Direct Biotic Plant–soil Feedback Promotes Dodonaea Viscosa Growth in a Dry-hot Valley, China

Xuemei Wang
School of Resource and Environmental Engineering, Mianyang Normal University
Bangguo Yan
Institute of Tropical Eco-Agriculture, Yunnan Academy of Agricultural Sciences
Liangtao Shi
Institute of Tropical Eco-Agriculture, Yunnan Academy of Agricultural Sciences
Gangcai Liu (liugc@imde.ac.cn)
Institute of Mountain Hazards and Environment Chinese Academy of Sciences

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Direct biotic plant–soil feedback promotes *Dodonaea viscosa* growth in a dry-hot valley, China

Xuemei Wang [1,2], Bangguo Yan [3], Liangtao Shi [3], Gangcai Liu [4*]

[1]School of Resource and Environmental Engineering, Mianyang Normal University, Mianyang, 621000, Sichuan Province, PR China

[2]Ecological Security and Protection Key Laboratory of Sichuan Province, Mianyang Normal University, Mianyang, 621000, Sichuan Province, PR China

[3]Institute of Tropical Eco-Agriculture, Yunnan Academy of Agricultural Sciences, Yuanmou 651300, Yunnan Province, PR China

[4]Institute of Mountain Hazards and Environment, Chinese Academy of Sciences, Chengdu 610041, Sichuan Province, PR China

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***Corresponding author:**

Gangcai Liu

NO.9, Block 4, Renmingnan Road, Chengdu, P. R. China

Email: liugc@imde.ac.cn

Post code: 610041

Fax/Tel: +86 028-85231287

Declarations

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Conflicts of interest/Competing interests

The Authors declare that there is no conflict of interest.

Availability of data and material

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Code availability

Not applicable.

Ethics approval

Not applicable.

Consent to participate

All authors agree to participate.

Consent for publication

All authors agree to publication.

Abstract Biotic plant-soil feedback has been widely studied, and may be particularly important in resource-poor areas. However, the roles of soil nutrient cycling in affecting plant growth in this process still remained unclear. The aim of this study was to explore the roles of soil biota in regulating nutrient cycling by conducting a two-phase feedback experiment in a dry-hot valley, with a conditioning phase during which there were *Dodonaea viscosa* or no *D. viscosa* growing in the soil, and a feedback phase in which the effect of the conditioned soil biota on *D. viscosa* performance was measured. The growth of *D. viscosa* significantly reduced soil N after the conditioning phase. However, *D. viscosa* showed a positive plant-soil feedback. In the feedback phase, the *D. viscosa* conditioned soil promoted the stem diameter, leaf area, and leaf dry mass content of *D. viscosa*. Total biomass was also significantly higher in *D. viscosa* conditioned soil than that in not conditioned soil. In contrast, soil sterilization had a negative effect on the growth of *D. viscosa*, with a significant reduction in plant biomass, especially in *D. viscosa* conditioned soil, and soil sterilization significantly increased the root: shoot biomass ratio and litter mass. Furthermore, we showed that although the biota-driven changes in enzyme activities correlated with the leaf N and P amount especially P amount, the enzyme activity was not the main reason to promote *D. viscosa* growth in the conditioned soil.

Keywords plant–soil feedback · microorganism · sterilization · dry-hot valley · *Dodonaea viscosa*

Introduction

There is substantial interest in plant–soil feedback, which acts to drive and maintain key ecosystem properties, such as community succession (Lozano et al. 2014), species invasion (Meisner et al. 2013) and plant species diversity (Mangan et al. 2010; Heinze et al. 2015). When plants of a given species affect the individual itself or other individuals of the same species, the plant–soil feedbacks are referred to as direct, intraspecific or conspecific; inversely, those that operate between species are referred to as indirect, interspecific or heterospecific (Van der Putten et al. 2013). Plant-soil feedback processes involve two phases: 1) changes in soil properties caused by a plant species or plant community; and 2) changes in soil properties in turn influence plant growth (Bever et al. 1997). The changes in soil properties by plant include changes in physical, chemical, and biotic properties (Perkins and Nowak 2013), with an increased number of studies focused on biota-mediated plant–soil feedback, which is also called biotic plant–soil feedback (Kardol et al. 2013).

The direct plant-soil feedback can be negative (changes in the soil properties exert a net growth-reducing effect to individuals of the same species), neutral (the net effect is that all influences of the soil are zero), or positive (growth of the plants or subsequent individuals of the same species is promoted by the net soil effect) (Van der Putten et al. 2013). Negative feedback is mainly caused by pathogens (Bever et al. 2012), while positive feedback may be mediated by the symbiotic microbes, such as arbuscular mycorrhizal fungi, ectomycorrhizal fungal and rhizobia, which can cause

78 an increase in nutrient absorption or the inhibition of pathogenic organisms (Van der
79 Putten et al. 2013). Besides, soil organisms can affect plants by their role in nutrient
80 cycling (Wardle et al. 2004). Soil enzymes, mainly secreted by soil microorganisms,
81 play an essential role in nutrient mineralization (Sinsabaugh and Follstad Shah 2012).
82 Different microbe groups show different ability to produce extracellular enzymes
83 (Romaní et al. 2006; Burke et al. 2011), and these enzymes can catalyze the
84 breakdown of soil organic matter, releasing nutrients that can be used by plants (Lau
85 and Lennon 2012). However, current studies of plant–soil feedback have mainly
86 focused on mutualists or pathogens on plant growth (Bever et al. 2012), and the
87 feedback effect of nutrient cycling by soil biota on plant growth has been less studied.
88 The dry-hot valley of the Hengduan Mountain region in southwestern China is an
89 ecologically fragile zone, characterized by low soil-water and nutrient availabilities.
90 The vegetation, dominated by grasses and shrubs with scattered trees, is classified as
91 valley-type savanna (Yan et al. 2016). Overgrazing, wood fuel consumption and
92 erosion have further reduced the cover of vegetation (Zhang et al. 2002). Vegetation
93 restoration has been widely developed in dry hot valley, and re-vegetation can
94 increase soil microbial activity and microbial biomass in this area (Peng et al. 2013;
95 Yan et al. 2020). On the other hand, the activities of soil organisms can modulate plant
96 responses to environmental stresses (Lau and Lennon 2012). Under severe limitation
97 of soil moisture and nutrients, adaptive traits are exploited by complex interactive
98 webs of plant-soil systems to allow plants to maximize the use of scarce resources
99 (Sardans and Penuelas 2013). However, although the characteristics of soil microbial

community in dry-hot valley have attracted the attention of researchers (Li and Zhao 2005; Li et al. 2010; Peng et al. 2020), the role of soil biota in plant growth remains unknown.

In this study, *Dodonaea viscosa*, the dominant species in dry-hot valley was used as the model plant to detect the role of soil biota in plant growth by conducting a two-phase feedback experiment. *D. viscosa* has resistance to drought and nutrient scarcity in dry-hot valley, and it is widely used for vegetation restoration (Peng et al. 2013). *D. viscosa* is considered as a native species in this area, but it originated from Australia and subsequently dispersed and established around the world within the last two million years (Harrington and Gadek 2009). The objective of this research was to test the direct biotic plant–soil feedback in dry-hot valley, and explore the respective roles of plant and soil biota in the process of the plant–soil feedback. We hypothesized that soil biota positively affect plant growth in this dry-hot valley, and nutrient cycling plays a critical role in this plant-soil feedback.

Material and methods

Study site and materials

The experiment was conducted in Yuanmou station of the Institute of Mountain Hazards and Environment, Chinese Academy of Sciences, located in Yuanmou county (101°35′–102°05′E, 25°25′–26°07′N) in the South-west of China. Yuanmou County is a typical dry-hot valley aside of the Jinsha River. The mean annual temperature of this area is 21.5 °C, and the average annual precipitation is 650 mm, with 90% of the rain

falling from May to September. The potential evaporation is 3400–3900 mm, approximately six times as great as the precipitation.

Mature seeds of *D. viscosa* were collected from mother trees in Yuanmou dry-hot valley where *D. viscosa* is abundant. Seeds were soaked in 98% sulfuric acid for 10 min to break the physical dormancy (Phartyal *et al*. 2005). Besides, the dry red soil (Luvisols in The Food and Agriculture Organization of the United Nations taxonomy), which is widely distributed in this area, was used in our experiment, and it was air dried, sieved (2 mm) and thoroughly mixed. The organic matter, available N, available P and available K of the soil used in our experiment were 3.05 (g kg^{-1}), 41.28, 4.90, and 106.46 (mg kg^{-1}), respectively.

Experimental design

To examine the biotic plant-soil feedback in this area, we performed a plant–soil feedback experiment. The experiment consisted of two phases, i.e., a conditioning phase with or without *D. viscosa* growing in dry red soil, and a feedback phase in which the effect of the conditioned soil biota on *D. viscosa* performance was measured. The design of the experiment included two soil origins and two biotic treatments.

In the conditioning phase, soils were conditioned by *D. viscosa* with a not conditioned control (Bare soil hereater). In the conditioned treatment, *D. viscosa* were planted in pots (upper diameter × lower diameter × height: 26×16×24 cm) in the greenhouse and allowed to develop the soil biota. Pots were filled with dry red soil,

and about ten *D. viscosa* seeds were sown in each pot. After the germination of most seeds, excess seedlings were then removed, leaving one seedling per pot. Besides, 20 pots not conditioned by *D. viscosa* were used as the bare treats. The pots of the bare treat were filled with the same amount of dry red soil as the conditioned treats. All pots including the conditioned pots and bare pots were watered regularly to keep the soil water content at 75 ± 5% field capacity approximately, and their positions were periodically rotated to minimize any effects of environmental heterogeneity. After 10 months, the plants with their roots were removed. The chemical properties of conditioned soil and bare soils were analyzed. Then the conditioned and bare soils were mixed respectively, and the mixed soils were sieved (2 mm) and subdivided into two equal aliquots for the feedback phase of the experiment.

In the feedback phase, one aliquot of the soil was used directly and the other was sterilized. Autoclaving has been shown previously to be effective for the sterilization of soil, causing only small changes in soil properties (Berns *et al*. 2008). Autoclaving was performed for one hour (121℃, 103.5 KPa) on three separate occasions, with a 24-hour interval between autoclaving. After autoclaving, each pot was sterilized using 80% alcohol solution and then filled with an equivalent amount (0.8 kg) of sterilized or non-sterilized soil. To reduce infection by exotic microorganisms, pots were transferred to climate chambers with 35/25 °C (day-night, 16/8 h) and 60% humidity. Seeds were then sown in each pot, and pots were watered regularly using sterile water. After the germination of most seeds, five seedlings were left in each pot and grown for three months. Three months later, the plants and soils were harvested.

Observation and measurements

At the end of the feedback phase, plant height and the diameter of the stem were measured. Leaf area was calculated from the scanned electronic pictures using Image J, and leaf dry mass content (LDMC, the ratio of leaf dry mass to fresh mass) were measured according to Garnier *et al*. (2001). During the feedback phase, the fallen leaves were collected and oven dried at 70℃ for 48 h to weigh the litter mass. When harvested, root, stem and leaf biomass were also oven dried at 70℃ for 48 h and weighted separately, and then the root: shoot biomass ratio and the percentage of litter mass in leaf biomass were calculated as follows:

$$\text{Root: shoot biomass ratio} = \frac{\text{root biomass}}{\text{stem biomass+leaf biomass}} \quad (1)$$

$$\text{Litter mass}(\%) = \frac{\text{fallen leaf biomass}}{\text{fallen leaf biomass+leaf biomass}} \times 100\% \quad (2)$$

Leaf N concentration was measured by the micro-Kjeldahl procedure with an Automatic Kjeldahl Azotometer (B-324, BUCHI, Switzerland), and leaf P concentration was measured by molybdenum blue colorimetric method in a spectrophotometer (Lambda 35, PerkinElmer, USA). Leaf N and P amounts were calculated as follows:

$$\text{Leaf N amount (mg pot}^{-1}) = \text{leaf N concentration} \times \text{leaf biomass} \quad (3)$$

$$\text{Leaf P amount (mg pot}^{-1}) = \text{leaf P concentration} \times \text{leaf biomass} \quad (4)$$

186 Soil in each pot was mixed well and passed through a 2-mm mesh sieve and
187 stored at 4 ℃ to measure the soil microbial biomass and soil enzyme activities within
188 28 days. Microbial biomass C and microbial biomass N were measured using the
189 fumigation extraction method (Vance *et al.* 1987). The activities of β-1, 4-glucosidase,
190 urease and acid phosphatase, which are tightly correlated with soil C, N and P cycling,
191 were measured as described by Wang *et al*. (2018).

192 Statistical analysis

193 Two-way analysis of variance (ANOVA) was used to test for the effects of the soil
194 origin, biotic treatment, and their interactions on measured values. The Tukey's
195 Honestly Significant Difference (HSD) Test was used to evaluate the significance of
196 differences at $P < 0.05$. Relationships of the related traits were analyzed using
197 Pearson correlation tests. All the statistical analyses were performed using SPSS 19.0.

198 **Results**

199 Changes of soil chemical properties after the conditioning phase

200 After the conditioning phase, total N and available N in conditioned soil were
201 significantly lower than those in the bare soil ($P < 0.05$). Soil organic matter in
202 conditioned soil was lower than that in the bare soil at the marginal significance level
203 ($P = 0.068$). Besides, soil P and K had no significant differences between the
204 conditioned and bare soil (Table 1).

205 Effects of treatment on D. viscosa traits after the feedback phase

206 Soil origin, biota, and their interactions significantly affected stem diameter, leaf area,
207 and LDMC of *D. viscosa*, but did not affect plant height (Table 2). Stem diameter and
208 LDMC of *D. viscosa* were significantly higher in conditioned soil than those in bare
209 soil. However, soil sterilization significantly reduced plant growth particularly in
210 conditioned soil. Growing on conditioned and non-sterilized soil, the stem diameter,
211 leaf area, and LDMC of *D. viscosa* were significantly higher than other treatments.

212 The overall biomass, including root, stem and leaf biomass, was significantly
213 higher in conditioned soil than that in bare soil. In addition, for conditioned soil,
214 sterilization significantly reduced stem biomass and leaf biomass by 47.8% and
215 74.6%, respectively. Sterilization also significantly reduced leaf biomass by 45.9% in
216 bare soil (Table 2). Biota, and biota × soil origin had significant effects on root: shoot
217 ratio and litter mass of *D. viscosa*. Soil sterilization significantly increased root: shoot
218 ratio in the conditioned soil, and significantly increased litter mass both in
219 conditioned and bare soil (Table 2).

220 The effects of soil origin, biota, and their interactions on leaf N concentration
221 were significant ($P < 0.001$). The presence of soil biota in the conditioned soil
222 significantly decreased leaf N concentration (Table 2), and leaf N concentration and
223 leaf biomass were negatively correlated ($r = -0.88$, $P < 0.001$). When considered leaf
224 biomass, the leaf N amount in the non-sterilized treatment was 98.55% higher than
225 that in the sterilized treatment. The presence of soil biota significantly increased leaf P
226 concentration ($P < 0.001$). After considering the leaf biomass, the presence of soil
227 biota increased leaf P amount by 348.14% and 110.80% in the conditioned and bare

soil, respectively. The leaf N: P ratios of *D. viscosa* under sterilized soil treatments for both the conditioned and bare soil were greater than those under non-sterilized conditions, and under the non-sterilized conditions, the leaf N: P ratio of *D. viscosa* in conditioned soil was significantly lower than that in bare soil. The leaf N: P ratio was negatively related to leaf biomass (r = -0.91, $P < 0.001$).

Effects of treatment on soil microbial characteristics after the feedback phase

The interaction of soil origin and biota on soil microbial biomass was significant ($P < 0.05$). The sterilized treatment significantly reduced soil microbial biomass C in the bare soil, but increased soil microbial biomass N in the conditioned soil (Table 3). Both soil microbial biomass C and microbial biomass N were positively correlated with soil organic matter and soil available N, but they were not significantly correlated with soil available P ($P >0.05$) (Fig. 1). Besides, the soil microbial biomass N amount was negatively correlated with leaf N amount (Fig. 2).

Sterilization significantly reduced the activity of β-1, 4-glucosidase and urease ($P < 0.01$) (Table 3). Sterilization and soil origin showed an interactive effect on phosphatase activity; sterilization decreased phosphatase activity especially in conditioned soil. In addition to quantitation of the enzyme activities per gram of soils, we also investigated the enzyme activities per microbial biomass, namely enzyme efficiency. The efficiencies of β-1, 4-glucosidase, urease and acid phosphatase were positively correlated with their enzyme activities significantly ($P < 0.001$). Correlation analysis showed that soil enzyme activities were positively correlated

with leaf N amount and leaf P amount, with the highest correlation coefficient between leaf P amount and phosphatase activity (Table 4).

Discussion

The growth of *D. viscosa* in the conditioning phase may have two most important effects on soil, i.e., the depletion of soil nutrients and the keep of soil biota. After the conditioning phase, the soil N was lower in conditioned soil than those in bare soil. From the perspective of nutrient depletion, *D. viscosa* growth depleted soil nutrients, which is disadvantage of the growth of the later plants. However, *D. viscosa* grew better in the conditioned soil than that in the bare soil, suggesting that the keep of soil biota in the conditioned soil promoted the growth and biomass accumulation of *D. viscosa* in the feedback phase. Soil sterilization significantly reduced *D. viscosa* growth, particularly for conditioned soil. These results are consistent with our hypothesis that soil biota promotes the growth of plant in dry-hot valley.

Positive effect of soil biota on the growth of *D. viscosa*

Compared with the non-sterilized soil, the root: shoot ratio was higher in the sterilized soil, indicating more serious nutrient limitation, which required increasing root biomass allocation to enhance nutrient uptake (Mccarthy and Enquist 2007). Defoliation can also promote nutrient reabsorption from the senescing tissue (Mao et al. 2013), with more nutrients allocate to new leaves (Vergutz et al. 2012). Thus, the increased litter mass also suggests nutrient limitation of *D. viscosa* in the sterilized soil treatment. This phenomenon suggests that the presence of soil biota can improve

plant nutrition.

The soil biota in the non-sterilized treatment indeed increased leaf nutrient, especially of P. The negative correlation between leaf N: P ratio and leaf biomass shows P limitation. The soil biota plays an important role in optimizing plant N: P ratios (Johnson et al. 2010). As an indicator of soil quality (Pajares et al. 2011), the activities of soil enzymes can be used to predict the capacity of nutrient supply to plants, thus, increased soil enzyme activities indicate improved soil nutrient availabilities (Sardans and Peñuelas 2010; Sinsabaugh and Follstad Shah 2012). Soil phosphatase is mainly secreted by phosphate-solubilizing bacteria and is involved in P mobilization. The increases of soil phosphatase activity in conditioned and non-sterilized soil increased soil available P, thus increasing P uptake by *D. viscosa* and alleviating P limitation to some degree. After alleviating the P limitation in conditioned and non-sterilized soil, the increased leaf biomass diluted the leaf N concentration, thus resulting in a negative correlation between leaf N concentration and leaf biomass. Therefore, the observed reduced leaf N concentration was due to the dilution effect of biomass growth on nutrient concentrations (Miyauchi et al. 2008; Ferreira et al. 2013). Our results indicate the importance of biotic effects in P cycling in dry-hot valley, which explains our previous finding that even though the available P content in dry red soil is very low, there was a greater effect of N addition on plant growth than P addition (Wang et al. 2018).

Interestingly, we found that soil microbial biomass C and biomass N did not increase significantly in non-sterilized soil, and the soil microbial biomass N

292 decreased significantly. The negative correlation between microbial biomass N
293 amount and leaf N amount (Fig. 2) suggesting that there may be nutrient competition
294 between *D. viscosa* and soil microorganisms. In nutrient poor soils, plants can uncork
295 the microbial bottleneck and actively control nutrient cycling (Chapman et al. 2006).
296 As mentioned above, the nutrient uptake of *D. viscosa* was increased in non-sterilized
297 treatment, thereby improving *D. viscosa* growth and biomass. The absorption of
298 nutrients by *D. viscosa* reduced the content of soil nutrients, resulting in nutrient
299 limitation of soil microorganisms, thus inhibiting the biomass of soil microorganisms.
300 On the contrary, the decreased nutrient absorption by *D. viscosa* in sterilized treatment
301 reduced the plant biomass, which in turn increased the nutrient content in soil, and
302 promoted the soil microbial biomass that contamination from the air or water supply
303 (Pernilla Brinkman et al. 2010). Therefore, microbial biomass was positively
304 correlated with soil nutrient availability (Fig. 1) and negatively correlated with leaf
305 nutrients amount (Fig. 2).

306 The positive plant–soil feedback observed here contrasts with the findings of
307 previous studies of negative plant–soil feedback for native species (van der Putten et
308 al. 2007; Kulmatiski et al. 2008), but is consistent with the report of positive plant-soil
309 feedback in arid ecosystems by Meijer et al. (2011). Emam et al. (2014) proposed that
310 the increase in biomass of native species in non-sterilized soil could be due to
311 biotic-mediated increases in nutrient availability, protection from pathogens,
312 stimulation of plant growth, or a combination of factors. The results of our study
313 suggest that the positive effect of soil biota is partly due to biotic-mediated increases

in nutrient availability. However, we did not reject other mechanisms, such as arbuscular mycorrhizal fungi, an important component in dry hot valley (Li and Zhao 2005; Li et al. 2010), which can promote plant nutrient uptake especially P (Smith and Smith 2011). The leaf P amount was significantly increased in bare and non-sterilized soil, and the leaf N amount was also significantly increased in the conditioned and non-sterilized soil, in the cases of no significant increases in enzyme activity after all. Anyway, the positive effect of soil biota on *D. viscosa* growth is superior to the negative effect.

Bare soil weakens the positive effect of soil biota on *D. viscosa*

The soil biota conditioned by *D. viscosa* significantly promoted the growth of *D. viscosa*, but the biotic effect for the bare soil was weaker than the conditioned soil. Carbon (C) is one of the most important limiting factors for the growth of microbes (Heuck et al. 2015). Microorganisms may use the C to synthesize enzymes to decompose organic compounds (Burns et al. 2013). In the conditioning phase, the organisms may be limited by C in the bare soil, thus reducing their enzyme activities significantly (Yan et al. 2020). However, at the end of the feedback phase, all the enzyme activities (β-1, 4- glucosidase, urease and acid phosphatase) were not affected by soil origin (Table 3). The response of enzyme activity to environmental change is sensitive, and *D. viscosa* growth in feedback phase may make up for the difference of enzyme activity caused by the conditioning phase. On the one hand, plant roots in the feedback phase provide soil microbes with an important source of labile C, mitigating

C limitation for microorganisms, thus promoting their enzymes activities (Kaiser et al. 2010; Brzostek et al. 2013). Yan et al. (2020) found that C addition in soils from bare plots increased enzyme activities more than those from planted plots. On the other hand, N is also the critical nutrient for enzyme synthesis and can limit soil microbial growth (Allison and Vitousek 2005; Yan et al. 2020). *D. viscosa* growth in the conditioning phase depleted soil N, and N competition between plant growth and organisms existed in the feedback phase as discussed above, which may lead to microbial N limitation and reduce enzyme activities of the conditioned soil in the feedback phase. Therefore, there was no significant difference in enzyme activities between the conditioned soil and the bare soil after the feedback phase.

Although soil origin had no significant effect on enzyme activities, it significantly affected the growth of *D. viscosa*, indicating that soil microbial enzyme activity was not the main reason to promote the growth of *D. viscosa* in the conditioned soil. Soil organisms positively affect plants directly by forming mutualistic relationships with their host plants and indirectly by their role in nutrient cycling (Wardle et al. 2004). Under the condition of no significant increase in phosphatase activity, the leaf P amount of the conditioned soil was significantly higher than that in the bare soil, which indicates that the direct promotional effect of soil biota on plant nutrient absorption might be more important than their effect on nutrient cycling. Therefore, inconsistent with our hypothesis, nutrient cycling caused by soil biota is not prominent in biotic plant-soil feedback. Instead, plants may change the microbial community composition, such as maintaining the beneficial soil

organisms (e.g. arbuscular mycorrhizal fungi) (Bever et al. 2009) to promote themselves. In a long-term process, the role of nutrient cycling may be obvious increasingly, which awaits further evidence.

Land degradation is a serious issue in dry-hot valley (Dong et al. 2014), and vegetation restoration is the most commonly used practice for rehabilitating the degraded land. Our results show that plants in dry-hot valley have an important impact on soil biotic function. On the contrary, the soil biotic effect on plant is significantly weakened after a period of plant remove. The results imply that the bare land will further lead to the depression of the positive effect of soil biota on plant growth. The microbial activity of bare land in Yuanmou dry-hot valley indeed significantly reduced (Yan et al. 2020). Therefore, our results here highlight the importance of vegetation restoration in ecological restoration in dry-hot valley.

Conclusions

Our results based on *D. viscosa* showed that, the soil biota in dry-hot valley can improve plant growth, biomass accumulation, and leaf nutrient content. However, the positive effect of soil biota was weakened by the disappearance of plant. Therefore, there was a positive biotic plant-soil feedback in dry-hot valley. The positive biotic plant-soil feedback plays an important role in ecosystem restoration, and helps in understanding plant adaptation to the local environment in this area.

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Tables

Table 1 Chemical properties of the conditioned and bare soil after the conditioning phase

Values	Conditioned soil	Bare soil
pH	6.42 ± 0.02 a	6.47 ± 0.03 a
Organic matter (g kg^{-1})	2.97 ± 0.25 a	3.81 ± 0.33 a
Total N (g kg^{-1})	0.21 ± 0.02 b	0.26 ± 0.01 a
Total P (g kg^{-1})	0.29 ± 0.02 a	0.32 ± 0.03 a
Total K (g kg^{-1})	30.68 ± 2.34 a	30.54 ± 1.54 a
Available N (mg kg^{-1})	36.72 ± 2.83 b	49.46 ± 3.35 a
Available P (mg kg^{-1})	5.36 ± 0.18 a	5.57 ± 0.29 a
Available K (mg kg^{-1})	126.75 ± 9.00 a	123.04 ± 7.02 a

Data in the table are means ± standard error, n=6. The different letters in the same row indicate significant differences between the conditioned and bare soil at $P < 0.05$

529 **Table 2** The growth characteristics of *Dodonaea viscosa* under different treatments after the feedback phase

Values	Conditioned soil		Bare soil		F value		
	Non-sterilized	Sterilized	Non-sterilized	Sterilized	Soil origin	Biota	Soil origin × biota
Height (cm)	8.78 ± 0.18 a	8.43 ± 0.41 a	9.22 ± 0.42 a	9.57 ± 0.53 a	3.76	0	0.75
Stem diameter (mm)	0.91 ± 0.03 a	0.69 ± 0.02b	0.76 ± 0.04 b	0.68 ± 0.02 b	9.27**	35.42***	6.47*
Leaf area (cm^2)	4.41 ± 0.22 a	2.37 ± 0.16 c	3.72 ± 0.11 b	2.76 ± 0.16 c	0.81	79.68***	10.42**
LDMC ($g\ g^{-1}$)	0.34 ± 0.01 a	0.28 ± 0.01 b	0.27 ± 0.01 b	0.25 ± 0.01 b	29.61***	25.32***	5.05*
Root biomass (g)	0.14 ± 0.01 a	0.12 ± 0.02 ab	0.08 ± 0.02 ab	0.06 ± 0.01 b	13.83**	1.84	0.01
Stem biomass (g)	0.23 ± 0.01 a	0.12 ± 0.01 b	0.16 ± 0.02 b	0.14 ± 0.01 b	4.55*	24.15***	11.55**
Leaf biomass (g)	0.67 ± 0.03 a	0.17 ± 0.01 c	0.37 ± 0.04 b	0.20 ± 0.01 c	30.61***	192.46***	46.20***
Root: shoot ratio	0.15 ± 0.01 b	0.40 ± 0.05 a	0.15 ± 0.02 b	0.19 ± 0.03 b	11.37**	20.80***	11.35**
Litter mass (%)	6.74 ± 0.51 c	51.62 ± 3.23 a	17.83 ± 2.51 b	41.99 ± 2.90 a	0.08	188.22***	16.95**
N concentration ($mg\ g^{-1}$)	10.93 ± 0.24 b	19.80 ± 0.52 a	19.94 ± 1.23 a	20.70 ± 0.50 a	47.37***	44.51***	31.70***

P concentration (mg g^{-1})	0.59 ± 0.02 ab	0.52 ± 0.01 b	0.64 ± 0.05 a	0.56 ± 0.01 ab	2.47	6.07*	0.15
N: P ratio	18.76 ± 0.65 c	37.84 ± 1.13 a	31.34 ± 1.23 b	37.17 ± 1.61 a	24.48***	107.00***	30.30***

530 Data in the table are means ± standard error, n=6. The different letters in the same row indicate significant differences among the four treatments

531 at $P < 0.05$ (Tukey's HSD test)

532 *, **, *** show statistical significance at the 0.05, 0.01, 0.001 level, respectively

533 **Table 3** The soil microbial characteristics under different treatments after the feedback phase

Values	Conditioned soil		Bare soil		F value		
	Non-sterilized	Sterilized	Non-sterilized	Sterilized	Soil origin	Biota	Soil origin × biota
Biomass C (mg kg^{-1})	244.7 ± 1.0 ab	252.2 ± 2.4 a	248.0 ± 4.1 a	237.7 ± 1.7 b	4.83*	0.31	12.12**
Biomass N (mg kg^{-1})	4.6 ± 0.1 b	5.5 ± 0.1 a	4.7 ± 0.1 b	5.0 ± 0.2 ab	2.07	19.88***	5.74*
β-1, 4- glucosidase (μmol g^{-1} h^{-1})	0.15 ± 0.02 a	0.02 ± 0.01 b	0.11 ± 0.05 ab	0.06 ± 0.02 ab	0.01	10.07**	1.65
Urease (μmol g^{-1} h^{-1})	3.66 ± 0.25 a	2.70 ± 0.57 a	3.48 ± 0.42 a	2.49 ± 0.46 a	0.19	4.88*	0
Acid phosphatase(μmol g^{-1} h^{-1})	0.20 ± 0.03 a	0.11 ± 0.01 b	0.14 ± 0.02 ab	0.11 ± 0.01 b	2.75	11.71**	4.56*

534 Data in the table are means ± standard error, n=6. The different letters in the same row indicate significant differences among the four treatments

535 at $P < 0.05$ (Tukey's HSD test)

536 *, **, *** show statistical significance at the 0.05, 0.01, 0.001 level, respectively

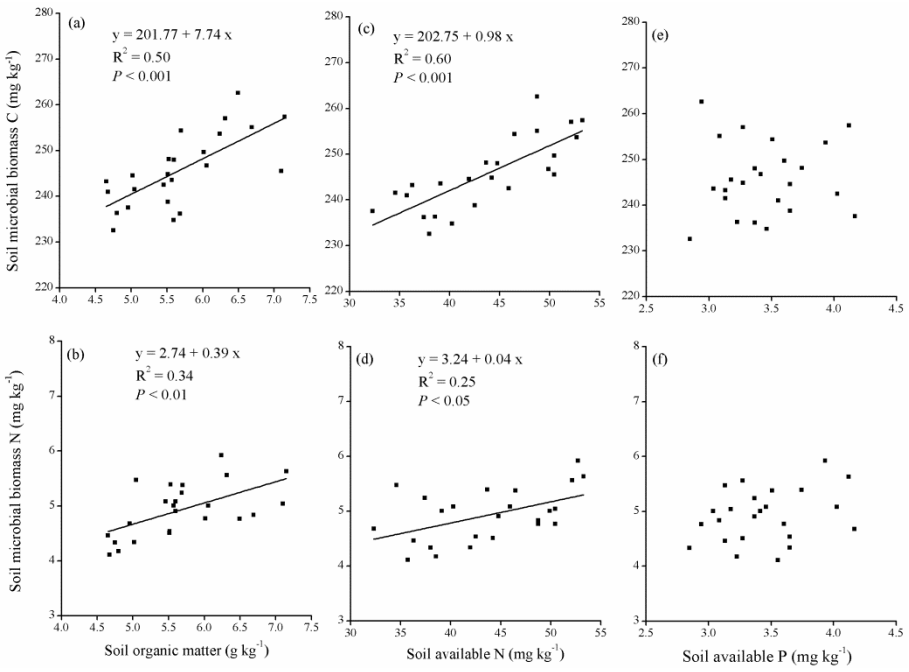
Table 4 Pearson's correlation coefficients (r) and their level of significance (*P*) showing the relationships between soil enzyme activities and leaf nutrient amount

Values	Leaf N amount		Leaf P amount	
	r	*P*	r	*P*
β-1, 4- glucosidase	0.596	0.002	0.580	0.003
Urease	0.420	0.041	0.409	0.047
Acid phosphatase	0.569	0.004	0.690	<0.001

Figures

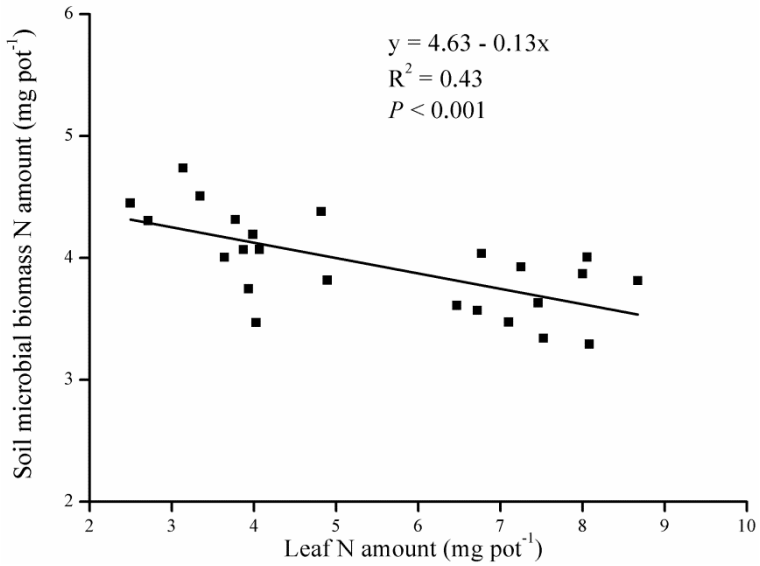
Fig. 1 Relationships between soil microbial biomass and soil nutrients. Relationship between soil microbial biomass C and soil organic matter (a), soil microbial biomass N and soil organic matter (b); relationship between soil microbial biomass C and soil available N (c), soil microbial biomass N and soil available N (d); relationship between soil microbial biomass C and soil available P (e), soil microbial biomass N and soil available P (f).

Fig. 2 Relationship between soil microbial biomass N amount and leaf N amount.


(a)
y = 201.77 + 7.74 x
R2 = 0.50
P < 0.001
(c)
y = 202.75 + 0.98 x
R2 = 0.60
P < 0.001
(e)
(b)
y = 2.74 + 0.39 x
R2 = 0.34
P < 0.01
(d)
y = 3.24 + 0.04 x
R2 = 0.25
P < 0.05
(f)
Soil microbial biomass C (mg kg-1)
Soil microbial biomass N (mg kg-1)
Soil organic matter (g kg-1)
Soil available N (mg kg-1)
Soil available P (mg kg-1)

547

548 Fig. 1


y = 4.63 - 0.13x
R2 = 0.43
P < 0.001
Soil microbial biomass N amount (mg pot-1)
Leaf N amount (mg pot-1)
2
3
4
5
6
7
8
9
10

549

550 Fig. 2

Figures

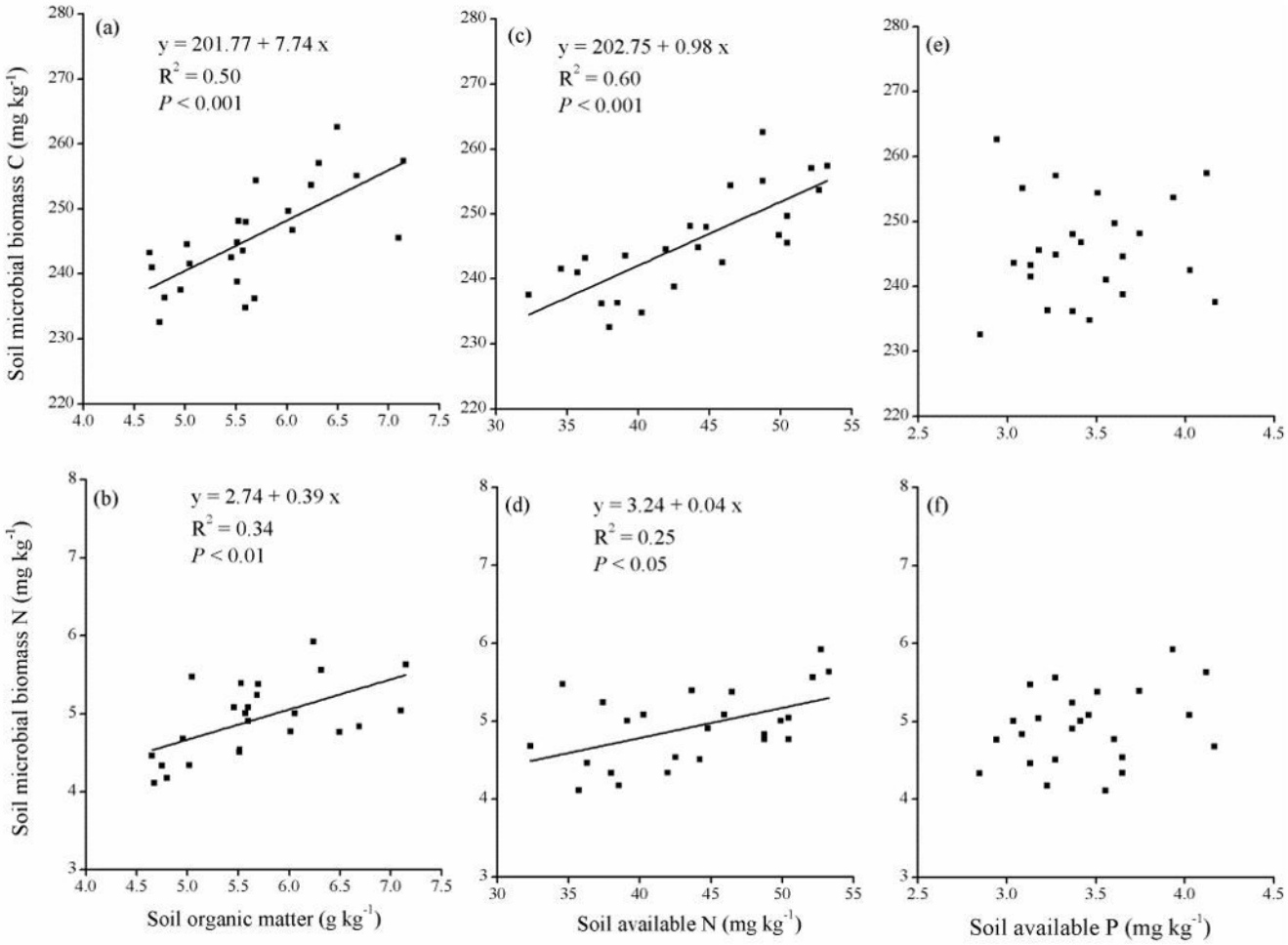


Figure 1

Relationships between soil microbial biomass and soil nutrients. Relationship between soil microbial biomass C and soil organic matter (a), soil microbial biomass N and soil organic matter (b); relationship between soil microbial biomass C and soil available N (c), soil microbial biomass N and soil available N (d); relationship between soil microbial biomass C and soil available P (e), soil microbial biomass N and soil available P (f).

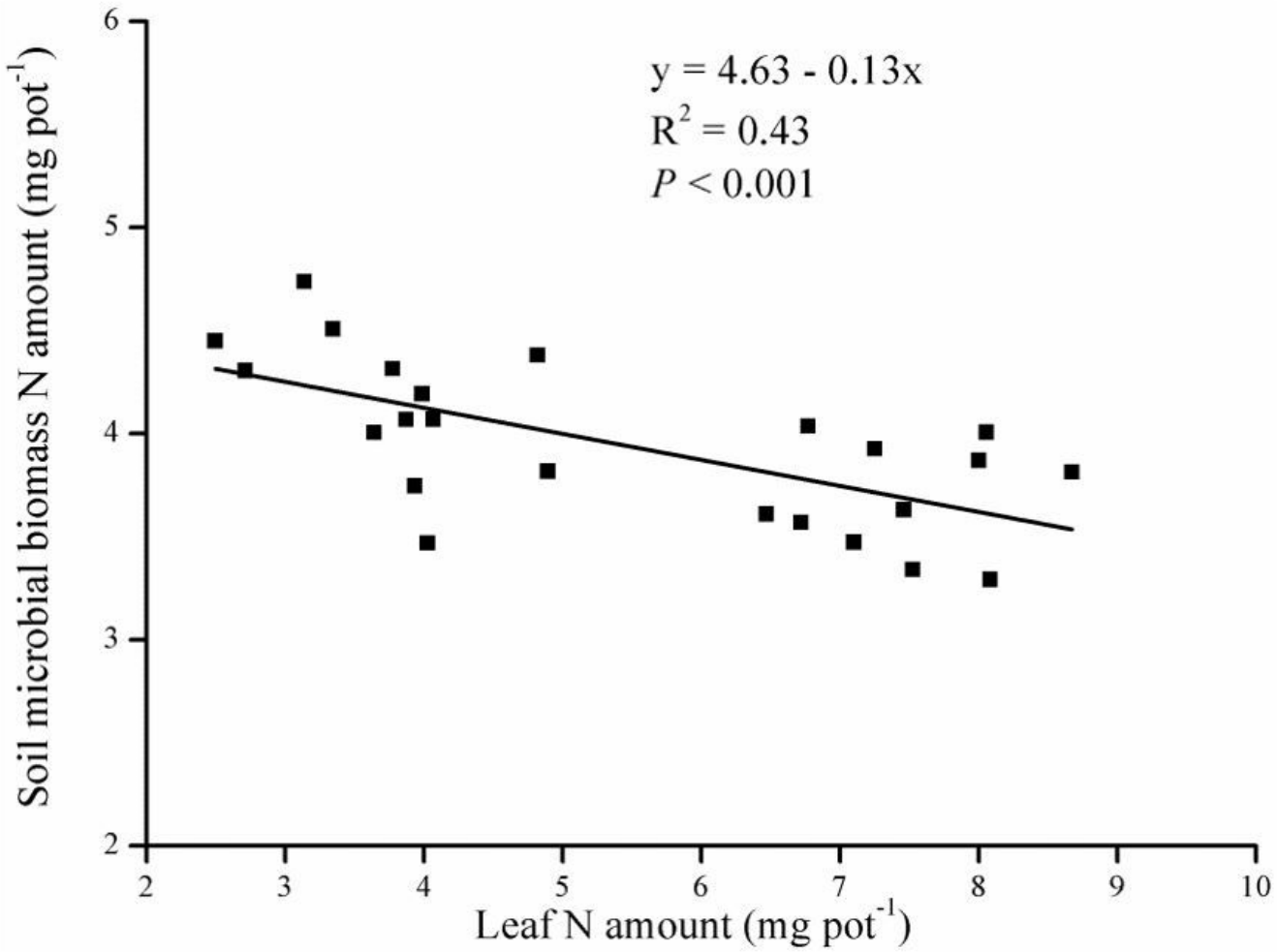


Figure 2

Relationship between soil microbial biomass N amount and leaf N amount.