*applied microbiology*

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# Impacts of Tillage Practices on Growth, Phosphorus Uptake, and Yield of Maize in Controlled and Field-Based Studies in Relation to Arbuscular Mycorrhizal Fungi

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**Abstract:** This study investigated the effects of arbuscular mycorrhizal fungi (AMF) on the growth, phosphorus (P) uptake, and yield of maize in the presence or absence of tillage. The two-year field experiment was conducted in Kanagawa, Japan. Firstly, we investigated whether the presence of indigenous AMF communities in the roots, as determined by amplicon sequencing analysis, contributed to maize growth in Experiment 1, a 2-year field-based study. The findings revealed that the maize (*Zea mays* L.) in rotary tillage had higher P uptake, growth at the six-leaves collar stage, and yield, compared to no tillage. The AMF communities colonizing maize roots were altered by the presence or absence of tillage; specifically, tillage increased the dominance of the *Gigasporaceae*, whereas no tillage increased the dominance of the *Acaulosporaceae*. Based on these findings, we confirmed whether the inoculation of similar AMF strains, as analyzed in the field study of tillage practices on maize roots, produces growth-promoting effects for maize growth in a controlled pot experiment consistent with the results of the field experiment. For experiment 2, *Dentiscutata cerradensis* TK-1, *Cetraspora pellucida* SZ-3 (*Gigasporaceae*), *Acaulospora morrowiae* AP-5, and *A. longula* F-1 (*Acaulosporaceae*) were inoculated as AMF inocula for a pot experiment. The results showed that aboveground biomass did not change with any inoculum compared to the control. The P concentration in maize was higher for *D. cerradensis* TK-1 and *C. pellucida* SZ-3 inoculation than for the control. However, inoculation with *A. morrowiae* AP-5 and *A. longula* F-1 did not change P concentrations from the control. This indicates that *D. cerradensis* TK-1 and *C. pellucida* SZ-3 are more effective in promoting P uptake in maize than in *A morrowiae* AP-5 and *A. longula* F-1. Based on field and pot experiments, our findings suggest that tillage practices lead to alterations in the AMF communities that colonize the roots, and this shift may also contribute to changes in P uptake and crop growth.

**Keywords:** arbuscular myccorhizal fungi; AMF communities; maize; tillage practice; phosphorus uptake



**Citation:** Tatewaki, Y.; Higo, M.; Isobe, K. Impacts of Tillage Practices on Growth, Phosphorus Uptake, and Yield of Maize in Controlled and Field-Based Studies in Relation to Arbuscular Mycorrhizal Fungi. *Appl. Microbiol.* **2023**, *3*, 358–374. https://doi.org/10.3390/applmicrobiol3020025

Academic Editor: Bong-Soo Kim

Received: 31 March 2023
Revised: 18 April 2023
Accepted: 20 April 2023
Published: 22 April 2023



## 1. Introduction

Rotary tillage is considered as a conventional agriculture practice. The significance of rotary tillage lies in its use to break up and soften the soil, and to evenly mix the organic matter and fertilizers. In contrast, no-tillage farming refers to a method in which the soil is not tilled before growing crops. Compared with rotary tillage cultivation, crop growth and yield have been reported to be decreased [1], unchanged [2], or increased [3]; the results are mixed. Therefore, it is important to identify the factors that affect crop yield in the presence or absence of tillage. It has been previously reported that tillage is a factor that affects soil hardness and the associated changes in root growth, which can increase or

decrease yield [4]. In addition, it has been suggested that differences in the composition of soil microbial species may affect crop yield [5], which is another factor that may alter crop growth and yield during tillage. Among soil microorganisms, arbuscular mycorrhizal fungi (AMF) are prevalent in terrestrial ecosystems and are known to enhance mineral and water uptake in addition to promoting plant growth. In return, the fungi obtain carbon from the host plant [6]. AMF grow external hyphae that supply phosphorus (P) to the host that cannot be obtained by the plant roots [6]. Consequently, there have been several reports of increased crop yield due to AMF colonization [7–9]. However, an increase in AMF colonization does not necessarily translate directly into increased crop yields. Approximately 300 species of AMF have been identified [10], although different species have been reported to have different capacities to acquire P [11,12]. It has been reported that there exists variations in the capacity of different AMF species or community levels to assimilate P for plant growth in controlled and field conditions [13–18]. Some studies have suggested that by allocating a greater proportion of resources towards extraradical hyphae, members of the *Gigasporaceae* family may be able to provide more P to the host plant compared to members of the *Glomeraceae* family, thereby increasing the carbon flux from the host to the symbiont [19]. Conversely, species belonging to the *Glomeraceae* family are thought to adopt a strategy of ruderality, which enables them to quickly colonize disturbed and low-nutrient environments by prioritizing fast growth rates and high hyphal turnover, at the cost of low investment in extraradical hyphae [20,21]. Previous studies have not only reported functional variations within AMF species but also investigated the potential impact of variations in AMF communities on crop growth [18].

It is also reported that rotary tillage generally disrupts the AMF network in the soil, resulting in a decrease in AMF colonization and crop yield [22]. Furthermore, the alteration of AMF communities in soil and plant roots as a consequence of tillage practices, as well as AMF colonization, has also been extensively documented [23–26]. The AMF communities are highly susceptible to variations in land-use types and agricultural management practices [27,28]. In a previous report, we combined two factors—different cover crop management and tillage—and found that the difference in AMF species colonizing the roots of fodder maize was influenced only by the presence or absence of rotary tillage [23]. However, this study did not clarify whether the AMF communities colonizing maize roots changed with the presence or absence of rotary tillage or affected the yield of maize. It is postulated that crop growth is improved when crops are colonized with a higher proportion of AMF species with high P acquisition capacity, whereas the percentage improvement in crop growth is smaller when colonized with a higher proportion of AMF species with low P acquisition capacity. Moukarzel et al. [18] have indicated that various species within diverse communities of AMF may possess the potential to exert a beneficial impact on plant biomass and nutrient uptake through the presence of specific AMF species. However, few reports have clarified whether the presence or absence of rotary tillage changes the AMF communities colonizing the roots and consequently affects crop yield. Therefore, the objective of this study was to clarify the factors that influence the yield of maize, depending on the presence or absence of rotary tillage, in terms of the AMF communities colonizing the roots. Knowing whether such tillage practice affects crop growth and its connections to AMF communities may help to determine the proper tillage practices under specific agricultural management. Our experiments were:

**Experiment 1.** *The AMF communities colonizing maize roots in a 2-year rotary or no tillage were analyzed to identify specific AMF taxa involved in crop growth in a field-based study.*

**Experiment 2.** *Based on the results of Experiment 1, a controlled pot study was conducted to confirm whether inoculation with some AMF strains similar to those identified in the field study had a similar growth-promoting effect.*

By addressing these issues, this study will provide a novel insight into the factors driving the differences in maize growth by AMF communities in tillage practices, thereby enhancing our comprehension of the functional role of AMF communities within the agri-

cultural ecosystem. Additionally, analysis of Illumina MiSeq sequencing is an extensively introduced and helpful technique for understanding the role of AMF communities in natural [29,30] and agricultural ecosystems [31,32]. Thus, we used this technique to investigate how and whether AMF communities in the roots of maize change in different types of tillage systems in the field-based study.

## 2. Materials and Methods

### *2.1. Experiment 1*

#### 2.1.1. Effect of Rotary Tillage on Growth, Yield, and AMF Colonization in the Roots of Maize (Field Experiments)

Field experiments were conducted from April 2019 to September 2020 at Nihon University (Fujisawa-city, Kanagawa, Japan; lat. 35°38′41″ N, long. 139°47′15″ E). Average temperature and accumulated precipitation during the growing season were obtained from the Amedas data station "Tsujido" of the Japan Meteorological Agency, located about 5 km away from the site of the field experiments. The average temperature during the growing season was 24.4 °C in 2019 and 24.8 °C in 2020. The accumulated precipitation was 738 mm in 2019 and 657 mm in 2020. The average temperature over the past 20 years was 23.4 °C and the accumulated precipitation was 796 mm (Figure S1). The soil in the field where the test was conducted was andosol. Soil chemical properties in the field experiments were: soil pH: 5.91, EC: 63.8 µS/cm, available soil P: 3.83 mg/100 g, nitrate N: 20.9 mg/100 g, and exchangeable K: 52.0 mg/100 g (Table S1). No-tillage and rotary tillage plots were established as test plots. The size of the test plot was 4.5 m (row direction) × 4 m (spacing direction), with three replicates per plot. The no-tillage plots were not tilled during the experimental period (April 2019 to September 2020), whereas the rotary tillage plots were tilled with a cultivator (KRA850, Kubota Corporation, Osaka, Japan) approximately 20 cm above the surface layer at 1 month before maize sowing and after harvesting. Maize (*Zea mays* L., variety: P1690, Pioneer Ecoscience Co., Ltd., Tokyo, Japan) was sown on 20 May 2019 and 14 May 2020 (Figure S2), at 2 cm below the surface layer with 75 cm between rows and 20 cm between plants, using 3 seeds per location. After 3 weeks, the seedlings were thinned to 6.7 plants/$m^2$. In both 2019 and 2020, nitrogen (ammonium sulfate) and potassium (potassium chloride) were applied as basal fertilizer in strips at 3 cm above the surface on the day before sowing at a rate of 10 g/$m^2$. After seeding, water was sprinkled daily until sprouting, and Sankei Denapon 5% bait (Sumitomo chemical garden products inc., Tokyo, Japan) was applied 1 week after germination to control insects. Alphard solution (Nippon Soda Co., Ltd., Tokyo, Japan) was applied 1 week before the 4-leaves collar stage (2019 and 2020: 28 days after sowing (DAS)) to manage weeds.

#### 2.1.2. Maize Sampling and Determination of Biomass, P Concentration, and Grain Weight

We collected aboveground plant parts and roots from 8 to 10 plants per replicate during the 6- leaves collar (1 July 2019: 42 DAS; 25 June 2020: 42 DAS) and tasseling stages (25 July 2019: 66 DAS; 23 July 2020: 70 DAS) (Figure S2). The roots were sampled with a shovel to a depth of 20 cm for a diameter of 15 cm. The aboveground was cut off from the roots at ground level and placed in a dryer (DRL823WA, Advantec Co., Ltd., Tokyo, Japan) at 80 °C for 48 h until completely dry, and the biomass was measured. After measurement, only the stems and leaves were ground into powder using a grinder (NR-02, Sansho Industry Co., Ltd., Osaka, Japan), and the aboveground P concentration was analyzed using the vanadomolybdate method [33] after acid decomposition. P uptake was calculated by multiplying the aboveground biomass by the P concentration. At the maturity stage (19 September 2019: 122 DAS, 9 September 2020: 118 DAS), we selected aboveground plant samples from 12 to 15 individuals per replication, which were subsequently separated into grain and stover components (Figure S2). The samples were then completely dried in an 80 °C dryer for 48 h, following which we determined the aboveground biomass of each component.

#### 2.1.3. AMF Colonization within Maize Roots

The roots were stained following the procedure of Kobae and Ohtomo [34]. The roots were washed with tap water, and approximately 100 mg of fresh weight of each root was collected from each individual, and the secondary or tertiary roots were cut into 1 cm lengths. The roots were soaked in a 10% solution of potassium hydroxide and heated in a microwave oven (DMW-P75D, Daewoo Sales Co., Ltd., Saitama, Japan) to soften the root tissue. The roots were then washed with distilled water and decolorized with 10% hydrogen peroxide for 15 min. After washing with distilled water, 2% hydrochloric acid was added and left for 5 min at room temperature to decolorize the tissue again. After the tissue was washed with distilled water, 2 mL of a mixture of 27 mL of PBS, 3 mL of 30% albumin solution, and 0.4 µL of WGA were added and left to stand at room temperature for at least 16 h. The roots were then washed with PBS solution, mixed with 200 µL each of 2 mL of PBS and three reagents of the peroxidase staining DAB kit (Nacalai Tesque, INC., Kyoto, Japan), and left at room temperature for 24 h to stain for AMF infection in the roots. The AMF colonization was measured in 5 mm square Petri dishes, and the presence or absence of infection at the intersection points was investigated at each iteration using the gridline intersect crossing method [35] at more than 200 points. If arbuscules or vesicles were observed in the roots, the roots were considered to be colonized by AMF.

#### 2.1.4. DNA Extraction from Maize Roots and Amplicon Sequence Analysis

The bead cell disruption device was used to crush secondary or tertiary roots weighing 100 mg in fresh weight, utilizing liquid nitrogen (MS-100, TOMY SEIKO Co., Ltd., Tokyo, Japan) at 3000 rpm for 30 s, and then a DNA extraction kit (NucleoSpin® Plant II, MACHEREY-NAGEL GmbH & Co. KG, Düren, Germany) was used to extract DNA. The extracted DNA was used for amplicon sequencing analysis of the 18S rRNA gene of AMF obtained by nested PCR. First, DNA was amplified by 1st-PCR using AM1 (5′-GTTTCCCGTAAGGCGCCGA-3′) [36] and NS31 (5′-TTGGAGGGCAGTCTGGTGCC-3′) [37] as primers. The 1st-PCR reaction was performed under the following conditions: 94 °C for 2 min, followed by 35 cycles of 94 °C for 10 s, 60 °C for 5 s, and 68 °C for 15 s. The 2nd-PCR was performed using AMV4.5NF (5′-AAGCTCGTAGTTGAATTTCG-3′) and AMDGR (5′-CCCAACTATCCCTATTAATCAT-3′) [38] with adapter sequences for amplicon sequencing analysis using Illumina MiSeq. The 2nd-PCR reaction was performed under the following conditions: 94 °C for 2 min, followed by 40 cycles of 94 °C for 10 s, 60 °C for 5 s, 68 °C for 15 s. The amplified PCR products were purified by NucleoSpin® Gel and PCR Clean-up (MACHEREY-NAGEL GmbH & Co. KG, Düren, Germany), and amplicon sequencing analysis was performed at 2 × 300 bp. Acquired amplicon sequence data were analyzed by Qiime2 [39]. We performed the bioinformatic analyses of AMF communities based on the procedure of Stefani et al. [40]. The raw demultiplexed sequences were processed in QIIME 2 v2022.8 ( http://benjjneb.github.io/dada2/tutorial.html, accessed on 9 September 2020) [41]. Paired-end sequences were denoised, dereplicated, and filtered for chimeras using the DADA2 [39], as implemented in QIIME 2. Sequences were trimmed in order to include only bases with quality scores >20. The first 21 and 20 nucleotides of the 5′ end of the forward and reverse sequences, respectively, were also trimmed. The 3′ end of the forward and reverse sequences were truncated at positions 230 and 210, respectively.

The taxonomic identification of each amplicon sequence variant (ASV) was performed by the procedure of Stefani et al. [40]. Each ASV was identified with the closest sequences found in GenBank [42] using NCBI BLAST. Only the first hit of BLAST results were saved (the hit with the highest pairwise similarity and a query coverage of >97%). A phylogenetic tree was inferred using reference sequences from well-identified AMF cultures to complement and refine the taxonomic identification of each ASV. The taxon name of each reference sequence was verified in NCBI GeneBank and updated when needed. A maximum likelihood tree was calculated in RAxML v8.2.10 (https://github.com/stamatak/standard-RAxML, accessed on 9 September 2020) [43]. Bootstrap resampling was set to 1000 and the GTRGAMMA sequence evolutionary model was chosen. The taxonomic

assignment of each ASV based on its position in the phylogenetic tree was compared with the taxonomic information retrieved from directly querying the MaarjAM [44] and NCBI GenBank databases. Relative abundance was calculated as the proportion of each family from the total AMFs. The BioProject Accession Number for the results of this analysis was PRJDB14201l; the results were registered through the DNA Data Bank of Japan.

For the community analysis, rarefaction analysis of the lowest reads (6-leaves collar stages: 27,284 sequences, tasseling stages: 33,793 sequences) per sample among the treatments was carried out using the "rarefy" function in the R package vegan v2.5.6 in R 4.0.2 (https://www.R-project.org/, accessed on 9 September 2020) [45]. After rarefaction analysis, we performed resampling to the lowest ASV abundance to assess differences between tillage treatments regardless of the sequencing depth for redundancy analysis (RDA) and permutational multivariate analysis of variance (PERMANOVA). To investigate whether tillage practice significantly changed the species communities of the AMF in the roots of maize, PERMANOVA was carried out with 999 permutations by using the "adonis" function in the R package vegan v2.5.6.

### *2.2. Experiment 2*

Effect of Different Colonized AMF Species on Maize Growth and P Uptake (Pot Experiment)

This experiment was conducted in an artificial weather growth chamber (Model FR-535A-S2, Koito Manufacturing Co., Ltd., Shizuoka, Japan) set at 25 °C during the day and 22 °C at night, with a day length of 14 h. Andosol and silica sand were sterilized at 121 °C for 60 min, mixed in a ratio of 1:1, and filled into 1/10,000 Wagner pots at a rate of 1000 g. The soil chemical properties of the soil mixture used in the pot experiment were: soil pH: 6.2, EC: 5.0 μS/cm, available soil P: 1.7 mg/100 g, and nitrate N: 1.7 mg/100 g (Table S2). The AMF inoculum consisted of 1000 spores of *Acaulospora longula* F-1, 1000 spores of *A. morrowiae* AP-5, 500 spores of *Dentiscutata cerradensis* TK-1, and 1000 spores of *Cetraspora pellucida* SZ-3. Cultures containing spores of each species were added directly under the maize seeds. The inoculum source was obtained from the Research Center of Genetic Resources (NARO GeneBank). The maize variety used, P1690, was the same as in the field experiment. Three seeds were sown per pot, and after 7 days of germination, the seedlings were thinned to one plant. Each inoculation treatment was established in triplicate. The aboveground plant and root samples were taken 35 days after sowing, and AMF colonization, aboveground biomass, aboveground P concentration, and aboveground P uptake were determined by the same methods as in the field experiment.

### *2.3. Statistical Analysis*

Significant differences in aboveground biomass, P uptake, and grain weight of maize in the field experiment were analyzed using two-way analysis of variance (two-way ANOVA) with R v.4.0.2. The AMF colonization and AMF relative abundance were angle-transformed to normalize the distributions before statistical analysis. Significant differences in the pot experiment were analyzed using a *t*-test with R v.4.0.2.

## 3. Results

### *3.1. Growth and Yield of Maize*

In both years, the aboveground biomass of maize at the six-leaves collar stage (2019 and 2020: 42 DAS) in the rotary tillage tended to be higher than that in the no-tillage, and significant differences were found between tillage practices when analyzed by two-way ANOVA (Figure 1a). P uptake in maize in the rotary tillage tended to be higher than that in the no-tillage, and significant differences were found between tillage practices (Figure 1b). The AMF colonization in the no-tillage tended to be higher than that in the rotary tillage from the two-year results, but no significant differences were found between tillage practices by two-way ANOVA (Figure 1c). Additionally, the aboveground plant biomass of maize at the maturity stage in the rotary tillage plots tended to be higher than

that in the no-tillage plots from the two-year results, and a two-way ANOVA showed significant differences among tillage practices. (Figure 1d).

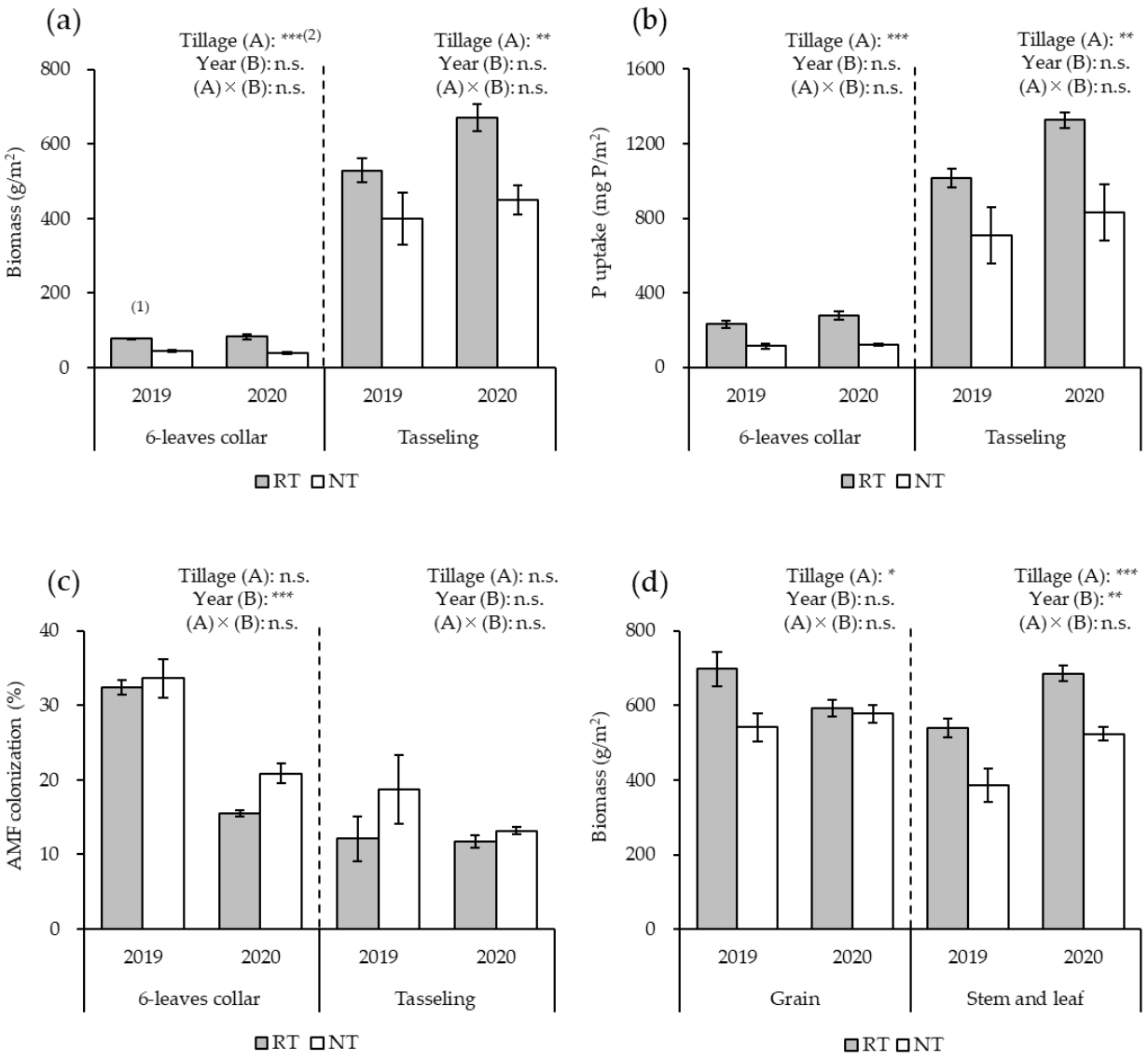


**Figure 1.** Effect of the different tillage practices on the arbuscular mycorrhizal fungal (AMF) colonization, maize growth, and maize yield in 2019 and 2020. (**a**) Aboveground biomass of maize at the 6-leaves collar (2019 and 2020: 42 DAS) and tasseling stages (2019: 66 DAS, 2020: 70 DAS) in 2019 and 2020; (**b**) aboveground P uptake in maize; (**c**) AMF colonization in the roots of maize at the 6-leaves collar (2019 and 2020: 42 DAS) and tasseling stages (2019: 66 DAS, 2020: 70 DAS) in 2019 and 2020; (**d**) aboveground biomass of maize at the maturity stage (2019: 122 DAS, 2020: 118 DAS). RT = rotary tillage, NT = no-tillage. [(1)] Error bars are the standard error of the mean; [(2)] n.s. indicates no significance and *, **, and *** indicate significant differences at the 5%, 1%, and 0.1% level according to two-way ANOVA, respectively.

### *3.2. Relative AMF Abundance in Maize Roots*

A total of 902,362 paired-end sequences corresponding to *Glomeromycota* were derived from the twelve libraries (Figure 2). We found a total of 104 amplicon sequence variants (ASVs) belonging to *Glomeromycota* in the roots. Additionally, we found that the relative abundance of AMF ASVs in maize roots tended to differ between tillage practices regardless of sampling stages (Figure 3a,b). We also used RDA to determine the differences in the structures of AMF communities in the roots of maize between tillage practices (Figure 3c,d).

The results of the RDA showed that tillage practices affected the shift in the structure of AMF communities. The results of PERMANOVA also indicated the significant differences in the structure of AMF communities in maize between tillage practices. Furthermore, the effect of different tillage practices on the relative AMF abundance in maize roots in the six-leaves collar and tasseling stages is shown in Figure 4. In the six-leaves collar stage, for both years, the relative abundances of *Diversisporaceae* in the no-tillage tended to be higher than those in the rotary tillage. The relative abundance of *Gigasporaceae* in the rotary tillage tended to be higher than that in the no-tillage plots, and significant differences were found between tillage practices in two-way ANOVA. In the tasseling stage, for both years, the relative abundance of Acaulospraceae in the no-tillage tended to be higher than that in the rotary tillage. The relative abundance of *Gigasporaceae* in the rotary tillage tended to be higher than that in the no-tillage, and significant differences were found between tillage practices.

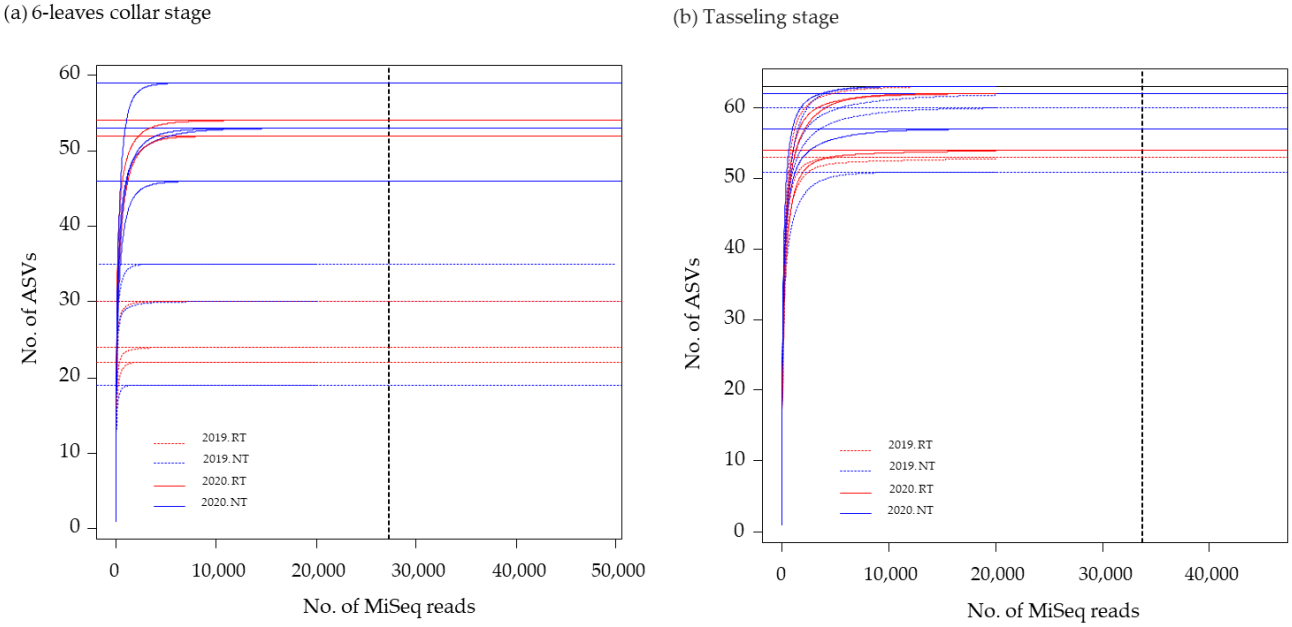


**Figure 2.** Depths of Illumina MiSeq amplicon sequencing in the maize roots by rarefaction analysis. The vertical dashed line was placed at 27,284 and 33,793 reads at the (**a**) 6-leaves collar (2019 and 2020: 42 DAS) and (**b**) tasseling stages (2019: 66 DAS, 2020: 70 DAS) in 2019 and 2020, respectively. The Amplicon Sequence Variant (ASV) of arbuscular mycorrhizal fungi (AMF) were defined at a cut-off level of 27,284 and 33,793 reads at the 6-leaves collar (2019 and 2020: 42 DAS) and tasseling stages (2019: 66 DAS, 2020: 70 DAS) in 2019 and 2020, respectively. RT = Rotary Tillage, NT = No Tillage.

### *3.3. Growth and P Uptake of Maize in Pot Inoculation Experiment*

The effects of different fungal species on maize growth and P uptake are shown in Table 1. The aboveground biomass in the maize tended to be highest in *A. morrowiae* AP-5 and lowest in *D. cerradensis* TK-1. The P concentrations in the maize tended to be highest in *D. cerradensis* TK-1 and lowest in *A. longula* F-1. The P uptake in the maize was highest in *C. pellucida* SZ-3 and lowest in *A. longula* F-1.

**Table 1.** Effect of the inoculation of different arbuscular mycorrhizal fungi (AMF) on the growth and phosphorus (P) uptake of maize in the pot experiment.

| Treatments | AMF Colonization (%) | | Aboveground Biomass (g/Plant) | | Aboveground P Concentration (mg P/g) | | Aboveground P Uptake (mg P/Plant) | |
|---|---|---|---|---|---|---|---|---|
| Control | - | | 0.75 ± 0.03 | | 0.68 ± 0.00 | | 0.60 ± 0.05 | |
| *A. morrowiae* AP-5 | 4.97 ± 3.27 [1] | a [2] | 0.99 ± 0.11 | n.s. [3] | 1.23 ± 0.24 | n.s. | 1.20 ± 0.22 | * |
| *A. longula* F-1 | 0.15 ± 0.15 | a | 0.87 ± 0.04 | n.s. | 0.88 ± 0.13 | n.s. | 0.76 ± 0.13 | n.s. |
| *D. cerradensis* TK-1 | 2.88 ± 1.57 | a | 0.75 ± 0.07 | n.s. | 1.54 ± 0.18 | ** | 1.14 ± 0.08 | n.s. |
| *C. Pellucida* SZ-3 | 5.52 ± 2.34 | a | 0.89 ± 0.07 | n.s. | 1.52 ± 0.05 | ** | 1.35 ± 0.12 | ** |

[1] Values show means of 3 replicates ± standard error. [2] Different letters show a significant difference according to Tukey's test ($p < 0.05$). [3] "n.s.", "*", and "**" mean no significance, 5%, and 1% according to Dunnett test, respectively.

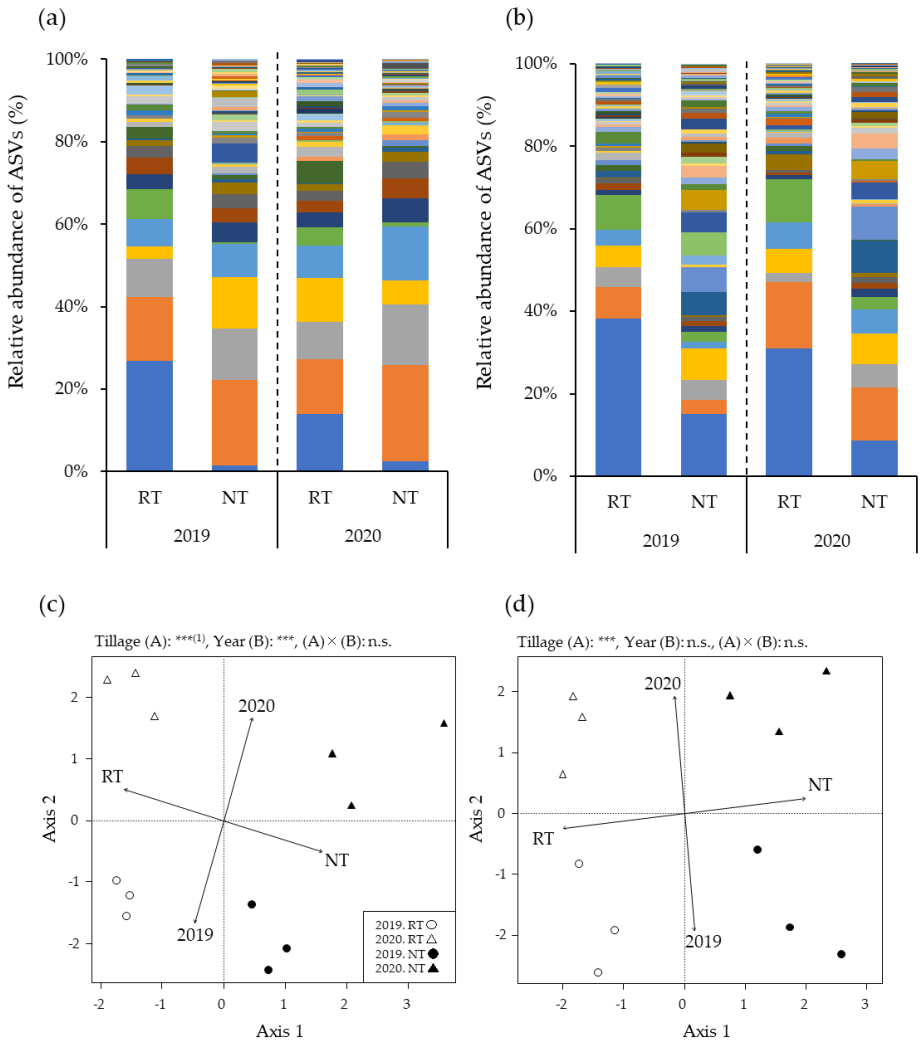


**Figure 3.** Effects of the different tillage practice on the arbuscular mycorrhizal fungal (AMF) communities colonizing maize roots at the 6-leaves collar (2019 and 2020: 42 DAS) and tasseling stages (2019: 66 DAS, 2020: 70 DAS) in 2019 and 2020. (**a**,**b**) Relative abundance of AMF ASVs in the tillage practice, (**c**,**d**) redundancy analysis (RDA) of the effects of tillage practice on the AMF communities in the roots of maize. [1] n.s. indicates no significance and *** indicates a significant difference at the 0.1% level according to permutational multivariate analysis of variance, respectively. RT = rotary tillage, NT = no-tillage.

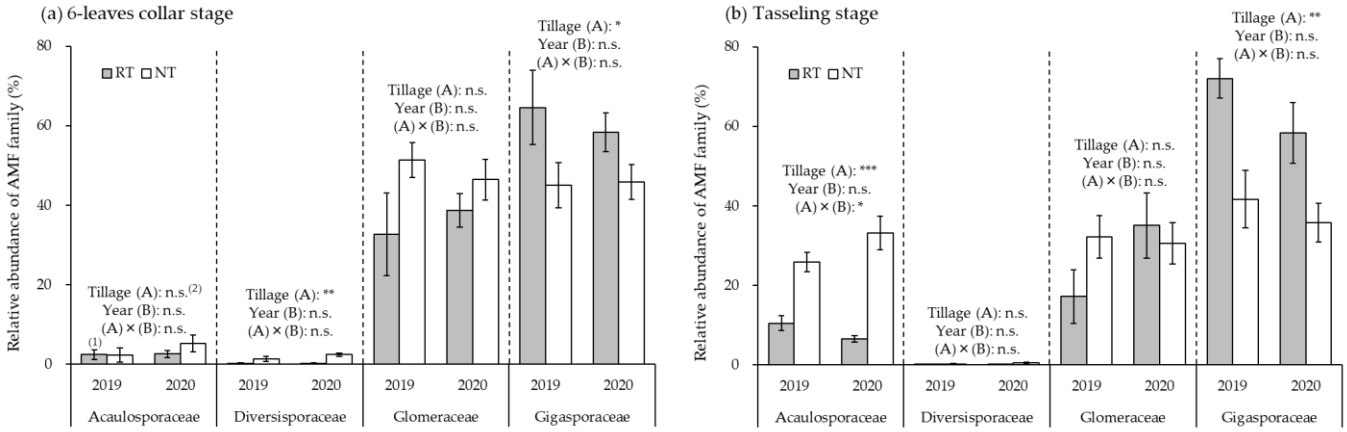


**Figure 4.** Effect of the different tillage practices on the relative abundance of arbuscular mycorrhizal fungal (AMF) families in the roots of maize plants at the (**a**) 6-leaves collar (2019 and 2020: 42 DAS) and (**b**) tasseling stages (2019: 66 DAS, 2020: 70 DAS) in 2019 and 2020. (1) Error bars show the standard error of the mean; (2) n.s. indicates no significance and *, **, and *** indicate significant differences at the 5%, 1%, and 0.1% levels according to two-way analysis of variance (two-way ANOVA), respectively. RT = rotary tillage, NT = no-tillage.

## 4. Discussion

It is generally believed that tillage disrupts the mycelial network of AMFs and reduces AMF colonization [46–48]. However, there are reports of rapid colonization in wheat roots caused by tillage [49] and reports of tillage not affecting AMF colonization [50,51]. Thus, the impact of tillage on AMF colonization varies. In this study, AMF colonization did not differ in the presence or absence of tillage and was not increased by the no-tillage treatment (Figure 1c). Holden [52] suggests that the residual state of the root system is a factor governing why tillage does not suppress AMF colonization. He found that a dense root system in the soil allows rapid mycorrhizal formation, even after the soil is physically destroyed by tillage. In this study, maize roots from the previous year were maintained after tillage, with a dense root system in the soil retained until the following year, which may have contributed to the fact that tillage did not affect AMF colonization. However, this study did not examine the number of roots in the soil; thus, this should be investigated in the future.

Recently, it has been reported that no-tillage and reduced tillage not only reduce production costs and soil disturbance, but also increase maize growth and yield [53–56]. In contrast, there have been many reports of increased maize yield with tillage practice compared to no-tillage [24,57,58], and our study had similar results to these reports (Figure 1d). In addition, tillage in this study also increased P uptake in maize (Figure 1b). In this experiment, the soil had low levels of available P (Table S1). Furthermore, in the absence of P fertilizer application, the growth of maize was constrained by the insufficiency of P, consequently rendering it vulnerable to variations in P uptake by the crop. These results suggest that the increased P uptake is one of the reasons for the higher growth and higher maize yield in the rotary tillage plots. Plant P uptake is increased by significant root elongation [59,60], and in addition, has been reported to be enhanced by AMF colonization in many cases [61–63]. Furthermore, it has been shown that the amount of P uptake of AMF varies with species [64,65]. As mentioned earlier, rotary tillage was not observed to have an effect on AMF colonization in this study, whereas differences were observed in the composition of the AMF communities colonizing the rotary tillage and no-tillage plots (Figures 1c and 3). In previous cases, it has been reported that the composition of AMF communities in soils and roots is strongly influenced by different tillage practices [23–26]. Specifically, in this study, rotary tillage increased the dominance of *Gigasporaceae*, and no-tillage increased the dominance of *Acaulosporaceae*. *Glomeraceae* was also prevalent in both tillage practices, however, the *Diversisporaceae* was scarce regardless of the tillage practice

(Figure 4). Usually, AMF belonging to *Gigasporaceae* do not rely on external mycelium to infect roots, but only on spores [66]. It has also been suggested that *Gigaspora* sp. have larger spores and can tolerate soil disturbances such as tillage [67,68]. These factors may have increased the dominance of *Gigasporaceae* in the rotary tillage plots in this study. In contrast, Jasper et al. [69] and Li et al. [70] reported that the mycelium of *Acaulospora* sp. loses its ability to colonize when the soil is disturbed. *Acaulosporaceae* have also been shown to have slow colonization [71]. Furthermore, this AMF often has low spore viability and prolonged dormancy [66,72]. These results suggest that the AMF of *Acaulosporaceae* is very vulnerable to soil disturbance, and that rotary tillage reduced root colonization in this study, resulting in higher presence in the no-tillage plots.

Additionally, several studies have frequently demonstrated variations in the composition of AMF communities in both soil and roots across diverse ecosystems [73–75]. Tillage practices can exert a certain impact on the AMF communities in soil. The variations in the soil AMF communities in the tillage systems, as well as the variations in the AMF communities in the maize roots, can potentially contribute to the growth performance of maize in this field study. However, we did not investigate the variation in the soil AMF communities in this tillage system. Further research would be required to gain a more comprehensive understanding of this aspect to fully capture the impact of tillage practices on maize growth through the composition of AMF communities in agricultural soil.

Previous studies have used a partial region of small subunit (SSU) [29,31,76–78] and large subunit (LSU) [79–84] rRNA genes as the PCR amplification target for AMF community analysis. In this study, we used nested PCR (1st primer pair: NS31/AM1, 2nd primer pair: AMV4.5NF/AMDGR) and the differences in the species communities of AMF colonizing maize roots at the early growth stage were significantly distinct between no-tilled and tilled plots (Figures 2 and 3). Higo et al. [31] and Suzuki et al. [84] demonstrated that the use of nested PCR (1st primer pair: NS31/AM1 or AML1/AML2, 2nd primer pair: AMV4.5NF/AMDGR) for AMF community analysis also showed more than a 90% rate of AMF detection and showed the highest frequency of AMF sequences in the amplicons, which corresponds to the results of our study. Thus, the coverage of AMF taxa in our results is considered enough to describe the species communities of AMF in the maize roots. However, Suzuki et al. [84] indicated that selecting several primer pairs should be considered for the analysis of AMF taxa communities; future work will be needed to describe more general conclusions regarding the molecular protocol on AMF taxa communities most suitable for next-generation sequencing analysis.

In our field experiment, the presence of *Gigasporaceae* increased in the rotary tillage plots, as along with P uptake and maize growth. In contrast, in the no-tillage plots, the existence of *Acaulosporaceae* increased, and maize P uptake and growth were correspondingly less than those in the tillage plots (Figures 1b and 4). Supposing that differences in AMF species communities due to the presence or absence of tillage cause changes in maize P uptake and growth, if only AMF of both families infected maize, the host maize would show differences in P uptake and growth. Therefore, in the second experiment, we investigated the effect of different AMF species on the P uptake and growth of maize. The results showed that P concentrations in maize were higher following inoculation with *D. cerradensis* TK-1 and *C. pellucida* SZ-3 than with control (Table 1). However, inoculation with *A. morrowiae* AP-5 and *A. longula* F-1 did not change P concentrations from the control. This suggests that *D. cerradensis* TK-1 and *C. pellucida* SZ-3 were more effective than *A. morrowiae* AP-5 and *A. longula* F-1 in promoting P uptake in maize. Functional variation (root and soil colonization, plant growth benefit) within AMF species has been well documented [12,17,85–87]. Indeed, some AMF species have been shown to have high growth-promoting effects on plants. Such differences in plant growth-promoting and nutrient acquisition capacity among AMF species have been reported [12,17,85–87]. Previous studies have also shown the effect of AMF on P or N accumulation in plant biomass for various plant species, including maize [88], tomato [78,89], and leek [90]. Lendenmann

et al. [91] found that differences in P acquisition between *R. intraradices* and *Cl. claroideum* were due to differences in the density of mycelial length and P transport.

In this study, the AMF colonization in the pot experiments was very low, ranging from 0.15% to 5.52%. Previous studies have shown increased plant P uptake even with low AMF colonization [92]. Säle et al. [17] reported cases of growth-promoting effects such as increased biomass in several AMF species that showed low AMF colonization. However, AMF colonization and growth-promoting effects on plants are inconsistent and diverse, with many cases showing no improvement in plant growth due to high AMF colonization [16,86,93]. There are also examples that the AMF group of *Gigaspora* can retain P in the mycelium before transport to the host plant [94,95]. Even if AMF-inoculated plants do not show high AMF colonization, P uptake via the mycorrhizal pathway is possible, and can contribute to plant nutrition by AMF [96]. Thus, it does not necessarily mean that the effect of AMF was not observed in this study.

In addition, several factors may have induced a lower rate of AMF colonization. It has been pointed out that AMF colonization by AMF inoculum depends on AMF isolates, plant species, soil, and environmental factors [97], and these factors may also have influenced AMF colonization in this study. In other words, the incompatibility of the soil mixture (the mix of andosol and sand) and the maize of the host plant may have been a factor in the very low AMF colonization. Furthermore, the AMF inoculum used in the pot experiments of this study was obtained from the NARO (National Agriculture and Food Research Organization) GeneBank, and no indigenous AMF species were used. Therefore, further studies are needed to isolate and culture indigenous AMF and conduct the next study under conditions with high AMF colonization. In addition, it has been reported that external hyphae spread extensively in *Gigasporaceae*, whereas those in *Acaulosporaceae* do not spread as widely [98–100], and this difference may have affected P uptake from the soil. Traditionally, it is believed that tillage increases crop growth and yield, mainly due to the improvement of soil hardness and the associated promotion of root elongation [4]. However, the results of this experiment suggest that tillage practice also changes the species communities of AMF colonizing the roots, which may also be a factor causing changes in crop growth. To clarify this new hypothesis, it is necessary to compare the actual P uptake from the soil within *Gigaspora* members, which was dominant in the rotary tillage plots, and that of *Acaulospora* members, which was dominant in the no-tillage plots.

In this study, a single inoculation with four AMF strains was utilized to analyze the growth and P uptake of maize in the pot experiment (Table 1). Previous research has shown that dual or mixed inoculation of AMF inoculants can induce a more significant enhancement of plant growth compared with single inoculation [87,101]. However, Van Geel et al. [102] indicated that inoculation with a single AMF species is more effective than inoculation with a mixture of diverse AMF taxa in stable and controlled environments. Furthermore, the potential benefits of field inoculation with AMF inoculants were investigated, as well as in controlled studies such as pot experiments. However, several field studies have demonstrated that the effective establishment of AMF inoculants has yielded inconsistent results [103–105]. Some studies suggest successful field establishment and improved crop yield [106,107], while others indicate a poor establishment of the inoculated AMF species [108,109]. In general, the single or mixed inoculation of AMF has been found to be unsuccessful in fields with highly diverse indigenous AMF communities [107,110]. However, a high density of the introduced AMF was observed to enhance the success of the establishment [111]. The selection effects on introduced AMF taxa are typically temporal, as evidenced in various field trials where the introduced AMF have been suppressed or eliminated from plant roots after a prolonged period of time [112–114]. These effects may also vary spatiotemporally as a result of the adaptation of the indigenous AMF community to local conditions. Therefore, Basiru and Hijri [110] have proposed that the impacts of exogenous single or mixed AMF inoculants on the indigenous AMF community may be minimal in ecosystems with highly diverse and functional indigenous microbial communities, but there remains a risk of failed inoculation attempts. This study was based on only

single inoculation in each different AMF strain as a pot experiment and did not consider the effects of the indigenous AMF community detected in our research field. Future investigations should incorporate the functional role of indigenous AMF communities to more fully examine the growth-promoting effects of maize plants in a controlled experiment.

## 5. Conclusions

The precise function of AMF species or community levels in agricultural and natural ecosystems remains elusive. In this experiment, the AMF communities in the tillage practices were investigated in a single region and soil type, and only for maize plants. However, it has been reported that different AMF communities colonizing roots and in soil vary among different crop identities [115,116], soil characteristics [117,118], and agricultural land use [119,120]. Differences in the AMF community compositions may elicit divergent growth responses in crop plants [85,121]. Therefore, further investigation into these differences will be essential to fully understand the role of AMF communities in agroecosystems. Additionally, our study yielded two primary novel findings. Firstly, we demonstrated that identifying certain AMF taxa in the roots can contribute to maize growth in the 2-year field-based tillage study through amplicon sequencing analysis. Secondly, we confirmed whether the inoculation of similar AMF strains, as analyzed in the field study of tillage practices on maize roots, elicits growth-promoting effects for maize growth in the controlled pot experiment corresponding to the results of the field experiment. In other words, we aimed to ascertain whether the growth-promoting effects observed in the field experiment can be replicated through the inoculation of comparable AMF strains belonging to the identified AMF taxa in the controlled pot experiment. From the second experiment, we confirmed that inoculation with similar AMF strains, which were analyzed in the maize roots in the field, elicited growth-promoting effects for maize growth in the controlled pot experiment, corresponding relatively to the results of our field study. By combining these findings, it will be imperative to proceed to the next phase of future research, which will involve inoculating indigenous AMF communities to confirm the consistency of results obtained in field tests with those obtained in the controlled pot study. Overall, further investigation into the practical features and variations of AMF communities in the roots and soil will provide valuable knowledge on the functional role of AMF and maize performance in tillage systems.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/applmicrobiol3020025/s1, Figure S1: Accumulated precipitation and average temperature during the growing season; Figure S2: Cultivation system in experiment 1; Table S1: Soil chemical properties in the field experiment; Table S2: Soil chemical properties in the pot experiment.

**Author Contributions:** Conceptualization, Y.T. and M.H.; methodology, Y.T., M.H. and K.I.; formal analysis, Y.T. and M.H.; investigation, Y.T. and M.H.; data curation, Y.T. and M.H.; writing—original draft preparation, Y.T.; writing—review and editing, Y.T., M.H. and K.I. All authors have read and agreed to the published version of the manuscript.

**Funding:** This study was financially supported by JSPS Grants-in-Aid for Scientific Research (C) Grant Number JP19K06005 and JP22K05603.

**Data Availability Statement:** Not applicable.

**Conflicts of Interest:** The authors declare no conflict of interest.

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