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Inference of allelopathy and autotoxicity to varietal resistance of asparagus (*Asparagus officinalis* L.)

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Abstract

The influence of varietal resistance to allelopathy and autotoxicity for growth, nutrient uptake and allelochemical characteristics were assessed under laboratory conditions. Two asparagus varieties; UC157 (U) and Gijnlim (G) from Europe and USA, respectively were cultivated in different rotational patterns in a continuous replanting system. Rotational combinations consisted of: UG, GU, GG, UU and GUG, GGU, GUU, UGU, UUG, UGG, GGG, UUU for the first and second replantings, respectively. The control planting was the first planting of each variety. The effects of potential allelochemicals on the growth and nutrient uptake for the two varieties in replant culture were investigated. Their contents were determined by high-performance liquid chromatography, and their phytotoxicity was assessed in agar medium during the replanting time. Identified allelochemicals were oxalic, succinic and tartaric acids. UC157 produced higher concentrations of total allelochemicals compared to Gijnlim. Root and shoot growth were inhibited by up to 77 and 73 %, respectively in the second replanting of UC157 (UUU) compared to the control (first planting of UC157). Growth inhibition was correlated with nutrient uptake inhibition; phosphorus (P) uptake was the most inhibited nutrient among nitrogen (N), potassium (K), calcium (Ca), and magnesium (Mg). The two varieties exhibited significant ($p< 0.05$) differences in growth, nutrient uptake and allelochemical characteristics. UC157 showed more varietal allelopathic and autotoxic activity than Gijnlim after two subsequent replanting. In Summary, selection of suitable asparagus varieties and varietal rotations are necessary in replantings in order to minimize the negative impacts of varietal allelopathy and autotoxicity.

Keywords: allelochemical; growth inhibition; nutrient uptake; rotational cultivation; replanting.
Abbreviations: ECD_Electro Conductivity Detector; HPLC_High Performance Liquid Chromatography; PCA_Principle component analysis.

Introduction

Asparagus (*Asparagus officinalis* L.) is a high-value perennial vegetable crop cultivated worldwide. Many studies have reported on yield reductions following its replanting in old asparagus fields (Han et al., 2008; Young and Chou, 1985; Schofield, 1991; Motoki et al., 2006). Successive culture of the same crop on the same land for years causes soil sickness or replanting injuries (Yeasmin et al., 2013). There are many reasons for the replanting problems, such as disease, insects, pathogens, microorganisms, soil physical and chemical properties, reduced number and diameter of stems, crowns and roots, and collapse of storage roots (Bais et al., 2006). Potential reasons for these problems include allelopathy and autotoxicity. Allelopathy refers to the effects of one plant on another caused by the release of inhibitory substances into the environment through root exudation, followed by leaching and volatilization, or through the decomposition of plant residues (Batish et al., 2009). Autotoxicity is a form of intraspecific allelopathy that occurs when a species releases chemical substances that inhibit or delay the germination and growth of plants of the same species (Han et al., 2008). Additionally, the chemical interactions between varieties within the same crop species can be classified as 'varietal allelopathy' and 'varietal autotoxicity' (Wu et al., 2007). Varietal allelopathy occurs when plants of a given variety release chemical substances that inhibit or delay germination and growth of other varieties of the same crop species. On the other hand, varietal autotoxicity occurs when plants of a given variety release chemical substances that inhibit the growth of the same variety. Many researchers have confirmed allelopathic activity of chemical substances released by asparagus (Motoki et al., 2006; Lake et al., 1993; Blok and Bollen, 1993; Hazebroek et al., 1989; Yeasmin et al., 2013). Allelochemicals are considered to be a potentially important cause of the asparagus replanting problem (Blok and Bollen, 1993). Allelochemicals produced by one crop species influence the growth, productivity, and yield of subsequent crops or the same crop (Batish et al., 2007) and the growth and activity of soil fungi and bacteria (Blok and Bollen, 1993). Allelopathy and autotoxicity are closely linked to environmental stresses such as nutrient deficiency (Young, 1984). Plant allelochemicals change the soil nutrients concentration, and conversely, soil nutrients also influence the concentration of plant allelochemicals. The avoidance of

Table 1. Percent (%) inhibition in asparagus seedling growth due to autotoxicity or allelopathy for UC157 (U) and Gijnlim (G) after the first and second replantings with different rotational combinations.

			Fresh Mass		Dry Mass	
		RC	Root	Shoot	Root	Shoot
First replanting	Autotoxicity	UU	41±1.3 a	36±0.9 a	40±1.9 a	35±3.2 a
		GG	21±0.8 b	17±0.5 b	26±5.6 b	19±2.4 b
First replanting	Allelopathy	UG	16±3.1 c	12±1.9 c	24±1.3 b	14±1.3 b
		GU	8±2.4 c	5±0.4d c	15±7.7 c	13±1.5 c
Second replanting	Autotoxicity	UUU	77±0.2 a	61±1.4 a	73±2.0 a	70±1.5 a
		GGG	46±0.1 b	41±0.3 b	47±0.4 b	44±0.8 b
Second replanting	Allelopathy	UUG	43±0.3 b	37±0.6 b	42±1.1 b	41±0.7 b
		GUU	41±0.2 b	35±0.4 b	40±0.8 b	38±0.7 b
		UGG	37±0.4 b	33±0.7 b	37±1.8 b	34±1.1 b
		GGU	35±0.1 b	30±0.6 b	33±0.6 b	30±2.6 b
		UGU	31±0.4 b	26±0.8 b	30±0.3 b	27±2.6 b
		GUG	26±0.8 b	21±0.4 b	29±0.5 b	22±0.4 b

Note: Listed fresh mass and dry mass suggests the values are actual fresh mass (g) and dry mass (g). Inhibition (%) was calculated by using equation 1. U = UC157; G = Gijnlim; the order of the letters represents the two varieties used in the first, second (first replanting), and third (second replanting) plantings, respectively. Lettering (a, b, c) in the table refers to comparisons for the first and second replantings separately (Tukey's protected multiple-comparison test, $p< 0.05$). Data presented as mean ± SE, replication ($n = 3$).

allelopathic effects between plants, or the exploitation of beneficial interactions in a rotation or a mixed cropping system, may have direct bearing on the crop yield (Yeasmin et al., 2013). Improved yields associated with crop rotation are often attributed to reduced disease incidence, maintained balance of mineral nutrients in soil, and are also believed to be due to the successful management of natural communities including soil microorganisms (Cook, 1993). There is no information on the varietal allelopathic and autotoxic effects of asparagus in a continuous replanting system with different rotational patterns. Therefore, the aim of this study was firstly, to evaluate varietal resistance of asparagus to allelopathy and autotoxicity with different rotational combinations under laboratory conditions and secondly, to identify the potential allelochemicals released from asparagus root exudates in two different varieties.

Results and Discussion

Varietal resistance to allelopathy and autotoxicity

The potential of allelopathy on root and shoot growth pattern between two asparagus varieties with different rotational combinations under laboratory conditions are illustrated in Table 1. There were significant ($p< 0.05$) differences in root and shoot growth patterns between the two varieties when grown under the different rotational combinations. The second replanting showed a higher inhibition in growth than the first replanting. Root growth was more severely inhibited than shoot growth in both varieties since the roots were directly in contact with the growing media. After the first replanting, the highest and lowest inhibitions for root and shoot growth were found in the UG and GU rotations, respectively. Following the second replanting, the highest and lowest inhibitions were found in the UUG and GUG rotations, respectively. This combined result indicated that UC157 might be producing more allelochemicals than Gijnlim. This inhibited growth is likely caused by varietal and rotational differences in the susceptibility to the type and total quantity of allelochemical constituents. Inhibitory effects of allelochemicals varied with varietal differences, and these allelochemicals are responsible for the growth inhibition (Chung et al., 2001). Allelochemical compounds including amino acids, organic acids, sugars, phenolic acids, and other secondary metabolites, serve as an important medium of root-based interactions with other microorganisms including bacteria, actinimycetes, pathogens, fungi, and insects in the growing media (Walker et al., 2003). Therefore, with increased number of replantings, allelochemicals could become more concentrated and cause severe plant growth inhibition. Growth inhibition by allelochemicals would be expected to reduce the competitiveness of the affected -11olplants, therefore selection of specific varieties under different rotational combinations may increase the security of future plant performance. Table 1 illustrates the potential of autotoxicity on root and shoot growth pattern after the first and second replantings in the same rotation with each variety. In autotoxic combinations, both the UU and UUU rotations showed significantly ($p< 0.05$) higher growth inhibition when compared to the GG and GGG rotations. Increased autotoxification by asparagus root exudates due to accumulation of allelochemicals from subsequent replantings might have been responsible for growth inhibition (Young and Chou, 1985). The present results indicated that asparagus is an auto-inhibited species which significantly inhibits the growth of seedlings of its own species. Aqueous extract of living asparagus roots were strongly inhibitory to the growth of asparagus (Hazebroek et al., 1989).

Nutrient uptake inhibition

The percentage inhibition for nutrient uptake in both UC157 and Gijnlim, with different rotational combinations is presented in Fig 1. There were significant ($p< 0.05$) differences in the uptake of mineral nutrients such as N, P, K, Ca and Mg between the two varieties grown under the different rotational combinations. The percentage inhibition for total N, P, K, Ca and Mg concentration ranged from 11-55; 14- 71; 8-45; 6-41; 5-33 %, respectively. The highest percentage inhibition was found for P, followed by N, while the others varied widely in the different rotational combinations. After the first replanting, the highest and lowest inhibitions for nutrient uptake under allelopathic combinations were found in the UG and GU rotations, respectively. After the second replanting, UUG and GUG rotations showed the highest and lowest inhibitions, respectively. Similarly, in the autotoxic combinations, the UU and UUU rotations showed significantly ($p< 0.05$) greater percentage inhibition than the GG and GGG rotations. Involvement of autotoxins from root exudates of previous asparagus crops was evaluated for the replanting problem (Young and Chou, 1985). Therefore, varying the varietal rotational combination could reduce the accumulation and concentration of the same autotoxins or allelochemicals. Wacker et al. (1990) noted several

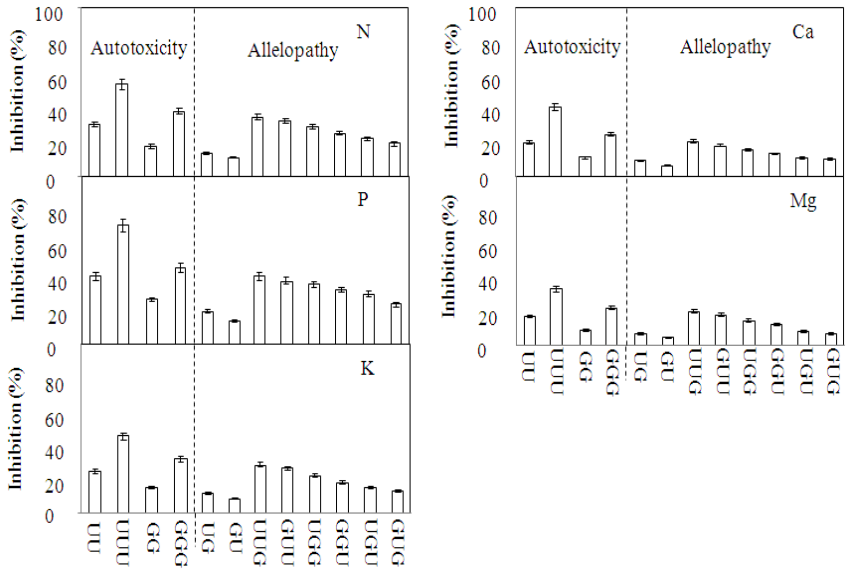

Fig 1. Percent (%) inhibition in asparagus seedling nutrient uptake due to autotoxicity or allelopathy after the first and second replantings with different rotational combinations. Listed nutrient uptake suggests the values are actual concentrations (mg g^{-1}) of N, P, K, Ca and Mg in asparagus seedlings. Inhibition (%) was calculated by using equation 1. The order of the letters (U and G) represents the varieties used in the first, second (first replanting), and third (second replanting) plantings, respectively. Values in each combination are differ significantly (Turkey's protected multiple-comparison test, $p < 0.05$). Data presented as mean ± SE, replication ($n = 3$).

allelochemicals isolated and characterized from asparagus root tissue, including ferulic acids which could inhibit phosphorus uptake in plant roots (McClure et al., 1978). Furthermore, plants have evolved special mechanisms to deal with nutrient deficiencies (Handreck, 1997), these could include mechanisms for the release of allelochemicals. Allelochemicals like benzoic, vanollic, cinamic and ferulic acids have been shown to inhibit P uptake; likewise, benzoic and trans-cinnamic acids reduce root and shoot dry biomass and lower the amounts of P, K, Mg, Mn (Baziramakenga et al., 2005). However, the effect of previously grown plants on subsequent asparagus P content correlates strongly with the growth of asparagus (Yeasmin et al., 2013). In contrast, the percentage inhibition of K, Ca and Mg concentration in tissue followed the same tendency as those of N and P. But it might be necessary to determine the particular reason for that inhibition especially for P under different rotational combinations with asparagus varieties.

Identification of potential allelochemicals

Table 2 illustrates the concentration of organic acids from root exudates in both UC157 and Gijnlim, after two replantings with different rotational combinations. There were significant (p<0.05) differences among the production of allelochemicals between the two varieties under different rotational combinations. On average, UC157 produced more oxalic, succinic and tartaric acids than Gijnlim; although both varieties had the tendency to produce the same allelochemicals. After the first replanting, the highest concentrations of oxalic, succinic and tartaric acids were found in the UG rotation and the lowest concentrations in the GU rotation. After the second replanting, the highest and lowest concentrations of those allelochemicals were found in the rotational combination UUG and GUG, respectively. These results reveal that allelochemicals produced by asparagus roots and released into the growing medium could be responsible for the replanting problem. For allelopathy to be an ecologically relevant mechanism influencing the growth of plants, allelochemicals must accumulate and persist at phytotoxic levels and come in contact with the target plant (Inderjit, 2005). Quantitative and qualitative differences in allelochemicals would be likely to lead to differential allelopathic and autotoxic effects which might be responsible for variations in growth and nutrient uptake. In autotoxic combinations, there were significant ($p < 0.05$) differences in the concentrations of oxalic, succinic and tartaric acids between the two varieties and their rotational combinations (Table 2). Both the UU and UUU rotations produced higher concentrations of these acids as compared to the GG and GGG rotations, respectively. The greatest growth and nutrient uptake inhibitions were also found in the UU and UUU rotational combinations. This suggests that inhibited growth and nutrient uptake could be caused by differences in the allelochemical substances released from asparagus root exudates. Autotoxicity of root exudates is an important feature for understanding replanting problems in agroecosystems as it represents one of the largest direct inputs of allelochemicals into the rhizosphere environment with potent biological activity and great variation in chemical components (Inderjit, 1996). Thus, in this study, results showed that organic compounds are the major allelochemicals causing varietal allelopathy or autotoxicity, which might be responsible for growth and nutrient uptake inhibitions even at a low concentration.

Overall physico-chemical characteristic variability

Principle component analysis (PCA) was used to differentiate the variation in different rotational combinations on the inhibitory effect of allelochemicals on the growth and nutrient uptake after the first and second replanting (Fig 2a.) and variability among physiochemical characteristics in Fig 2b. Fig 2a. shows the correlation within the same replanting treatments among different rotational combinations. GU and UG rotational combinations showed a strong positive

Table 2. Effects of the identified organic acids at different concentrations (mg L^{-1}) on growth and nutrient uptake of asparagus after the first and second replantings.

		RC	Oxalic acid	Succinic acid	Tartaric acid
			(mgL^{-1})		
First planting	Control	U	1.1±0.6 c	1.8±0.9 c	1.2±0.3 c
First planting	Control	G	0.2±0.1 c	1.3±0.5 c	0.7±0.1 c
First replanting	Autotoxicity	UU	5.3±0.8 a	11.4±1.4 a	7.5±1.4 a
		GG	4.0±0.0 a	8.5±0.1 a	5.4±1.0 a
First replanting	Allelopathy	UG	2.9±0.1 b	7.4±0.4 a	4.6±0.6 a
		GU	0.6±0.2 c	2.2±0.3 b	1.3±0.3 b
Second replanting	Autotoxicity	UUU	7.6±1.7 a	17.1±0.1 a	11.1±2.2 a
		GGG	5.7±0.2 a	13.8±0.8 a	9.3±0.1 a
Second replanting	Allelopathy	UUG	4.5±0.1 a	10.2±0.4 a	8.2±0.8 b
		GUU	3.5±0.3 a	8.0±0.2 a	6.7±0.6 b
		UGG	2.9±0.3 b	6.6±0.8 a	4.6±0.3 b
		GGU	2.2±0.2 b	5.3±0.5 b	4.4±0.5 b
		UGU	1.8±0.4 b	4.2±0.4 b	2.9±0.9 c
		GUG	1.3±0.1 c	2.5±0.1 c	1.8±0.5 c

Note: U = UC157; G = Gijnlim; the order of the letters represents the two varieties used in the first, second (first replanting), and third (second replanting) plantings, respectively. Lettering (a, b, c) in the table refers to comparisons for the first and second replantings separately (Tukey's protected multiple-comparison test, $P < 0.05$). Data presented as mean ± SE, replication ($n = 3$).

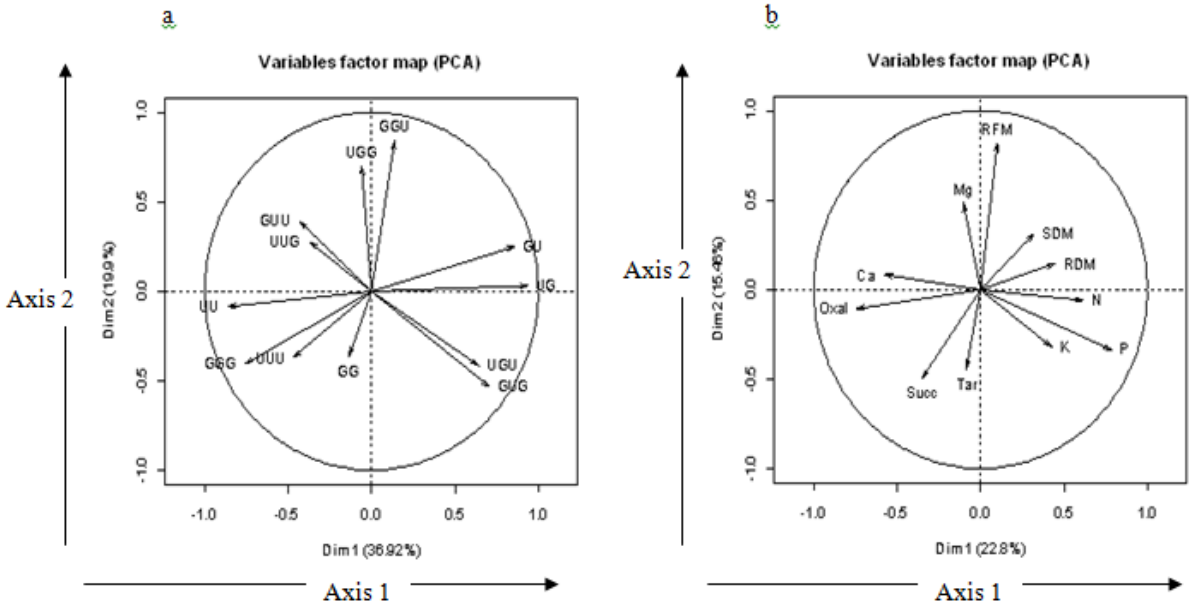

Fig 2. (a) Variable factor map (PCA) for total variation in different rotational combinations after the first and second replantings. Dim 1 and Dim 2 explain 36.92 and 19.9 % of the variation observed, respectively. U = UC157; G = Gijnlim; the order of the letters represents the varieties used in the first, second (first replanting), and third (second replanting) plantings, respectively. (b) Variable factor map (PCA) for total variation in the physiochemical characteristics throughout all replantings. Dim 1 and Dim 2 explain 22.8 and 15.45 % of the variation observed, respectively. Here, RFM = root fresh mass, RDM = root dry mass, SDM = shoot dry mass, Oxal = oxalic acid, Succ = succinic acid and Tar = Tartatic acid.

correlation, while UU, GGG and UUU rotational combinations displayed a negative correlation. Rotational combinations with same cultivar showed very high factor loading, and are denoted by axis 1 in this analysis. Axis 2 denotes the various rotational combinations with different cultivar. Fig 2b. shows the strong positive correlation among dry mass of root, N, and P suggested that N might have been regulated the dry mass and P nutrient, although negative correlation observed with oxalic, succinic and tartaric acids. Identified allelochemicals showed very high factor loading, and are denoted by axis 1 in this analysis. Axis 2 denotes the various physicochemical characteristics monitored during the replanting period. This result indicated that with an increased allelochemical concentration, growth and nutrient uptake could be decreased. This decline could have resulted from allelochemical substances released from asparagus root exudates. This reconfirms the significant inhibitory effect of allelochemicals in all replanting stages as earlier described. There is now ample evidence that root exudates produces sufficient quantities of allelochemical substances to inhibit growth and nutrient uptake (Yeasmin et al., 2013). In this study, results reveal that the rotational effect, allows asparagus seedling roots to exude varied amounts of organic acids into the growth medium and could be responsible for variations in asparagus varieties growth and nutrient uptake.

Materials and methods

Planting materials

The seeds of two asparagus varieties; UC157 and Gijnlim of USA and European origin, respectively, were procured from

a local commercial seed company (Pioneer Ecoscience Co. Ltd. Tokyo, Japan).

Assessment of varietal allelopathy and autotoxicity

A replant culture system was employed to identify growth inhibitory activity of asparagus. The plant boxes (65 × 65 × 100 mm, Magenta, New Milford, CT, USA) were filled with 250 ml autoclaved agar (Nacalai Tesque, Inc., Kyoto, Japan) medium in a clean bench (M-377, Sanyo, Osaka, Japan). After cooling the autoclaved agar 0.75% (w/v) (gelling temperature 30-31^{o} C) to 40 ^{o} C, it was poured into the plant box and, kept on ice. After gelatinizing the agar, a total of 12 seeds of UC157 and Gijnlim were separately sown in each plant box. Prior to sowing, asparagus seeds were covered with a double layer of gauze and surface-sterilized in 70% ethanol and then rinsed in deionized water several times. Sterile culture techniques were adopted to rule out the possibility of interference by microorganisms in the culture medium. The plant boxes were wrapped with cling film between the cap and upper part of the box to prevent drying and also covered with aluminum foil to darken the roots. They were incubated at: 25 ℃; 12-h light/12-h dark; relative humidity 80% and 200 µmol m^{-2} s^{-1} intensity of light in a growth chamber (MLR-351H; Sanyo, Tokyo, Japan) for 56 days. First planting of each variety served as the control. After 56 days, seedlings were harvested and seeds of both UC157 and Gijnlim were then replanted in the same agar (the agar media that was used for first planting) for the first replanting (second planting) and left to grow in the growth chamber (conditions are same as above) for another 56 days. The above procedures were done in the clean bench to reduce contaminations. The third (second replanting) planting also followed the same procedures as above. At the end of each planting, 12 seedlings average values (fresh or dry mass of the roots or shoots) were calculated, termed as a one seedling value (fresh or dry mass of the roots or shoots) for each treatment. All treatments were replicated three times.

Inhibition, expressed as a percentage, was calculated using the following equation:

$$\text{Inhibition (\%)} = (1 - Xt/Xc) \times 100 \qquad (1)$$

Where Xc denotes the fresh or dry mass of the roots or shoots of the control and Xt represents the mean values of the corresponding fresh or dry mass in the second (first replanting) and third (second replanting) plantings. The above equation was used to compare the performance of the two varieties; UC157 (U) and Gijnlim (G) in the following rotational combination patterns for varietal allelopathy: UG, GU (first replanting) and UGU, UUG, UGG, GUG, GGU, GUU (second replanting) and autotoxicity: UU, GG (first replanting) UUU, GGG (second replanting), respectively.

Measurements of plant growth and nutrient uptake

After harvesting at the end of each planting, all seedlings were carefully separated into roots and shoots, thoroughly cleaned, blotted dry between absorbing paper and their fresh mass measured. Root and shoot dry masses were measured after oven drying at 70℃ for 72h. To determine nutrient uptake, all dried root and shoot parts were combined and ground to a fine powder using a stainless ball mill. Total nutrients N, P, K, Ca and Mg were analyzed using standard procedures. Total N content was determined by the dry combustion method with an automated C-N coder (Model MT 700; Yonaco, Tokyo, Japan), total major mineral nutrients K, Ca and Mg were determined after digestion with a H_2O_2-H_2SO_4 mixture. Total P in the digested mixture was determined calorimetrically with a spectrophotometer (Model U-2001, Hitachi Co., Tokyo, Japan) using the phosphomolybdate blue method (Murphy and Riley, 1962). The total amounts of K, Ca, and Mg were determined with an atomic absorption spectrophotometer (Model Z-8100, polarized Zeeman; Hitachi Co., Tokyo, Japan). Inhibition, expressed as a percentage, for nutrient uptake was calculated by using equation 1.

Identification of potential allelochemicals

The separation and identification procedures of selected allelochemicals were conducted according to Fujii et al. (1991) with some modifications. Three standard chemicals including oxalic acid, succinic acid, tartaric acid at concentrations of 0, 50, 100, 150, 200 and 250 mgL^{-1} and asparagus root exudate samples were injected in 20 µl quantities and subjected to HPLC (ELITE LaCrom, Hitachi Co., Tokyo, Japan, column oven L-2350) analysis. Concentrations in the sample were calculated by comparing peak areas of samples with those of the standards. Conditions of HPLC were as follows: ODS - RS pack DC- 613, guard cartridge column (6.0 mm LD X 15mm), temperature in column: 40°C, equipped with ECD (Electro Conductivity Detector) and eluted with 0.1 M phosphate buffer. This experiment was conducted with three replications.

Statistical analysis

Experimental data presented are the means of three replicates. Statistical analyses were executed using Stat View software. The percentage data was $\log_e$-transformed before analysis where necessary to equalize variances between treatments (Yeasmin et al., 2013). Tukey's protected multiple-comparison test (at $P < 0.05$) was used to compare the percentage of inhibition in root and shoot growth. Principle component analysis (PCA) was performed using XLSTAT 2011 to clarify total data variability with respect to co-relationships between growth, nutrient uptake, and allelochemical characteristics after the first and second replantings. Additionally, each rotational combination was treated as categorical data, converted to dummy variables and PCA performed along with other variables. Due to a very low cumulative contribution ratio, some dummy variables were omitted.

Conclusion

This study provided additional evidence of asparagus varietal allelopathy and autotoxicity in different rotational combinations under laboratory conditions. The varying degree of inhibition with differential responses to the allelopathic and autotoxic compatibility may be valuable in predicting the potential growth and nutrient uptake inhibitions of subsequent asparagus cultivation. Therefore, we are currently taking steps to explore the specific causes of these problems and how to improve growth and nutrient uptake especially for P under different rotational combinations with asparagus varieties.

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