Chemical diversity of crop root mucilages: Implications for their maximal water content and decomposition

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Abstract

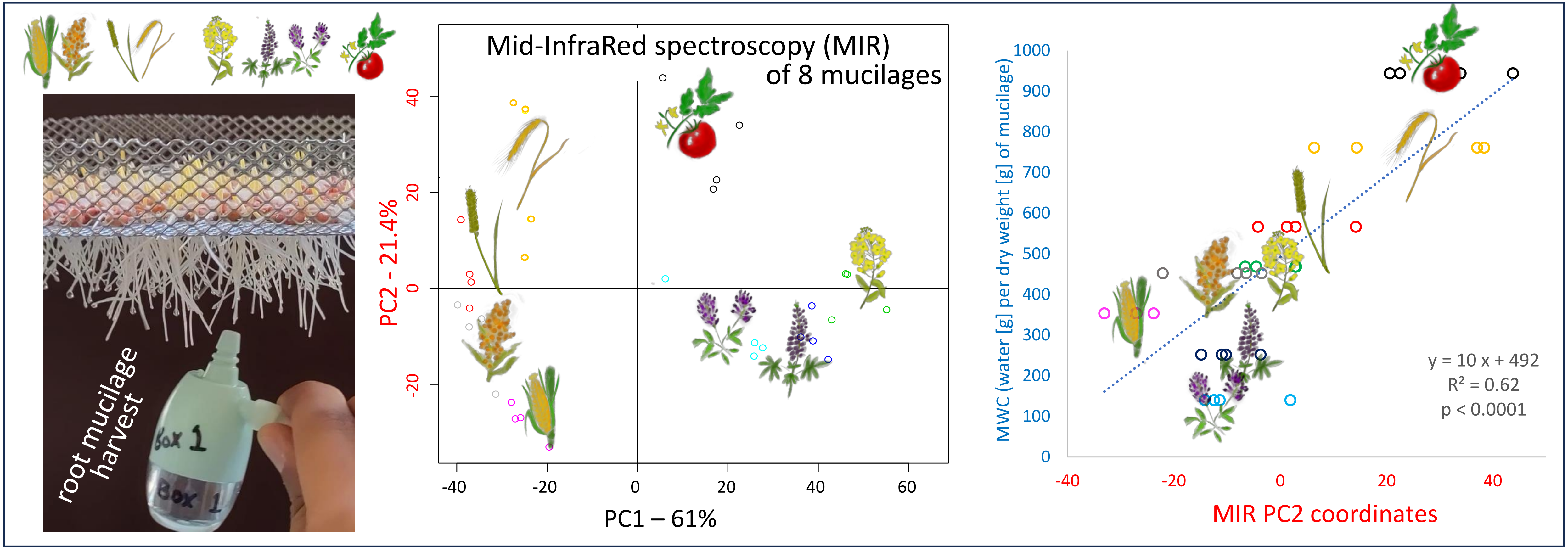
The biophysical functioning of the rhizosphere can act on plant water use efficiency through root mucilage release and their stimulation of microorganisms' activity. Mucilage characteristics and roles are still poorly studied for the diversity of agronomic plant species. We compared mucilages collected from roots of germinated seeds (aerohydroponics technique) of eight plant species (four Eudicotyledons, four Monocotyledon) in terms of total sugars content, Medium Infrared (MIR) spectra, mucilage maximal water content and induced respiration in contrasting soils. Our results suggest that the "chemical fingerprint" of these mucilages could be discriminated according to the phylogenetic proximity of the plant species. In addition, the maximal water content that mucilage retain seems to be linked to their chemical composition and seems more related to the presence of high molecular weight sugars than their total sugar amounts. If mucilage-induced respiration by soil microbiota appeared to be independent from phylogeny, some mucilages induced more respiration than others regardless of the soil studied. Microbial communities and soil physico-chemical properties interact in decomposition with variations in mucilage's chemical composition.

Keywords: root, mucilage, crop, Medium Infrared spectra, exopolymers, water content, decomposition

Highlights

- Chemical composition of root mucilage is related to plant phylogenetic proximity
- Composition of mucilage affects their maximum water content
- Mucilage-induced respiration varies with soil type and probably the plant

Graphical abstract



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Improvements in the efficiency of water use and resistance to water deficits are required for the agroecological transition (Ahmed et al., 2018) and need new production systems as well as new cultivars. To this aim, we need to understand the functional traits of the plant that could improve its resistance to water deficit.

In relation with the root system (Vetterlein and Doussan, 2016), the biophysical functioning of the rhizosphere *(e.g variation in soil water retention, wettability, porosity, microorganisms activity, due to root activity)* is a characteristic that could modify plant water use efficiency. Peculiar biophysical characteristics of rhizospheric soil (water retention and aggregation) are thought to be linked in part to exopolymers (EPS) produced by plant roots via their mucilages and also by rhizospheric microorganisms, themselves stimulated by rhizodeposits (including mucilage, Brax et al., 2019). Root mucilages are mainly composed of exopolysaccharides (EPSac), with minor amount of proteins, minerals and lipids (Nazari, 2021). Their fate in the soil in relation to their decomposition and according to their plant origin has been little studied to date (Naveed et al., 2017) and no comparison between different soils (with different microbial communities) has been made to our knowledge. In relation with the diversity of agronomic plant species, their variability in characteristics and roles are however poorly studied (Galloway et al., 2020).

Our aim was to characterize the root mucilage of various crop species, through their chemistry (sugar content, MIR spectra), physical parameter (maximal water content) and decomposition potential in contrasting soils (MicroResp™ bioassays).

We used an aero-hydroponic method adapted from Zickenrott et al. (2016), Holz et al. (2018) and Brax et al. (2019) to harvest the mucilage of eight plant species of agronomic interest (four Eudicotyledons, four Monocotyledons, Tab. 1). After sterilization the seeds (Isopropanol 70%, NaOCl 1% then tween 20 0.1%, followed by a wash with ultrapure water), the seeds were germinated on a tray (3x3 mm stainless steel mesh, adding a very thin layer of glass wool for very small seeds such as tomato, rapeseed and sorghum), incubated in the dark at 25°C +/- 1°C, in an hermetic box above a solution of CaSO4 (2 mM) aerated continuously with two pumps. After 2-3 days of incubation, mucilage is collected from the tip of each root daily using a baby fly connected to a suction pump over a further 1-2 days, until the roots reach the CaSO4 solution. For each species, five growth box systems were set up and run in parallel. From four growth boxes, the mucilage was collected and pooled to obtain enough material for analysis and experimentation. Globally, the mucilage pools were obtained from 1100 to 29800 germinated seeds, depending on the species tested (Tab.1). The fifth growth box was used to get the amount of mucilage (in total sugar equivalent) produced per dry mass of roots. In this box, after the first mucilage collection, the roots were cut along the grid surface, dried and weighed.

The collected mucilage was pooled into tubes, weighed and first stored at -20°C. An aliquot was freeze-dried to measure mucilage maximal water content (MWC, calculated as mucilage wet weight minus dry weight divided by dry weight, Nazari et al., 2020) and for analyses with Medium Infrared (MIR) spectroscopy. Total sugars were analyzed using the Dubois method (Dubois et al., 1956). MIR measurements were performed with a Tensor 27 FTIR spectrometer (Bruker Optics, Wissembourg, France). The samples were scanned between 4000 and 600 cm^{-1} and each spectrum was obtained by averaging 16 successive scans. For each sample, four replications on different aliquots were made (Bérard et al., 2020). MIR data were processed with ChemFlow chemometrics software (GalaxyProject). Principal component analysis (PCA) of the MIR spectra of the eight species mucilage showed that the first two axes explained 82 % of variance.

We also performed a MicroResp™ assay (Bérard et al., 2011; De Vries et al., 2019) of respiration induced by the different mucilages in three contrasting soils selected for their distinct microbial biomass, texture, organic C, and water holding capacity. These include a sandy clay loam from an irrigated permanent grassland ("Crau"), a silty clay loam soil from a conventional agricultural field ("Lysi") and a sandy soil from a pine forest ("Tavel") (Bérard et al., 2020, SuppMat1). We introduced 25 µl of fresh mucilage per well of the microplate system (containing 0.48 to 0.57 g in dry mass equivalent per well depending on the soil type), with 4 replications per mucilage and per soil tested (the moisture content of the test soils was 40% of their water holding capacity). Respiration measurements were recorded after six hours' incubation at 23°C and respiration induced by each mucilage was normalized by the total sugars amount introduced per soil sample. Non-parametric tests (Kruskal Wallis, Dunn Bonferroni test, $p<0.05$) were used for data analysis.

From the results obtained, the variations of the eight species root mucilage in its chemical, physical and degradation characteristics enabled to address the three points below:

- The chemical composition of plant root mucilage seems related to their phylogenetic proximity

The PCA of MIR measurements shows that the species are relatively well separated from each other (Fig.1). The dendrogram of relative distances between points effectively separates Monocotyledons (negative part of PC1) from Eudicotyledons (positive part of PC1), Asterids (Tomato) from Rosids, Malvids (Rapeseed) from Fabids, and Roinoids (Lupins) from Genisteae (Alfalfa) (SuppMat2). In the Monocotyledons, Panicoideae having C4 photosynthesis strategy (Maize and Sorghum) are at the bottom left of the PCA, and Pooideae with C3 photosynthesis (Wheat and Barley) at the top left. This suggests that these plant mucilage chemical compositions are related to phylogenetic proximity, at least up to the family scale, corroborating earlier studies by (Vančura and Hovadík, 1965) who observed similar molecular compositions of root exudates whose plant species were closely related. More recently, similar observations have been made on the phylogeny-chemical composition link of root exudates from different plant families using GC-MS (Herz et al., 2018; Williams et al., 2022) or using ESI FT-ICR MS (Miao et al., 2020).

According to MIR spectra acquired, dicots are located on the positive part of PC1 (Fig.1a), characterized by a high absorption in a broad band of wave numbers between 1217 and 1681 cm^{-1} (Fig.1b). This zone is largely represented by nitrogenous molecules of the amine, amide (I, II, III types), proteins, as well as phosphates and fats (phospholipids, triglycerides, lipids, fatty acids). Benzene (1328; 1489 cm^{-1}), phenyl (1500 -1510 cm^{-1}) and quinoid (1588 cm-1) rings are also in this band. Wave numbers between 1419 and 1444 cm-1 indicate pectin- and cellulose-type polysaccharides (Talari et al., 2017).

The negative part of PC1 is represented by Monocots-Poaceae with MIR absorption bands at 932-1064 cm-1 and 1140 and 1198 cm-1. These zones are mainly represented by simple carbohydrates (sucrose, mannose, galactose, fructose), polysaccharides (pectin, cellulose, glycogen) and, to a lesser extent, phosphate, phosphodiester, amino acid (thyrosine) and aromatic molecules (Talari et al., 2017).

Setting aside the redundancies between spectra regions, these results suggest that PC1 is structured primarily by a gradient of fat abundance (lipids, fatty acids, triglyceride; wave numbers above 1300 cm-1). Nitrogenous molecules also drive PC1, with an abundance of tertiary amides to its positive part (wave numbers above 1400 cm-1). This joins the observations of (Miao et al., 2020): the degree of unsaturation and the proportion of nitrogen in the molecules studied were the two main factors discriminating species mucilage chemical composition according to their phylogenetic families. So although mucilage from different phylogenetic families possess a "largely common composition" (Herz et al., 2018), particularly for their carbohydrate base (Vančura and Hovadík, 1965), the abundance of fat and nitrogenous molecules (amide III), albeit minor in mucilage composition (Nazari, 2021; Miao et al,. 2020) seem the primary factors in their variability.

- The chemical composition of mucilages seems linked to their MWC

A positive correlation arises (R^2=0.568, p=0.051) between amount of sugar (per g of mucilage dry matter) and maximal water content of mucilage, only if maize is excluded. Nazari et al. (2020) also found no correlation for maize cultivars. Furthermore, the PC2 axis structured by a wavelength band between 1100 and 1250 cm^{-1}, corresponding to polysaccharide (pectin and cellulose) and sugar type molecules (Talari et al., 2017), appears to rank mucilages according to the quantity of high molecular weight sugar (at the top is the tomato whose exudates are rich in pectin, Jeong et al., 2018) and therefore also to their ability to retain water (Kazanskii and Dubrovskii, 1992). This is underlined by the positive correlation between the coordinates of the PC2 axis and MWC values (R^2=0.623, $p<0.0001$) (Fig.2).

- Mucilage-induced respiration depends on the type of soil and probably also on its plant origin.

Irrespective of the mucilage tested, we observed a ranking of respirations according to the 3 soils, with mucilage-induced respirations systematically higher in Crau and Lysi soils than in Tavel soil ($p<0.0001$). This shows an effect of microbial communities and their edaphic environment (with Crau>Lysi>Tavel for MO content, Microbial Biomass, CEC, WHC and Basicity, Bérard et al., 2020 ; Riffaldi et al., 1996) greater than the effect of the mucilage's chemical composition on its induced respiration. However, some mucilages are classified (in terms of induced respiration intensity) in the same way whatever the soil (wheat, lupin, maize mucilage being the least degraded, while tomato, rapeseed mucilage the most - Fig. 2). In particular, respiration induced by tomato mucilage was always much higher than that induced by maize mucilage ($p<0.002$). The water content of tomato mucilage is higher than that of maize mucilage (Tab.1), probably making the first more available to microorganisms. In addition, these two mucilages are very far apart on the PCA of the MIR spectra (Fig.1), suggesting different compositions. To a lesser extent than Naveed et al. (2017), we observe the same trend when comparing maize and barley mucilage. This suggests that the chemistry and/or physics of the mucilage have a dominant role on its availability/degradation by soil microorganisms. It would be interesting to develop chemical and physical analyses to characterize, for example, the size and branching of the polymers, and their water retention and viscosity (parameters likely to influence the degradability of these mucilages) in order to confirm these hypotheses. On the other hand, plant phylogeny does not seem to be related to mucilage-induced respiration levels. Finally, in some cases, mucilage-induced respiration differently according to soil type. For example, rapeseed mucilage-induced respiration is higher than wheat or lupin mucilage in Crau soil ($p<0.001$), whereas this difference fades in Lysi and Tavel soils ($p>0.05$). The soil, through its microbial community and its physicochemical properties, can therefore interact with the degradation of the different mucilages.

The sugar amount of mucilage produced per seed is extremely variable (Tab.1) and not associated with phylogeny but strongly correlated with seed weight ($R^2= 0.92$, $p=0.0001$). This suggests that species involve more or less the same fraction of seed's C reserve in sugars of mucilage production. As a corollary, this also results in a large range of amounts of mucilage-derived sugars delivered to soil among species (according to seed weights), which may impact considerably in soil the shaping and interactions in this "early stage rhizosphere" at a critical stage in plant establishment. Analyzes of C stored in the seeds, in relation with mucilage-derived sugars could strengthen these findings. We also observed that the sugars amount produced per root weight was highly variable between different species (6-fold, Tab.1), which in real plant conditions in soils could impact rhizospheric soil water retention. This exploratory study, based on mucilage harvested in aero-hydroponics from various plant species, needs to be extended to later phenological stages in real field conditions, with a variety of soils and water availability conditions, as done for maize (Nazari et al., 2023) and tomato (Le Gall et al., 2021).

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Figures and Table captions

Figure1: Results of the Principal Component Analysis (PCA) performed on MIR spectra (four spectra per species) of mucilages harvested from the roots of aero-hydroponically germinated seeds of eight plant species. **a-** PCA representing the eight species. **b-** PCA eigenvector of the PC1 (black curve) and PC2 (red curve) axes of Fig.1a were built from the wavenumbers of the MIR spectra.

Figure.2: Correlation between the chemical characteristics of the different mucilages (harvested from the roots of aero-hydroponically germinated seeds of eight plant species) (x-axis: coordinates of the PC2 axis of the PCA performed with the MIR spectra, see Fig.1) and a physical characteristic (y-axis: mucilage maximal water content, see Tab.1) of these mucilages.

Figure.3: Respiration measurements induced by different mucilages (harvested from the roots of aero-hydroponically germinated seeds of eight plant species) in three contrasting soils (MicroResp^{TM} technique). **a-** Respiration in Tavel soil. **b-** Respiration in Lysi soil. **c-** Respiration in Crau soil. Different letters indicate significant differences (four replications, Kruskal-Wallis, Dunn Bonferroni test). Tom: Tomato, Sor: Sorghum, Rap: Rape, Alf: Alfalfa, Bar: Barley, Lup: Lupin, Wht: Wheat, Mze: Maize.

Table.1: Phylogeny of the eight vegetal species studied, experiment characteristics, mucilage characteristics harvested from the roots of aero-hydroponically germinated seeds of these eight plant species. MWC= maximal water content (calculated as mucilage wet weight minus dry weight divided by dry weight).

SuppMat.1: Main physical, chemical and microbial properties of the three soils used for MicroResp^{TM} bioassay with the eight different mucilages tested. SOC: Soil Organic Carbon, TN : Total Nitrogen, CEC: Cation Exchange Capacity, WHC: Water Holding Capacity, MB: Microbial Biomass, WSA : Water Stable Aggregates

SupMat2.a: Results of the Dendogram (Agglomerative Nesting Hierarchical Clustering) performed on MIR spectra (four spectra per species) of mucilage harvested from the roots of aero-hydroponically germinated seeds of eight vegetal species. **SupMat2.b:** Years of phylogenetic phyla from compilations of articles from the Angiosperm Phylogeny Website hosted by the Missouri Botanical Garden: http://www.mobot.org/MOBOT/Research/APweb/welcome.html.

SuppMat.3 Discussion of the limitations of the mucilage collection method

Figure 1

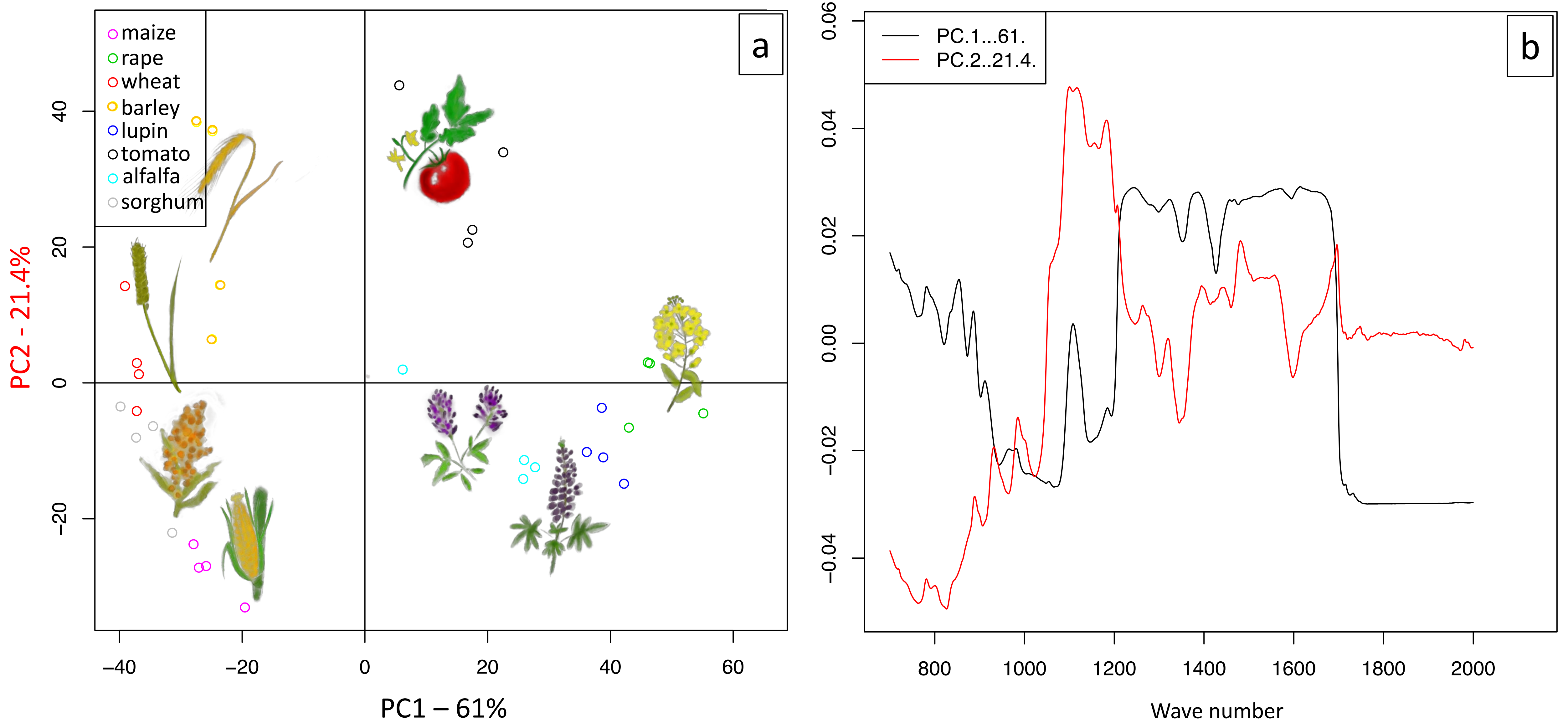
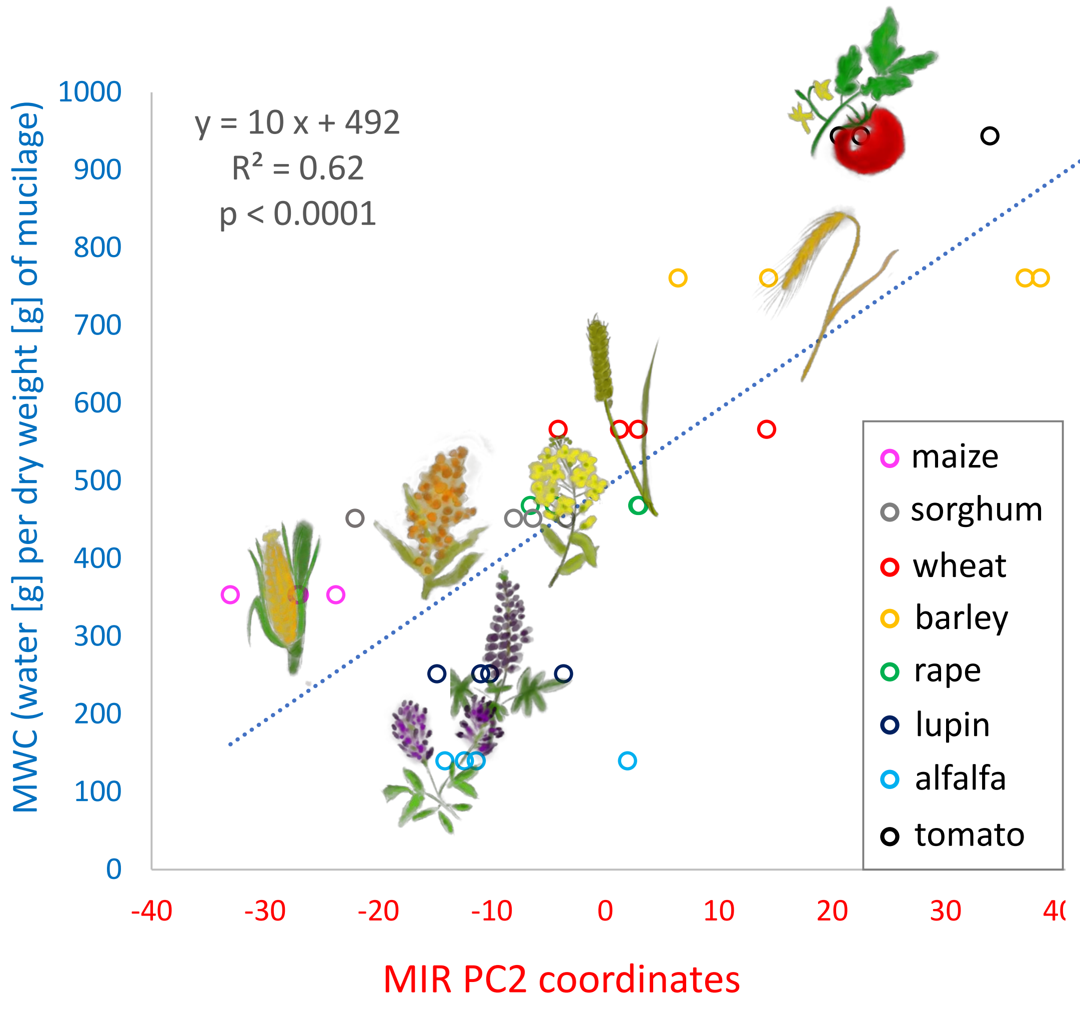
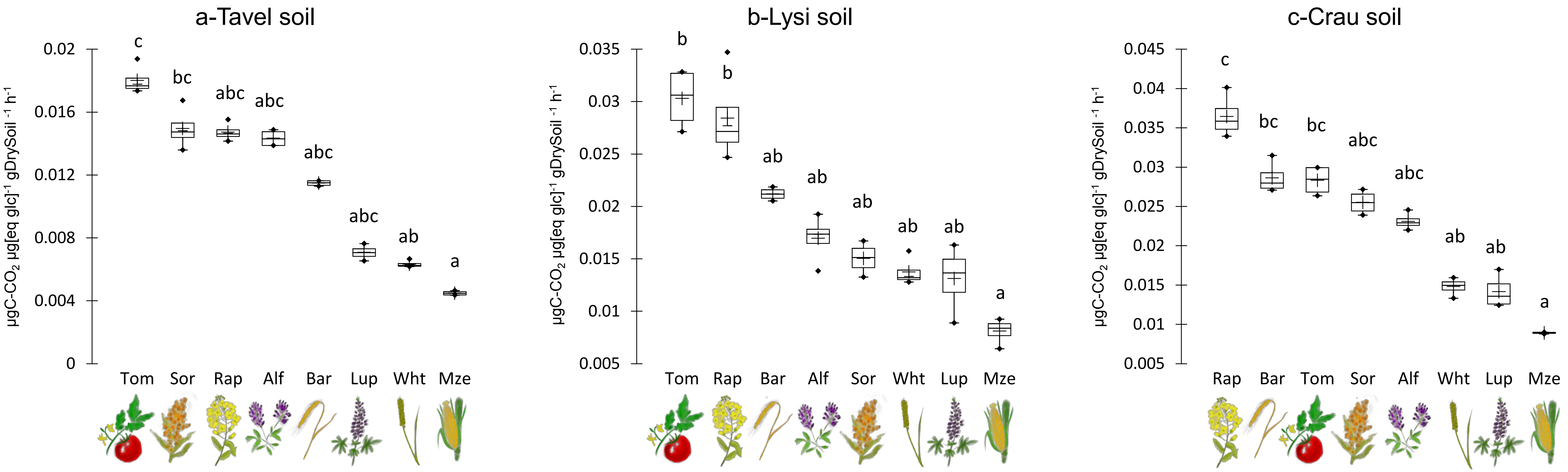

a
maize
rape
wheat
barley
lupin
tomato
alfalfa
sorghum
PC2 - 21.4%
PC1 – 61%
−40
−20
0
20
40
60
b
PC.1...61.
PC.2..21.4.
0.06
0.04
0.02
0.00
−0.02
−0.04
800
1000
1200
1400
1600
1800
2000
Wave number

Figure 2



y = 10 x + 492
R² = 0.62
p < 0.0001
MWC (water [g] per dry weight [g] of mucilage)
1000
900
800
700
600
500
400
300
200
100
0
-40
-30
-20
-10
0
10
20
30
40
MIR PC2 coordinates
maize
sorghum
wheat
barley
rape
lupin
alfalfa
tomato

Figure 3


a-Tavel soil
b-Lysi soil
c-Crau soil
µgC-CO2 µg[eq glc]-1 gDrySoil -1 h-1
Tom
Sor
Rap
Alf
Bar
Lup
Wht
Mze
c
bc
abc
ab
a
b

Tab.1

Table.1: Phylogeny of the eight vegetal species studied, experiment characteristics, mucilage characteristics of these vegetal species. SWC= saturation water content (calculated as mucilage wet weight minus dry weight divided by dry weight).

Plant and experiment characteristics										Mucilage characteristics			
Species	Variety	Tribe	Sub-family	Family	Clade	Clade	Thousand seed weight (g)	Number of Seeds per tray	Germination time (day)	Total sugar per dry root [eq glc] mg/g	Total sugar per dry matter [eq glc] mg/g	Total sugar per 1000 seed [eq glc] mg	SWC water [g] per dry weight [g]
Maize	MAS 26.R	Triticeae	Pooideaeae	Poaceae	Commelinids	Monocot	286	277	3	0.89	8.16	1.97	353
Sorghum	Solarius	Triticeae	Pooideaeae	Poaceae	Commelinids	Monocot	11	2846	3	1.28	3.48	0.07	452
Wheat (Spring wheat)	Togado	Andropogoneae	Panicoideae	Poaceae	Commelinids	Monocot	37	865	3	0.28	6.31	0.38	566
Barley (Spring barley)	RGT Planet	Andropogoneae	Panicoideae	Poaceae	Commelinids	Monocot	43	794	3	0.95	5.41	0.65	761
Alfalfa	Europe	Robinoids	Faboideae	Fabaceae	Rosids	Eudicot	2	7456	2	0.70	1.37	0.05	140
Lupin	Rumba	Genisteae	Faboideae	Fabaceae	Rosids	Eudicot	154	520	3	0.20	4.05	0.68	252
Rape	Cleopatra	Brassiceae	Brassicoideae	Brassicaceae	Rosids	Eudicot	5	3804	3	0.67	2.92	0.04	468
Tomato	Saint Pierre	Solaneae	Solenoideae	Solanaceae	Asterids	Eudicot	2	6138	3	0.19	5.47	0.10	944
								Mean for all species		*0.64*	*4.65*	*0.49*	*492*
								standard deviation for all species		*0.40*	*2.13*	*0.65*	*263*

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: