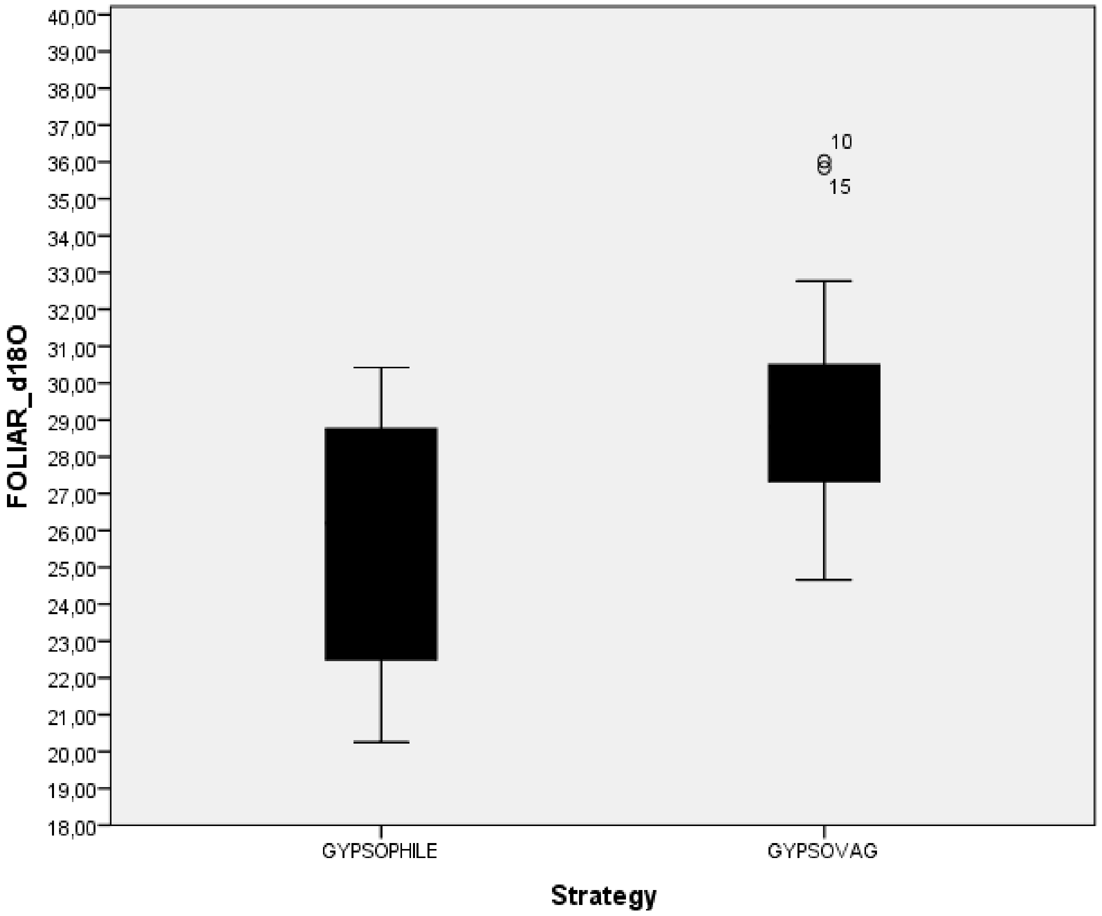


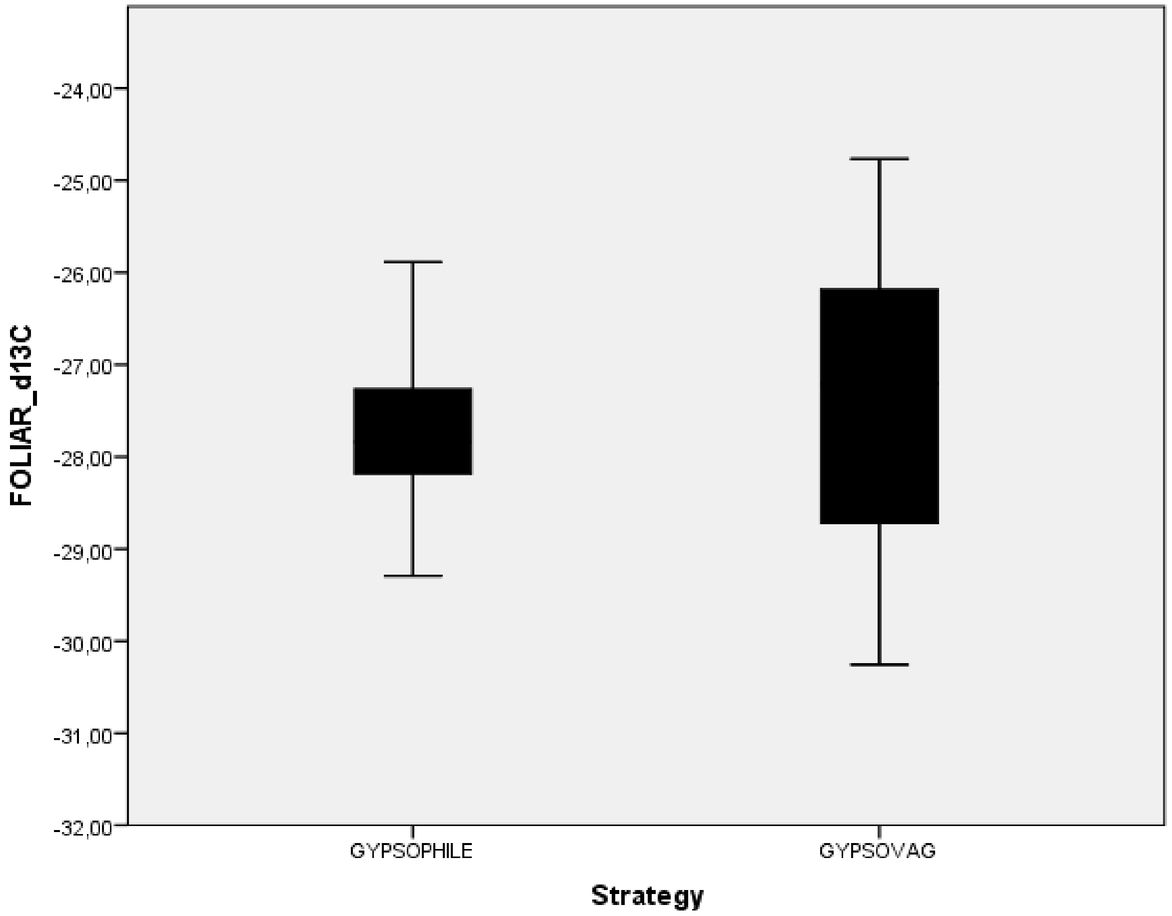




Strategy
GYPSOPHILE
GYPSOVAG
StemWater_d18O
2,50
,00
-2,50
-5,00
-7,50
6,0
4,0
2,0
0,0
Frecuencia

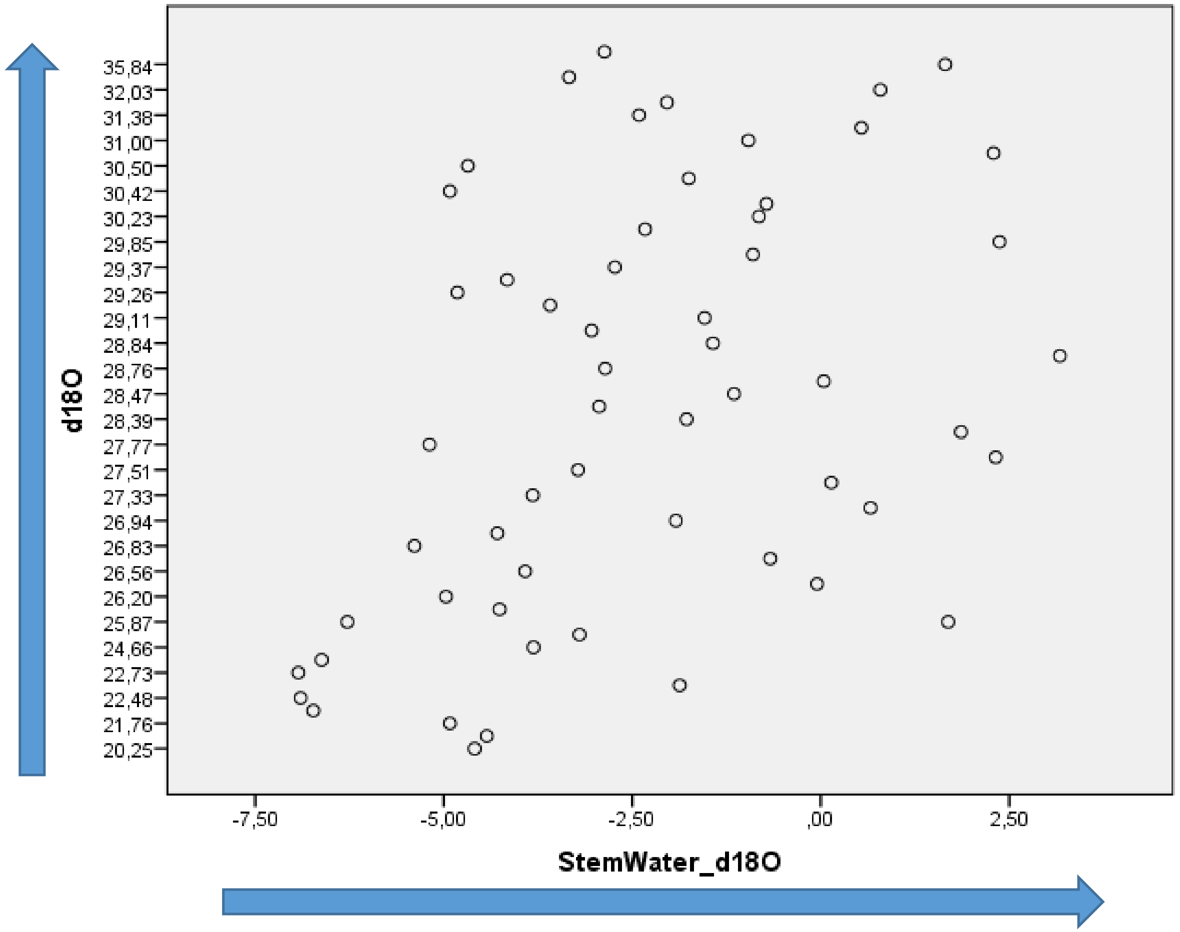
Across species, gypsophiles generally have lower leaf d18O values tan gypsovags (P<0,001), indicating higher stomatal conductance and cumulative transpiration and/or utilization of deeper, less evaporated water in gypsophiles. In contrast, time-integrated water use efficiency (inferred from leaf d13C) is not different between gypsophiles and gypsovags (P=0,822). Foliar d13C is weakly positively correlated with leaf d18O enrichment above source water across species (P=0,040), suggesting some degree of shared stomatal control over both variables.





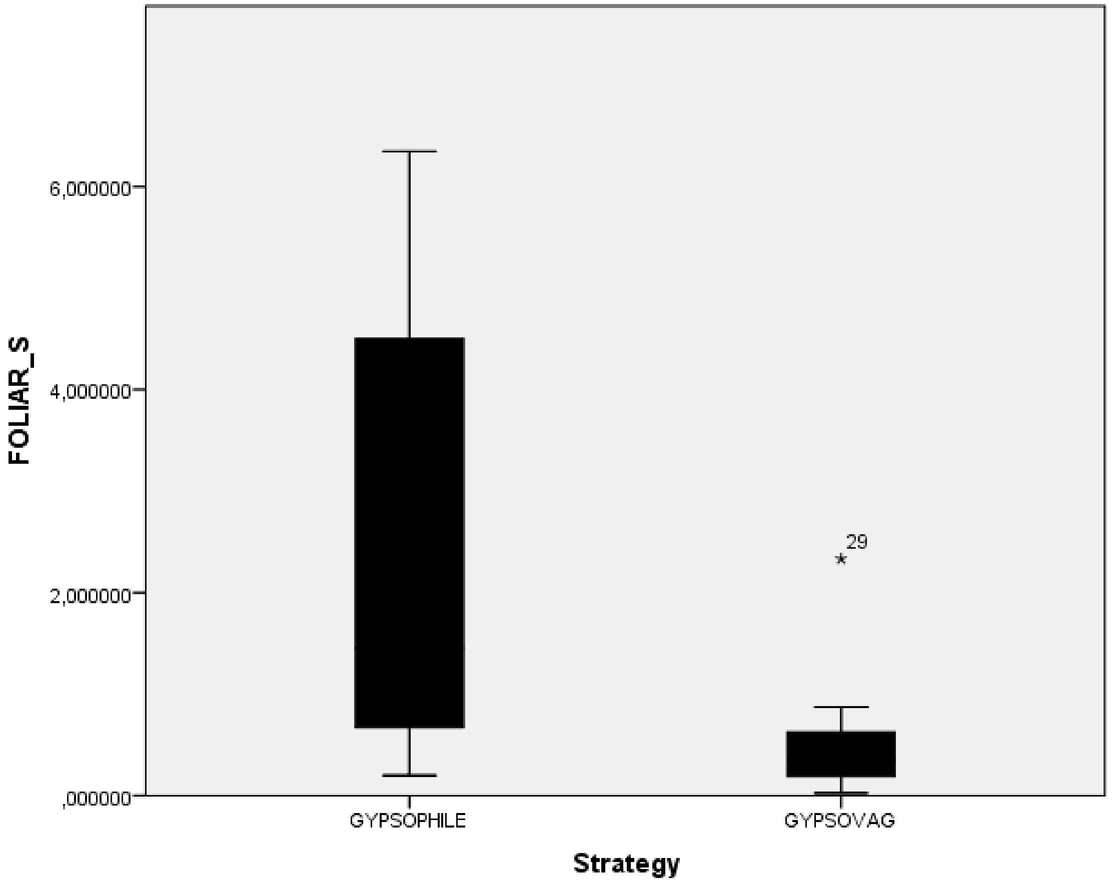
Across shrub species, higher leaf d18O is coupled to utilization of water stored in shallower soil layers (strongly evaporated)

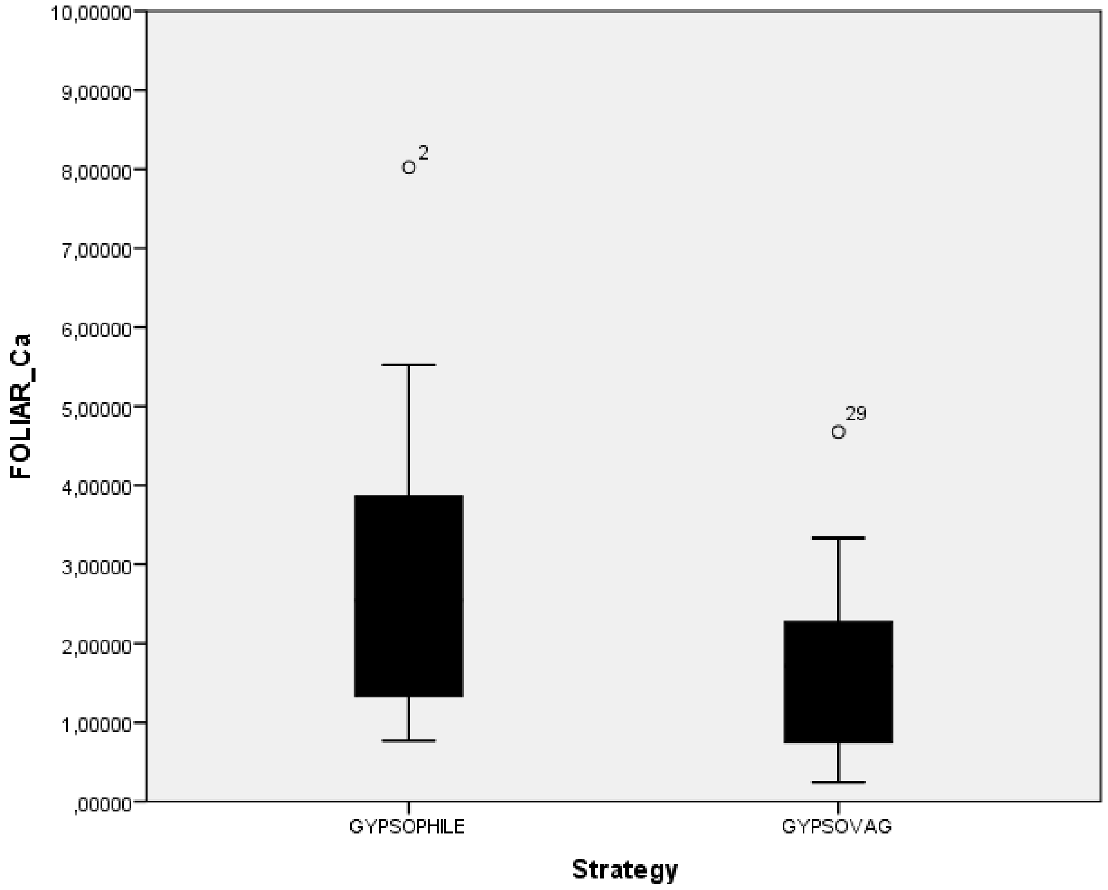
Higher foliar d18O indicates tighter stomatal control of transpiration and thus lower cumulative transpiration over the growing season



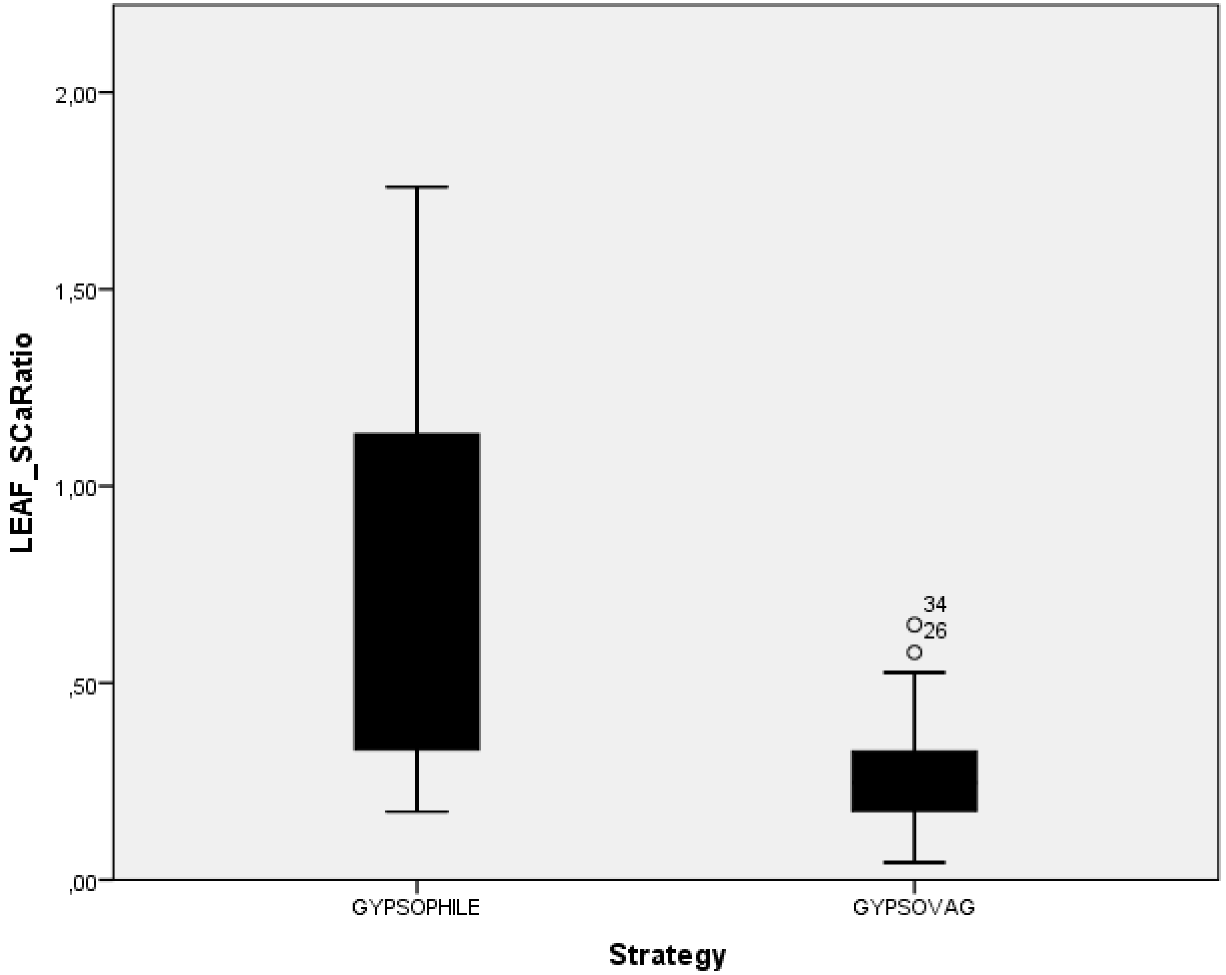
Higher stem water d18O indicates utilization of shallower, more evaporated water sources from surface soil layers

Gypsophiles show significantly higher concentrations of sulphur and calcium in their leaves than gypsovags (P<0,001 for both)

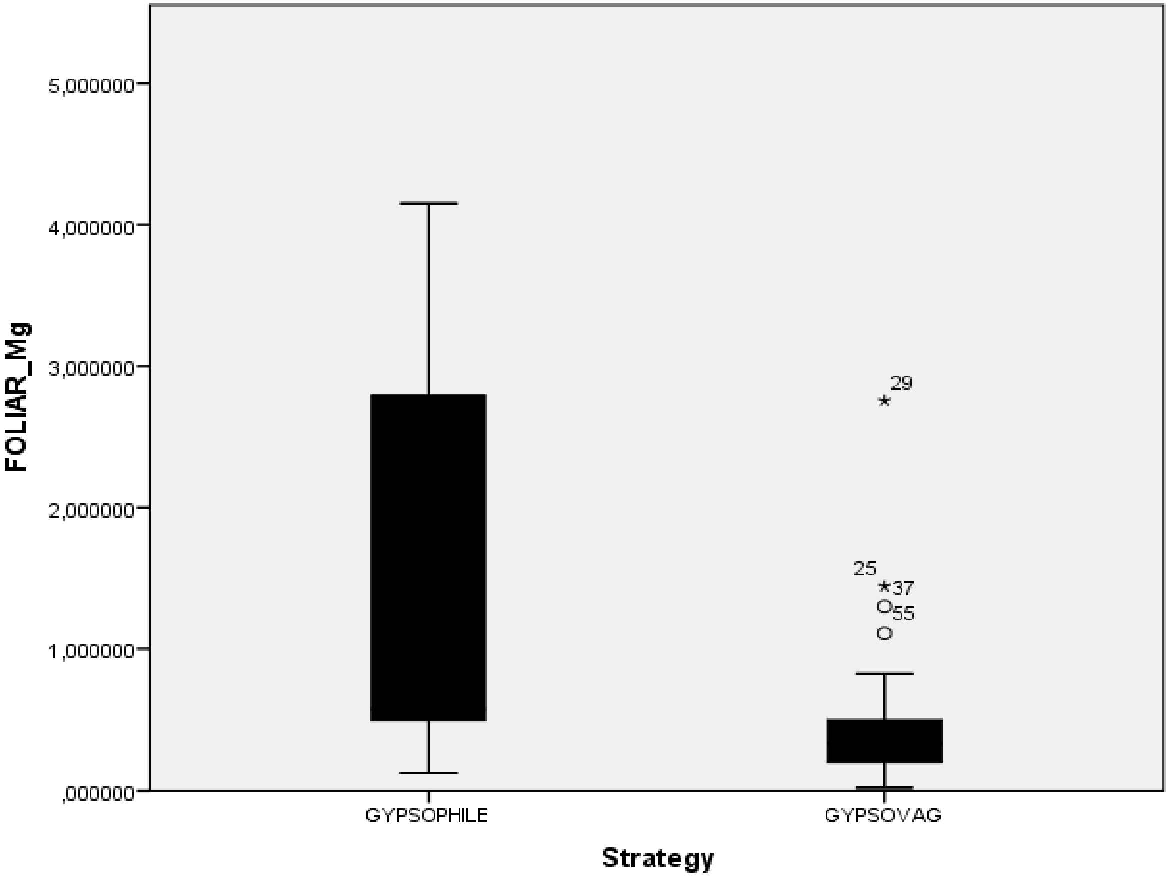


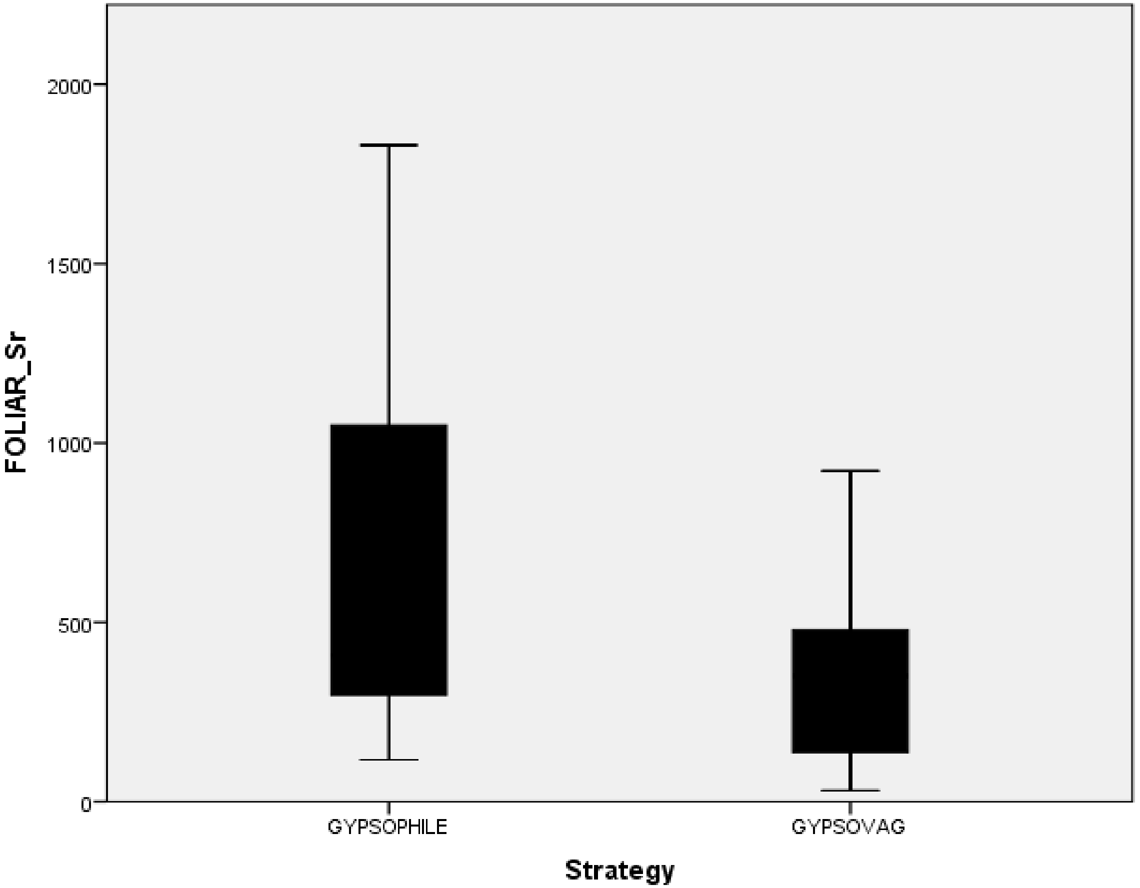


Gypsophiles show significantly higher foliar S:Ca ratios than their gypsovag neighbours (P<0,001), indicating differential accumulation of sulphur over calcium.

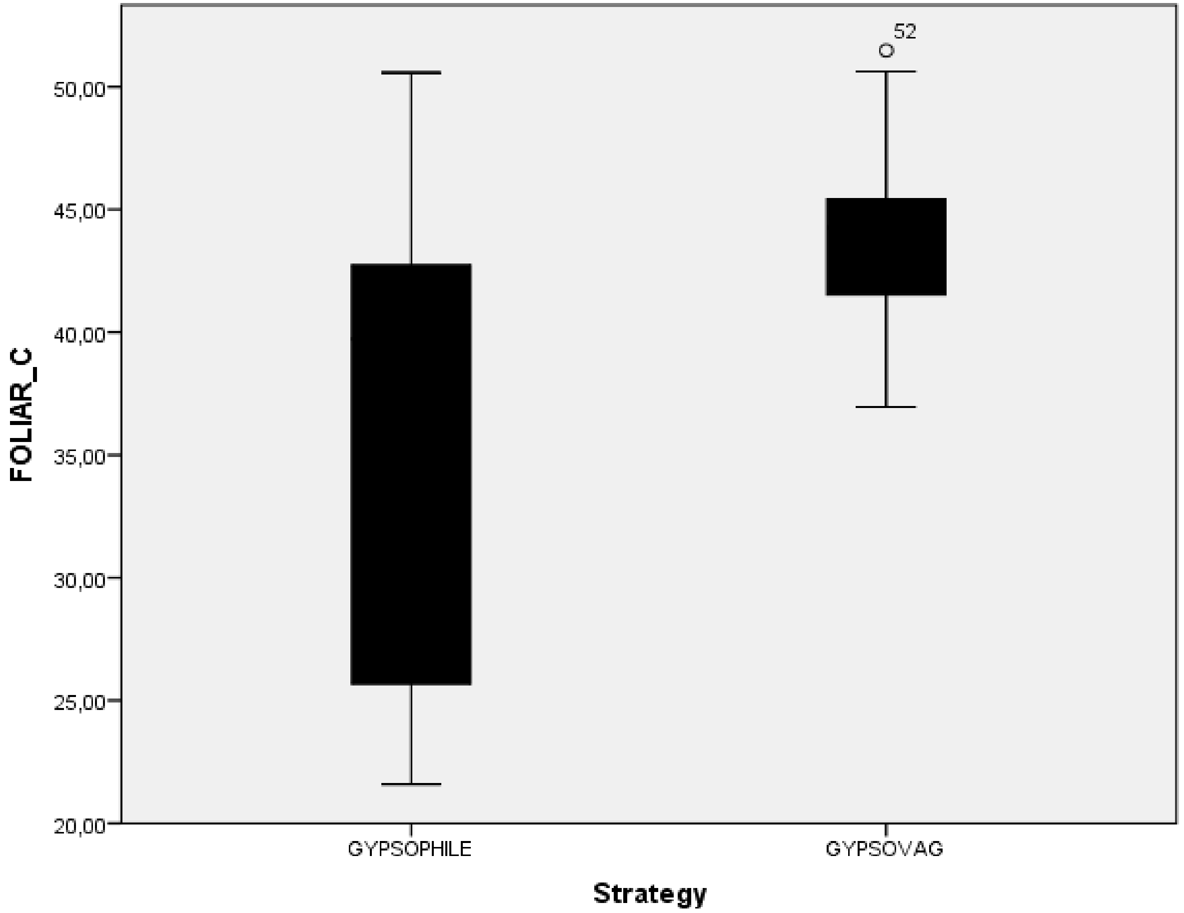


Gypsophiles also show significantly higher concentrations of magnesium and strontium in their leaves than gypsovags (P<0,001 for both)

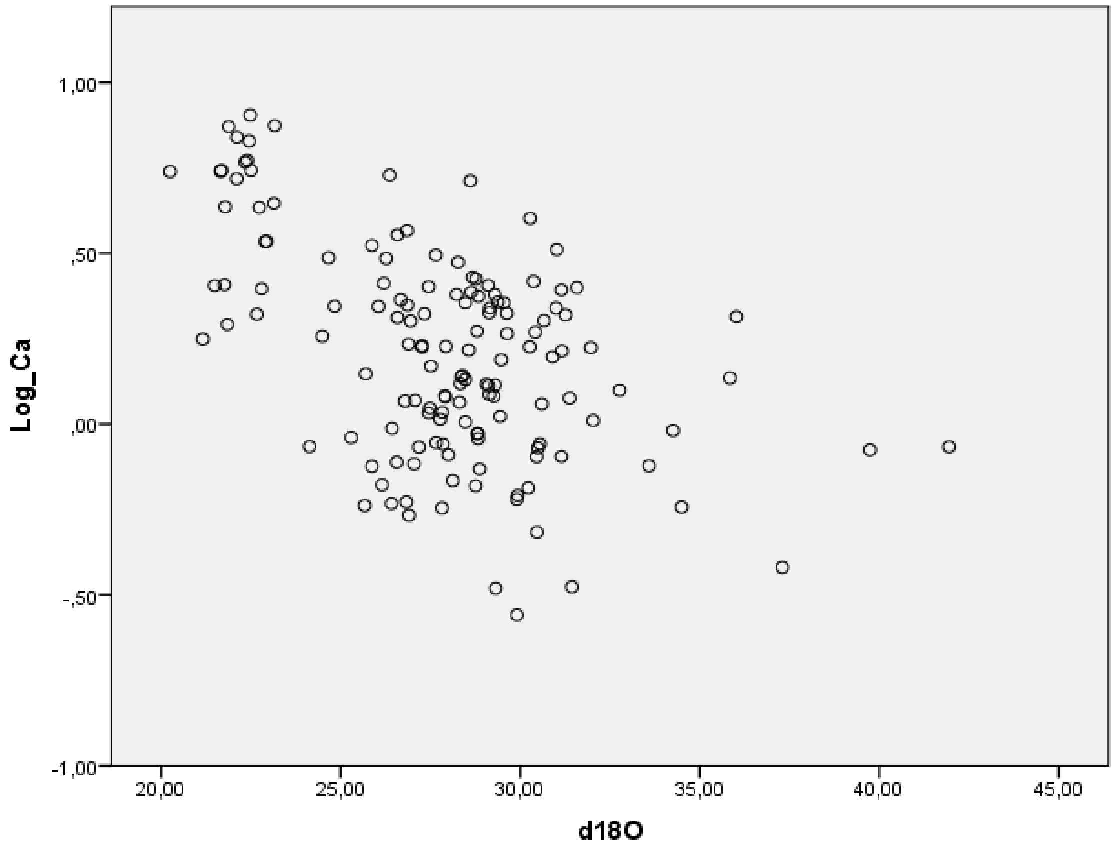


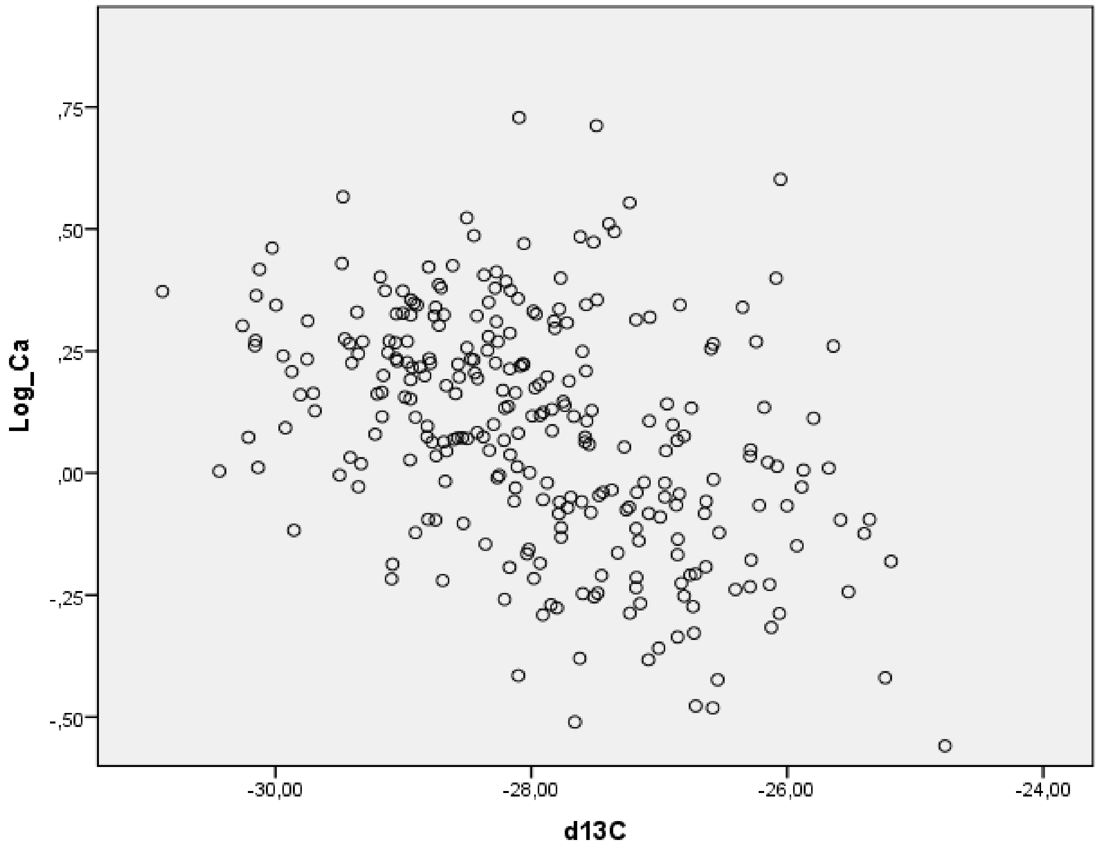


Extremely high accumulation of S, Ca, Mg, Sr and other mineral elements in the leaves of some gypsophiles leads to strikingly low concentration of carbon in foliar tissue dry matter (as low as 25% in some Ononis tridentata individuals). Plant leaves normally have 40-55% carbon (global average).

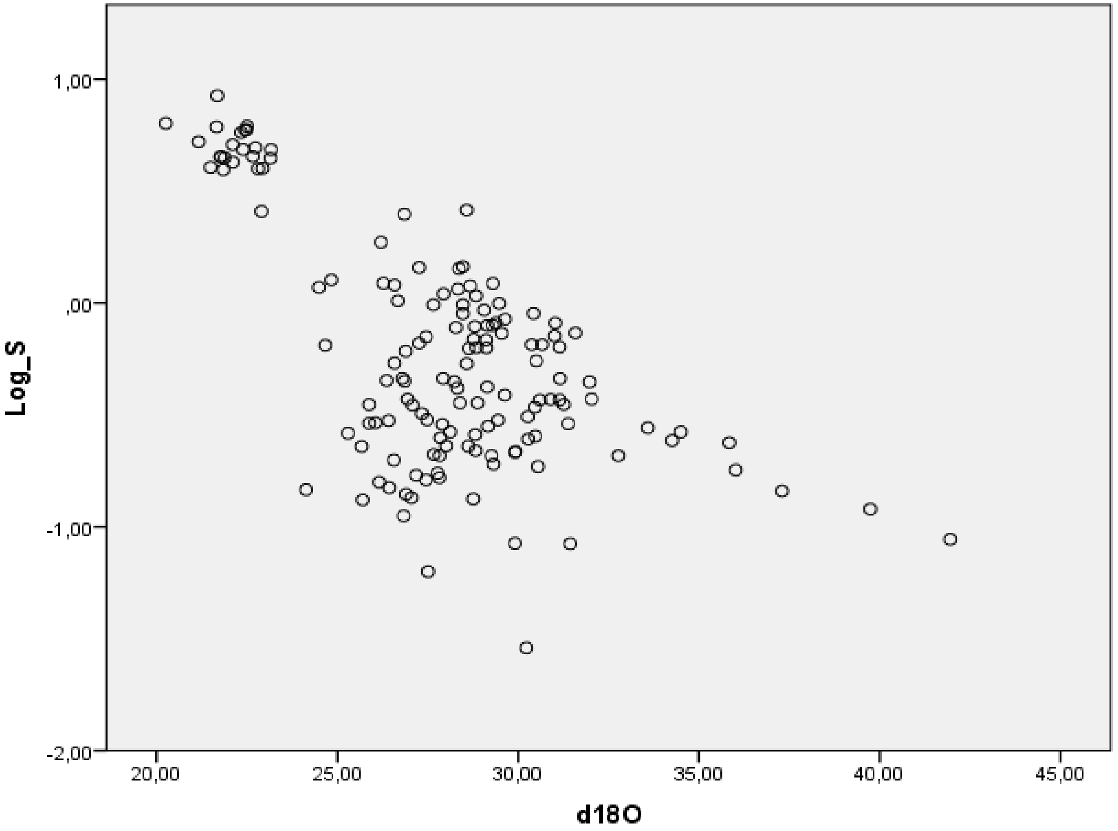


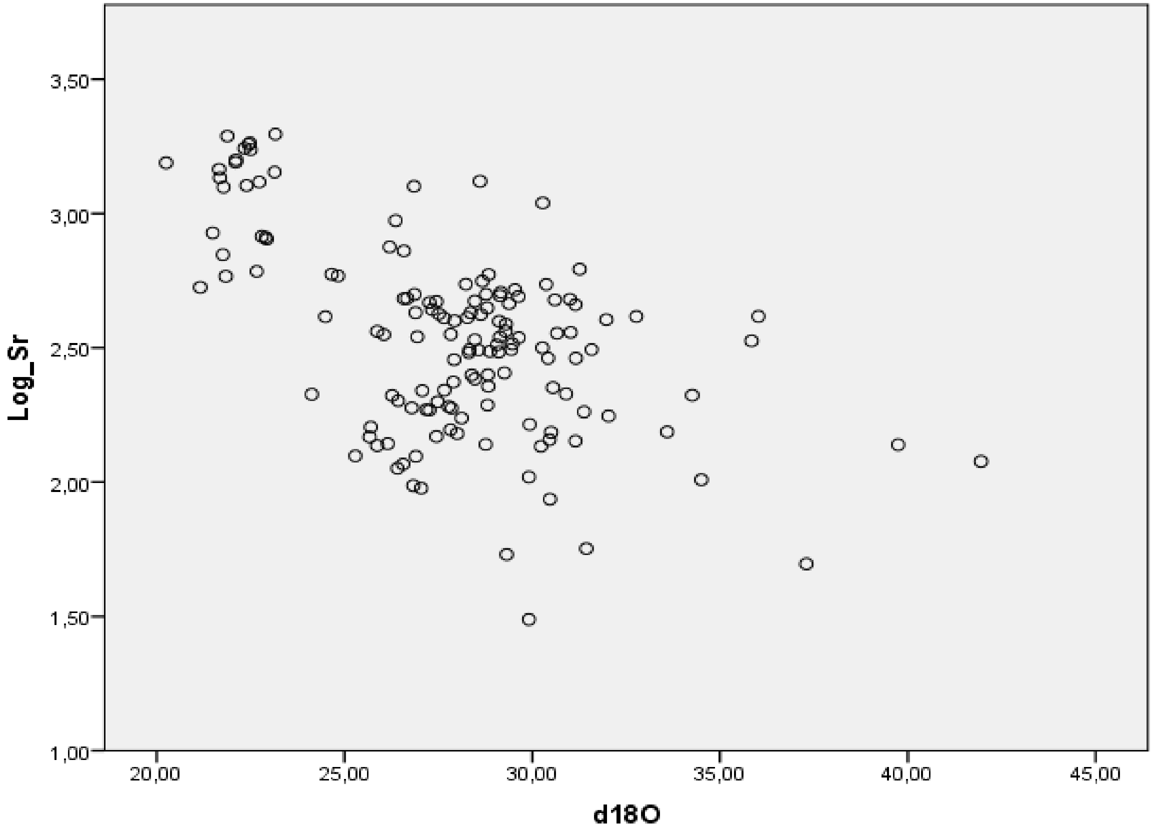
Across shrub species, lower leaf d18O (indicative of high cumulative transpiration and/or utilization of deeper soil water) is linked to higher accumulation of calcium in leaves. Lower leaf d13C (indicative of a profligate, water-spender strategy) is also linked to high accumulation of calcium in leaves. Similar results obtained with d18O enrichment above source water.





Across shrub species, lower leaf d18O (indicative of higher cumulative transpiration and/or utilization of deeper soil water) is also linked to higher accumulation of sulphur and strontium in leaves. Similar results obtained with d18O enrichment above source water.





Low accumulation of S and Ca in leaves
Tighter stomatal control of transpiration, low cumulative transpiration
Utilization of shallow soil water

Mainly gypsovags

A single PCA axis accounts for 67% of cross-species variability in Leaf Ca and S concentration, stem water d-excess and Foliar d18O across species

Gypsophiles have significantly higher scores along this axis than gypsovags (P<0,001)

High accumulation of S and Ca in leaves
Profligate water use strategy, high cumulative transpiration
Utilization of deep soil water

Mainly gypsophiles

“Provisional” conclusions:

1. Gypsohiles tend to rely on deeper, less evaporated sources of soil/bedrock water than gypsovags during the dry season.

2. Gypsophiles may on average achieve higher cumulative transpiration over the entire growing season than gysovags, which suggests a more profligate water use strategy in the former (facilitated by root access to deeper, more reliable sources of soil moisture during drought).

3. High accumulation of S, Ca, Mg and other elements in the leaves of gypsophiles may in part be the consequence of the above: greater proportional consumption of water stored in subsoil or bedrock gypsum layers where the soil solution is saturated with S and Ca, along with higher transpiration-driven mass flow of S and Ca to roots.

Important caveat: limited number of species included in the field survey (4 gypsophiles + 8 gypsovags) and only 3 study sites (Sax, Novelda, Petrer in the Alicante Province, Southeastern Spain).

Further studies including a larger number of study sites and coexisting gypsophile and gypsovag species will be needed to empirically test the wider generality of this pattern.

Leaf gas exchange measurements (LICOR) will be needed to confirm our interpretation of leaf isotopic data.