Artículo de investigación

Legume reaction to soil acidity

Отношение бобовых растений к кислотности почвы

Reacción de las leguminosas a la acidez del suelo

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Abstract

Most legumes grow and develop better in neutral soils, with the exception of lupine, which grows at pH 4.0–5.0. Red clover secretes hydrogen ions into the soil through its roots, changing soil pH. Legume root nodules form better at pH 6.5–7.0, and at pH values less than 3, the root cells' cytoplasm breaks down. At pH 8.7, the plants are deficient in NO_3^-, phosphates, iron, manganese, copper, and zinc. In acidic soils, an excess of aluminium inhibits the uptake of phosphorus, calcium, potassium, iron, sodium, and boron by root cells. Legumes are sensitive to the concentration of aluminium ions in the soil. In aluminium-sensitive pea varieties, nutrient absorption is suppressed; lectin, hemicellulose, and cellulose synthesis is inhibited in root cell walls; membrane water permeability decreases; the number of SH groups in cells decreases; and enzyme activity is inhibited. In an acidic medium, clover growth is inhibited, nodules form poorly, and nitrogen fixation rate decreases. The higher the acidity, the harder it is to assimilate soil magnesium. Magnesium deficiency leads to

Аннотация

Большинство бобовых растений лучше растут и развиваются на нейтральных почвах, исключением является люпин, растущий при pH 4,0-5,0. Клевер луговой через корни выделяет ионы водорода в почву, меняя pH. Клубеньки на бобовых растениях лучше формируются при pH 6,5-7,0. При pH менее 3 нарушается структура цитоплазмы клеток корня. При pH 8,7 растения испытывают дефицит NO_3^-, фосфатов, железа, марганца, меди, цинка. В кислых почвах избыток алюминия подавляет поглощение клетками корня фосфора, кальция, калия, железа, натрия, бора. Бобовые растения чувствительны к содержанию ионов алюминия в почве. У чувствительных к алюминию сортов гороха: подавляется поглощение элементов питания; тормозится синтез лектина, гемицеллюлозы и целлюлозы клеточных стенок корня; снижается проницаемость воды через мембраны; уменьшается количество SH- групп в клетке; подавляется активность ферментов. В кислой

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reduced photosynthesis and decreased sugar transport to roots and nodules. As a result, nitrogen fixation stops, and the plant's leaves turn yellow and fall off. For legumes, the Ca:Mg ratio is important. The combined application of calcium and magnesium increases plant biomass yield, reduces nodule formation in lupine, and increases it in beans. This difference is related to the fact that beans, clover, and haricot are calciphiles, whereas is calciphobous. The use of waste beet sugar production – defecate, calcium fertilizer, is very effective. Decreased acidity increases leghemoglobin content in nodules, increases nodule weight, and increases nitrogen fixation 3–4 times.

Keywords: Hydrogen and aluminium ions, legumes, nitrogen fixation, productivity, soil solution reaction.

среде у клевера тормозится рост, слабо формируются клубеньки, снижается азотфиксация. Чем выше кислотность, тем труднее усваивается почвенный магний. При недостатке магния снижается активность процессов фотосинтеза, резко снижается транспорт сахаров в корни и клубеньки, фиксация азота останавливается, листья желтеют и опадают. Для бобовых растений важно соотношение Ca:Mg. Совместное внесение кальция и магния повышает урожай биомассы растений, снижало формирование клубеньков у люпина и повышало у бобов. Разная реакция растений связана с тем, что бобы, клевер и фасоль относятся к группе кальциефилов, тогда как люпин – к группе кальциефобов. Высокой эффективностью отличается применение отхода свеклосахарного производства – дефеката, кальцийсодержащего удобрения. Снижение кислотности повышает содержание легемоглобина в клубеньках, растет масса клубеньков, а фиксация азота увеличивается в 3-4 раза.

Ключевые слова: азотфиксация, бобовые растения, ионы водорода и алюминия, продуктивность, реакция почвенного раствора.

Resumen

La mayoría de las legumbres crecen y se desarrollan mejor en suelos neutros, con la excepción del lupino, que crece a un pH de 4.0 a 5.0. El trébol rojo secreta iones de hidrógeno en el suelo a través de sus raíces, cambiando el pH del suelo. Los nódulos de la raíz de las leguminosas se forman mejor a pH 6.5–7.0, y a valores de pH inferiores a 3, el citoplasma de las células de la raíz se descompone. A pH 8.7, las plantas son deficientes en NO_3^-, fosfatos, hierro, manganeso, cobre y zinc. En suelos ácidos, un exceso de aluminio inhibe la absorción de fósforo, calcio, potasio, hierro, sodio y boro por las células de la raíz. Las legumbres son sensibles a la concentración de iones de aluminio en el suelo. En las variedades de guisantes sensibles al aluminio, se suprime la absorción de nutrientes; la síntesis de lectina, hemicelulosa y celulosa se inhibe en las paredes celulares de la raíz; la permeabilidad del agua de la membrana disminuye; disminuye el número de grupos SH en las células; y se inhibe la actividad enzimática. En un medio ácido, el crecimiento del trébol se inhibe, los nódulos se forman mal y la tasa de fijación de nitrógeno disminuye. Cuanto mayor es la acidez, más difícil es asimilar el magnesio del suelo. La deficiencia de magnesio conduce a una fotosíntesis reducida y a un menor transporte de azúcar a las raíces y nódulos. Como resultado, la fijación de nitrógeno se detiene y las hojas de la planta se vuelven amarillas y se caen. Para las legumbres, la relación Ca: Mg es importante. La aplicación combinada de calcio y magnesio aumenta el rendimiento de la biomasa vegetal, reduce la formación de nódulos en el altramuz y aumenta en los frijoles. Esta diferencia está relacionada con el hecho de que los frijoles, el trébol y la judía son calciphiles, mientras que son calciphobous. El uso de la producción de residuos de azúcar de remolacha - defecar, fertilizante de calcio, es muy efectivo. La disminución de la acidez aumenta el contenido de leghemoglobina en los nódulos, aumenta el peso de los nódulos y aumenta la fijación de nitrógeno de 3 a 4 veces.

Palabras clave: Iones de hidrógeno y aluminio, legumbres, fijación de nitrógeno, productividad, reacción de solución del suelo.

Introduction

In recent decades, soil acidity has increased due to a negative balance of calcium and magnesium (Kosolapova et al., 2018; Litvinovich, Lavrischev, Bure, Pavlova, & Kovleva, 2017; Naliukhin, Vedeneeva, & Vlasova, 2017; Sychev & Ahanova, 2019). Acidity is among the most important indicators of soil fertility, and increased acidity serves as a deterrent to increasing productivity and degrading the quality of leguminous plants. Legumes' role in agriculture is considerable: they improve soil structure, enrich soil with organic matter and biological nitrogen, and saturate humans and farm animals' diets with protein.

In legumes, soil acidity determines the nature of mineral nutrition, the intensity of nitrogen fixation, metabolic activity, productivity, and yield quality. The majority of leguminous plants grow and develop better in neutral soils; the exception is lupine, which grows in low-pH soils. The optimal pH values for leguminous plants are as follows: pea – 6.0–7.5, melilot – 7.0–8.7, clover – 6.0–6.5, lupine – 4.0–5.0, alfalfa – 7.0–8.3, soybean – 5.5–6.5, haricot – 7.0–8.0 (Appunu & Dhar, 2006; Moiseenko & Zajtseva, 2009; Nebolsin & Nebolsina, 1997; Valkov, 1986). Rhizosphere microbiocenoses are involved in the transformation of substances and actively affect soil composition and acidity. When clover was grown on low-fertility soil, soil pH under the clover decreased from 7.0 to 4.2 because the H^+ ions released by the roots outnumbered absorbed cations. Soil pH under ryegrass, however, remained at the initial level (Dzyun, 2018; Kaufman & Blinnikova, 2018; Valentine, Benedito, & Kang, 2010).

Neutral or weak acid reactions in the medium are optimal for atmospheric nitrogen fixation. Nodules form at pH values of 4.5–6.0, and optimum reactions occur in a medium close to neutral. *Azospirillum* develops better at pH 6.5–7.0, *Klebsiella* develops better at 6.8–7.0, and *Enterobacter* develops better at 7.0 (Belyshkina, 2018; Ferguson & Gresshoff, 2015; Gao, Wang, Fu, & Zhao, 2017).

Increased acidity and alkalinity negatively affect legume growth and development, adversely impacting a number of mineral nutrition processes. Therefore, at pH values less than 3, the structure of the root cells' cytoplasm is disturbed. Under alkaline conditions (pH 8.7), plants lack NO_3^-, phosphates, iron, manganese, copper, zinc, and contain an excess easily soluble salts (Nebolsin & Nebolsina, 1997; Voloshin, 2018). In acidic soils, excess aluminium inhibits the uptake of phosphorus, calcium, potassium, iron, sodium, and boron by the root cells due to decreased cytoplasm membrane permeability. At the same time, in the root tip meristem, cells with two nuclei develop (Black, 1973; Klimashevsky, 1991; Stefan et al., 2018).

Soil acidity affects the mobility of heavy metals and their absorption by plants' root systems. In soils with a pH below 5.5, manganese is soluble, but at pH 7.5, its mobility decreases due to the transition of Mn^{+2} to Mn^{+4} and the formation of insoluble compounds. Legumes are resistant to high manganese concentrations due their roots' ability to release excess manganese into the environment (Ivashikina & Sokolov, 2006; Jaiswal, Naamala, & Dakora, 2018).

In acidic soils, legume productivity decreases unequally (Table 1).

Table 1. Legume yield change at various soil pH values, %

Crop	pH value				
	4.7	5.0	5.7	6.6	7.5
Alfalfa	2	9	42	100	100
Melilot	0	2	49	89	100
Meadow clover	12	21	53	98	100
Swedish clover	16	27	72	100	95
Soybean	65	79	80	100	93

Melilot and alfalfa productivity decrease to the greatest extent, but soybeans experience the smallest decrease because the crop is acidophilic. Alfalfa and melilot develop better in neutral and alkaline soils.

Nitrogen's influence on legume growth and development is closely related to the competition of NH_4^+ and NO_3^- ions with other ions, and the participation of H^+ and OH^- ions and the products of their assimilation are not always taken into account. Nevertheless, the pH gradient of absorbing root cells' plasma membranes is among the driving forces of membrane ion transport in plants (Denk et al., 2017; Ivashikina & Sokolov, 2001; Osmolovskaya & Ivanova, 1989, 1992).

When using the ammonium form of nitrogen, dry matter synthesis decreased 1.6 times in beans and 2 times in haricot with respect to the control (urea) (Table 2).

Table 2. Influence of nitrogen forms on bean and haricot dry mass synthesis (Osmolovskaya & Ivanova, 1989)

Nitrogen form	Weight of dry biomass, % of control	
	haricot	beans
$CO(NH_2)_2$	100.0	100.0
NH_4^+	49.5	63.5
NO_3^-	94.7	100.7

When using ammonium, haricot and beans accumulated the greatest amount of mineral anions in leaves and the least amount of mineral cations and organic acid anions. However, in the case of nitrate, the plants contained the largest amount of organic acid cations and anions and the smallest amount of mineral anions.

Ammonium and nitrates influence legumes' ionic balance directly and indirectly through pH change in the root medium due to the release of H^+ and OH^- ions into it. These ions are the products of plant assimilation (Osmolovskaya & Ivanova, 1989, 1992). Mixed nitrogen nutrition is more advantageous than pure ammonium only in solutions with pH values of 4.0–5.8. When the medium's pH increases to 8.2, total nitrogen absorption from both solutions levels off. Optimisation of plants' ionic balance through ammonium nutrition during medium neutralisation results from a change in the direction and magnitude of the pH gradient in the membranes of the absorbing root cells, which maintain the plants' ionic and pH homeostasis.

Legumes are sensitive not only to hydrogen ions, but also to aluminium ions. Aluminium ions, which form the exchangeable acidity of sod-podzolic soils and the soils of the northern chernozem zone, affect plant metabolism and productivity (Jaiswal et al., 2018; Klimashevsky, 1991) (Table 3).

Table 3. Effects of aluminium ions on various legumes

Sensitive variety	Resistant variety
The sensitive soybean variety synthesises less organic matter per unit of nutrients (^{15}N, ^{32}P, ^{40}K).	The resistant (tolerant) soybean variety synthesises more organic matter per unit of nutrients.
Aluminium inhibits ^{32}P uptake by pea roots, and aluminium interacts with phosphates not only on the surface of root cells, but also with internal phosphorus-containing protoplasm proteins.	Resistant legume varieties isolate aluminium from roots' sensitive metabolic sites.
In the sensitive pea variety, 3 times more phosphates are fixed in the root hair zone.	In the resistant pea genotype, 66% of aluminium is localised in the root epidermis; the sensitive genotype accumulates 82% of aluminium there.

P_2O_5 accumulation in pea root cell mitochondria and nuclei is higher (4.2 and 1.7 times, respectively).	In resistant forms, aluminium precipitation on the root surface is faster, and the root hairs play the role of an active ion exchanger.
Aluminium more strongly inhibits ^{14}C synthesis of pectin, hemicellulose, and cellulose of the cell walls of pea roots.	Aluminium has a weaker effect on synthesis enzyme (hydrolase) activity, binding and inactivating aluminium ions.
Cell wall water permeability in the elongation and cell division zones is significantly reduced.	The aluminium-resistant pea variety accumulates 84% of dry matter relative to the control, whereas the sensitive variety accumulates 35%.
The number of SH-groups is reduced 2–3 times.	The number of SH-groups remains at control levels.
Accumulation of malic and citric acids is suppressed.	Organic acid content is high.
ABA content increases 4.7 times compared with resistant varieties.	ABA content decreases compared with the control.
Free nucleotide accumulation in root cells increases.	Aluminium does not affect ATP content in root cells.
Aluminium significantly inhibits oxidative and phosphatase activity in root tissues and separates oxidation and phosphorylation processes.	Roots absorb more NO_3^-, and a larger amount of ^{15}N is included in the amine and amide fractions.
Aluminium suppresses nitrate reductase (NR) activity in pea roots by 73%.	Aluminium suppresses NR activity in pea roots by 50%.
The suppression of glutamine synthetase activity is similar to the suppression of the NR activity.	Non-cyclic photophosphorylation occurs 3.5 times faster than in the sensitive form, and cyclic photophosphorylation occurs 2.2 times faster.
Chloroplast ATPase activity decreases by 34%, and acid phosphatase activity increases 3 times.	Chloroplast non-cyclic photophosphorylation activity decreases slightly, and cyclic photophospholation activity increases.
	Pea roots exhibit higher excretory function (by ^{32}P).

The main factor limiting clover cultivation in the non-black soil zone is increased soil acidity. At pH 4.5–5.0, clover's growth is inhibited, nodules form poorly, and nitrogen fixation decreases (Vavilov & Posypanov, 1983). However, VIK-7 clover has high symbiotic nitrogen fixation rates in sod-podzolic loamy soil with high acidity and low phosphate availability (Trepachev, 1999). This is explained by the nature of soil acidity, which is caused less by H^+ ion concentration and more by aluminium ions, which have low mobility. At the same time, biological factors, such as microsymbionts and macrosymbionts' high resistance to of hydrogen and aluminium ionic toxicity levels, play an important role.

Acidity has another peculiar effect: the higher the soil acidity, the more difficult it is for plants to absorb magnesium. With increased magnesium content, lupine's above-ground mass and grain yield increase (Trepachev, 1999). When soil lacks magnesium, it moves from vegetative to reproductive organs, photosynthesis stops, and the plant's leaves turn yellow and fall off. Sugar transport in the roots and nodules decreases sharply, and nitrogen fixation stops.

For leguminous plants, Ca:K, Mg:K, and Ca:Mg ratios are important. In soil with high mobile potassium content and reduced mobile phosphates when compared to the background without phosphorus and potassium fertilizers, plants' leaves fell off during the reproductive phase. Phosphorus and potassium fertilizers (PK-background, applied together) reduced the yield of lupine and fodder beans (Table 4).

Table 4. The effect of calcium and magnesium on leguminous plants' accumulation of above-ground mass, roots, and nodules, g container^{-1} (Trepachev, 1999)

Fertilizer	Lupine			Fodder beans		
	above-ground mass	roots	nodules	above-ground mass	roots	nodules
Without fertilizers	91.6	38.4	1.7	16.4	23.0	0.05
PK-background	73.9	38.8	1.8	11.0	13.8	-
PK-background + Mg	136.9	35.2	3.1	44.8	25.8	1.51
PK-background + Ca	117.2	49.5	2.3	21.0	14.2	0.30
PK-background + Ca + Mg	145.1	31.8	2.4	62.3	27.7	1.72

Magnesium, against the PK-background, significantly increased the above-ground yield and nodule development (1.8 times in lupine and 4 times in beans). The combined application of calcium and magnesium increased the yield of the above-ground mass in leguminous plants, reduced nodule formation in lupine, and increased it in beans. This ambiguous response to nutritional conditions is related to the fact that beans, haricot, and clover belong to the calciphile group, whereas lupine belongs to the calciphobous group.

On leached chernozem at acidic pH values (5.1–5.4), the activity of the vetch photosynthetic apparatus decreased, which decreased grain yield (Table 5). On unlimed soil, fertilizer efficiency reached 8.0–9.9% compared to the control, whereas on limed soil, it was 9.0–11.5%. When lime was added, the vetch yield increased by 0.22–0.28 t ha^{-1} (10–12%).

Table 5. The effect of liming and mineral fertilizers on the spring vetch harvest (Akanova & Dvoynikova, 2014)

Fertilizer application	Unlimed soil			Limed soil				
	grain yield, t ha^{-1}	increase		grain yield, t ha^{-1}	increase		increase from lime application	
		t ha^{-1}	%		t ha^{-1}	%	t ha^{-1}	%
Without fertilizers	2.12	-	-	2.34	-	-	0.22	10.4
$P_{45}K_{45}$	2.29	0.17	8.0	2.55	0.21	9.0	0.26	11.4
$N_{20}P_{45}K_{45}$	2.33	0.21	9.9	2.61	0.27	11.5	0.28	12.0
$LSD_{0.5}$	0.12			0.13				

Grey forest soils are characterised by low humus content (3–4%) and pH value (3.8–4.5), which negatively affects the development and activity of the bacteria *Rhizobium leguminosarum* and reduces pea yields (Table 6).

Table 6. Formation of symbiotic system and pea yield depending on lime scum dose (Stupina, 2010)

Lime scum dose, t ha^{-1}	pH$_{salt}$	GSP*	ASP**	Grain yield, t ha^{-1}
Control	4.8	76.5	0.37	1.05
Lime scum, 6	5.8	130.7	17.6	1.16
Lime scum, 12	5.8	143.9	20.2	1.47
Lime scum, 24	6.6	157.2	22.6	1.79

*general symbiotic potential (GSP); **active symbiotic potential (ASP).

Calcium in lime scum (sugar beet production waste) regulates soil solution pH$_{salt}$ (Shishkin, 2002). Lime scum in the dose of 24 t ha^{-1} ensured the greatest activity of the symbiotic legume–rhizobial system and contributed to better development of the leaf apparatus assimilation surface, which resulted in high pea yield (Stupina, 2010). Mineral fertilizers ($N_{60}P_{60}K_{60}$) inhibited the development of active nodules compared to lime scum due to decreased pH value.

In the Northern Trans-Urals, legumes sometimes do not enter into symbiosis with rhizobia, suffer from a lack of nitrogen, and produce low yields. Among the limiting factors is the acidic reaction of grey forest soil (pH$_{salt}$ is 4.6–5.4). A decrease in the acidity from 4.6 to 5.5 increased the content of leghemoglobin (Lb) in nodules 1.5–2 times; the amount of nitrogen fixed by vetch plants increased by 130 mg container^{-1}, and the amount fixed by pea plants increased by 330 mg container^{-1} (Table 7).

Table 7. Indicators of symbiotic and photosynthetic activity in vetch and pea plants depending on soil pH (Petukhov, 1995)

Indicator	Vetch			Pea		
	4.6	5.5	6.2	4.6	5.5	6.2
Weight of active nodules, g container^{-1}	1.2	1.6	2.1	1.1	1.8	3.0
Lb content, mg g^{-1} of raw nodules	5.4	7.9	8.2	3.9	7.8	8.4
Nitrogen content in plants, g container^{-1}	1.03	1.16	1.55	0.92	1.25	1.82
Increase in fixed nitrogen content, mg container^{-1}	-	130	520	-	330	900
Leaf area, sq. dm container^{-1}	18.0	20	25	13	18	23
Active symbiotic potential, g container^{-1}	34.0	39.5	51.8	32.2	38.8	55.1
Seed yield, g container^{-1}	7.5	9.0	14.3	10.0	13.3	19.9

A further decrease in soil acidity to pH 6.2 increased the weight of vetch nodules by 31% and pea nodules by 67%; Lb content decreased by 4% and 8%, respectively; the amount of fixed atmospheric nitrogen increased 2.8–4.0 times, and the seed yield increased by 50–59%. In acidified sod-podzolic soil with a pH of 5.5, the weight of alfalfa roots decreased by a factor of 3, and the supply of nitrogen to the soil decreased by 5 times, which depleted the soil of nitrogen due to the suppression of nitrogenase activity by 2.5–2.8 times (Petukhov, 1995).

Increased H^+ and Al^{+3} ion concentration in the soil solution adversely affects leguminous plants: membrane ultrastructure and permeability change; membrane potential depolarisation or hyperpolarisation occurs due to a change in the equilibrium of H^+ ions in the root; and proton pump activity, which determines the creation of a membrane potential, energy storage, and absorption of mineral ions by the roots, changes; and K^+ and Ca^{+2} channel activity changes (Chirkova, 1988; Ivashikina & Sokolov, 2006; Stefan et al., 2018).

Thus, under the influence of H^+ and Al^{+3} ions in the roots of leguminous plants, membrane ultrastructure, proton pump activity, ion equilibrium, and ion channel activity change. With increased acidity, aluminium toxicity increases, magnesium absorption decreases, sugar transport to nodules is suppressed, and nitrogen fixation stops. As pH rises, it increases the total symbiotic potential (2 times) and active symbiotic potential, nodule Lb content (1.5–2.0 times), active nodule mass (1.8–2.7 times), and the amount of fixed nitrogen (2.8–4.0 times).

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