

Gradu Amaierako Lana / Trabajo Fin de Grado Biologia Gradua / Grado en Biología

# Reactivity of dry riverbed's to rewetting: a worldwide vision

Egilea/Autor/a: Yosune Echeverría Colado Zuzendaria/Director/a: Daniel von Schiller Calle

© 2017, Yosune Echeverría Colado

# **INDEX**

- Abstract / Resumen (page 3)
- Introduction (pages 3 to 5)
- Materials and methods (pages 5 to 9)
- Results and discussion (pages 9 to 16)
- Conclusions (pages 16 to 17)
- Acknowledgements (page 17)
- References (pages 17 to 20)
- Annex I (pages 21 to 24)
- Annex II (page 25)

#### **ABSTRACT**

Intermittent rivers and ephemeral streams (IRES) that naturally cease to flow and run dry comprise a notable fraction of the world's river network. Moreover, their temporal and spatial extent is increasing due to land use and climatic changes. Nonetheless, IRES have been traditionally overlooked by soil and stream ecologists because of their double condition of soil and water. Recent studies have demonstrated the relevance of the dry phase of IRES with respect to carbon dioxide (CO<sub>2</sub>) emissions to the atmosphere. In this study, we focused on the effect of rewetting on microbial respiration in IRES sediments. Therefore, we measured microbial respiration under dry, slightly wet and severely wet conditions. Our results show a strong effect of rewetting on respiration, indicating that great amounts of CO<sub>2</sub> can be emitted to the atmosphere during first flush events. In addition, microbial respiration was higher in sediments with smaller particle size (e.g. clay and silt), and higher carbon (C) and nitrogen (N) content.

*Keywords*: intermittent, river, stream, rewetting, carbon, emissions, microbial respiration, particle size, interdisciplinarity.

#### **RESUMEN**

Los ríos intermitentes y arroyos efímeros (IRES) que de forma natural cesan de fluir y se secan constituyen una notable fracción de la red fluvial mundial. Sin embargo, los IRES han sido tradicionalmente ignorados por los ecólogos terrestres y fluviales debido a su doble condición de suelo y agua. Sin embargo, estudios recientes han demostrado su relevancia en relación a las emisiones de dióxido de carbono (CO<sub>2</sub>) a la atmósfera. En el presente estudio, centrado en la fase de rehumedecimiento de los IRES, se ha medido la respiración microbiana bajo condiciones de sequedad y humedad ligera y severa. Nuestros resultados muestran un fuerte efecto del rehumedecimiento en la respiración, indicando así que pueden ser emitidas grandes cantidades de CO<sub>2</sub> a la atmósfera durante los primeros pulsos de agua. Además, la respiración microbiana resultó ser mayor en sedimentos con un menor tamaño de grano (ej. arcilla y limo) y mayor contenido en carbono (C) y nitrógeno (N). *Palabras clave*: río, arroyo, intermitente, rehumedecimiento, carbono, emisiones, respiración microbiana, tamaño de partícula, interdisciplinaridad.

#### INTRODUCTION

Intermittent rivers and ephemeral streams (IRES) are those rivers and streams which stop flowing or dry up at some point in time and space (Acuña et al., 2014). IRES represent a substantial proportion of the total number, length and discharge of the world's rivers and are the dominant freshwater type in arid and semiarid regions (Larned et al., 2010). Moreover, given the land use and climatic changes,

their temporal and spatial extent is increasing (Palmer et al., 2008). They have been long time avoided because of their double functioning of soil and water, typically studied by different experts in separate works. This condition has created a knowledge gap on their functioning and biogeochemistry, and consequently, they have been widely neglected in water legislation and management (Datry et al., 2014).

IRES have very important values: they are places of human cultural significance, seed or egg "banks" for aquatic biota with desiccation-resistant stages, habitats containing a variety of aquatic, amphibious and terrestrial biota, dispersal corridors for terrestrial and aquatic biota, and sites for retention and transformation of organic matter and nutrients (temporary aquatic-terrestrial ecotones) (Steward et al., 2012). In addition, their improper consideration may cause the incorrect estimation of nutrient and carbon (C) fluxes in river networks. Fortunately, they have recently received increased attention by scientists and water resources managers, leading way to its proper study and knowledge, although it remains insufficient (Acuña et al., 2014; Datry et al., 2014).

IRES have a unique 'biogeochemical heartbeat' with high temporal and spatial variation in nutrient and organic matter dynamics (von Schiller et al., in press). In terms of biogeochemistry, the most important phases that characterize IRES are desiccation and rewetting, in which carbon dioxide (CO<sub>2</sub>) emissions to the atmosphere can be very significant (Gallo et al., 2014; von Schiller, 2014). The CO<sub>2</sub> emissions from dry IRES cannot be considered terrestrial. The C processed in dry IRES has either already left terrestrial ecosystems and entered the river network or has been produced within the river network. Moreover, the sediments from dry IRES, and the terrestrial soils are different environments in terms of physical structure and biogeochemical dynamics (McIntyre et al., 2009; Larned et al., 2010; Steward et al., 2012). Thus, not considering CO<sub>2</sub> emissions from dry IRES may overlook the role of a fundamental component of river networks in the C balance of inland waters.

In most IRES, fragmentation typically evolves towards complete stream desiccation. Low water availability reduces overall microbial activity through direct physiological effects, reduced diffusion of soluble substrates and lowered microbial mobility (Amalfitano et al., 2008; Humphries and Baldwin, 2003). Nonetheless, the dry riverbeds of IRES do not remain inactive and, biofilms can process organic C in dry IRES (Pohlon et al., 2013; Timoner et al., 2012; Zoppini and Marxsen, 2011) and CO<sub>2</sub> can be released from these systems when they are dry (Gallo et al., 2014; Gómez-Gener et al., 2016; von Schiller et al., 2014). When sediments of IRES dry up, they come into direct contact with the air, thus creating an oxygenated environment that favors aerobic transformation processes (Baldwin and Mitchell, 2000; Mitchell and Baldwin, 1999). Moreover, the high mortality of animals, plants and microbes during sediment drying results in low immobilization and in release of high amounts of nutrients and organic matter (Amalfitano et al., 2008; Zoppini and Marxsen, 2011).

The recovery of stream flow after the dry phase in IRES occurs because of decreases in evapotranspiration and the occurrence of heavy rainfalls, resulting in a gradual, intermediate or abrupt first flow event (Butturini et al., 2003; Jacobson and Jacobson, 2013; Stanley et al., 1997). Many in-

stream microbial activities tend to recover very quickly after flow resumption (Amalfitano et al., 2008; Dodds et al., 2004; Sabater et al., 2016) and the relative importance of allochthonous terrestrial nutrient and organic matter sources increases with respect to those from in-stream origin (Bernal et al., 2013). High amounts of particulate and dissolved materials, including nutrients, are mobilized downstream during these first flow pulses (Fisher and Minckley, 1978; Obermann et al., 2009; Tzoraki et al., 2007; von Schiller et al., 2011). This phenomenon was first characterized by Birch (1964) in soils, and henceforth termed "Birch effect". Birch showed that cycles of drying and wetting of soils stimulated the mineralization of soil organic matter, leading to the rapid release of mineral nitrogen (N) and CO<sub>2</sub>, thus having a significant influence on the sink capacity of the system. Nowadays the "Birch effect" is seen as a result of a hypoosmotic stress response of the soil microbial community and the rapid assimilation of dead microbial biomass (Unger et al., 2010), that increases with drought length (Fierer and Schimel, 2002).

The aim of the present study was to investigate the effect of rewetting (first pulses) on sediment microbial respiration in IRES, which is an important source of CO<sub>2</sub> emissions (Gallo et al., 2014). With this purpose, we conducted a laboratory experiment within the framework of the international initiative "The 1000 Intermittent Rivers Project" (<a href="http://1000\_intermittent\_rivers\_project.irstea.fr">http://1000\_intermittent\_rivers\_project.irstea.fr</a>; Datry et al., 2016). Sediment samples were collected consistently during the dry period from 100 IRES across 16 countries spanning a wide range of conditions (e.g. climate, land use). In a centralized laboratory, we measured sediment characteristics (e.g. C and N content, texture, moisture) as well as microbial respiration under dry and rewetting conditions. We hypothesized that sediment respiration would increase significantly when rewetted because of the increase in moisture. We further hypothesized that this reactivity would be modulated by sediment characteristics.

# MATERIALS AND METHODS

Study sites

The sampling was conducted in 100 IRES located in 16 countries (Figure 1): Algeria (1 site), Australia (9 sites), Czech Republic (4 sites), Ecuador (3 sites), France (13 sites), Germany (11 sites), Israel (1 site), Italia (8 sites), La Reunión (France; 2 sites), Namibia (2 sites), Portugal (1 site), South Africa (4 sites), Spain (17 sites), Switzerland (9 sites), United Kingdom (2 sites) and USA (13 sites).

The sampled IRES had an active channel width between 0.3 and 10 m; a catchment area between 0.1 and 6000 km<sup>2</sup>; a length of the drying period duration between 0.5 and 800 days; an aridity index between 5 and 108; a potential evapo-transpiration (PET) between 480.4 and 1817.5; a mean annual temperature between -1.2 and 24.1 °C; and a mean annual precipitation between 5 and 1516 mm. See Annex I for details.

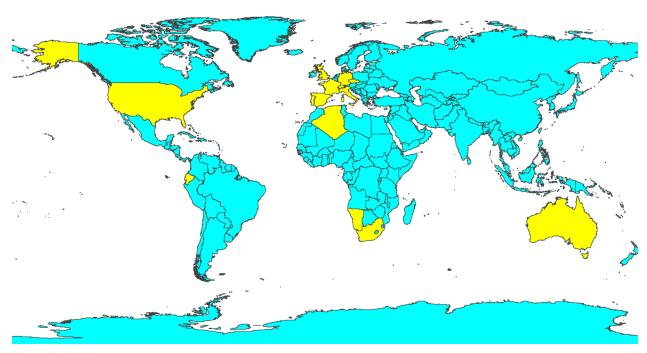


Figure 1: Map of the world with the sampled countries in yellow.

## Field sampling

Samples were obtained following the 1000IRP protocol

(http://1000\_intermittent\_rivers\_project.irstea.fr/wp-content/uploads/The-1000-intermittent-rivers experiment\_proposal\_protocols\_procedures\_27may2015.pdf). Our team from the University of the Basque Country (UPV/EHU) took samples from 4 rivers located in the Basque Country and Navarre (Figure 2).

The length of the reach sampled was defined as 10 times the average active channel width to ensure consistent sampling effort across IRES and to cover a representative area. The active channel is defined here as the area of inundated and exposed bed sediments between established edges of perennial, terrestrial vegetation and/or abrupt changes in slope.

Dry riverbed sediments were collected in a standardized way during the dry period, before the flow resumption. The area of the selected reach was estimated (length \* average active channel width). Then, the surface from which sediments were collected was calculated, to sample at least 5 % of the reach surface using 1 m² quadrats.

Back in the laboratory, the material was processed as soon as possible. The sediment was sieved through a 2 mm sieve and only the fine fraction was kept. One subsample of ~160 g dry riverbed sediments was prepared, packed in Ziplock bags or a solid plastic container and sent to our laboratory for further analyses.



**Figure 2**: Dry riverbeds sampled in the rivers Arantzazu (top left) and Begiolatza (bottom right) located in Guipuzkoa, as well as in an unnamed Barranco (top right) and Barranco de las Cortinas (bottom left) located in Navarre.

## Laboratory analyses

Original sediment samples (of about 160 g, air-dried and 2 mm sieved) were stored in a dry and dark place until analyzed. First, samples were homogenized and shared out to perform five different analyses: C and N content (20 g), sediment texture (3 g), water content (20 g), MicroResp<sup>®</sup> (10 g) and bottle incubations (40 g). The rest was stored in the dark in case further analyses were needed. Structural variables were estimated in different laboratories.

Samples for the percent of organic C (OC) and total N (TN) were grinded in our laboratory and analyzed at the Catalan Institute for Water Research (ICRA). The OC and TN content was estimated after acidifying (to eliminate the inorganic fraction; e.g. carbonates) by acidification with 2N HCl on an Elemental Analyzer, using two replicates per sediment sample. The C/N molar ratio was also estimated as OC/TN.

Main textural fractions (% sand, % silt and % clay) and their median particle size were determined with a laser-light diffraction instrument (Coulter LS 230, Beckman-Coulter, USA), after organic matter was eliminated with  $H_2O_2$ . Processing and analysis were performed at the University of Barcelona (UB). In this case, we used one replicate per sediment sample.

Water content was estimated at the UPV/EHU. Before grinded, about 20 g of each sample (well homogenized) were weighted (wet weight, WW) into pre-weighted crucibles, and dried in the

laboratory oven at 60 °C for 24 h. After that, samples were again weighted into pre-weighted crucibles to calculate the dry weight (DW). Water content (%) was then obtained based on the wet and dry weight of the samples: (WW-DW)\*100/WW.

Sediment microbial respiration was measured with two methods: MicroResp® and bottle incubations, to obtain 3 measures of microbial respiration. MicroResp® method was measured under dry and wet conditions, to reproduce dry and low intensity rewetting (e.g. rain) conditions, respectively. Bottle incubations were used to reproduce microbial respiration under high intensity rewetting conditions (e.g. reflooding).

Respiration with MicroResp® (Macaulay Scientific Consulting Ltd, UK) was measured at ICRA following Campbell et al. (2003). First, 0.5 g of sediment was weighted into a deep well microplate. Samples were placed at the same temperature that was used later for incubations (20 °C), for at least 24 h. Three of the replicates were left in dry conditions and rewetted with  $50\mu$ L of Volvic® mineral water. Replicates were incubated for 6 h at 20 °C and a colorimetric method was used to measure the evolution of  $CO_2$  immediately before and after the incubation. To finish, the % change of  $CO_2$  to basal respiration ( $\mu$ g  $CO_2^{-1}$  h $^{-1}$ ) was converted considering the incubation time and temperature, the gas constant, the headspace volume and the soil dry weight as indicated in the MicroResp® technical manual.

Sediment microbial respiration was also measured using bottle incubations, based on dissolved oxygen decline (Ely et al., 2010) at the UPV/EHU. Samples were placed at the same temperature used for incubations (20 °C) at least for 24 h. We used two replicates of 5 g approximately per sediment sample, and several controls without sediment for each run. Samples and controls were introduced in 250 mL incubation bottles filled with Volvic® mineral water and closed without air. They were then incubated for 20 h at 20 °C in an incubation chamber (Figure 3). DO decline (mg  $L^{-1}$ ) was measured at the end of the incubation with a PreSens Microx 4 DO meter with a Needle-type Oxygen Microsensor (Figure 3). DO decline (obtained considering the DO difference between the control and the sample) was converted to  $CO_2$  production using RQ (Respiratory quotient) = 0.85.



Figure 3: Set up and equipment used for the microbial respiration measurements using bottle incubations.

# Data analysis

To examine the effect of rewetting on sediment microbial respiration, we compared respiration values obtained in dry, wet (both with MicroResp®) and bottles (bottle incubations) conditions using a non-parametric Kruskal-Wallis test. To examine the relationship between microbial respiration and sediment characteristics, we used non-parametric Spearman-rank correlations. Statistical analyses were done using Past 3.15 (PAleontological STatistics software package for education and data analysis).

## RESULTS AND DISCUSSION

#### Sediment characteristics

Sediment variables showed a wide range of values indicative of the wide variety and worldwide representativeness of sampled IRES (Table 1). However, this could also be an impediment to characterize rivers of specific regions and to study differences between areas (e.g. countries, climatic regions).

Water content proportions were low, which makes sense taking into account that sediment samples were taken in the dry phase of IRES. Thus, the difference between water content in samples is due to the span of time since the dry phase started. Samples with higher water content must have passed a shorter period of drought, whereas samples with the lowest water content had a long-term desiccation.

Overall, sediment texture was dominated by sand, with only few dry riverbeds dominated by silt. The proportion of clay was generally low, but relevant (up to 17%) at some sites. The median particle size falls in the sand classification, that is, the biggest one. Grain size is an important factor because it is related with the soil profile (smaller particles are usually found in the surface and larger ones in profound layers), in which microbial communities are distributed declining in depth and activity (Fierer et al., 2003).

Recent studies have shown that biofilms process organic C in dry IRES (Pohlon et al., 2013; Timoner et al., 2012; Zoppini and Marxsen, 2011) and that CO<sub>2</sub> can be released from these systems when they are dry (Gallo et al., 2013; Gómez-Gener et al., 2016; von Schiller et al., 2014). Heterotrophic processes such as exoenzymatic activities are more resistant to stream desiccation than autotrophic processes, especially in subsurface sediments (Acuña et al., 2015; Timoner et al., 2012; Zoppini and Marxsen, 2011). Thus, these heterotrophic processes, along with the dead biomass (Bottner et al., 1998), explain the high organic C content measured in the sediments.

The C:N ratio was high, showing a prevalence in C percentage (liberated in higher amounts than N). Even so, N content was not negligible. Its liberation due to leaf litter decomposer

communities, along with stream microbial communities during the dry phase, contributes considerably to the high nitrate export typically observed in intermittent streams during first flush events (Merbt et al., 2016).

 $\label{thm:characteristical} \textbf{Table 1:} \ \ Main \ statistical \ values \ (horizontal) \ \ of \ the \ proximal \ \ variables \ (vertical) \ from \ the \ analyzed \ sediments.$  Sediment characteristics are labeled with the following initials: WC (Water Content, % of weight), Median\_size (median particle size, \$\mu m), Clay\_coult (% particles < 2\$\mu m), Silt\_coult (% particles 2-63 \$\mu m), Sand\_coult (% particles 63 to 2000 \$\mu m), C (% of organic C content), N (% of total N content), CN (C to N molar ratio, NA).

	Median	25 percentil	75 percentil	Range
WC	0.9	0.5	2.3	0.1-10.9
Median_size	404.2	40.9	631.2	7.5-1276.7
Clay_coult	3.1	1.3	8.5	0.2-17.3
Silt_coult	15.8	6.2	48.6	0.9-83.1
Sand_coult	81.4	39.2	92.3	4-98.8
С	0.7	0.3	1.4	0.1-8.5
N	0.042	0.018	0.094	0.009-0.553
CN	16.1	12.9	19.8	6.5-206.8

## Rewetting effect on respiration

Microbial respiration differed significantly among the different incubation methods and conditions (Figure 4). The highest respiration was measured in the bottle incubations (median = 47.2 nmol C/gDW\*h, range = 0-349.3), followed by MicroResp® respiration in wet conditions (median = 23.3 nmol C/gDW\*h, range = 5.7-147.1) and MicroResp® respiration in dry conditions (median = 1 nmol C/gDW\*h, range = 0-14.1). These results indicate that microbial respiration in IRES sediments is generally low during the desiccation phase, but that rewetting events can create a rapid increase of microbial respiration and CO<sub>2</sub> release as a result of stimulation of microbial activity (Jarvis et al., 2007). These findings are in line with those of Gallo et al. (2014), who described biogeochemical hot moments of CO<sub>2</sub> release during rewetting experiments conducted in IRES in Arizona (USA).

A similar response has been reported as the "Birch effect" in soil studies (Birch, 1964), caused by rapidly increased respiration and mineralization rates in response to changing moisture conditions. Results suggest that this effect is bigger for a reflooding (represented by the bottle incubations method) than for a small rewetting (represented by the wet MicroResp® method). These results agree with previous rewetting effects reported from soils (Fierer and Schimel, 2002), in which microbial activity raised because of the eventual availability of water.

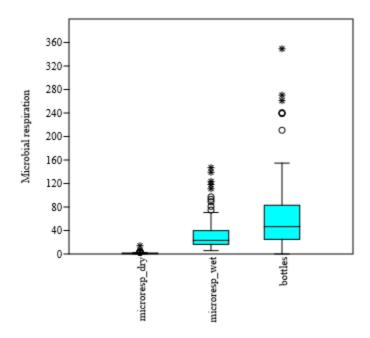


Figure 4: Box plot of the respiration values (in nmol C g DW<sup>-1</sup> h<sup>-1</sup>) measured with MicroResp<sup>®</sup> (dry and wet) and bottle incubations methods, showing a significant difference between sample medians.

Kruskal-Wallis test for equal medians: chi square = 183, p value < 0.001.

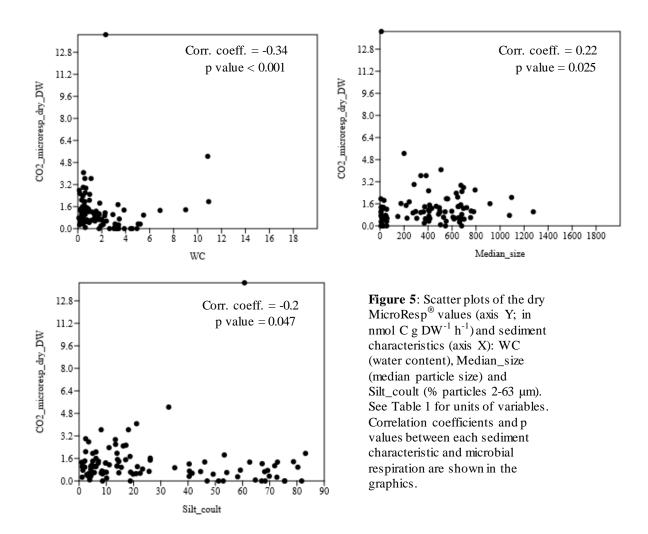
Relationships between respiration and sediment characteristics

A table with all correlation values and their related p values can be found in the Annex II. In this section, we only show results of significant correlations (p value < 0.05).

MicroResp® microbial respiration in dry conditions was negatively correlated with water content and silt fraction and positively correlated with mean particle size (Figure 5). Many field and laboratory studies have shown that soil respiration rates are strongly influenced by average water content (Howard and Howard, 1993), and that frequency of drying-rewetting events has clear ecosystem consequences for soil C mineralization rates (Fierer and Schimel, 2002; Miller et al., 2005). Our results indicate that a greater content of water results in a lower respiration. Water content could be related with the desiccation term period. In this way, IRES with more water content in dry conditions must have had a short-term dry period, and thus microbial communities are still not adapted. A number of organisms that live in intermittent river sediments need oxygenic conditions to carry out their metabolism. That is the case of some stream microbial communities with ammonia oxidation activity (Merbt et al., 2016). Those conditions appear, thus, under severe dry periods.

Results suggest that when particles are larger, respiration increases (median particle size positively correlated with microbial respiration) whereas it decreases when they are smaller (silt fraction negatively correlated with microbial respiration). Microbial communities vary through the soil profile. Not only does biomass decline exponentially with depth (Fierer et al., 2003) but so does relative activity, while the community composition shifts to a less diverse community of starvation-tolerant microbes (LaMontagne et al., 2003; Fierer et al., 2003; Holden and Fierer, 2005). Surface soils (with particles of a smaller size) are resource rich, but experience wide variation in temperature and moisture while deeper soils (with particles of a bigger size) are resource poor, but experience a more

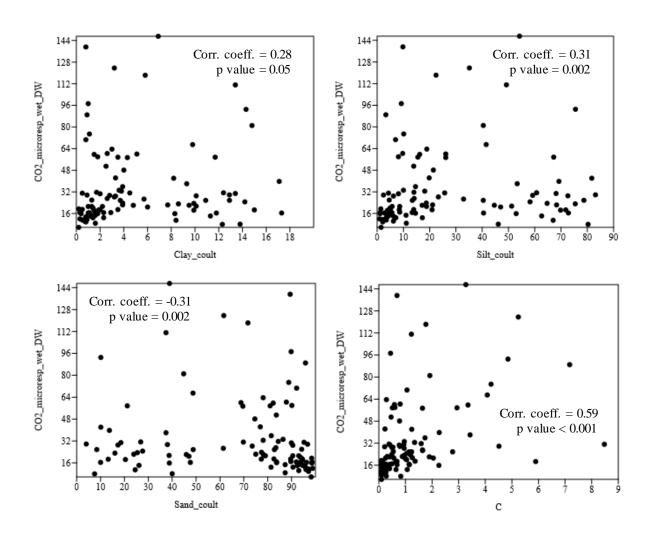
constant environment (Fierer et al., 2003). In this way, surface microbes have a greater C supply thus fuel enhanced growth and respiration, and subsurface soil microbes are C-starved (Fierer at al., 2003). Microbial respiration should be higher in sediments with a low median particle size. However, in dry conditions our results indicate the opposite conclusion, being microbial respiration positively correlated with median particle size. Nonetheless, these correlations were strongly affected by the outlier with the highest respiration, and being p values proximal to 0.05, maybe these variables are not so strongly correlated to microbial respiration.

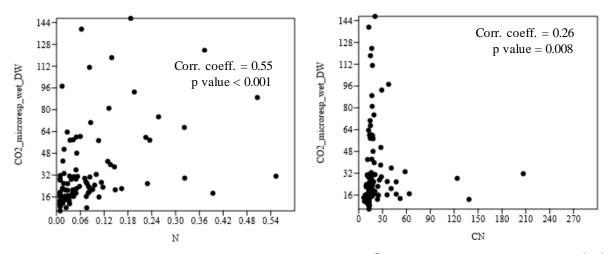


MicroResp® microbial respiration in wet conditions was positively correlated with clay fraction, silt fraction, C content, N content and negatively correlated with sand fraction (Figure 6). Under dry conditions the correlation between respiration and silt fraction was negative. However under wet conditions, it was positive, as well as with the clay fraction. In this case, results agree with previous explanations for the microbial respiration in the soil profile. As reported, surface microbes (that live between small size particles) have a greater C supply and thus an enhanced growth and respiration, whereas subsurface soil microbes (that live between big size particles) are C-starved

(Fierer at al., 2003). Thus, microbial respiration increases in clay and silt fractions, and decreases in the sand fraction.

For the C and N content, the correlation was positive. In that way, respiration gets higher in sediments with a larger amount of those elements. As we have previously said, with a first flush event, a large amount of nutrients is released due to riparian groundwater and leaching from accumulated detritus. In this case, wet conditions simulate the rewetting of the soil. Therefore, soils that have stored these nutrients in the dry phase release them when rewetted (making sediments rich in nutrients) as a result of an osmotic shock to the populations of microbes (Jarvis et al., 2007; Unger et al., 2010) what makes respiration larger.



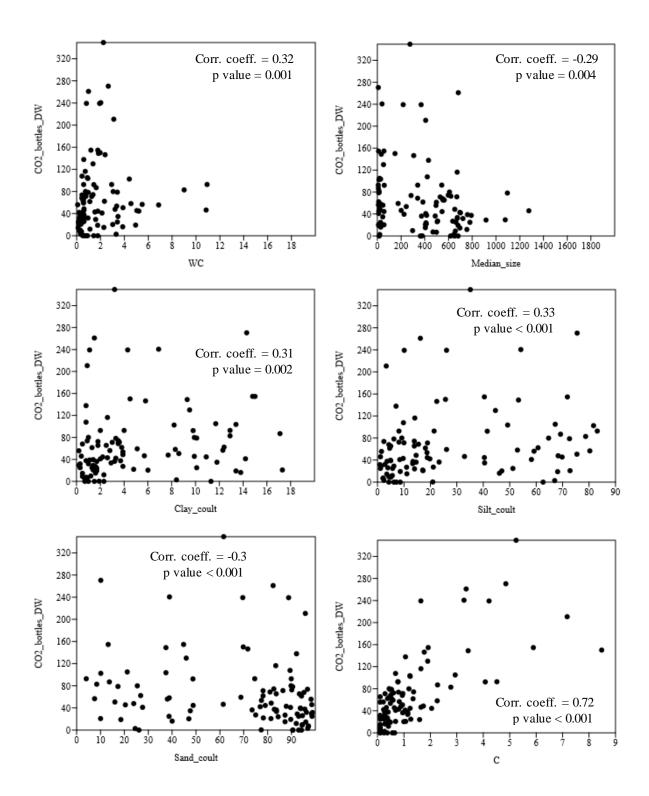


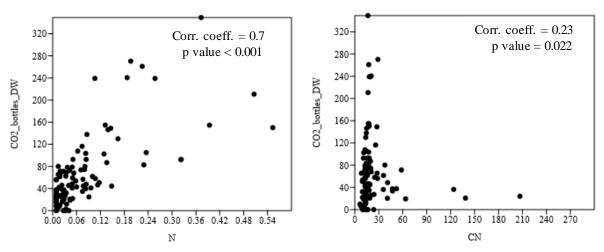
**Figure 6**: Scatter plots showing correlations between wet MicroResp<sup>®</sup> respiration (axis Y; in nmol C g DW<sup>-1</sup> h<sup>-1</sup>) and sediment characteristics (axis X): Median\_size (median particle size), Clay\_coult (% particles < 2μm), Silt\_coult (% particles 2-63 μm), Sand\_coult (% particles 63 to 2000 μm), C (organic C content), N (total N content), CN (C to N molar ratio). See Table 1 for units of variables. Correlation coefficients and p values between each sediment characteristic and microbial respiration are shown in the graphics.

Correlations between respiration results obtained with the bottle incubations method and the sediment characteristics are shown in figure 7. Correlations between microbial respiration and the environmental variables (mean particle size, clay fraction, silt fraction, sand fraction, C, N, and CN) explained for the wet MicroResp<sup>®</sup> condition agrees with the ones of the bottle incubations. This makes sense because in both cases respiration has been measured under wet conditions, simulating the rewetting event (of a lower or greater magnitude).

Nevertheless, for the bottle incubations method two more correlations appeared. The first one was a positive correlation with water content (on the contrary to dry MicroResp® conditions, in which it was negative), indicating that respiration increases in sediments with a higher amount of water. Many studies have proved that under dry conditions, metabolism of many organisms decreases (Amalfitano et al., 2008; Humphries and Baldwin, 2003), so in sediments with a larger quantity of water their activity can remain higher. Thus, those sediments show a bigger respiration when measured.

Finally, median particle size was also significant, with a negative correlation. As presented in the Table 1, sand percentage is the biggest and mean particle size remains quite big. Like this, the explanation for the negative correlation of the mean particle size is the same as the one told for the sand fraction. When particles are bigger they offer a difficult surface to grid and live for the organisms, and so microbial respiration decreases.





**Figure 7**: Scatter plots of the correlations between bottles incubations respiration (axis Y; in nmol C g DW<sup>-1</sup> h<sup>-1</sup>) and sediment characteristics (axis X). Environmental values are expressed in this way: WC (Water Content), Median\_size (median particle size), Clay\_coult (% particles < 2um), Silt\_coult (% particles 2-63 um), Sand\_coult (% particles 63 to 2000 um), C (organic C content), N (total N content), CN (C to N molar ratio). See Table 1 for units of variables. Correlation coefficients and p values between each sediment characteristic and microbial respiration are shown in the graphics.

#### **CONCLUSIONS**

Our results show that, rewetting of IRES accomplishes a first flush event in which high amounts of CO<sub>2</sub> are emitted to the atmosphere (Gallo et al., 2014). These emissions are affected by the number of drying-rewetting cycles, which are increased after long-term periods of drought (Fierer and Schimel, 2002). Dry watercourses can emit a similar or even greater amount of CO<sub>2</sub> than running waters (von Schiller et al., 2014; Gómez-Gener et al., 2016). When these emissions in dry conditions are summed up to those of the first flush events, a considerable quantity of emissions can be attributed to IRES. So far, CO<sub>2</sub> fluxes have been largely overlooked because of the lack of studies and comprehension of IRES, even though they may have an important role in the land C sink (Unger et al., 2010; von Schiller et al., 2014), and that their nature and biogeochemistry differs from those of soils or perennial rivers.

Microbial respiration rates have been proved to be greater in sediments with a smaller particle size, as typically found in the surface of soils, and with a higher C and N content. This fact can be of importance when considering sediment types of different places of the world. Those IRES with prevalence of small-sized particle sediments and higher organic matter content will show greater emissions during rewetting events.

This work has important implications in face of climatic change. The future scenario of the world will probably suppose an increase in the number of IRES around the world, driven by an increase in the mean temperature. Thus, a correct understanding of this type of rivers seems necessary,

allowing their proper consideration in water legislation and management (Datry et al., 2014). However, this is a challenge in which we have to work together. Interdisciplinarity is important not only in science, but in all aspects. Many knowledge gaps would be easier resolved if we cooperate together. In the IRES case, the lack of communication between soil and stream ecologists because of their different thinking and methodology led to their avoidance over many years. Nevertheless, their current unity is helping in progressing our understanding of IRES, and also in learning across disciplines.

#### **ACKNOWLEDGEMENTS**

First of all, I would like to thank my mom, without whom I would not have had enough courage to arrive where I am today. I feel also very grateful to my mentor, Dani, who has helped me in all this TFG process with all the doubts I had, also for giving me the opportunity of participating in this big and important project. And along with him, thanks to all the Group of Stream Ecology for their support, especially to Arturo, who accepted my collaboration in the Group. I would also like to thank the classmates that have been most important for me (they know who they are) and have given me strength along these four years. Also, the good Professors whose dedication towards their job has encouraged me to finish my bachelor's degree. Finally, my whole gratitude to the UPV/EHU, in which I have learnt so much, and which has been like my second home. To all of them, just THANK YOU. This work has been supported by the EU 7th Framework Programme Funding under Grant agreement no. 603629-ENV-2013-6.2.1-Globaqua and by COST (European Cooperation in Science and Technology) Action CA15113 SMIRES.

### **REFERENCES**

- Acuña, V., Datry, T., Marshall, J., Barceló, D., Dahm, C.N., Ginebreda, A., McGregor, G., Sabater, S., Tockner, K., Palmer, M.A. (2014). Why should we care about temporary waterways? Science (80-.) 343, 1080–1081.
- Amalfitano, S., Fazi, S., Zoppini, A., Caracciolo, A.B., Grenni, P., Puddu, A. (2008). Responses of benthic bacteria to experimental drying in sediments from Mediterranean temporary rivers. *Microb. Ecol.* 55, 270-279.
- Bernal, S., von Schiller, D., Sabater, F., Martí, E. (2013). Hydrological extremes modulate nutrient dynamics in mediterranean climate streams across different spatial scales. *Hydrobiologia* 719, 31–42.
- Baldwin, D.S., Mitchell, A.M. (2000). The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-foodplain systems: a synthesis. *Rivers Res. Manag.* 16, 457-467.

- Birch, H.F. (1964). Mineralisation of plant nitrogen following alternate wet and dry conditions. *Plant Soil* 20, 43-49.
- Bottner, P., Austrui, F., Cortez, J., Billes, G., Coûteaux, M.M. (1998). Decomposition of 14C- and 15N- labelled plant material, under controlled conditions, in coniferous forest soils from a northsouth climatic sequence in western Europe. *Soil Biol. Biochem.* 30, 597-610.
- Butturini, A., Bernal, S., Hellin, C. (2003). Influences of the stream groundwater hydrology on nitrate concentration in unsaturated riparian area bounded by an intermittent Mediterranean stream. *Water Resour. Res.* 39, 1110.
- Campbell, C.D., Chapman S.J., Cameron C.M., Davidson M.S., Potts J.M. (2003). A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. *Applied and environmental microbiology* 69, 3593-3599.
- Datry, T., Larned, S.T., Tockner, K. (2014). Intermittent Rivers: A Challenge for Freshwater Ecology. *Bioscience* 64 (3), 229-235.
- Datry, T., Corti, R., Foulquier, A., von Schiller, D., Tockner, T. (2016). One for all, all for one: a global river research network. *EOS Earth & Space Science News, American Geophysical Union* 97 (15), 13-15.
- Dieter, D., von Schiller, D., García-Roger, E.M., Sánchez-Montoya, M.M., Gómez, R., Mora-Gómez, J., Sangiorgio, F., Gelbrecht, J., Tockner, K. (2011). Preconditioning effects of intermittent stream flow. *Aquat. Sci.* 73, 599–609.
- Dodds, W.K., Gido, K., Whiles, M.R., Fritz, K.M., Matthews, W.J. (2004). Life on the edge: the ecology of Great Plains prairie streams. *Bioscience* 54, 205-216.
- Ely, D.T., von Schiller, D., Valett, H.M. (2010). Stream acidification increases nitrogen uptake by leaf biofilms: implications at the ecosystem scale. *Freshw. Biol.* 55, 1337-1348.
- Fierer, N., Schimel J.P. (2002). Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology & Biochemistry* 34, 777-787.
- Fierer, N., Schimel, J.P., Holden, P.A. (2003). Variations in microbial community composition through two soil depth profiles. *Soil Biology & Biochemistry* 35, 167–176.
- Fisher, S.G., Minckley, W.L. (1978). Chemical characteristics of a desert stream in flash flood. *J. Arid Environ*. 25-33.
- Gallo, E.L., Lohse, K.A., Ferlin, C.M., Meixner, T., Brooks, P.D. (2014). Physical and biological controls on trace gas fluxes in semi-arid urban ephemeral waterways. *Biogeochemistry* 121, 189-207.
- Gómez-Gener, L., Obrador, B., Marcé, R., Acuña, V., Catalán, N., Casas-Ruiz, J.P., Sabater, S., Muñoz, I., von Schiller, D. (2016). When water vanishes: magnitude and regulation of carbon dioxide emissions from dry temporary streams. *Ecosystems* 19,710.
- Hellawell, J.M. (1988). Toxic substances in rivers and streams. Environmental Pollution 61-85.

- Holden, P.A., Fierer, N. (2005). Microbial processes in the Vadose Zone. *Vadose Zone Journal* 4, 1–21.
- Howard, D., Howard, P. (1993). Relationships between CO<sub>2</sub> evolution, moisture content, and temperature for a range of soil types. *Soil Biology & Biochemistry* 25, 1537-1546.
- Humphries, P., Baldwin, D.S. (2003). Droght and aquatic ecosystems: an introduction. *Freshw. Biol.* 48, 1141-1146.
- Jacobson, P.J., Jacobson, K.M. (2013). Hydrologic controls of physical and ecological processes in Namib Desert ephemeral rivers: Implications for conservation and management. *J. Arid Environ*. 93, 80-93.
- Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., Valentini, R. (2007). Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the "Birch effect". *Tree Physiology* 27, 929–940.
- LaMontagne, M., Schimel, J., Holden, P.A. (2003). Comparison of subsurface and surface soil bacterial communities in California grassland as assessed by terminal restriction fragment length polymorphisms of PCR-amplified 16S rRNA genes. *Microbial Ecology* 46, 216–227.
- Larned, S.T., Datry, T., Arscott, D.B., Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshw. Biol.* 55,717-738.
- McIntyre RES, Adams MA, Grierson PF. (2009). Nitrogen mineralization potential in rewetted soils from a semi-arid stream landscape, north-west Australia. *J. Arid Environ*. 73, 48–54.
- Merbt, S.N., Proia, L., Prosser, J.I., Martí, E., Casamayor, E.O., von Schiller, D. (2016). Stream drying drives microbial ammonia oxidation and first flush nitrate export. *Ecology* 2192–2198.
- Miller, A.E., Schimel, J.P., Meixner, T., Sickman, J.O, Melack, J.M. (2005). Episodic rewetting enhances carbon and nitrogen release from chaparral soils. *Soil Biology & Biochemistry* 37, 2195-2204.
- Mitchell, A.M., Baldwin, D.S. (1999). The effects of sediment desiccation on the potential for nitrification, denitrification, and methanogenesis in an Australian reservoir. *Hydrobiologia* 392, 3-11.
- Obermann, M., Rosenwinkel, K.-H., Tournoud, M.-G. (2009). Investigation of first flushes in a medium-sized mediterranean catchment. *J. Hydrol.* 373, 405-415.
- Palmer, M.A., Liermann, C.A.R, Nilsson, C., Flörke, M., Alcamo, J., Lake, P.S., Bond, N. (2008). Climate change and the world's river basins: anticipating management options. *Front. Ecol. Environ.* 6(2), 81–89.
- Pohlon, E., Fandino, A.O., Marxsen, J. (2013). Bacterial community composition and extracellular enzyme activity in temperate streambed sediment during drying and rewetting. *PLoS One* 8, e83365.

- Sabater, S., Timoner, X., Borrego, C., Acuña, V. (2016). Stream biofilm responses to flow intermittency: from cells to ecosystems. *Front. Environ. Sci.* 4, 14.
- Stanley, E.H., Fisher, S.G., Grimm, N.B. (1997). Ecosystem expansion and contraction in streams. *Bioscience* 47, 427–435.
- Steward, A.L., von Schiller, D., Tockner, K., Marshall, J.C., Bunn, S.E. (2012). When the river runs dry: human and ecological values of dry riverbeds. *Front. Ecol. Environ.* 10, 202-209.
- Timoner, X., Acuña, V., von Schiller, D., Sabater, S. (2012). Functional responses of stream biofilms to flow cessation, desiccation and rewetting. *Freshw. Biol.* 1565-1578.
- Tzoraki, O., Nikolaidis, N.P., Amaxidis, Y., Skoulikidis, N.T. (2007). In-stream biogeochemical processes of a temporary river. *Environ. Sci. Technol.* 41, 1225-1231.
- Unger, S., Máguas, C., Pereira, J.S., David, T.S., Werner, C. (2010). The influence of precipitation pulses on soil respiration - Assessing the "Birch effect" by stable carbon isotopes. *Soil Biology & Biochemistry* 42, 1800-1810.
- von Schiller, D., Acuña, V., Graeber, D., Martí, E., Ribot, M., Sabater, S., Timoner, X., Tockner, K. (2011). Contraction, fragmentation and expansion dynamics determine nutrient availability in a Mediterranean forest stream. *Aquat. Sci.* 73, 485-497.
- von Schiller, D., Marcé, R., Obrador, B., Gómez, L., Casas, J.P., Acuña, V., Koschorreck, M. (2014). Carbon dioxide emissions from dry watercourses. *Inl. Waters* 4, 377-382.
- von Schiller, D., Bernal, S., Dahm, C.N., Martí, E. (in press). Nutrient and organic matter dynamics in intermittet rivers. In: Intermittent Rivers and Ephemeral Streams, edited by Datry T, Bonada N & Boulton A. ISBN-97-80128038-3-52. pp. 496. *Academic Press*.
- Zoppini, A., Marxsen, J. (2011). Importance of Extracellular Enzymes for Biogeochemical Processes in Temporary River Sediments during Fluctuating Dry– Wet Conditions. In: Shukla, G., Varma, A. (Eds.), Soil Enzymology SE 6, *Soil Biology*. Springer Berlin Heidelberg, pp. 103-117.

# **ANNEX I**

Table with sampled variables measured *in situ*, labels indicating: Unique identification for the sediment samples (ID\_sed), Sampling country (Samp\_country), Latitude of the sampling reach (Lat), Longitude of the sampling reach (Long), Active channel width (R\_width), Area of the sampling catchment (Catch\_area), Duration of the dry period (Dry\_period), Aridity index based on the WorldClim Global Climate Data (<a href="http://www.cgiar-csi.org/data/global-aridity-and-pet-database">http://www.cgiar-csi.org/data/global-aridity-and-pet-database</a>; Aridity), Potential Evapo-Transpiration based on the WorldClim Global Climate Data (<a href="http://www.cgiar-csi.org/data/global-aridity-and-pet-database">http://www.cgiar-csi.org/data/global-aridity-and-pet-database</a>; PET), and Mean annual precipitation based on wordclim 1.4. database (<a href="http://www.worldclim.org/current">http://www.worldclim.org/current</a>; Prec).

ID_sed	Samp_country	Lat	Long	R_width	Catch_area	Dry_period	Aridity	PET	Prec
1	Switzerland	47.5650	9.3478	1.0	1.7	28	716.2	789.2	1015
2	France	48.4428	7.0619	2.9	2.2	70	622.3	708.3	962
3	France	48.8240	6.8951	1.4	0.6	35	589.2	793.5	738
4	France	49.0424	8.7761	1.2	0.2	28	603.2	813.0	721
5	United Kingdom	53.0484	-1.8662	6.8	58.1	30	543.5	636.8	982
6	Spain	41.9446	2.9683	5.0	321.5	140	582.8	895.2	689
7	Switzerland	46.4099	9.8576	0.6	1.0	270	480.4	480.4	1424
8	Australia	-27.4723	152.9216	3.8	3.4	152	1058.8	1433.8	1245
9	Australia	-27.7736	152.7681	3.5	9.2	151	776.5	1539.3	936
10	Spain	36.8822	-4.4222	5.5	152.3	165	497.2	1158.2	590
11	Ecuador	-1.4084	-78.7615	0.5	0.1	15	680.0	1500.0	630
12	Australia	-27.4658	152.9603	4.4	1.4	6	1081.0	1397.3	1201
13	USA	37.9547	-122.7135	1.7	1.2	185	589.8	1035.2	1030
14	USA	37.1008	-121.4725	5.1	132.0	70	440.4	1368.8	547
15	USA	36.4711	-121.1948	1.2	3.0	184	410.4	1447.8	463
16	USA	37.9487	-122.7075	2.5	1.5	210	588.0	1033.8	1004
17	Ecuador	-1.4069	-78.7569	0.6	0.2	0.5	680.0	1500.0	630
18	USA	33.4186	-111.0089	4.2	96.6	38	412.5	1520.8	501
19	USA	33.7972	-110.9597	2.7	2.8	17	555.5	1269.0	646
20	Ecuador	-1.4750	-78.8442	0.3	0.5	0.5	530.0	1500.0	619
21	Spain	39.4129	-3.3098	4.7	2557.0	99	354.0	1211.0	414
22	Spain	41.1282	0.9069	1.2	12.4	30	516.8	971.8	617
23	Switzerland	46.2296	8.7143	2.8	0.4	37	772.2	790.4	1286
24	Switzerland	46.2246	8.7292	2.4	0.5	37	786.8	807.8	1286
25	Australia	-29.0553	152.3785	5.5	4.1	37	878.3	1454.0	1090

26	France	47.0809	5.7060	2.5	145.2	87	667.2	854.8	930
27	Portugal	38.6471	-7.7084	6.0	75.2	185	908.8	1455.0	1139
28	Switzerland	47.5835	9.2962	0.6	1.8	28	712.0	782.8	985
29	France	48.8275	6.9127	1.2	1.3	47	588.2	794.0	738
30	Germany	51.6654	8.7465	3.8	90.8	54	564.7	700.3	835
31	Germany	50.2759	9.4327	1.0	13.0	69	577.8	753.8	740
32	USA	38.3678	-123.0021	5.0	1.8	140	595.0	1050.0	787
33	Germany	50.2498	9.4384	2.0	27.3	91	571.7	763.3	755
34	Germany	50.2524	9.3769	1.5	8.0	76	567.6	771.8	669
35	United Kingdom	53.1014	-1.8571	9.3	91.1	50	548.0	635.4	1006
36	France	48.8368	6.8787	1.5	0.7	35	589.3	793.3	739
37	Switzerland	47.6543	9.0513	0.4	1.4	45	703.6	765.6	1023
38	Switzerland	45.9022	9.0334	3.6	0.4	45	746.2	761.3	1282
39	Switzerland	45.9006	9.0481	5.5	3.0	43	754.8	771.0	1273
40	Spain	42.9778	-2.4034	3.0	3.4	70	704.6	875.2	1057
41	Spain	36.5059	-5.5204	8.0	367.3	105	609.3	1071.5	775
42	Germany	51.6208	8.6577	10.0	761.3	7	566.3	695.4	869
43	France	45.8584	5.6184	2.0	140.0	40	688.7	804.3	1122
44	Germany	52.4051	14.2044	2.0	9.0	50	461.8	740.2	543
45	Spain	42.1142	2.4481	4.0	40.0	75	704.0	865.2	880
46	Spain	37.6312	-1.5820	4.4	10.2	800	275.8	1198.0	329
47	USA	37.9919	-122.7493	3.6	3.0	110	593.3	1052.8	1060
48	Germany	52.4515	13.6950	2.5	150.0	90	463.7	744.5	546
49	USA	38.3572	-122.9817	4.0	3.5	105	595.0	1050.0	787
50	Germany	52.3610	14.1817	3.0	37.8	50	461.0	743.8	543
51	Spain	42.9782	-2.4025	4.0	8.2	70	704.6	875.2	1057
52	France	47.2481	6.3463	3.0	389.2	26	684.3	799.3	1135
53	USA	37.9542	-122.7119	2.2	1.6	176	589.8	1035.2	1030
54	Spain	42.2153	-1.5075	5.0	1.6	9	477.8	1057.0	573
55	France	48.8459	6.9161	1.2	1.0	20	587.4	792.8	739
56	France	44.4886	4.4838	4.5	153.9	140	660.0	971.0	805
57	Namibia	-21.0102	14.6879	1.0	0.1	300	72.5	1817.5	89
58	Switzerland	46.4197	9.8611	1.0	1.0	270	480.4	480.4	1416
59	Spain	39.0933	-2.5718	2.0	129.0	125	375.8	1183.4	439
60	Spain	39.7850	2.7495	1.6	2.9	70	529.5	945.0	592

61	France	48.8374	6.9761	1.4	0.5	47	587.6	787.6	742
62	France	48.8898	7.0066	2.0	1.3	15	585.4	788.8	735
63	France	49.0408	6.4821	2.2	1.8	28	591.7	796.3	768
64	Spain	37.5990	-1.2528	3.4	8.1	800	256.8	1220.4	302
65	Spain	37.5884	-1.1866	3.0	17.9	800	261.3	1216.3	318
66	Spain	37.6227	-1.5758	4.6	7.8	800	278.3	1194.3	364
67	Spain	37.5756	-1.4429	2.5	3.5	800	259.3	1207.3	298
68	Namibia	-20.9875	14.6332	2.0	0.2	300	76.0	1802.5	98
69	Reunion Island (France)	-21.3425	55.6463	5.0	5.5	175	983.8	1140.0	1300
70	Reunion Island (France)	-21.1004	55.6337	4.0	62.2	134	998.0	1101.0	1516
71	USA	32.8735	-116.6209	3.5	25.0	15	497.8	1355.2	582
72	USA	32.5860	-116.5630	2.0	1.4	45	328.8	1529.0	430
73	Australia	-35.3306	148.8849	2.0	24.6	8	777.5	1241.3	897
74	Australia	-35.3259	148.8872	4.0	1.2	8	769.5	1244.7	897
75	Australia	-33.7402	144.9170	5.0	400.0	312	310.5	1459.0	367
76	Czech Republic	48.8667	16.0260	2.5	16.9	46	520.3	817.0	615
77	South Africa	-27.7459	31.7082	4.0	65.0	60	5.0	1691.0	5
78	Czech Republic	48.8619	17.3977	2.0	7.3	62	582.6	810.4	699
79	South Africa	-27.9168	31.8448	6.0	130.0	150	711.5	1391.8	870
80	South Africa	-27.9865	31.6097	5.0	45.0	120	665.3	1444.8	795
81	South Africa	-28.2322	31.1868	10.0	6000.0	30	673.2	1440.0	802
82	Czech Republic	48.8437	17.3136	3.2	18.3	55	571.5	816.8	664
83	Czech Republic	49.8177	16.0045	3.2	7.9	118	533.8	730.8	635
84	Australia	-19.3250	146.7624	8.0	10.0	300	869.8	1537.2	1057
85	Spain	38.1352	-1.3443	3.5	11.5	350	265.4	1276.2	320
86	Italy	41.4066	15.1946	3.0	3.4	75	490.2	953.2	577
87	Italy	41.4445	15.1792	2.5	11.5	75	496.5	965.5	581
88	Italy	41.3740	15.2208	3.0	1.8	75	482.7	938.8	567
89	Italy	41.4256	15.1995	4.0	26.3	75	490.8	959.0	581
90	Italy	41.3672	15.2265	3.0	2.8	75	480.8	943.5	567
91	Italy	44.6268	10.1090	3.0	42.0	60	633.2	870.2	858
92	Italy	41.4728	15.1600	2.0	2.2	75	500.0	952.6	589
93	Australia	-19.3172	146.5760	7.0	47.0	300	841.5	1560.8	995
94	USA	37.9522	-122.3209	3.5	18.9	120	545.8	1044.5	664
95	Algeria	34.8500	1.1667	5.0	288.9	82	319.8	1135.3	377

96	Germany	52.2476	13.0790	1.3	1.9	146	475.7	763.2	560
97	Germany	52.6458	13.4832	1.2	0.2	143	485.1	734.4	573
98	Germany	50.2508	9.3983	0.4	6.0	72	572.3	766.8	669
99	Italy	41.7660	14.7855	3.0	33.0	80	591.0	927.0	696
100	Israel	33.0122	35.1900	4.5	52.0	150	537.3	1246.8	664

# **ANNEX II**

Table with correlations between respiration and sediment characteristics, labels meaning: MicroResp® respiration in dry conditions (microresp\_dry), MicroResp® respiration in rewetted conditions (microresp\_wet), respiration in reinundated bottles (bottles), water content (WC), C to N molar ratio (CN), organic carbon content (C), total nitrogen content (N), median particle size (Median\_size), % particles <  $2\mu$ m (Clay\_coult), % particles 2-63  $\mu$ m (Silt\_coult), and % particles 63 to 2000  $\mu$ m (Sand\_coult).

	microresp_dry		microresp_wo	et	bottles		
	correlation coefficient	p value	correlation coefficient	p value	correlation coefficient	p value	
WC	-0.33908	0.00055858	0.14516	0.14959	0.31899	0.0012398	
Median_size	0.22372	0.025254	-0.16859	0.093599	-0.2876	0.0037147	
Clay_coult	-0.1395	0.16627	0.27655	0.0053489	0.30563	0.001987	
Silt_coult	-0.19958	0.046504	0.30832	0.0018033	0.33387	0.00068718	
Sand_coult	0.18669	0.062913	-0.31128	0.0016193	-0.3396	0.00054688	
С	-0.15012	0.13601	0.58816	1.24E-10	0.72359	1.8342E-17	
N	-0.15692	0.11895	0.55128	2.79E-09	0.70114	4.5598E-16	
CN	-0.057186	0.57199	0.2631	0.0081757	0.22966	0.021533	