Essay

Oxygen in the root zone and its effect on plants

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Abstract

The information presented analyzes the state of the art of the evidence in the last 20 years of the importance and the effects of the availability of oxygen in the rhizosphere on the growth and development of plants. Adverse conditions of biotic (microorganisms) and abiotic factors (temperature, waterlogging, salinity, others) that influence the oxygen concentration in the rhizosphere, can lead to a rapid drop in oxygen levels and affect morphology, metabolism and physiology from the roots, with a negative effect on the growth of the plant. Radiation medium oxygenation techniques can be favorable, both in soils and in substrates, in situations where there is a risk of hypoxia, but specific studies are required on the effect of oxygen application in each species, as well as the measurement of the answers to identify the oxygen requirements that maximize the yield and quality of the harvested products, both in the field and in the greenhouse. In the agricultural sector, techniques that are sustainable and economically viable are required, even with the high costs of using new technologies.

Keywords: anoxia, hypoxia, oxygenation.

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Oxygen in the growth medium plays a critical role, as it determines the root orientation and the metabolic state of the root. Oxitropism allows roots to avoid areas of the substrate with low oxygen levels and could also be a physiological mechanism to reduce competition between roots for water, nutrients and oxygen itself (Porterfield and Musgrave, 1998).

The availability of oxygen at the radical level is fundamental for the optimal development of plants, since it is required in different priority metabolic processes such as: carbohydrate metabolism, nitrate reduction, symbiotic nitrogen fixation, protein renewal, maintenance of the proton gradient and the absorption of nutrients by the roots (M'Bou *et al*., 2010; Makita *et al*., 2015; Bhatla, 2018), with immediate effects on root growth and shoot, which has an impact on the general development of the plant (Morard *et al.*, 2000; Dutilleul *et al*., 2003; Eckhard *et al*., 2013).

Plant respiration is an oxidative process controlled by different metabolic pathways, in order to avoid situations of low energy availability (Toro and Pinto, 2015) even in situations of hypoxia (van Dongen *et al*., 2011; Gupta *et al*., 2015), although the knowledge of its regulation is limited (Fernie *et al*., 2004; Ishizawa, 2014). There are frequent oxygen deficiencies in the rhizosphere, as a result of high rates of radical respiration, either due to high temperatures, deficiencies in the aeration capacity of the culture medium or inadequate irrigation management (Carazo *et al*., 2015).

This has given rise to different cultural practices and oxygenation techniques (aeroponia, oxygenation, oxyfertigation) of the radical medium, the irrigation water or the nutrient solution (Marfa *et al*., 2005; Bhattarai *et al*., 2006; Midmore, 2007). Based on the above, the objective of this work is to review the evidence on the effects and importance of oxygen availability in the rhizosphere for plant growth and development, as well as the benefits of oxyfertigation by minimizing the risk of hypoxia and increase yield and quality of products harvested from agricultural crops.

Oxygen requirements in plants

It is difficult to define the availability of oxygen for plants with specific concentration values. The terminology to describe this condition is based on the comparison with the atmospheric oxygen level (21% v/v), known as normoxia. Higher or lower oxygen concentrations are called superoxia and hypoxia, respectively; while anoxia is the situation in which there is no free oxygen available.

Anoxia is also used to describe oxygen concentrations within tissue that are very close to zero. The interpretation of hypoxia is complicated because it is used both to refer to the concentration of O_2 in the environment and its concentration within the plant tissue; for example, a fabric that is kept in a normoxic environment may be hypoxic indoors; therefore, the O_2 concentration must be specified in each situation (Fagerstedt *et al*., 2013; van Dongen and Licausi, 2015).

Root respiration in aerobic conditions requires a continuous supply of O_2 to the rhizosphere. Radical respiration depends on various factors: temperature (Rachmilevitch *et al*., 2006), salinity (Bernstein *et al*., 2013), heavy metals, water stress (Jiménez *et al*., 2013) and saturation of the pore space (Liao and Lin, 2001), but the factor that has the most direct relationship is the availability of O_2, which allows or not the process, making it a limiting factor both in soil and in substrates (Urrestarazu and Mazuela, 2005; Fagerstedt *et al*., 2013).

As a result, plants can exhibit decreased water consumption, wilting, and reduced stomatal conductance (Bhatla, 2018), slow growth, and decreased yield (Bhattarai *et al*., 2008; Maestre and Martínez, 2010). Damage and death of flooded plants have been attributed to lack of oxygen at the root (Boru *et al*., 2003; Bhatla, 2018).

Due to the central role in energy metabolism (respiration), N metabolism, substrate in desaturation reactions of fatty acids and synthesis of phytohormones such as ethylene, abscisic acid and gibberellins (van Dongen and Licausi, 2015). In hypoxic conditions, in addition to the physical properties that restrict the availability of O_2 (Friedman and Naftaliev, 2012), the respiratory activity of the microorganisms also decreases it's content, since they compete with the plant for the available O_2, especially in unstable or immature organic substrates with high microbial activity (Lemaire, 2005). Also the low content of O_2 increases the susceptibility to infection by pathogens, since spores are stimulated with exudates in the rhizosphere, as is the case of *Phytophthora infestans*, where waterlogging generates anaerobic respiration with the release of ethanol that stimulates the production of infection structures (Lal *et al*., 2018).

Although the serious effects of anoxia on the plant (Gibbs and Greenway, 2003) are unlikely in the porous substrates used in soilless cultivation systems (Morard *et al*., 2000) and plants exhibit tolerance to deficiency of O_2 for several hours (Geigenberger, 2003), since when these conditions are reversed the plants do not suffer side effects, positive responses to oxygenation have been observed in conditions of hypoxia and anoxia in studies with cultures in nutrient solution (Marfá *et al*., 2005; Urrestarazu and Mazuela, 2005; Urrestarazu *et al*., 2006).

In corn (*Zea mays* L.) roots, a gradient of 10 to 5% O_2 was observed from the cortex to the wake. In castor (*Ricinus communis* L.) the gradient was established between 21% of the exterior to 7% in the phloem. In pea roots (*Pisum sativum*) an internal concentration of 8% of O_2 was measured and in potato tuber (*Solanum tuberosum* L.) the oxygen gradient was established from 11-15% of the periderm to 2-5% of oxygen in the center (Papke *et al*., 2014).

Oxygen in the water

The solubility of O_2 in water depends on temperature, O_2 partial pressure, atmospheric pressure, water salinity, and the area of contact between water and air. But under normal conditions (20 °C, 1 pressure atmosphere, 20-21% O_2 in air), the maximum amount in solution is between 8 and 9 mg L^{-1}. This concentration decreases as the temperature and the concentration of dissolved salts increases (Table 1) (Murad *et al*., 2005; Massol, 2005).

Table 1. Oxygen solubility (mg L^{-1}) as a function of temperature and salinity (Massol, 2005).

Temperature (°C)	Salinity (%) of saturation in the solution					
	0.03	9.055	18.08	27.105	36.13	45.155
0	14.624	13.728	12.888	12.097	11.355	10.657
5	12.77	12.024	11.32	10.656	10.031	9.441
10	11.288	10.656	10.058	9.493	8.959	8.454
15	10.084	9.541	9.027	8.54	8.079	7.642
20	9.092	8.621	8.174	7.749	7.346	6.964
25	8.263	7.85	7.457	7.083	6.728	6.39
30	7.559	7.194	6.845	6.513	6.1	5.806
35	6.95	6.624	6.314	6.017	5.734	5.464
40	6.412	6.121	5.842	5.576	5.321	5.078
45	5.927	5.665	5.414	5.174	4.944	4.724
50	5.477	5.242	5.016	4.799	4.591	4.392

The dissolved O_2 concentration (COD) is an important parameter of the quality of irrigation water that can become a limiting factor in some intensive agricultural systems (Raviv *et al*., 2004; Marfá *et al*., 2005). In hydroponics, Morard (1995) established the critical partial pressure of O_2 at 4-6% in the nutrient solution, which corresponds to COD values of approximately 3 mg L^{-1}.

Oxygen in the soil

The porosity of air in the soil is determined by the texture, the size of the aggregate and the degree of compaction. Smaller particles (silt and clay) reduce aeration because they bond very tightly, directly and indirectly limiting the air spaces between them, as they hold more water against drainage forces (Rengasamy, 2000).

Larger particles (sand), aggregates, and organic matter increase aeration because they leave pores that drain and are easily filled by air. In sandy soils at field capacity (CC), air occupies 25% or more of its volume, but at higher aeration, evaporation and leaching increase rapidly. In clay soils, the air volume at CC is between 15 and 20%, but it can be less than 10% (Peverill, 1999).

Due to pressure differences, the oxygen in the atmosphere diffuses through the air-filled pores to the vicinity of the roots, since their diffusion; through, the pores with water is slower. Then it dissolves in the water film that surrounds the roots and by diffusion it is introduced into the cells where respiration and will generate energy for other metabolic processes (Bonachela *et al*., 2008).

Oxygen in substrates

High water availability, adequate air supply, low bulk density and high structural stability are the main physical characteristics of the ideal substrate, in which the oxygen diffusion rate (TDO) is related to the aeration capacity, the highest values of which 30% will not have a limiting TDO for the absorption of water and nutrients (Bonachela *et al*., 2008; Pineda *et al*., 2012). Plants that grow in containers, especially those that remain confined for long periods, develop more roots at the bottom and in the space between the substrate and the container walls (Gallegos *et al*., 2020).

This is due to the fact that compaction produces oxygen deficiency and root death in the center of the container, a phenomenon that is more accentuated in compacted substrates that have mechanical resistance to radical penetration and in substrates with a high content of organic matter that enter decomposition by oxygen consuming microorganisms. Downward vertical growth is a natural response to gravitropism and hydrotropism, typical of all active roots.

However, in containers, this results in a tangle of roots at the bottom of the container exposed to oxygen deficiency due to competition between them aggravated by frequent accumulations of water (Lemaire, 2005; Pineda *et al*., 2012). In containers, sands tend to compact due to manipulation, physical impacts on the surface of the substrate when containers are moved, and over-irrigation generate compaction, a process that is irreversible, reducing root growth (Kafkafi, 2008).

The most common consequences are: a) saline accumulation when the root zone is not sufficiently washed by the irrigation water; b) ammonium toxicity due to high concentrations of fertilizers during periods of high temperature; and c) overheating due to exposure of the containers to direct sunlight and consequently root death due to oxygen deficiency that is accentuated by excessive irrigation, especially during the hot season (Lemaire, 2005; Kafkafi, 2008).

The saturation of the substrate causes a decrease in the gas exchange between the atmosphere and the rhizosphere, therefore, the concentration of O_2 for radical respiration will be a limiting factor (Raviv *et al*., 2004). Even in well-aerated substrates, O_2 deficiencies can occur in periods or areas where high growth rates and root respiration coincide with high temperatures and a decrease in the concentration of dissolved O_2 in the substrate solution (Raviv *et al*., 2004; Bonachela *et al*., 2007; Acuña *et al*., 2008).

Mechanisms of tolerance to oxygen deficiency

In soils and substrates with O_2 deficiency, plants adapt by modifying their morphological, anatomical, physiological and metabolic characteristics, depending on the degree of O_2 stress (Table 2) and they vary widely between plant species and between genotypes of the same species (Fagerstedt *et al*., 2013; Larsen *et al*., 2015; Bhatla, 2018).

Table 2. Negative effects and modifications in plants under hypoxic conditions.

O_2 deficiency stress	Mechanism of adjustment or adaptation by the plant
High sensitivity to the lack of O_2 in internal tissue	Morpho-anatomical modifications: Extension of stem and leaf petioles to the water surface (flooded areas) Thinning of the leaves to facilitate underwater photosynthesis Arenchyme formation to transport O_2 from aerial structures to submerged roots Formation of adventitious roots, which develop an arenchyma to transport O_2 from the outside to the O_2-deficient tissue Lenticels for gas exchange between the exterior and interior of the tissues
Decreased redox potential (Eh) and formation of reduced toxic chemical species (Mn^{2+}, Fe^{2+}, H_2S) and loss of NO_3^- by denitrification	Development of barriers against solutes and gases (suberization in exodermis and lignification in sclerenchyma cells, greater thickness of hypodermis) to decrease the loss of O2 supplied by aerenchyma and prevent the entry of reduced toxic chemical species (Mn^{2+}, Fe^{2+}, H_2S) Smaller wake thickness to minimize O2 demand at root center Shallow roots to avoid areas with lower redox potentials (Eh)
Alteration in carbohydrate metabolism (starches and sucrose) in aerobic respiration as a central precursor process of substrates and ATP for different reactions of primary and secondary metabolism (energy crisis)	Physiological and metabolic adjustments and modifications: The metabolism of carbohydrates (starches and sucrose) in respiration as a central precursor process of substrates for different reactions of primary and secondary metabolism ATP energy metabolism to minimize its requirements in different processes
Accumulation of oxidants and free radical’s ROS (O_2^-, HO^-, HO_2^-, H_2O_2, NO, $ONOO^-$)	Antioxidant production (SOD-Fe, SOD-Mn, SOD-Zn. SOD-Cu, GSH/GSSG) for detoxification of ROS free radicals
Cytosolic acidosis generation	Adjustment in N metabolism for stabilization of cytosolic pH (homeostasis)
Accumulation of toxins: lactic acid, ethanol, acetaldehyde	Avoid accumulation of final products (lactate, ethanol) with internal metabolism and extrusion abroad
Phytohormone imbalance: increased ACC/ethylene in the root and decreased cytokinins and gibberellins in the aerial part.	Regulation of the aerial part/root ratio to increase efficiency in the absorption of water, nutrients and transport of hormones. Increased O_2 supply through the aerenchyma

Adapted from Eckhard *et al*. (2013); Fargestedt *et al*. (2013); Ishizawa (2014); Limami (2014); Larsen *et al*. (2015); Bhatla (2018).

Plants' tolerance to O_2 deficiency depends on their ability to mitigate the detrimental effects of the energy crisis and cytosolic acidosis. Lactic and ethanolic fermentation are activated under O_2 stress in order to regenerate NAD^+ to maintain a high rate of glycolysis that becomes the main route for ATP production. Paradoxically, lactic acid worsens cytosolic acidosis and carbon is consumed for the formation of ethanol, a metabolically useless dead-end product.

This adaptation saves ATP, regenerates NAD^+, and saves carbon in the form of alanine, a removable form of C/N storage after formation. Alanine accumulation indirectly contributes to pH homeostasis by consuming pyruvic acid and competing with lactate dehydrogenase (Eckhard, 2013; Limami, 2014).

In this regard, Ishizawa (2014) reported that in corn the cytoplasmic pH of dead cells decreased from 7.5 to 6.2, but remained at 6.8 after 12 h of hypoxia in normal roots, demonstrating that cytoplasmic acidosis alters pH homeostasis in cells, which leads to cell death in hypoxic and anoxic conditions.

Oxygen enrichment in the rhizosphere

Various methods have been tried to improve O_2 supply to crop roots; in soils the structure must be improved through tillage (Abu-Amdeh, 2003), create artificial aeration routes, establish drainage and select tolerant plants (Stepanova *et al*., 2002). O_2 deficiency can be complicated even more so when wastewater is used, since the dissolved O_2 content in this water is low or close to zero, especially when stored in closed tanks (Bonachela *et al*., 2007), in addition, this water generally has a high content of organic matter leading to increased microbial activity within the soil, which increases competition for oxygen in the root environment (Bonachela *et al*., 2008). Low O_2 concentration in irrigation water can be avoided using various O_2 enrichment methods.

Oxy-fertigation has been developed to improve the oxygen availability of the rhizosphere and consists of supplying dissolved O_2 in irrigation water at supersaturated concentrations using fertigation equipment (Marfá *et al*., 2005). Information on the dynamics of oxygen content in the substrate solution in greenhouse vegetable crops is scarce (Bonachela *et al*., 2007) and most of the studies have been carried out in short growing periods under controlled conditions of climate (Shi *et al*., 2007).

Pressurized air is injected into the drip irrigation system (Bhattarai *et al*., 2006; Bonachela *et al*., 2010; Maestre and Martinez, 2010) or oxygen gas to the nutrient solution (Marfá *et al*., 2005; Urrestarazu and Mazuela , 2005), peroxyacetic acid (CH_3CO_3H) is also added (Carrasco *et al*., 2010), hydrogen peroxide (H_2O_2), urea peroxide ($CH_6N_2O_3$), calcium peroxide (CaO_2), potassium peroxide (K_2O_2) or ozone (O_3) to irrigation water (Urrestarazu and Mazuela, 2005; Mazuela, 2010). These compounds are considered as oxygen fertilizers (Mazuela, 2010).

Most methods seek to keep dissolved oxygen concentrations above 3-4 mg L^{-1}, to avoid a decrease in radical growth and a browning of the roots (Urrestarazu *et al*., 2006). In practice, the oxygenation of the soil or substrate is complex since there are other factors that can affect both the demand and the supply of O_2 and cause its deficiency or hypoxia (partial pressure of oxygen between 1 and 4%), a condition that reduces the plant activity (Urrestarazu *et al*., 2006).

Most of the horticultural crops grown in substrate and in greenhouse have high growth rates associated with high respiration rates and water demand, they form a high density of roots at the bottom of the container, where conditions close to saturation usually occur. The gas exchange within the substrate can be decreased by the container (usually plastic) that surrounds the substrate.

Oxygenation and its influence on crops

Although some contradictory results have been reported regarding the use of methods to enrich the growth medium of crops with oxygen, especially with uncontrolled environment conditions (Urrestarazu and Mazuela, 2005; Bonachela *et al*., 2007), various experiments with production of plants under greenhouse, either in nutrient solution or in substrate, indicate that high levels of oxygenation they accelerate development and increase yields, as a result of the improvement in anatomical-physiological processes and increase in the hydraulic conductivity of the roots, greater mineral absorption and more efficient photosynthesis (Urrestarazu *et al*., 2006).

Morard *et al*. (2000) reported in melon (*Cucumis melo* L.), with a radical development of 25 g L^{-1} and nutrient solution at 20 °C, that the saturation concentration of 8 mg L^{-1} is reduced to 0 mg L^{-1} in 60 min, if there is no oxygen replenishment. The oxygen supply in rose (*Rosa* sp.) Increased the activity of the enzyme alcohol dehydrogenase (ADH), improved the growth and development of roots and stems. In tomato (*Solanum lycopersicum* L.).

Experiments by Goorahoo *et al*. (2002) with drip tape 12-15 cm deep and studies by Bhattarai *et al*. (2006) with tape at 8 to 30 cm depth, showed the benefits of oxygenation. The data showed that the increase in yield of pepper fruit (*Capsicum annuum* L.) reached its maximum value at 25 m from the aeration source and then decreased over 35 m, equaling the yield of the pitches without aeration.

In oxygenation tests with air injection with venturi and hydrogen peroxide in a clay soil cultivated with tomato, soybean (*Glycine max* L.) and cotton (*Gosipium irsutum* L.), yield increases of 12, 84 and 21% were obtained , respectively, compared to the control (Bhattarai *et al*., 2006). Similarly, in clay and sandy loam soil, venturi oxygenation produced an increase of 33 and 39%, respectively, in the total weight of pepper fruit (Goorahoo *et al*., 2002).

Soy adapted to prolonged oxygen deficiency producing adventitious roots, the stem showed hypertrophy and developed an aerenchyma for the transport of O_2 to the roots (Boru *et al*., 2003). The efficiency of the use of water (EUA) with oxygenation was 11% higher (39.1 *versus* 35.2 g L^{-1}) for tomato, 70% (3.65 *versus* 2.15 g L^{-1}) for soybeans and 18% (0.45 versus 0.38 g L^{-1}) for cotton in a clay soil (Bhattarai *et al*., 2006) and 36% (1.46 *versus* 0.94 kg m^{-3}) for corn in a clay-sandy loam soil (Abuarab *et al*., 2012).

Other EUA effects, such as the photosynthesis/net leaf transpiration ratio, were also greater with oxygenation (Bhattarai *et al*., 2006). Urrestarazu and Mazuela (2005) supplied O_2 with potassium peroxide (1 g L^{-1}) to pepper and melon, finding a yield of 20 and 15% higher, respectively, with oxygenation; but there were no significant differences in cucumber.

In this regard, Urrestarazu *et al*. (2006) indicate that the application of a chemical oxygenator to the irrigation solution significantly increases the availability of O_2, translating into higher fruit yield per plant. Underground irrigation with 12% air in the water, stimulated growth and improved reproductive performance by advancing flowering and fruiting in tomatoes, and increased yield by 21%, the effect of aeration was greater in soil at field capacity (CC) in relation to the soil with water stress; while in saline soil, the increase was 38% in relation to the soil without aeration.

In both cases, the efficiency of water use increased, 16% in humidity experiments and 32% in salinity. The increase in yield with aeration was also accompanied by a higher harvest index (IC), higher fruit weight, and a lower water stress index. The benefit obtained by the oxygenation of the irrigation water was not only observed in conditions in which the air porosity was low (sodium soils with poor structure or at CC in clay soils), but also in soils with less moisture availability.

CC irrigation in clay soil generated a lower concentration of O_2 in the rhizosphere, but aeration improved the concentration of dissolved O_2 and increased tomato yield, since aeration avoided hypoxia (Bhattarai *et al.*, 2006). Another study by Bonachela *et al*. (2007) demonstrated that oxygenation of the substrate solution in pepper and tomato cultivation avoided hypoxic conditions, while O_2 deficiencies occurred in melon during the second half of the cultivation cycle, when high environmental temperatures occurred and the plant had developed its radical system and complete canopy.

In rose plants that received oxifertigation treatments, the leaf area, the dry weight of leaves and flowers were higher, especially in those that grew on fine particle substrates with the presence of hypoxia (Carazo *et al*., 2008). In these periods, enriching the nutrient solution provided with O_2, by managing irrigation rafts or artificial contributions of O_2, can improve crop growth conditions and consequently their productivity (Bonachela *et al*., 2008).

In the arugula culture (*Eruca sativa* Mill), different doses of peroxyacetic acid (CH_3CO_3H) were evaluated in the nutritive solution, determining that 40 mg L^{-1} produced higher yield compared to plants grown in perlite without addition of this acid (Carrasco *et al*., 2010). In the parameters of fertigation, production and quality of melon fruits, the application of the oxygenating potassium peroxide increased the absorption and the efficiency of water use in terms of kilograms produced per liter of water consumed.

There were no differences in fruit yield and quality, which was attributed to the absence of O_2 deficiency in the control treatment and to periods of hypoxia of insufficient intensity or duration to significantly affect productivity (Mazuela, 2010). With the injection of air in subsurface drip irrigation, potato productivity increased, the yield was 27.11 and 17.8%. Also, it was higher in the air injection treatment, compared to drip irrigation (RG) and underground drip irrigation (RGS), respectively, in the first cycle, but it was 38.2 and 7.66% higher than RG and RGS, respectively, in the second cycle. In the air injection treatment, compared to the treatments without aeration (RG) and (RGS), the efficient use of water (UEA) was 46.41 and 30.52% higher in the first cycle, and was 61.78 and 19.33% higher than in RG and RGS, respectively, for the second cycle.

The plant height was 14.7 and 6.07% higher in the air injection treatment than in the control (RG) and (RGS), respectively, for the first cycle, while it was 14.13 and 9.7% higher than in the controls in the second cycle. The weight of the shoots per plant was 14.8 and 4.61% higher in the air treatment than in RG and RGS, respectively, for the first cycle, while it was 37.6 and 1.94% higher for the second cycle.

These data indicate that potato yield can be improved in underground drip irrigation if the water is aerated (Mohamed *et al.*, 2014). Carazo (2015) reported that oxy-irrigation favored productivity in rose (number of flowers, number and weight of fruits), quality (weight and length of cut flower, duration of cut flower, weight and leaf and root surface of cuttings, rooted seedling) and development in various aspects (biometric parameters, mineral content).

When air is injected into the water within the root zone, the diffusion of ethylene and carbon dioxide outside the rhizosphere increases, leading to better plant growth conditions. Increased yields and potential improvement in soil quality associated with aeration of the root zone implies the adoption of air injection technology in the irrigation system as a tool to increase crop productivity (Mohamed *et al*., 2014).

Conclusions

The information presented summarizes the evidence on the effects and importance of oxygen availability in the rhizosphere for plant growth and development. It is necessary to expand the studies on the benefits of the constant or intermittent supply of oxygen, through different methods, during the stages of plant development or conditions where there is a high demand for oxygen.

Specific studies on the effect of oxygen in different plant species are required, as well as the measurement of responses to identify oxygen requirements that maximize the yield and quality of products harvested in agrosystems both in the field and in the greenhouse. The results to date indicate that oxifertigation can be a management factor to increase the efficiency of natural resources used in intensive production systems for agricultural crops.

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