

1 Irrigation agriculture affects organic matter decomposition **in** semi-
2 arid terrestrial and aquatic ecosystems

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4 Maite Arroita¹, Jesús Causapé², Francisco A. Comín³, Joserra Díez⁴, Juan José
5 Jiménez³, Juan Lacarta³, Carmen Lorente³, Daniel Merchán², Selene Muñiz³, Enrique
6 Navarro³, Jonatan Val³ and Arturo Elosegi¹

7

8 ¹ Faculty of Science and Technology, University of the Basque Country. PO Box 644, 48080 Bilbao,
9 Spain

10 ² Geological Survey of Spain. C/ Manuel Lasala nº 44, 50006 Zaragoza, Spain

11 ³ Instituto Pirenaico de Ecología (CSIC). Av. Montañana 1005, 50059 Zaragoza, Spain

12 ⁴ Faculty of Education, University of the Basque Country. J. Ibañez Sto. Domingo 1, 01006 Vitoria–
13 Gasteiz, Spain

14

15 * Corresponding author at: Faculty of Sciences and Technology, the University of the Basque Country, 48080
16 Bilbao. Tel.: +34 946015939 E-mail address: maite.arroita@ehu.es (Maite Arroita)

17

18 Abstract

19 Many dryland areas are being converted into intensively managed irrigation crops, what
20 can disrupt the hydrological regime, degrade soil and water quality, enhance siltation,
21 erosion and bank instability, and affect biological communities. Still, the impacts of
22 irrigation schemes on the functioning of terrestrial and aquatic ecosystems are poorly
23 understood. Here we assess the effects of irrigation agriculture on breakdown of coarse
24 organic matter in soil and water. We measured breakdown rates of alder and holm oak
25 leaves, and of poplar sticks in terrestrial and aquatic sites following a gradient of
26 increasing irrigation agriculture in a semi-arid Mediterranean basin transformed into
27 irrigation agriculture in 50% of its surface. Spatial patterns of stick breakdown

28 paralleled those of leaf breakdown. In soil, stick breakdown rates were extremely low in
29 non-irrigated sites ($0.0001\text{--}0.0003\text{ day}^{-1}$), and increased with the intensity of agriculture
30 ($0.0018\text{--}0.0044\text{ day}^{-1}$). In water, stick breakdown rates ranged from 0.0005 to 0.001 day^{-1} ,
31 and increased with the area of the basin subject to irrigation agriculture. Results
32 showed that irrigation agriculture affects functioning of both terrestrial and aquatic
33 ecosystems, accelerating decomposition of organic matter, especially in soil. These
34 changes can have important consequences for global carbon budgets.

35

36 *Keywords:* irrigation agriculture, ecosystem functioning, breakdown, stream, soil

37

38 1. Introduction

39

40 Human activities are transforming dramatically the world's landscape [1], what
41 probably represents the most important component of global environmental change [2].
42 Extensive natural areas are being converted for human use, and management practices
43 are intensifying in already human-dominated lands [3]. The area of cultivated land
44 increased globally 466% from 1700 to 1980 [4], to such an extent that croplands and
45 pastures have become one of the largest biomes on the planet [5–6]. More recently, this
46 expansion has slowed down, but, even so, yields keep increasing considerably [7]. This
47 increase is a consequence of the so-called "Green Revolution", which promoted the
48 expansion of high-yielding crops that depend on the use of potentially hazardous
49 materials such as synthetic fertilizers and pesticides, and on the implementation of
50 irrigation and mechanization. As a result, the irrigated surface has doubled during the
51 last 50 years [8–9] and the use of fertilizers increased seven-fold [10]. Moreover, future
52 projections related with global change claim for further expansion of irrigated lands

53 [1,11] in order to compensate the rising temperatures [12], the altered seasonality [13]
54 and the enhanced torrentiality [14]. Highly populated areas with a shortage of water
55 availability, like the Mediterranean region, will be most dependent on the increase of
56 irrigation to ensure their agricultural supply, and this will likely imply transformation of
57 non-irrigated croplands as well as of non-agricultural lands.

58

59 Modern agricultural techniques result in increased productivity, but often at a high
60 environmental cost leading to unacceptable environmental alterations [3,15]. Irrigation
61 disrupts the hydrological regime [16–17], whereas fertilizers and pesticides pollute soils
62 and nearby aquatic ecosystems [18–20]. These impacts can lead to soil acidification
63 [21], salinization [22], eutrophication and hypoxia [23], water quality issues [24], as
64 well as being a critical source of greenhouse gases [1,3,25]. Moreover, agricultural
65 streams are often associated with high siltation, erosion and bank instability [22,26],
66 which reduce habitat quality [27] and affect the composition and structure of biological
67 communities [28–29]. These environmental impacts could affect the functioning of
68 aquatic and terrestrial ecosystems, eroding their resilience and undermining many
69 ecosystem services [30–31]. Therefore, for a sustainable future it is crucial to understand
70 how ecosystem functioning is altered by irrigation agriculture.

71

72 Ecosystem functioning includes a wide variety of processes that change at different
73 spatial and temporal scales and respond to environmental changes specifically [32].

74 Decomposition, usually measured in terms of leaf litter breakdown, is one of the most
75 broadly used functional variables to assess the impacts of environmental changes on the
76 functioning of both terrestrial [33–34] and aquatic [35–36] ecosystems. Standard wooden
77 sticks are a cost-effective alternative to leaf bags to assess the functional impairment of

78 ecosystems [37–39]. Breakdown of organic matter integrates physical abrasion,
79 microbial colonisation, and invertebrate fragmentation [40] and is a key process in the
80 cycling and storage of carbon and nutrients in terrestrial and aquatic ecosystems [41–
81 42]. In addition, it is sensitive to many anthropogenic stressors including flow
82 regulation [43], pollution [44–45], eutrophication [46], changes in riparian vegetation
83 [47–48], or loss of biodiversity [49–50]. However, because each stressor can push
84 breakdown in a different direction and interactions between stressors are common in
85 agro–ecosystems exposed to multiple stressors simultaneously, it is difficult to forecast
86 the overall effect on decomposition [38].

87

88 This study assesses the impacts of **intensive irrigation agriculture** on the functioning of
89 terrestrial and aquatic ecosystems in a semi–arid landscape. The main goal is to compare
90 the breakdown of standard wooden sticks in terrestrial and aquatic sites exposed to a
91 gradient of irrigation intensity. Because this tool has only been validated recently, we
92 also compared the response of wooden sticks with that of classical leaf bags. We
93 hypothesized that: a) the breakdown of wooden sticks will follow the same patterns than
94 leaf bags; b) irrigation will promote breakdown in soils, as water availability is strongly
95 limiting in semi–arid regions; and c) irrigation will also result in higher breakdown in
96 aquatic ecosystems because of higher nutrient contents in the returning water from
97 agricultural fields to streams.

98

99 2. Materials and Methods

100

101 2.1 Study area

102

103 Breakdown experiments were performed in the the Lerma Creek basin, in the Ebro
104 Depression (Spain). It is located south from the pre-Pyrenees, in the semi-arid Bardenas
105 sector of the Mediterranean region. The climate is continental with an annual
106 precipitation of 468 mm, occurring mostly in spring and fall, whereas severe droughts
107 occur in summer. The annual mean temperature is 14 °C, and the monthly mean varies
108 between 5 °C in January/February and 23 °C in July/August (data from the nearby town
109 of Ejea de los Caballeros).

110

111 The Lerma Creek drains a basin of 752 ha that has been recently transformed to
112 irrigation agriculture in almost 50% of its surface. Sprinkler (86%) and drip irrigation
113 (14%) are used to grow mainly maize, winter cereals and tomato. Irrigation in the area
114 enabled double cropping, thanks to an increase in the amount of water, fertilizers and
115 pesticides applied annually per hectare. The common agricultural practices consist of
116 sowing fertilization with NPK compounds, followed by urea (46% N) and/or multiple
117 applications of liquid fertilizers (16% urea, 8% ammonia and 8% nitrate). The
118 predominant active principles of the pesticides used are metolachlor, terbuthylazine and
119 chlorpyrifos, and also included atrazine in the recent past [51].

120

121 Irrigation had deep effects on the hydrological regime. The median of daily flow at the
122 Lerma basin increased significantly, the intermittent main creek became perennial and
123 seasonality shifted from a rain-driven to an irrigation-driven pattern [52]. This increased
124 the export of salt from the basin, reduced water salinity due to dilution, and increased
125 the concentration and export of nitrate [53]. Abrahao et al. [51] found slightly elevated
126 **values of endrin in the soil, pp'-DDT** in water and Ni and Zn in the sediments.

127 However, overall, no serious contamination was detected related to the substances they

128 analyzed (44 pesticides and metabolites, 11 organochlorinated compounds, 17
129 polycyclic aromatic hydrocarbons, 13 polychlorinated biphenyls and several metals and
130 metalloids).

131

132 We selected terrestrial and aquatic sites following a gradient of increasing irrigation
133 intensity (Fig. 1). Terrestrial sites ranged from natural shrubby vegetation above the
134 irrigated area (Shrubland) to irrigated crops (Cropland), passing through non-irrigated
135 pine plantations (Pine Plant), with some differences in soil characteristics (Table 1).
136 Non-irrigated sites were set in the valleys of the Lerma gully, predominated by
137 emerging tertiary materials with a small effective depth limited by limestone and tabular
138 gypsum, and slow drainage. On the contrary, croplands were located in the quaternary
139 glacis consisting of deeper layers of gravels with a sandy loam matrix and layers of
140 tertiary materials [52]. Aquatic sites included the main irrigation canal, and 3 stream
141 reaches with increasing area of irrigation **agriculture** in their drainage basins, and
142 considerable differences in conductivity and nutrient concentration (Table 2).

143

144 *2.2 Breakdown experiment*

145

146 Breakdown experiments were carried out with tongue depressors (15 × 1.8 × 0.2 cm)
147 made of untreated Canadian poplar wood (*Populus nigra* × *canadiensis*, Moench 1785).
148 Wooden sticks were numbered, oven-dried (70 °C, 72 h), weighed and assembled in
149 strings of 5 with fishing line. Sticks were buried (5–10 cm) in terrestrial sites, and tied to
150 metal bars or roots in water. In order to check whether the response of wooden sticks
151 was consistent to that of traditional leaf bags, we also incubated fine (100 µm) and
152 coarse (5 mm) mesh bags with leaves of holm oak (*Quercus rotundifolia* Lam.) in two

153 of the sampling points in soil (Gully and Cropland²), and fine (100 µm) and coarse (5
154 mm) mesh bags with leaves of alder (*Alnus glutinosa* (L.) Gaertner) in the four
155 sampling points in water. Fine mesh bags exclude invertebrates, enabling to discern the
156 contribution of microbial and invertebrate communities to the overall decomposition.
157 Freshly fallen holm oak and alder leaves were collected in autumn 2010, air-dried at
158 room temperature (21 °C), enclosed in labelled bags (3 ± 0.05 g in holm oak bags and in
159 fine alder bags; 5 ± 0.05 g in coarse alder bags) and buried and tied like wooden sticks.
160

161 All materials were retrieved after 43, 75, 219 and 371 days (5 replicates per site and
162 material), except for alder bags which were collected after 14, 43 and 75 days due to
163 their faster decomposition. The rainfall during the incubation period was 260 mm, lower
164 than the long-term average but within the natural interannual variability. Upon removal,
165 sticks and bags were stored in individual zip-lock bags and carried to the laboratory on
166 ice. Samples were rinsed with tap water to remove invertebrates and mineral particles.
167 The material was oven-dried (70 °C, 72 h) and ashed (500 °C, 5 h) to determine the ash
168 free dry mass (AFDM). Initial dry mass of sticks and alder bags incubated in water was
169 corrected for leaching to exclude the effect of this site-independent chemical process,
170 and the remaining AFDM was fitted to the negative exponential model to calculate
171 breakdown rates [54].

172

173 2.3 Data treatment

174

175 The response of different materials was compared by two-way ANCOVAs (k rate as
176 dependent variable, site and material as fixed factor, and time as covariable) and by
177 computing ratios of breakdown rates between different sites for each material [35].

178 Differences in breakdown rates of wooden sticks were analysed by means of one-way
179 ANCOVAs (k rate as dependent variable, site as fixed factor, and time as covariable)
180 and post-hoc **Bonferroni tests. Pearson's correlation coefficients were calculated**
181 between breakdown rates and the rest of the variables, and a Principal Component
182 Analysis (PCA) was also performed to identify the main factors explaining the
183 differences among breakdown rates in soil.

184

185 3. Results

186

187 3.1 *Wooden sticks versus leaves*

188

189 There were large differences among materials in breakdown rates in both terrestrial and
190 aquatic ecosystems (soil: $F_{1,132} = 132.6$, $p < 0.0001$; water: $F_{2,206} = 115.1$, $p < 0.0001$;
191 Fig. 2). Leaf litter in coarse mesh bags broke down the fastest and wooden sticks the
192 slowest, except for Cropland2, where holm oak in fine mesh bags broke down slower
193 than sticks. Differences among sites were also statistically significant (soil: $F_{2,132} =$
194 $27.03.6$, $p < 0.0001$; water: $F_{3,206} = 4.35$, $p = 0.005$), but spatial variations depended on
195 the material. The increase in breakdown rate was much higher for coarse mesh than for
196 fine mesh bags, especially in soil, and the interaction site \times material was significant
197 (soil: $F_{2,132} = 21.7$, $p < 0.0001$; water: $F_{6,206} = 2.27$, $p = 0.038$). Moreover, ratios of
198 breakdown rates computed with different materials were highly variable and showed no
199 consistent pattern (Table 3). Nevertheless, coarse mesh bags and sticks displayed
200 consistent patterns and the site \times material interaction became non-significant when fine
201 mesh bags were removed from the analysis (soil: $F_{1,86} = 0.595$, $p = 0.442$; water: $F_{3,134} =$
202 2.09 , $p = 0.105$).

203

204 *3.2 Impacts of irrigation agriculture*

205

206 In the terrestrial environment irrigation agriculture accelerated decomposition. Stick
207 breakdown rates were extremely low in non-irrigated sites (0.0001–0.0003 day⁻¹), and
208 increased significantly with the intensity of irrigation (0.0018–0.0044 day⁻¹; Fig. 3).

209 According to the post-hoc Bonferroni test, the sampling points could be grouped in
210 three groups regarding breakdown rates: they were slowest in non-irrigated sites, 5–16
211 times faster in Cropland3, and fastest in Cropland1 and Cropland2.

212

213 The regression between water availability and breakdown rates was only marginally
214 significant ($p = 0.054$), being content of CaCO₃, sand and silt the only variables
215 significantly correlated with stick breakdown rates in soil, all of them strongly inter-
216 correlated ($p < 0.05$). However, breakdown rates were strongly correlated with the first
217 of the two main components extracted for the PCA analysis, which together accounted
218 for 81.8% of the variance (Fig. 4). The first axis was significantly correlated with water
219 availability, carbon content, granulometry and number of bacteria (both alive and
220 harmed or dead) in soils. The second axis was correlated with N content and pH.
221 Differences between the non-irrigated sites and the three croplands were mainly
222 influenced by the main component, whereas the second axis explained the differences
223 between the non-irrigated sites.

224

225 In the aquatic environment stick breakdown rates ranged from 0.0005 to 0.001 day⁻¹,
226 and increased significantly downstream, with the area of the basin subject to irrigation
227 agriculture (one-way ANCOVA: $F_{3,62} = 18.8$, $p < 0.0001$; Fig. 5). The only variable

228 significantly correlated with stick breakdown rates in water was PO_4^{3-} ($R^2 = 0.9$, $p =$
229 0.049). The regression between NO_3^- and the area under irrigation was statistically
230 significant ($R^2 = 0.98$, $p = 0.007$), but neither NO_3^- nor the area under irrigation were
231 strongly correlated with breakdown rates ($p > 0.05$). Besides, spatial differences in
232 water were not as abrupt as in soil, and according to the post-hoc Bonferroni test the
233 sampling points could be grouped in two highly overlapping groups (Fig. 5). Maximum
234 differences in breakdown rate were also smaller in water (5X) than in soil (44X).

235

236 4. Discussion

237

238 4.1 *Wooden sticks versus leaves*

239

240 The response of wooden sticks to environmental stressors caused by irrigation
241 agriculture was consistent to that of coarse mesh bags in both terrestrial and aquatic
242 ecosystems, thus suggesting their breakdown integrates the effects of microbial activity
243 and consumption by invertebrates. Sticks have been used in streams as indicators of
244 functional impairment [37–38], as they are a cheaper and less time consuming
245 alternative to leaf bags [39]. Our results suggest their use can be expanded to assess soil
246 functioning. Their slow decomposition would make them especially suitable for routine
247 use with one year incubations, less so for shorter time frames. A related question is how
248 to define thresholds for functional impairment based on breakdown rates. Gessner and
249 Chauvet [35] proposed to use the ratio of breakdown rates between test and reference
250 sites, and gave specific values to indicate moderate and strong impairment in streams.
251 Nevertheless, in the present experiment these ratios resulted extremely variable
252 depending on the material used, a result paralleling those reported by Arroita et al. [39]

253 in large streams. Therefore, although wooden sticks offer a cheap, quick and reliable
254 method to measure breakdown in different ecosystem types, clearly more research is
255 needed to adequately define the metrics and the thresholds for functional impairment.

256

257 *4.2 Impacts of irrigation agriculture*

258

259 Agricultural practices have deep effects on the characteristics and functioning of soil
260 and nearby water ecosystems [55]. As hypothesized, intensive irrigation agriculture
261 affected the functioning of terrestrial and aquatic ecosystems, accelerating
262 decomposition rates of organic matter irrespective of the type of material. Besides, the
263 fact that irrigation accelerated more the breakdown of leaf litter in coarse than in fine
264 mesh bags indicates that it affected both microbial and invertebrate activities. Our
265 limited dataset precludes attributing enhanced breakdown rates to specific
266 environmental variables, but increased water and nutrient availability seems to be the
267 main factor promoting biological activity in this semi-arid area.

268

269 Regarding the terrestrial environment, our results confirm the well-known effect of
270 agriculture on enhancing the cycling of materials in soils. Organic matter breakdown
271 depends on soil moisture, temperature and nutrient contents [56-57], and tends to be
272 promoted in agricultural soils, up to the point of reducing their contents on organic
273 matter [58-64]. In agricultural areas, primary production greatly increases as a
274 consequence of irrigation, thus amounting to a large sequestration of CO₂ in biomass.
275 Nevertheless, the effects of agriculture on the global carbon budget depend largely on
276 the fate of agricultural products. There are no data on agricultural primary production in
277 the study area, but it clearly increased when irrigation was implemented, as the number

278 of crops per year doubled, and low-biomass crops such as wheat were substituted by
279 high biomass ones such as corn. Nevertheless, for most of the irrigated crops such as
280 corn or tomato, only grain or fruits are harvested and most of the biomass is left on the
281 ground. Therefore, the fact that we found lower contents of organic matter in the
282 irrigated soils indicates that breakdown also increases greatly, to the extent of matching
283 primary production.

284

285 The most important factor accelerating breakdown of organic matter seems to be water
286 availability [65], especially in semi-arid regions, as moisture promotes microbial
287 activity, thus enhancing decomposition [66–67]. In the Lerma gully, the implementation
288 of irrigation led to a progressive increase in evapotranspiration [52], which has been
289 shown to result in accelerated breakdown [68]. Furthermore, artificial remoistening of
290 dried soil by irrigation disrupts soil structures, increasing substrate availability for
291 bacteria, further enhancing microbial activity [69]. Concerning temperature, irrigation
292 agriculture has been shown to contribute to the reduction of the diurnal temperature
293 range [70], what could slow down decomposition [71]. However, our results suggest
294 that factors enhancing breakdown (moisture) were much stronger than factors
295 decelerating it (reduced temperature oscillations).

296

297 Other potential factors behind enhanced breakdown are soil texture, ploughing, and
298 fertilization. Soil texture affects decomposition [69] through their effects on vertical
299 migration of organisms and aeration [72], both of them decisive factors in breakdown
300 [73]. The fact that breakdown rate was located close to the first axis in our PCA, and not
301 close to the nutrient contents, suggests soil texture to be a determinant factor of the
302 observed differences. Nevertheless, a potential confounding factor is the fact that non–

303 irrigated sites in the Lerma basin are mainly located on tertiary clays, whereas most
304 croplands are located in more sandy quaternary glaciis. Their composition makes
305 quaternary glaciis more suitable for irrigation, explains part of the differences in soil
306 texture, and might play a role in breakdown rates. A point of concern is the higher
307 percentage of dead bacterial cells in croplands in the present experiment, which might
308 reflect soil toxicity, probably as a consequence of pesticides and heavy metals, which
309 appear in fairly high concentrations in the Lerma basin [51]. The combination of heavy
310 metals and organic pollutants causes synergistic cytotoxic effects on microorganisms
311 [74].

312

313 Although we lack any data previous to the implementation of irrigation agriculture in
314 the Lerma basin, the observed spatial patterns suggest that it enhanced the breakdown of
315 organic matter. On one hand, irrigation converted the Lerma Creek from intermittent to
316 perennial [52], and it is known that stream intermittency results in slow breakdown [75–
317 77]. On the other hand, the spatial gradient of intensification produced an acceleration
318 of breakdown rates. Nutrient concentrations in water enhance breakdown rates [78–80]
319 up to a point beyond which they can fall again [36]. Additionally, agricultural practices
320 can have multiple effects on river ecosystems, from altered hydrology to siltation or
321 pesticide toxicity, all of which can have important consequences for ecosystem
322 functioning [81–82]. Therefore, it is not rare to find large variability on breakdown rates
323 in rivers subject to multiple stressors [38]. Nevertheless, our results show that in the
324 Lerma Creek the spatial differences can be explained by nutrient concentration, thus
325 suggesting other factors to play a minor role.

326

334

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Table 1. Irrigation water applied, water availability, content of soil organic carbon (SOC), soil inorganic carbon (SIC), total nitrogen (N_{TOT}), $CaCO_3$, sand, silt and clay, pH and number of bacteria alive (B_A) and bacteria harmed or dead (B_{HD}) in the sampling points in soil.

SITE	Irrigation (mm)	Wat. Avail. (mm)	SOC (%)	SIC (%)	N_{TOT} (%)	$CaCO_3$ (%)	Sand (%)	Silt (%)	Clay (%)	pH	B_A (cell·g ⁻¹)	B_{HD} (cell·g ⁻¹)	B_{HD} (%)
SHRUBLAND	0	7.15	4.39	2.32	0.167	34.6	46.8	33.1	20.1	8.41	7.88E+06	9.55E+04	1.2
PINE	0	7.15	4.81	2.49	0.285	34.1	57.8	31.2	10.9	5.74	3.05E+07	1.14E+06	3.6
GULLY	0	10.8	4.10	2.14	0.060	34.3	47.9	38.0	14.1	7.98	9.01E+06	1.53E+05	1.67
CROPLAND1	726	17.4	3.67	1.55	0.114	29.7	65.2	22.9	11.9	7.98	2.47E+07	8.63E+06	25.9
CROPLAND2	683	14.3	4.01	1.64	0.101	29.0	73.5	17.4	9.1	8.23	1.25E+07	2.40E+06	16.1
CROPLAND3	706	12.0	3.31	1.31	0.141	28.3	66.4	22.8	10.9	8.28	4.57E+07	9.86E+06	17.8

Table 2. Characteristics of study sites in water (mean \pm SE).

SITE	Irrigated area		Cond. ($\mu\text{S}\cdot\text{cm}^{-1}$)	pH	O ₂ ($\text{mg}\cdot\text{L}^{-1}$)	NO ₃ ⁻ ($\mu\text{gN}\cdot\text{L}^{-1}$)	PO ₄ ⁻³ ($\mu\text{gP}\cdot\text{L}^{-1}$)
	ha	%					
CANAL	0	0	246 \pm 10	8.50 \pm 0.08	9.0 \pm 1.89	269 \pm 89	2.21 \pm 0.8
CROPLAND1	22	87	1906 \pm 140	8.45 \pm 0.04	7.8 \pm 1.87	1689 \pm 73	5.38 \pm 0.9
GULLY	36	35	295 \pm 31	7.40 \pm 0.90	10.6 \pm 0.79	124 \pm 95	8.16 \pm 3.2
GAUGING STAT.	320	43	3461 \pm 319	8.37 \pm 0.03	12.1 \pm 0.63	22265 \pm 380	3.32 \pm 1.5

Table 3. Ratios of breakdown rates between different sites for each material.

	Bag 5 mm	Bag 100 μ m	Sticks
Gully: Cropland2	0.20	0.46	0.06
Canal: Cropland1	0.69	1.56	0.42
Canal: Gully	0.92	1.30	0.20
Canal: GaugingStat	0.59	0.94	0.43
Cropland1: Gully	1.34	0.83	0.47
Cropland1: GaugingStat	0.85	0.60	1.02
Gully: GaugingStat	0.64	0.72	2.18

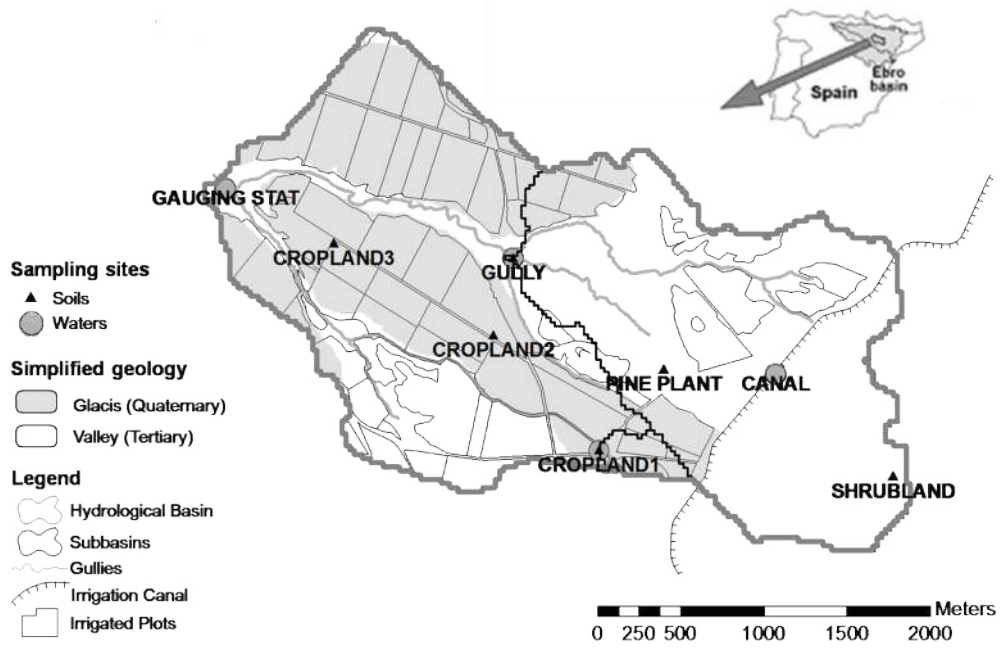


Fig. 1. Physical setting of the Lerma basin and sampling sites.

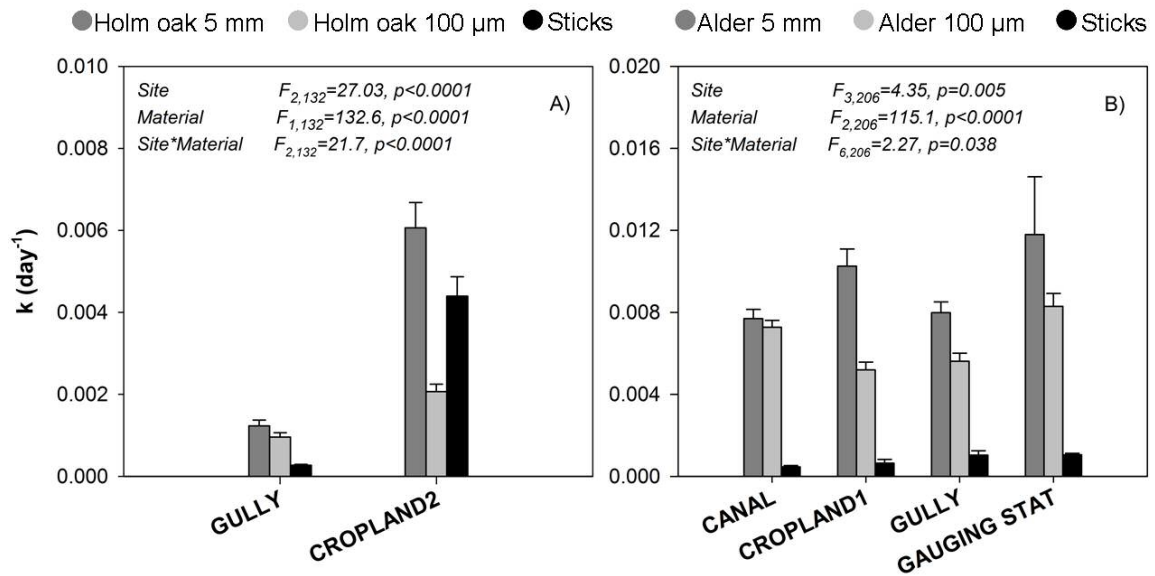


Fig. 2. A) Breakdown rates in soil (day^{-1}) of holm oak in fine and coarse mesh bags, and of poplar sticks. B) Breakdown rates in water (day^{-1}) of alder in fine and coarse mesh bags, and of poplar sticks. Error bars show SE. Results from two-way (site \times material) ANCOVA are also shown.

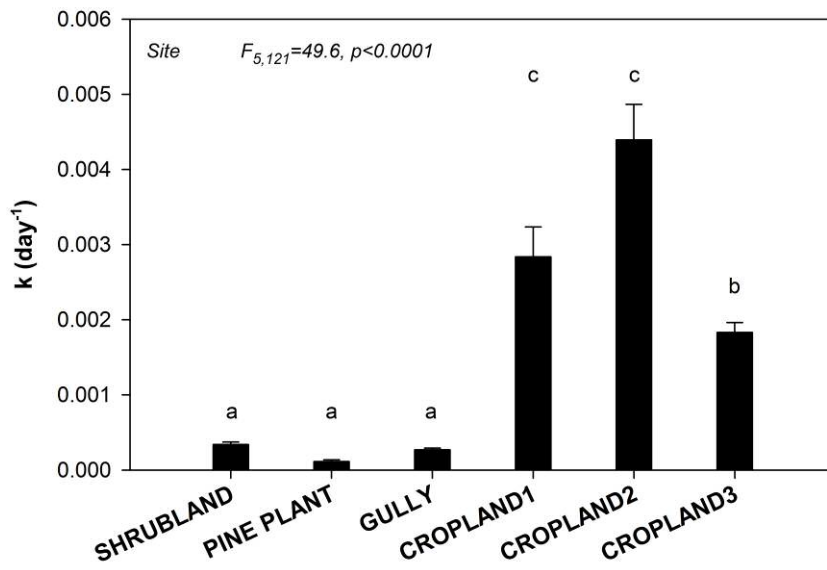


Fig. 3: Breakdown rates (day⁻¹) of wooden sticks in soil. Error bars show SE. Results from post-hoc Bonferroni test after one-way ANCOVA with site as a factor are also shown.

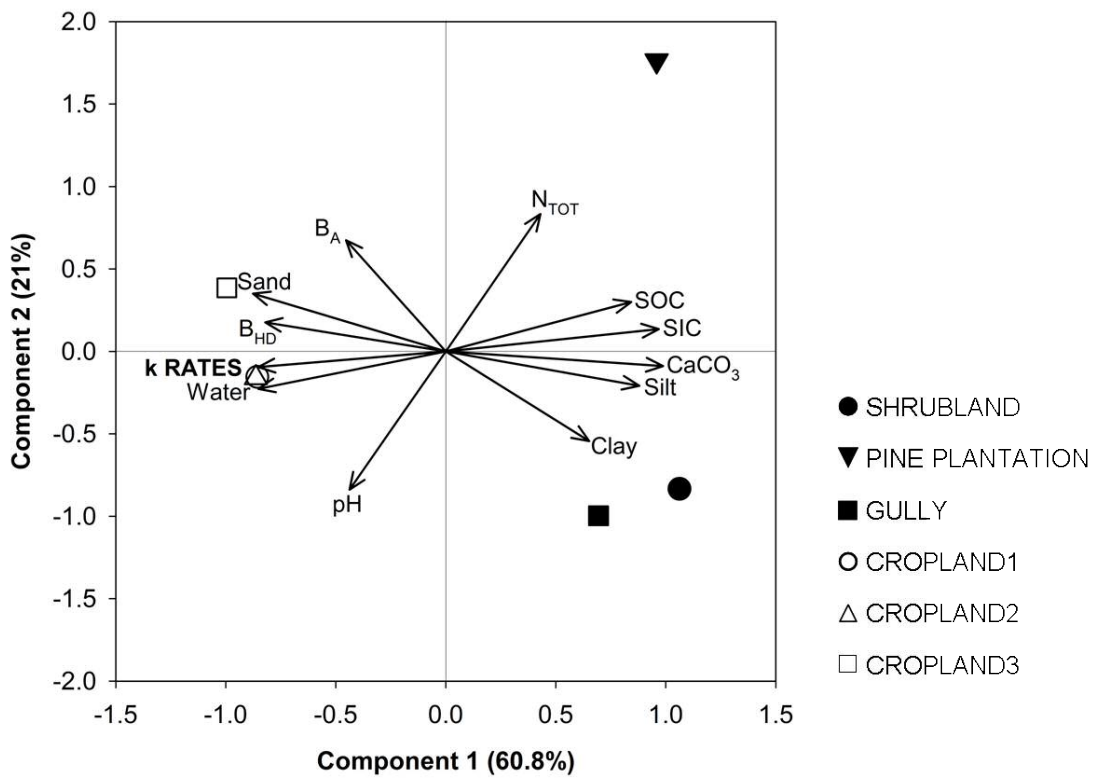


Fig. 4. Principal Component Analysis with breakdown rates, water availability, soil organic carbon (SOC), soil inorganic carbon (SIC), total nitrogen (N_{TOT}), $CaCO_3$, content of sand, silt and clay, pH and number of bacteria alive (B_A) and bacteria harmed or dead (B_{HD}) in each site.

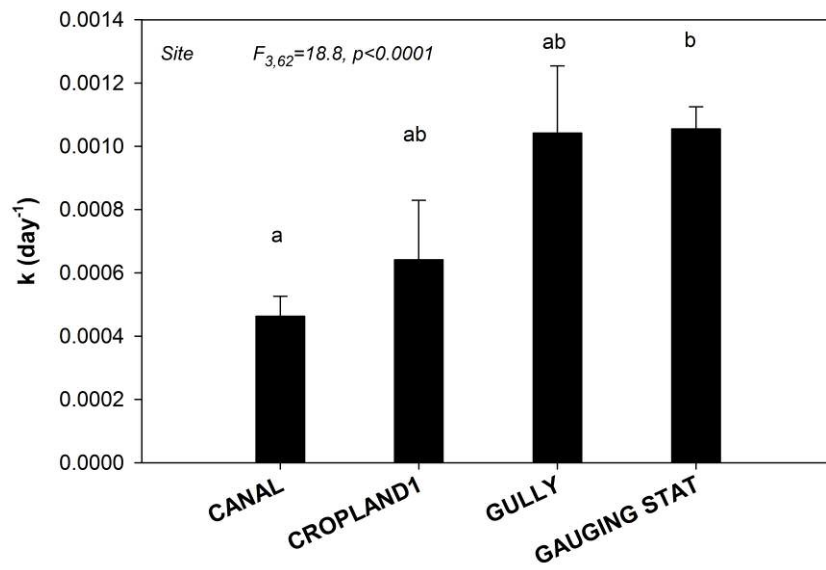


Fig. 5. Breakdown rates (day⁻¹) of wooden sticks in water. Error bars show SE. Results from post-hoc Bonferroni test after one-way ANCOVA with site as a factor are also shown.