Revista Mexicana de Ciencias Agrícolas

DOI: https://doi.org/10.29312/remexca.v14i5.3090

Article

Allelopathic activity of alfalfa root exudates in *Arabidopsis thaliana*

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Abstract

Alfalfa (*Medicago sativa*) is native to Central Asia, this legume is sown throughout Mexico, contributes to the regeneration of soil fertility, in addition, its high content of proteins and amino acids helps reduce costs of meat and milk production. The objective of this study was to evaluate different sowing densities and the effectiveness of the extract based on alfalfa exudates on seedlings of *Arabidopsis thaliana* (L.) Heynh. Seeds of the alfalfa varieties San Miguelito and Belleza Verde were used. Sowing was established in Petri dishes at the National Technological Institute of Mexico, Roque campus in November 2018. Three sowing densities, 3, 6 and 9 kg ha^{-1}, were used. All variables were subjected to an analysis of variance and a comparison of means, with the SAS 9.0 package. The sowing density affected the root development of alfalfa, in particular the development of lateral roots and the presence of root hairs, but not the root length. The sowing density with the highest root development was with 9 kg ha^{-1}. The exudates of alfalfa presented a very marked antagonistic effect on *Arabidopsis thaliana* by reducing its growth, this effect was higher for the density of 9 kg ha^{-1}. A concentration of 50% or more of alfalfa exudates slows the growth until death of this *Arabidopsis thaliana*.

Palabras clave:

Arabidopsis thaliana, allelopathy, forage.

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Introduction

Alfalfa (*Medicago sativa*) is a Fabaceae with origin in Central Asia, currently this legume is sown practically throughout Mexico. It is the main forage crop worldwide for its contribution to the agroecological system, as well as its bromatological and nutritional characteristics (Jing-Wei *et al*., 2015). On average, one kilogram of alfalfa seed contains 480 000 seeds. If all seeds germinated and emerged, with only 5 kg ha^{-1} of seed there would be a desirable density of plants, with a distance between furrows of 50 cm (Lara and Jurado, 2014).

Alfalfa forage production in Mexico in 2016 was 33 172 950 t. Regarding the behavior by state, the highest production is shown by the state of Chihuahua with 7 426 087 t for 2016, followed by Hidalgo and Guanajuato with 4 573 392 and 3 489 919 t, respectively. In an analysis of the state of Guanajuato, production has remained relatively constant from 2012 to date and it is the main source of food for dairy cattle in the region (SIAP, 2017).

On the other hand, plants depend on the root for their nutrition, it explores the soil in search of nutrient and water uptake, by developing a taproot, the formation of adventitious roots and root hairs (Ortiz-Rojas, 2017). These roots have functions that confer the survival and ecology of the plant, in addition to being a site of high physiological activity where the synthesis, accumulation and release of compounds (flavonoids, alkaloids, phenolic acids, among others) that interfere in intra- and interspecies population patterns originate (Gilroy and Jones, 2000) . In response to biotic or abiotic stress or fluctuations, the root system secretes compounds with a wide variety of physical and chemical properties into the rhizosphere (Faure *et al*., 2009).

In this same sense, rhizodeposition is the release of carbon from the roots and its products can be categorized as exudates, secretions and fats. In the case of root exudates, they are chemical in nature and have different biological functions. In these cases, the plant species will determine the type and amount of exudates, with differences between genotypes, age and phenological status of the plant (Badri and Vivanco, 2009). For example, flavonoid-type root exudates influence some soil bacteria (Szoboszlay *et al*., 2016).

In this sense, exudates have an allelopathic effect, so allelopathy is defined as a chemical-ecological phenomenon in which a plant species produces secondary metabolites that, when released, interfere with the germination and growth of other plants in its environment, being able to affect the growth and productivity of crops, therefore, allelopathy has recently begun to be considered as an alternative for pest, disease and weed control (Rodriguez *et al*., 2014).

Among the substances with allelopathic activity are flavonoids, phenolic acids, quinones, terpenoids and alkaloids, which can be found in most plant tissues of the plant and seeds. Phenolic acids act by destroying the hormone indoleacetic acid (IAA or auxin), while terpenoids interfere with respiratory enzymes (Flores *et al*., 2015). In the case of alkaloids, these compounds inhibit the activity of DNA and RNA of some enzymes, affect protein biosynthesis and membrane permeability. Alkaloids are by nature toxic and help plants protect themselves from their enemies for their own survival (Rodriguez *et al*., 2014).

For this reason, alkaloids act as allelopathic compounds, providing the plant with a natural herbicide potential (Goyal, 2013). The study of allelopathy continues to be dynamic and very complex, the possible methods of action of allelochemical compounds in an ecosystem are shown (Oliveros-Bastidas *et al*., 2015).

The *Arabidopsis thaliana* plant belongs to the group of Brassicaceae, it is a plant that has served as a model for the study of various fundamental physiological processes, cellular and molecular, thanks to its small size, small genome and easy genetic manipulation, the understanding of the variation of the intraspecific genome has greatly improved, therefore, it has become one of the most important systems for the study of many aspects of plant physiology and model plant for genetics (Koornneef and Meinke, 2010; Kawakatsu *et al*., 2016).

The root of the DR5-gfp (green fluorescent protein) line, its root grows due to the production of new cells in the root meristem, located in the distal part of the root, region where cell division

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takes place. After cell division, elongation begins and then differentiation. The cells of the pericycle give rise to the lateral roots, the pericycle being a tissue adjacent to the vascular system that forms a new meristem. The function of lateral roots is to explore the soil and increase the nutrient absorption area.

The interaction of two hormones, auxins and cytokinins, regulates the growth of the taproot, the formation of root hairs and lateral roots. The different concentrations of auxins and cytokinins enable organ regeneration and are the basis of *in vitro* plant propagation (Ortiz-Rojas *et al*., 2017). The determination of the production or alterations of auxins in the root of *Arabidopsis thaliana* makes use of the line that carries the auxin response marker DR5 coupled with the green fluorescent protein gfp, which is a genetic encoder that is intrinsically fluorescent (Tatsuo *et al*., 2015). Therefore, the objective of this research was to evaluate different sowing densities and the effectiveness of the extract based on alfalfa exudates on seedlings of *Arabidopsis thaliana* (L.) Heynh.

Materials and methods

The project was developed at the National Technological Institute of Mexico, campus Technological Institute of Roque, in 2018 with location Celaya-Juventino Rosas Road km. 8 (20° 57’ 94.4” north latitude, 100° 82’ 50.0” west longitude and 1 760 masl) and an average temperature of 22 °C. The San Miguelito variety is landrace, it is very persistent in the field and produces good yields of forage of excellent nutritional quality, its life cycle is perennial, the largest of its uses is cut, it prefers temperate climates, it has a dormancy 9 and the optimum soil temperature to germinate is at least 12 °C, it has a life span of 3 to 4 years, its sowing season is autumn-winter, the sowing density is 60 kg of pelleted seed per hectare, the sowing depth is maximum 2 cm.

The average height per plant is 65-70 cm, the days to the first cut are 85-90 days, the days between cuts are 30-32 in spring, summer and autumn and 35-40 in winter, the minimum fertilization required in pre-sowing is 60-120-40 and the minimum annual fertilization is 80-100 kg of phosphorus ha^{-1}, its potential dry matter forage yield is 20-25 t ha^{-1}, the cutting height is 4-6 cm and it has a very good drought tolerance (Semillas Berentsen, 2019). The Belleza Verde variety is considered the best producer of green forage of high nutritional quality and long productive life. Perfectly adaptable to the intensive management of forage production in Mexico, with dormancy 9-10.

Nine to ten cuts are obtained per year, it has a moderate resistance to salinity, a very fast recovery after cutting, a life span of 3-5 years, its main qualities are resistance to diseases such as root rot, anthracnose and *Fusarium* wilt, likewise it has a high resistance to insects such as pea aphid (*Acyrthosiphum pisum*), spotted aphid (*Therioaphis maculata*) and blue aphid (*Acyrthosiphum kondoi*) (Versa, 2019).

The work was carried out in the laboratory, seeds of the varieties San Miguelito and Belleza Verde were placed in Petri dishes for germination and root growth, at three sowing densities (3, 6 and 9 kg ha^{-1}), each with three repetitions, to analyze the relationship between root proximity and exudate production. Fifty seeds were placed in Eppendorf tubes to sterilize the surface, washing them with 95% ethanol for 5 min and then rinsing with 20% commercial bleach for 5 min more and at the end with sterilized water five times.

Once the seeds were washed, they were placed on paper for 10 min to remove excess moisture. They were then placed in Petri dishes with MS (Murashige and Skoog) culture 0.1 X at pH 5.7+/-1 added with 10% bacteriological agar. Petri dishes with seeds and MS culture were kept in the plant culture growth zone (laboratory). The boxes were placed with an angle of inclination of 65° in an incubation chamber at 22 °C, with a photoperiod of sixteen hours of light and eight hours of darkness.

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During the development of the seedling, root growth was measured for twelve days. In each seedling, the length of the main root, its lateral roots and root hairs were measured, with this the difference in growth of the roots at different proximities was analyzed.

Antagonism of alfalfa on *Arabidopsis*

Seed of *Arabidopsis* line DR5-gfp was sown at a distance of 1 cm between seedlings, and seed of the alfalfa varieties San Miguelito and Belleza Verde, each with three repetitions, at a sowing density of 3, 6 and 9 kg ha^{-1}. The growth of *Arabidopsis* seedlings was monitored and when they reached an average length of 1.3 cm, they were transplanted to the Petri dishes containing the alfalfa seedling, this was about the eighth day after sowing alfalfa and fourteen days after sowing *Arabidopsis*. During the following twelve days, the growth of both seedlings was monitored. Using an inverted fluorescence microscope, auxin production in *Arabidopsis* roots was analyzed to verify whether or not the growth of these seedlings stopped.

Seedlings of both alfalfa and *Arabidopsis* were extracted from the Petri dishes. The medium used as a substrate for the seedlings was mixed in Eppendorf tubes at a ratio of 10, 25 and 50% medium and water and 95% ethanol as a solvent. Obtaining with this, a total of 38 treatments. The tubes with the different mixtures were stirred at room temperature for 30 min, then centrifuged at 3 000 rpm for 10 min.

Seeds of *Arabidopsis* of the line used in previous experiments (DR5-gfp) were sown in MS medium with a pH of 5.7, allowing the seedling to reach a length of 1.3 cm to add 5 µl of each sample, two controls were used, one water and the other ethanol. The effect of the treatments on root growth was monitored for twelve days. For the analysis of root development, antagonism of alfalfa seedlings on *Arabidopsis thaliana* L., and the effects of alfalfa extracts, a completely randomized design was used, with factorial arrangement, as factor A, two varieties, factor B, three densities and factor C, two concentrations, with three repetitions, and a Tukey mean comparison test through the statistical package SAS version 9.0.

Results

Sowing density did not significantly affect radicle length, a statistical effect significant at 5% was found for lateral root development and a statistical effect highly significant at 1% on the development of alfalfa root hairs. These differences are attributed to competition for nutrient acquisition between neighboring seedlings. In the case of the source of variation, varieties of alfalfa, these were statistically affected at 1% for root length, although the development of root hairs and lateral roots was not significant, which indicates that both genotypes behaved similarly in these last two variables. For the interaction between varieties and densities, no statistical differences were detected for these study variables. The coefficients of variation range from 2.7 to 17.8% and were considered acceptable.

As indicated above, root length was not statistically different, therefore, all means were in the same group (a), which indicates that they presented the same pattern of behavior (Table 1). However, the length varied from 3.7 cm to 4.1 cm and with a difference of 9.75% more biomass in favor of the lowest sowing density, it is important since, at a greater volume, better and greater obtaining of nutrients by the root is expected; nevertheless, the root hairs were superior with the density of 9 kg ha^{-1}, these can absorb more water and molecules that the plant needs for its development and survival and in the same way greater amount of exudates that protect the plant.

In the case of the number of root hairs and lateral roots, where two groups formed (a and b), they indicate that the higher the density of sowing, the greater the development of both root hairs and lateral roots. When using 9 kg ha^{-1}, the development of lateral roots increased almost twice as much as when working with 3 and 6 kg ha^{-1}, the same for the number of root hairs. This is attributed to competition for nutrients in a smaller space by neighboring plants. With the data obtained, it was possible to analyze that, as the number of lateral roots increases, also the

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number of root hairs is higher, although the root length was higher with the density of 9 kg ha^{-1}, thus having less area.

Table 1. Comparison of means for root length, root hairs and lateral roots in sowing densities in alfalfa (*Medicago sativa*) San Miguelito and Belleza Verde in 2018.

Sowing density (k ha^{-1})	Root length (cm)	Number of root hairs	Number of lateral roots
9	4 a	9 a	13 a
6	3.7 a	5 b	7 ab
3	4.1 a	5 b	6 b
Tukey (5%)	0.0111	0.0365	0.061

Means with equal letters are not statistically different (Tukey= 0.05).

For the source of variation 'varieties', the behavior of the root length was influenced by the genotype used, with a superior result for the variety Belleza Verde (Table 2). In the case of the development of root hairs and lateral roots, they had no significant statistical difference with α at 0.05. Therefore, it is concluded that root development behaved uniformly among the genotypes used, with Belleza Verde being superior in root length.

Table 2. Comparison of means for root length, root hairs and lateral roots in two varieties of alfalfa (*Medicago sativa*) in 2018.

Variety	Root length (cm)	Number of root hairs	Number of lateral roots
San Miguelito	3.8 b	6 a	8 a
Belleza Verde	4 a	7 a	9 a
Tukey (5%)	0.0074	0.0243	0.0407

Means with equal letters are not statistically different (Tukey= 0.05).

The length of the alfalfa root was not affected when the seedlings of *A. thaliana* L. were transplanted, compared to its control, even the seedlings with higher density were slightly higher in length (Table 3). However, in *A. thaliana* L., the antagonism produced by alfalfa on them completely stopped their growth five days after transplantation, with an average length of 1.5 cm in contrast to its control (4.9 cm), and it showed symptoms of chlorosis eight days after transplantation. The growth and development of the root of *Arabidopsis* seedling was affected to a greater degree by the alfalfa density of 9 kg ha^{-1} and the density of 3 kg ha^{-1} showed 12.65% higher root length than highest density.

Table 3. Comparison of means for root length of alfalfa (*Medicago sativa*) and *Arabidopsis* through sowing densities in 2018.

Sowing density (kg ha^{-1})	Root length alfalfa (cm)	Root length *Arabidopsis* (cm)
9	7.03 a	1.38 b
6*	6.3 ab	1.45 ab
3	5.98 b	1.58 a
Control	6.8 a	4.9 a
Tukey (5%)	0.0086	0.0056

*= commercial control for seed production. Means with equal letters are not statistically different (Tukey= 0.05).

In Figure 1, the behavior of the treatments was observed: a) just after transplantation, both alfalfa (the two varieties) and *Arabidopsis* are not yet affected by the interaction in the same Petri dish; b) alfalfa and *Arabidopsis* seedlings at twelve days after transplantation, it was clearly verified that alfalfa seedlings were not affected by the presence of *Arabidopsis*, while the latter were severely affected when compared with the control; and c) *Arabidopsis* control seedlings from the same sowing date.

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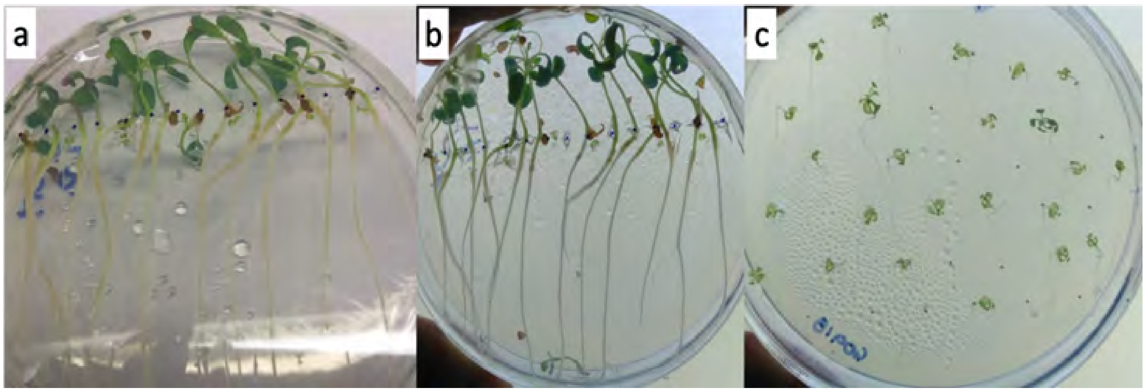
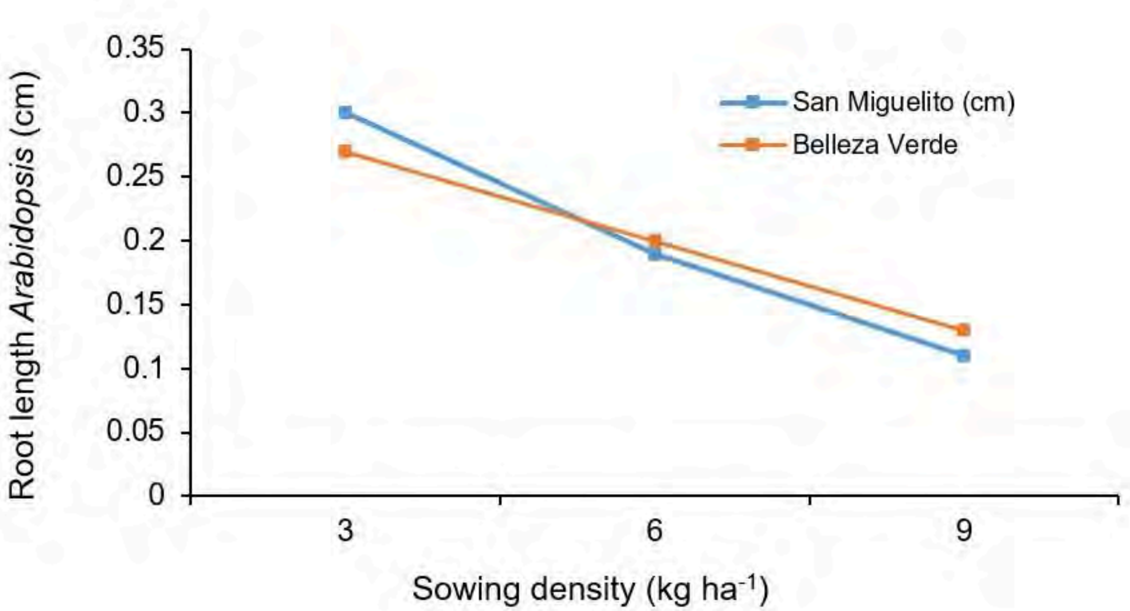
Figure 1. Root length of the two varieties of alfalfa (*Medicago sativa*) with transplantation of *Arabidopsis* a) day one after transplantation; b) day 12 after transplantation; c) control *Arabidopsis* same day of point b in 2018.



The effect of the sowing density used for the alfalfa variety San Miguelito in the medium with which the extracts were made was more effective when 9 kg ha^{-1} were used, because the average root length of *Arabidopsis* seedlings was only 0.11 cm, in contrast to the density of 3 kg ha^{-1} where seedlings grew up to 0.3 cm, which means 63.3% less root length with the highest density, attributable to the competition of plants, both alfalfa-alfalfa and alfalfa-*Arabidopsis*.

For the Belleza Verde genotype, the response corresponded to the same sowing densities, with the average root length of *A. thaliana* seedlings being 0.13 and 0.27 cm respectively, in this case, with 51.8% difference in root length between the highest and lowest sowing density. The San Miguelito variety was approximately 15% more effective for *Arabidopsis* root growth inhibition compared to Belleza Verde (Figure 2).

Figure 2. Root length of *Arabidopsis thaliana* L. at twelve days after applying the extracts of the medium + exudates of alfalfa (*Medicago sativa*) with three sowing densities in 2018.



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The most effective concentration of medium to affect the normal development of *Arabidopsis* seedlings in both cases was medium + exudate 50%, with an average root length of 0.14 and 0.08 cm in San Miguelito and Belleza Verde, respectively. In the case of the Belleza Verde variety, the concentration of 50% was 75% more effective when compared to that of 10%. The extract that the Belleza Verde variety contained was more effective in reducing the development and average growth of *Arabidopsis* root. When it had a concentration of medium + exudates at 50%, the Belleza Verde variety was 43% more effective than the San Miguelito variety, when using the concentration at 25%, again Belleza Verde was 6% more efficient. However, with a concentration of 10%, the San Miguelito variety reduced growth speed by 21% more than the Belleza Verde variety (Figure 3).

Figure 3. Root length of *Arabidopsis thaliana* L. at 12 days after applying 3 concentrations of extracts (medium + exudates of alfalfa (*Medicago sativa*) in 2018.

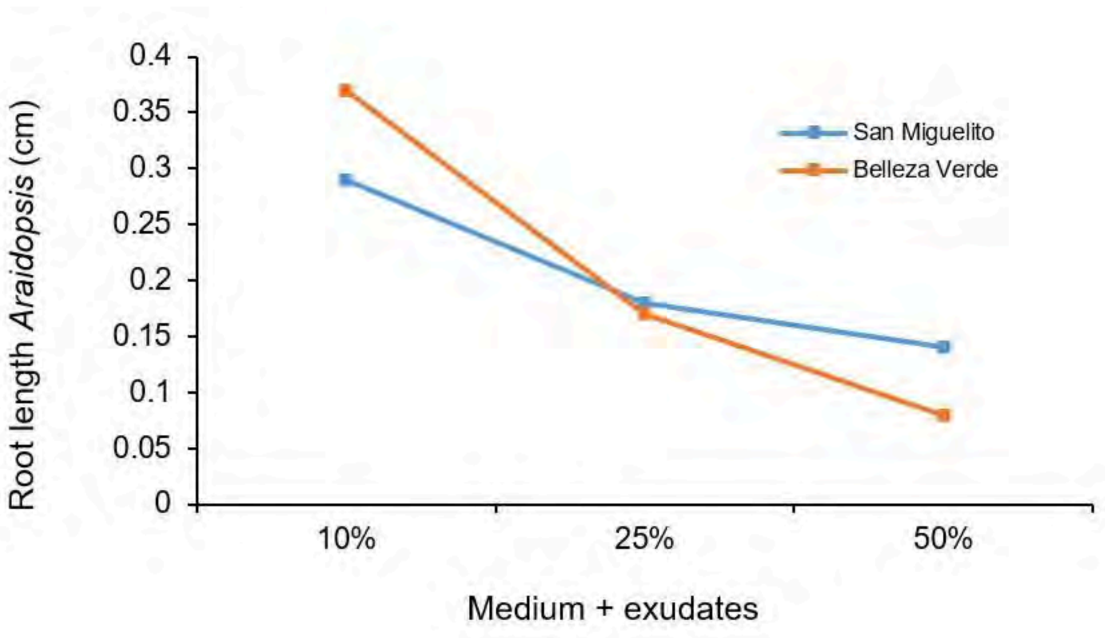

Figure 4 shows *Arabidopsis* seedlings after applying treatments based on alfalfa extracts, in photograph 4a, seedlings with a normal green color one day after application are observed; that is, seedlings with normal leaves and radicle and in Figure 4b, eight days after applying the alfalfa extract, both the seedlings and the rootlets began to present chlorosis until death.

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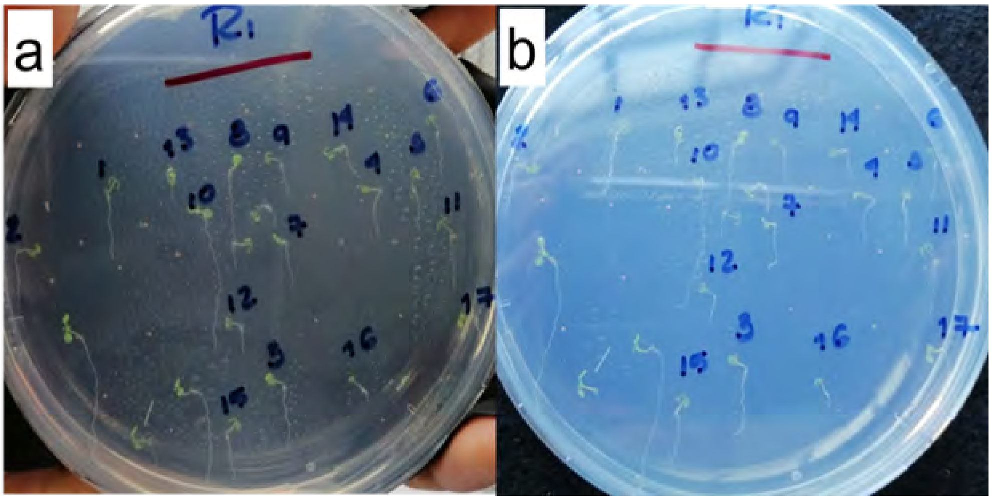
Figure 4. Growth of *Arabidopsis* seedlings with extracts of MS medium previously sown with alfalfa (*Medicago sativa*) in interaction with *Arabidopsis* a) day one after application, b) day eight after application in 2018.



Discussion

The demand for nutrients has a strong relationship with sowing density, due to competition for space, they influence the formation of aerial biomass and also the development of the root system. In this regard, Castaldo *et al*. (2018), in a work on two sowing densities (8 and 16 kg ha^{-1}) and two varieties of alfalfa (WL 611 and WL 903), reported results similar to those of the present work, where the sowing densities that were used did not show statistical differences for a higher yield and dry weight of alfalfa, but they were statistically significant at 5% between the varieties used.

The differences between varieties are attributed to the genetic origin and sowing densities, these impact to a greater degree on root length, number of root hairs and number of lateral roots.

In this sense, Ortiz-Rojas *et al*. (2017) conclude from their work on root development of *Arabidopsis thaliana* with foliar extract of *Moringa oleifera* that there were differences in root development, being attributed to competition with neighboring roots for nutrient uptake. When there are different conditions for the development of a plant, it is expected that the plants in each of the treatments express their growth according to their needs. The increase of the root system is determined by the number and position of the lateral roots (Palleros, 2015) for this statement, it can be observed that when there is a higher density of sowing, there is also greater development of root hairs as there is more growth of lateral roots.

Antagonistic effect was observed on the root growth of *Arabidopsis thaliana* L. seedlings with alfalfa, but it was to a greater degree until chlorosis was reached with the highest sowing densities. Some species have been shown to have autotoxicity and heterotoxicity effects (Chocarro and Lloveras, 2014). Toxicity occurs when some plants release chemicals that alter the establishment of neighboring plants. They usually affect the germination or establishment ability of new seedlings, as well as morphology, similar results are reported in a work of allelopathic potential of alfalfa on different forage legumes, they found that the root of the plants neighboring alfalfa is the one that is most affected in its development, which corroborates the results of the present work (Chocarro and Lloveras, 2014). Some authors, López-Bucio *et al*. (2005) found in their work with *Bacillus megaterium* that it modifies the root architecture of *Arabidopsis*, independently of auxins and ethylene.

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Some referential studies, such as that of Martínez-Mera *et al*. (2016), they express in their work the effect of extracts of three different legumes (crotalaria, jack and pigeon peas), they found an interaction between cultures by aqueous extract in germination. Inhibition was generated in the growth of coleoptile, and the radicle of corn, in the coleoptile and hypocotyl and radicle in sorghum and lettuce. Results that coincide with the present work as the growth of the root and in general the aerial part of *Arabidopsis* seedlings was inhibited until reaching their death, eight days after sowing.

Conclusions

Alfalfa presents high antagonism against the seedlings of *Arabidopsis thaliana* L. With exudates of all sowing densities, antagonism was observed since they stopped the growth of the *Arabidopsis* seedling; nevertheless, the one with the greatest effect was with the density of 9 kg ha^{-1}, which caused death in the two varieties, which indicates that the antagonistic effect does not depend on the variety but on the sowing density.

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Revista Mexicana de Ciencias Agrícolas

DOI: https://doi.org/10.29312/remexca.v14i5.3090

Allelopathic activity of alfalfa root exudates in *Arabidopsis thaliana*

Journal Information
Journal ID (publisher-id): remexca
Title: Revista mexicana de ciencias agrícolas
Abbreviated Title: Rev. Mex. Cienc. Agríc
ISSN (print): 2007-0934
Publisher: Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias

Article/Issue Information
Date received: 01 May 2023
Date accepted: 01 July 2023
Publication date: 26 July 2023
Publication date: July 2023
Volume: 14
Issue: 5
Pages: 66-77
DOI: 10.29312/remexca.v14i5.3090

Categories

Subject: Articles

Keywords:

Keywords:

Arabidopsis thaliana

allelopathy

forage

Counts

Figures: 8

Tables: 6

Equations: 0

References: 22

Pages: 12