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Soil Bacteria and Nematode Functional Diversity: A Comparison Across Vegetation Types

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Abstract. Vegetation types are an above-ground component that plays an important role in shaping soil community through their different life history. Plant organic material as the main source for the below-ground community is available at various time and amount based on plant growth. The objective of this study was to compare the bacteria and nematode functional diversity on soil planted with five plant types. These greenhouse experiments are selected *Oryza sativa* L. (grass), *Amaranthus* sp. (herb), *Solanum lycopersicum* (L.) Karst. (shrub), *Citrus reticulata* Blanco (tree), and *Arachis hypogaea* L. (legume). To create seven treatments, control and plant mixture were included. Soil samples and plants were collected after five weeks for bacteria and nematode enumerations, plant biomass and specific leaf area measurements. Plant growth was followed approximately every two weeks. The bacteria were separated into the heterotrophic or autotrophic group and nematodes were classified into their functional group after identification. Canonical Correspondence Analysis was used to investigate the correlation between plant types and the soil organism composition. The preliminary results showed that the plant types determined the soil bacteria and nematode composition, except for *O. sativa* and *S. lycopersicum* with the greatest similarity of composition (eigenvalue: 0.33 and 0.24, correlation: 0.80, cumulative variance: 84.1 %). This was consistent with stem growth rate, leaf growth rate, specific leaf area and plant biomass allocation. Strong to medium correlations were observed between soil organisms and above-ground plant biomass allocation (r = -0.81), plant growth rate (r = -0.59) and leaf growth rate (r = -0.46) indicating below-ground resources most likely influenced soil food web development.

Keywords: Bacteria, biota soil composition, functional groups, nematodes, vegetation types.

INTRODUCTION

The function of the terrestrial ecosystem depends on the interaction between above-ground and below-ground community [1, 2]. Below-ground community such as bacteria and nematodes provide necessary nutrients for the plants and, in turn, plants supply the necessary resources for them. This interaction however, is more complicated than previously supposed, and requires a detailed study on how plant affects soil community [3]. Plant surface litter was reported to be the important carbon source for the soil community while other reports claimed the significance of below-ground root input [4]. In a terrestrial ecosystem, plants are available to saprotrophic and detritivorous soil community as litter and root deposition. Litter quality, commonly measured by its C and N ratio, has been reported to affect nematode abundance [5]. Plant diversity through litter they produce, in addition, influenced soil micro-fauna diversity [6]. Many studies on ecosystem succession following the changes of plant community revealed that bacterivorous nematode abundance was greater in the early stages in which high quality of soil organic content was available and then decreased at the later stages due to the low quality of organic matter. In a forest ecosystem, nematode diversity did not correspond to changes in tree diversity [7–9].

An ecosystem mostly consists of more than one type of vegetation. Thus, it is not easy to separate the effect of each plant type to soil community. Each type of plant grows at various rates that might produce different quality of litter and root deposition at a different time. How this affects soil community, to our knowledge, is less understood. Grasses and herbs, for example, are two types of plants that mostly are short-lived with the rapid life cycle.

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Therefore, resources are quickly available for soil community. Species with slow life cycle such as shrubs and trees have slow growth rates thus longer turn over [10]. Well understood development of soil community due to plant type effects is believed to support soil management in the agroecosystem. The data will contribute to plant selection and mixture to cultivation, thus maintaining soil community to function in the agroecosystem. Our study, as a consequence, focuses on common agricultural plants selected based on vegetation types. Bacteria and nematodes are the main soil organisms establishing the soil micro-food web [11]. Therefore, they were selected in our study with the main objective was to compare the bacteria and nematode functional diversity on soil planted with five vegetation types.

METHODS

Greenhouse Experiments

Five vegetation types, i.e., grass, herb, shrub, tree, and legume, were used for the greenhouse experiments. Grouping of vegetation types was based on their growth form and life cycle. The agricultural plants which included paddy (*Oryza sativa* L.), spinach (*Amaranthus* sp.), tomato (*Solanum lycopersicum*) (L.) Karst, orange (*Citrus reticulata* Blanco) and peanut (*Arachis hypogaea* L.) were selected and planted in separate pots. The soil was mixed with sand (1 : 1 volume) to dilute the soil organisms. Resource soil was *Agathis alba* forest soil freed from large organic matter (visible to bare eyes). Overall, seven treatments were created by adding control of no plant and plant mixture (all plants), with five replicates for each treatment. The pots were sampled destructively three times during the study period. Because the experiments are still running, this paper, however, reported the results of the first sampling (five weeks after planting). Soil samples and plants were collected for evaluation of bacteria and nematode diversity, as well as quantification of plant variables.

The plant measured variables consisted of growth rates (leaf and stem) taken approximately every two weeks, biomass allocation and specific leaf area. Other plant chemical analyses including plant organic matter content, leaf N and C, root N and C were incomplete, thus, would be excluded in the results and discussion. Nematodes were extracted from the soil with the Baerman [12] funnel method for further analysis.

Soil Bacteria and Nematode Enumeration

Nematode diversity was measured by enumerating their abundance and by assigning into their functional groups based on their mouth structures [13, 14], which separated them into bacterivore, fungivore, omnivore, predator and root feeder. The morphotype of each nematode observed in each functional group was recorded for further genus or species identification. Bacterial abundance was quantified by plate count method by growing them on nutrient agar [15] and Burk's N-free media [16]. They were identified afterwards [17]. The bacteria were then categorized into autotrophic or heterotrophic groups. In addition, soil temperature, moisture and pH were measured as components of soil physical and chemical properties.

Canonical Correspondence Analysis (CCA) was used to investigate the correlation between vegetation types and the soil organism composition. The environment variables applied in CCA were plant types, growth rate, biomass allocation and specific leaf area, soil temperature, moisture, pH and bacterial richness whereas the species variables consisted of bacteria and nematode diversity. Biplot ordination followed the CCA, which illustrated the distribution of bacteria and nematodes in relation to the environmental variables applied. This also showed bacteria and nematode composition according to vegetation types.

RESULTS

Plant Properties

The plants differed in their growth strategy. Comparison of growth and biomass allocation across vegetation types revealed that *A. hypogaea* plant appeared to allocate most of the energy for stem and leaf growth, as well as below-ground biomass during the first five weeks. *S. lycopersicum* and *C. reticulate* plants, in contrast, favored above-ground biomass, whereas *Amaranthus* sp. preferred leaf growth. Specific leaf area varied between 0.05 mm^2 ·

mg^{-1} and 0.50 $mm^2 \cdot mg^{-1}$ across the vegetation types. The greatest specific leaf area was observed in *C. reticulate* tree and with decreasing values in *O. sativa*, *A. hypogaea*, *Amaranthus* sp., and *S. lycopersicum* plants (Fig. 1).

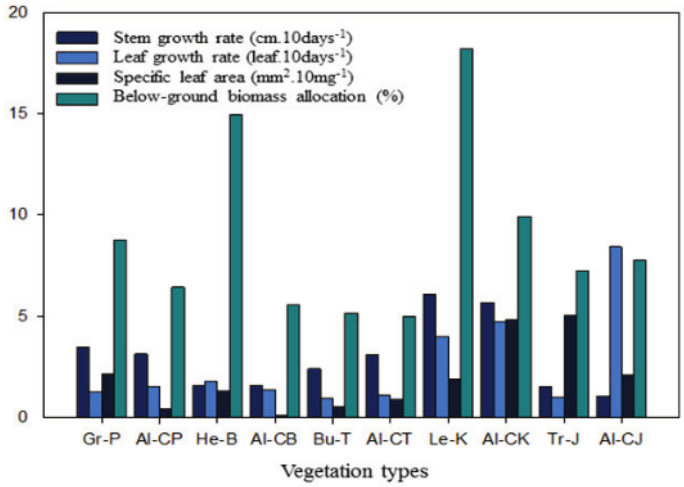

FIGURE 1. Comparison of stem growth, leaf growth, below-ground allocation, and specific leaf area across vegetation types. (axis-y was multiple with the unit represented in the legend; GriP: Grass-*O. sativa*, AI-CP: *O. sativa* of mixed plants, He-B: Herb-*Amaranthus* sp., AI-CB: *Amaranthus* sp. of mixed plants, Bu-T: Shrub-*S. lycopersicum*, AI-CT: *S. lycopersicum* of mixed plants, Le-K: Legume-*A. hypogaea*, AI-CK: *A. hypogaea* of mixed plants, Tr-J: Tree-*C. reticulate*, AI-CJ: *C. reticulate* of mixed plants).

The preliminary results on plant growth rate showed that leaf growth was the fastest in *A. hypogaea* and the slowest in *S. lycopersicum* plants when they were planted alone, but it was in *C. reticulate* tree when they grow together. It took 2.5 d for *A. hypogaea* plants to produce one leaf, but it needed 11.11 and 12.5 d for *S. lycopersicum* plant and *C. reticulate* trees respectively. Similar patterns occurred for the stem growth, in which *A. hypogaea* plants required 1.64 d to produce 1 cm stem, whereas *C. reticulate* tree was between 6.67 d and 9 d. All plants are allocated most of their biomass (> 80 %) above-ground. Two plants demonstrated greater below-ground biomass compared to the others. *A. hypogaea* plant spent 18.22 % of its biomass into below-ground growth, and *Amaranthus* sp. allocated as much as 14.93 % (Table 1).

TABLE 1. Plant characteristics across vegetation types

Vegetation Type	Plant Species	Leaf Growth Rate (leaf · day^{-1})	Stem Growth Rate (cm · day^{-1})	Below-ground Biomass Allocation (%)	Above-ground Biomass Allocation (%)	Specific Leaf Area ($mm^2 \cdot mg^{-1}$)
Grass	*O. sativa*	0.13	0.34	8.77	91.23	0.22
Herb	*Amaranthus* sp.	0.18	0.16	14.93	85.07	0.13
Shrub	*S. lycopersicum*	0.09	0.24	5.16	94.84	0.05
Tree	*C. reticulate*	0.10	0.15	9.05	90.95	0.50
Legume	*A. hypogaea*	0.40	0.61	18.22	81.78	0.19
Mixture:						
- Grass	*O. sativa*	0.15	0.31	6.44	93.56	0.41
- Herb	*Amaranthus* sp.	0.14	0.16	5.56	94.44	0.13
- Shrub	*S. lycopersicum*	0.11	0.31	4.98	95.02	0.09
- Tree	*C. reticulate*	0.08	0.11	7.76	92.24	0.21
- Legume	*A. hypogaea*	0.47	0.57	9.93	90.07	0.48

Bacteria and Nematode Diversity

Heterotrophic and autotrophic bacteria were common in the soil of varied vegetation types. Based on the morphological characters of a bacterial colony, the bacterial richness differed according to plant types. The greatest bacterial richness was observed in soil without plant [11] and soil planted with *A. hypogaea* [11]. In most cases, heterotrophic bacteria richness was greater than that of autotrophic bacteria, which was between 2 and 7 different isolates. The higher richness of autotrophic compare to heterotrophic bacteria was observed in the soil of *Amaranthus* sp (56 %) and *S. lycopersicum* (60 %). Isolate-1, isolate-3, isolate-4 and isolate-12 were specific isolates of heterotrophic bacteria while isolate-10 was common autotrophic bacteria. Isolate-18 was a specific bacterium inhabiting soil of *A. hypogaea* and isolate-20 in the soil of *C. reticulata.* The most abundant bacteria ware observed from the soil of *A. hypogaea* (22.60×10^6 cfu · g^{-1}soil). The soil without plant also showed high bacterial abundance (21.40×10^6 cfu · g^{-1}soil). Bacterial abundance in soil of *Amaranthus* sp. was twice of that in *O. sativa* (Table 2).

TABLE 2. Bacterial diversity based on colony morphology across vegetation types (Res. Soil: resource soil, Med. Soil: soil used as plant growth medium, Hetero: heterotrophic, Auto: autotrophic)

Vegetation Type	Plant Species	Bacterial Richness	Hetero-Richness	Auto-Richness	Specific Hetero.	Specific Auto.	Abundance ($X10^6$ cfu · g^{-1}soil)
Res. Soil	*A. alba*	12	5	7	-	Isolate 15	381.10
Med. Soil	-	11	6	5	Isolate 12	Isolate 15	22.80
No plant	without plant	11	7	4	Isolate 13	Isolate 6	21.40
Grass	*O. sativa*	8	5	3	Isolate 2	Isolate 10	8.97
Herb	*Amaranthus* sp.	9	4	5	Isolate 1	Isolate 6	16.70
Shrub	*S. lycopersicum*	5	2	3	Isolate 2	Isolate 10	9.60
Tree	*C. reticulate*	8	5	3	Isolate 13	Isolate 20	9.92
Legume	*A. hypogaea*	11	6	5	Isolate 3	Isolate 18	22.60
Mixture	all plant species	9	6	3	Isolate 4	Isolate 10	9.76

Isolate-1: heterotrophic, G+, coccus (1.25 µm); yellow, round, less shiny and raised colony with the smooth perimeter.
Isolate-2: heterotrophic, G-, rod-shape [(4.36 × 1.25) µm]; white, round, less shiny and raised colony with the smooth perimeter.
Isolate-3: heterotrophic, G-, ovoid [(2.5 × 0.750 µm]; milky-white, round, shiny and raised colony with the smooth perimeter.
Isolate-4: heterotrophic, G+, rod-shape [(2.75 × 0.5) µm]; milky-white, irregular, less shiny and raised colony with the undulate perimeter.
Isolate-6: autotrophic, G-, rod-shape [(2.50 × 0.50) µm]; white, round, shiny and raised colony with the smooth perimeter.
Isolate-10: autotrophic, G+, rod-shape [(2.50 × 1.25) µm]; cloudy-white, irregular, less shiny and raised colony with the undulate perimeter.
Isolate-12: heterotrophic, G-, rod-shape [(2.5 × 1.25–1.88) µm]; brownish-white, round, shiny and raised colony with the smooth perimeter.
Isolate-13: heterotrophic, G-, coccoid (1.88 µm); brownish-white, round, dull and raised colony with the smooth perimeter.
Isolate-15: autotrophic, G+, rod-shape [(2.5 × 0.75–1.25) µm]; clear-white, round, shiny and raised colony with the smooth perimeter.
Isolate-18: autotrophic, G-, rod-shape [(4.5 × 2) µm]; dark-cream, a round, shiny and umbonate-crateriform colony with the smooth perimeter.
Isolate-20: heterotrophic, G+, rod-shape [(1 × 1.5) µm]; brownish-white, round, dull and raised colony with the smooth perimeter.

Overall, all nematode functional groups, except predator, inhabited the soil of all vegetation types. However, their functional diversity varied with plant types. Only bacterivorous and fungivorous nematodes occupied soil of *O. sativa* and *A. hypogaea.* The soil of all plants was slightly richer by the present of root feeder nematodes. Bacterivorous nematodes were the most diverse of all functional groups across vegetation types both in morphotype richness (55 % to 82 %) and abundance (55 % to 87 %). This bacterial feeder reached 86 individuals at 10 g^{-1} soil in the soil of *A. hypogaea* which was the greatest abundance among vegetation types. The lowest nematode abundance (eight individuals × 10 g^{-1} soil) was detected in the soil of *O. sativa.* Fungivorous nematodes were most abundant in

the soil of *S. lycopersicum* (24 individuals × 10 g^{-1} soil). The most abundant of omnivorous and root feeder nematodes were in soil of *C. reticulate* (six individuals × 10 g^{-1} soil) and soil of *S. lycopersicum* (Nine individuals × 10 g^{-1} soil) respectively. The ratio between bacterivorous and fungivorous nematodes varied between 1.38 in the soil of mixed plants and 6.44 in the soil of *A. hypogaea.*

TABLE 3. Nematode's functional diversity of soil planted with five types of vegetation (Res. soil: resource soil, Med. soil: soil used as plant growth medium (inds: individuals, B: bacterivore, F: fungivore)

Vegetation Type	Plant Species	Morphotype Richness	Bacterivore Richness	Fungivore Richness	Omnivore Richness	Root Feeder Richness
Res. Soil	*A. alba*	20	11	4	4	1
Med. Soil	-	8	5	2	-	1
No plant	without plant	20	14	3	2	1
Grass	*O. sativa*	11	9	2	-	-
Herb	*Amaranthus sp*	22	12	4	3	3
Shrub	*S. lycopersicum*	19	11	5	3	2
Tree	*C. reticulate*	21	12	4	4	1
Legume	*A. hypogaea*	14	11	3	-	-
Mixture	all plant species	16	12	3	-	1

TABLE 4. Nematode's functional diversity of soil planted with five types of vegetation (Res. soil: resource soil, Med. soil: soil used as plant growth medium (inds: individuals, B: bacterivore, F: fungivore) [continued]

Vegetation Type	Plant Species	Bacterivore Abundance (inds × 10 g^{-1})	Fungivore Abundance (inds × 10 g^{-1})	Omnivore Abundance (inds × 10 g^{-1})	RootFeeder Abundance (inds × 10 g^{-1})	Total Abundance (inds × 10 g^{-1})	B:F
Res. Soil	*A. alba*	13.43	9.90	1.98	1.98	27.29	1.36
Med. Soil	-	3.47	4.95	-	0.99	9.41	0.70
No plant	without plant	15.94	3.28	1.20	0.40	20.82	4.86
Grass	*O. sativa*	5.60	2.60	-	-	8.20	2.15
Herb	*Amaranthus sp*	17.59	6.40	4.80	2.40	31.19	2.75
Shrub	*S. lycopersicum*	41.19	23.79	0.80	9.20	74.97	1.73
Tree	*C. reticulate*	20.99	3.40	6.40	0.20	30.98	6.17
Legume	*A. hypogaea*	86.82	13.48	-	-	100.30	6.44
Mixture	all plant species	11.59	8.40	-	0.80	20.79	1.38

Correlation Analysis

CCA revealed a strong correlation between environmental variables and species variables (0.80) with the eigenvalues of axis-1 was 0.33 and axis-2 was 0.24. The cumulative percentage variance of species and environment relation for both axes was 84.1. Figure 2 presented the bi-plot of the CCA. It showed that soil bacteria and nematode composition varied with the vegetation type except those of *O. sativa, S. lycopersicum* and all plants. This was consistent with plant growth and above-ground biomass allocation. The soil organism was fairly to strongly correlated to leaf growth rate (axis-1 = -0.46, axis-2 = 0.55), stem growth rate (axis-1 = -0.59, axis-2 = 0.55) and correlated stronger to above ground biomass allocation (axis-1 = -0.81), but showed weak correlation to specific leaf area (axis-1 = 0.14, axis-2 = 0.10). Bacterial richness revealed fair correlation to the soil community (axis-1 and 2 = 0.37), with slightly more prominent correlation to autotrophic bacteria (axis-2 = 0.49). Soil properties seemed to show weak correlation to the soil community, in which soil temperature showed a correlation of 0.04 (axis-1) and of -0.38 (axis-2) while soil moisture was of 0.09 for axis-1 = 0.09 and -0.42 for axis-2.

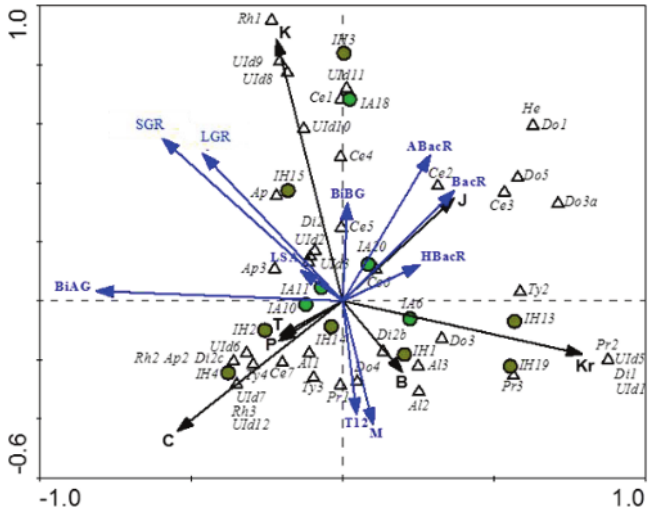

FIGURE 2. CCA biplot of bacteria and nematode community in seven different plant variation of five vegetation types (LGR: leaf growth rate, SGR: stem growth rate, BiBG: below-ground biomass allocation, ABacR: autotrophic bacterial richness, BacR: bacterial richness, HBacR: heterotrophic bacterial richness, M: soil moisture, T12: soil temperature at 12 cm depth, BiAG: above-ground biomass allocation, LSA: specific leaf area; K: *A. hypogaea*, J: *C. reticulate,* Kr: without plants, B: *Amaranthus* sp., C: all plants, P: *O. sativa,* T: *S. lycopersicon*; Ap: Aphelenchidae, Di: *Ditylenchus*, Ce: Cephalobidae, He: *Heliotylenchus,* Do: Dorylamidae, Pr: Prismatolaimidae, Al: Alamidae, Ty: Tylenchidae, Rh: Rhabditidae, UId: unidentified; IA: autotrophic isolate, IH: heterotrophic isolate; triangle: nematode, green filled circle: autotrophic isolate of bacteria, brown filled circle: heterotrophic isolate bacteria).

DISCUSSION

Our preliminary results showed that over 5 wk, vegetation types determined soil bacteria and nematode diversity and composition. Plant growth rate and biomass allocation were more prominent factors contributing to the soil community than other measured environment factors. Based on the bacteria and nematode diversity of the soil used as growth medium before planting, vegetation types seemed to change bacteria into the less diverse community in term of isolates, although their functional diversity remained the same. Nematode community, however, was more diverse in term of morphotypes but varied in term of functional diversity. The composition of bacteria and nematode community also changed and developed into a less similar community.

Particular bacteria isolate developed during the 5 wk period, and depending on plant type; autotrophic bacteria isolate 10 was more common than heterotrophic isolate 1 and 4, which only inhabited soil of *Amaranthus* sp. and all plants. It was unclear as what mechanisms affected this specificity. Based on the environmental factors measured, the soil of *Amaranthus* sp. showed higher moisture and temperature than the soil of others. Thus, it might be that soil temperature selected particular bacteria while moisture provided water vapor as a resource. Soil chemical and physical properties of all plants were approximately similar to that of *Amaranthus* sp. but below-ground biomass was more available in all plants than in soil of *Amaranthus* sp. This might shift the environment into more favorable to heterotrophic bacteria of isolate 4. This, nevertheless, requires further analysis. Another possible explanation was the presence of bacterivorous nematodes that slightly greater in the soil of *Amaranthus* sp. and different nematode morphotype. The different nematode morphotype might be different species that had preferences in particular bacteria species as food choice.

Nematode community followed vegetation types in most cases. Based on the bacterivore to fungivore ratio, it indicated that most nematode community developed from fungal based toward bacterial based food web. This trend was most noticeable in the soil of *A. hypogaea* and *C. reticulate,* but the least in the soil of *S. lycopersicum* and all plants. Development of bacterial based food web could be related to root deposition during the plant growth.

Availability of root deposition provides more nutrients, particularly N, to enhance the development of opportunist bacterivorous nematodes [18].

Three bacterivorous nematode morphotypes, i.e., Rhabditidae-1, unidentified-9 and -8, were numerous in the soil of *A. hypogaea,* which also dominated by heterotrophic bacteria of isolate-3 and autotrophic bacteria of isolate-18. It was possible that these nematodes were large consumers of these bacteria. Cephalobidae-1 also appeared to consume them. The soil of *C. reticulate* demonstrated different soil community to the soil of *A. hypogaea.* Although bacterivores were abundance, this community was rich in omnivorous nematodes of Dorylamidae-1, -3a, and -5. This indicated that nematode food web was the most stable of all vegetation types. This perhaps related to less soil disturbance due to slow plant growth but the steady availability of organic soil matter [19]. Again, however, soil organic matter content need to be measured. Soil community of *Amaranthus* sp. with high numbers of bacteria isolate-1 and -6 was occupied mostly by bacterivorous nematodes of Alamidae-3 and -2, as well as omnivorous Dorylamidae-3. Compared to the soil of *C. reticulata,* nematode food web was less stable. In the soil of *S. lycopersicum, O. sativa* and all plants, bacteria and nematode community were highly similar.

In summary, our preliminary results showed vegetation types shifted bacteria and nematode community mostly through plant growth and below-ground biomass allocation. The functional diversity of bacteria persisted in all vegetation type soil, but different isolates specified the soil community. Nematode functional groups varied with the plant types but shifted toward bacterial based food web. Plant types determined richness and abundance of nematode morphotypes in all soil, in particular, greater richness and abundance of omnivorous nematodes appeared in slow growing plants. More data and further analyzes are required to provide a more detailed process and good conclusion.

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