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How does soil nutritional stress limit restoration in the Amazon? Physiological, biochemical and anatomical responses of arboreal species

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ABSTRACT: Forest restoration is an urgent demand in the national and global scenario, especially in the Amazon due to the advance of forest cover loss. On the other hand, the nutritional limitation of soils in this biome is a challenge for this practice, considering the entire impact of stress on plants. Considering it, this review sought to compile the findings on the impacts of nutritional stress on tree species, as well as the strategies used to reverse this impasse in the Amazon. As a result, it was possible to observe biochemical, physiological, and morphological responses in tree species. In general, we found that nutritional stress results in changes in the biochemical and physiological activities of the plant since most nutrients are related to the function, structure, and/or composition of cellular elements. For morphological characteristics, a decrease in height, biomass and leaf area are the most recurrent damages. Regarding restoration methods used to minimize nutritional stress, besides conventional techniques such as phosphate fertilization and liming, it was observed the scientific community has invested in strategies mainly based on the reuse of waste. Furthermore, the application of biostimulants, biochar, and biofortification is increasingly common and promising. In this context, the promotion of research in the Amazon biome is strongly recommended to reduce existing gaps.

Como o estresse nutricional do solo limita a restauração na Amazônia? Respostas fisiológicas, bioquímicas e anatômicas de espécies arbóreas

RESUMO: A restauração florestal é uma demanda urgente no cenário nacional e global, especialmente na Amazônia devido ao avanço da perda de cobertura florestal. Por outro lado, a limitação nutricional dos solos do bioma é um gargalo para esta prática, tendo em vista uma série de impactos causados pelo estresse às plantas. Diante disso, está revisão buscou compilar os achados sobre os impactos do estresse nutricional para espécies arbóreas, bem como as estratégias utilizadas para reverter este impasse na Amazônia. Por meio da revisão, foi possível observar respostas bioquímicas, fisiológicas e morfológicas em espécies arbóreas. De maneira geral, constatou-se que o estrese nutricional resulta nas alterações de atividades bioquímicas e fisiológicas do vegetal, já que a maioria dos nutrientes constituem funções relacionadas à função, estrutura e/ou composição de elementos celulares. Para as características morfológicas, decréscimo em altura, biomassa e área foliar são os prejuízos mais recorrentes. Em relação aos métodos de restauração utilizados para minimizar o estresse nutricional, além de técnicas convencionais como a adubação fosfatada e a calagem, observou-se que a comunidade científica tem investido em estratégias orgânicas, baseadas principalmente no reaproveitamento de resíduos. Ademais, o uso de bioestimulantes, do biochar e da biofortificação são cada vez mais usuais e promissores. Nesse contexto, recomenda-se incisivamente o fomento de pesquisas no bioma, visando diminuir as lacunas existentes.

Introduction

Biotic or abiotic conditions that affect the development of the plant are known as stress (Kaur and Gautam 2021). Examples of biotic conditions that limit plant growth include competition, pest attacks, and insectivorous action (Mertens et al. 2021), while light intensity, soil pH, and temperature exemplify the abiotic conditions (Nowicka et al. 2018). Although both have a large influence on plant growth, abiotic conditions are the main factors limiting plant growth, and generally facilitate pathogen activity (Kaur and Gautam 2021).

In Amazon, for instance, high soil acidity reduces the availability of essential elements, and makes the forest dependent on the nutrient cycle (Machado et al. 2016) to perform physiological and biochemical activities essential to the plant cycle (Hoosbeek et al. 2023). The impacts are intensified with the advance of deforestation caused by activities such as agriculture, mining, livestock, and logging, which although they contribute significantly to the Brazilian Gross Domestic Product (GDP) (Sauer 2018, Patharkar and Walker 2019), cause the interruption of biogeochemical cycles and the reduction of the carbon sink (Carvalho et al. 2019, Silva, Bento, et al. 2020).

In order to decrease and mitigate the negative environmental impacts of these activities, especially in the Brazilian portion of the ecosystem that corresponds to more than 60% of the territory, global goals and agreements were established (Muthee et al. 2022). In the Bonn challenge, Brazil committed to restoring 12 million hectares by the year 2030 (Suding et al. 2015, Guerra et al. 2020). To do so, investments in research and restoration technology have become indispensable, even if the edaphic conditions of the Amazon are an obstacle to this practice (Ribeiro et al. 2021). For these locations, the use of structural indicators such as DBH, height, and increment rates stands out due to the low cost and facility of data collection (Williams-Linera et al. 2021).

Generally, due to prolonged stress, the high mortality of species is evidenced (Elias et al. 2019) that is characterized as feedback from the plant, needing a better comprehension of the biochemical and physiological responses that lead to morphological consequences. However, one of the main obstacles is the accumulation of research focused on forest cultures (Chandrasekaran; Boopathi; Manivannan, 2021; El-Esawi Et Al., 2018; Ohanmu; Ikhajiagbe; Edegbai, 2018). Thus, aiming at advancing forest restoration in the Amazon, this review searched to gather findings on the impacts of nutritional stress on tree species, as well as the strategies used to reverse this impasse in the Amazon.

Factors that intensify nutritional stress

Soil-plant interaction is fundamental to the regulation of biogeochemical processes and therefore to the supply of ecosystem goods and services (Elias et al. 2019). In fact, in all soil phases (solid, liquid and gas) there are interactions with the mineral components. However, abiotic factors such as light and water availability, and temperature may interfere with the availability of nutrients in the system (Nowicka et al. 2018). Light availability regulates the photosynthetic processes of the plant, which are responsible for the production of ATP and NADPH (Shafiq et al. 2021). On the other hand, temperature intensifies the degradation of the litter layer, which is the main route of nutrient entry into the soil-plant system (Bufacchi et al. 2020), besides having a strong correlation with the denaturation of proteins and lipids (Estravis-Barcala et al. 2020).

In addition to these factors, soil pH plays an important role in nutrient availability, in establishing soil microorganisms, and therefore in plant development (Rocha et al. 2023). In the case of essential nutrients, the appropriate pH to optimize nutrient availability ranges from 4.5 to 6.5, so any variation above or below these values implies lower nutritional availability for the soil-plant system (Taiz et al. 2017). For example, a pH greater than 6.5 reduces the availability of phosphorus, magnesium, manganese, iron, boron and zinc, whereas a pH lower than 4.5 reduces the availability of nitrogen and calcium (Rocha et al. 2023).

The implications for plant development may be justified by Liebig's law of the minimum, which explains the nutritional limitations of Amazon soils, most of which are classified as acids. In the tropics, due to intense leaching, stress is usually caused by nutritional scarcity or low availability (Zhou et al. 2018), while in temperate regions excess is the main reason (Wheeler et al. 2017). The responses can be seen in both functional (biochemistry and physiology) and structural (anatomy) aspects of the plant (Luo et al. 2019). Added to that, pH also influences the action of microorganisms, because for the establishment of the microbial community, it is more effective at pH greater than 5.5 (Reyes et al. 2019, Jones et al. 2019).

Impacts of nutritional stress on tree growth

Biochemical and physiological responses

Nitrogen (N), absorbed by plants in the forms of ammonium (NH4+) and nitrate (NO3), is one of the main drivers and/or limiters of plant growth, depending on its availability, as it is a key constituent of cellular elements (Fig. 1), such as proteins, nucleic acids, and hormones (Xie et al. 2022). Thus, the absence or insufficiency of available N in the soil delays the biochemical processes vital to the development, especially the transport of solutes, consequently inhibiting plant growth (Luo et al. 2019). Nitrogen deficiency in the forest is also capable of reducing 41% of photosynthetic capacity and increasing starch production in the root, thereby increasing root biomass (Luo et al. 2019, Jaquetti et al. 2022).

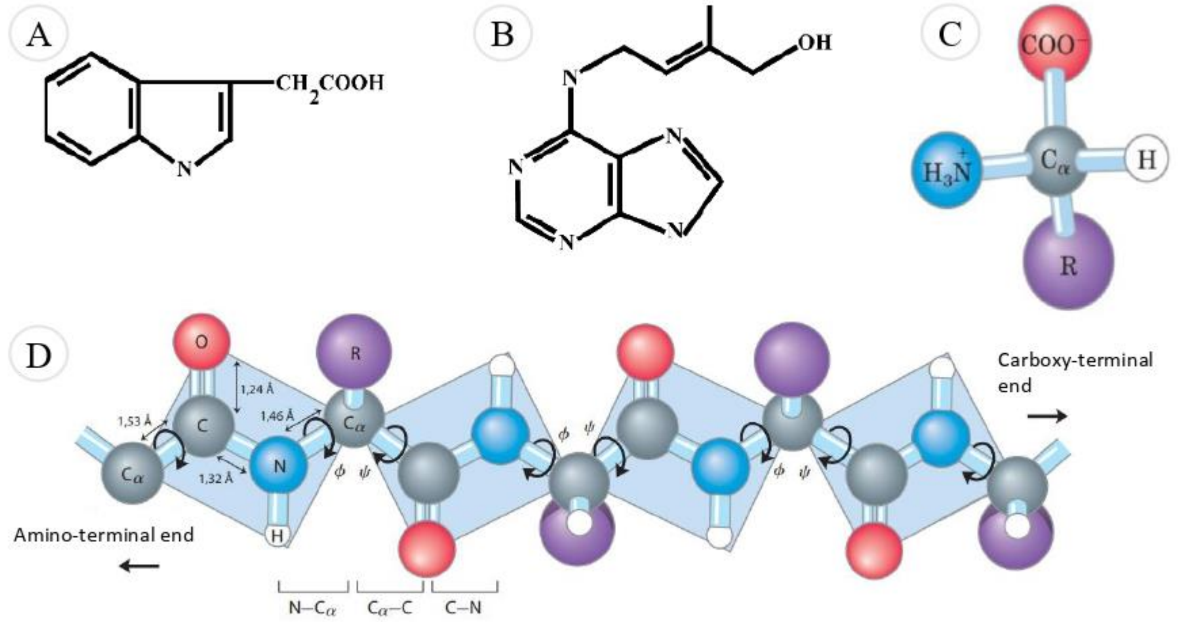

Figure 1. Nitrogen as a key element of plant hormones (A = auxin; B = Cytokinin); amino acids (C); and protein (D). Source: Adapted from Taiz et al. (2017) and Gray (2004).

Considering the role of phosphorus (P) in reactions involving NADPH and ATP (Fig. 2A), limiting this element mainly affects the synthesis of sugars and the fixation of carbon. Consequently, damage to the structural integrity of the cell is also easily visualized (Meng et al. 2021), as it is directly related to the enzymes involved in photosynthesis, such as ribulose 1,5-bisphosphate carboxylase (RuBisCo).

The omission of potassium (K) delays the activation of numerous enzymes involved in energy metabolism, such as energy production and osmotic control of cells (Cornut et al. 2021). The stomatal control provided by this nutrient is directly related to transpiration, since it acts in the activation of ATPase (Mostofa et al. 2022). In addition to that, the low availability of K reduces the use of photoassimilates, consequently reducing CO2 fixation and increasing ionic availability. The application of K in plants under salinity stress was responsible for a 65% increase in root length and a reduction in sodium in fine and medium roots (Larbi et al. 2020), probably due to the action of ethylene (Zhang et al. 2021), besides providing greater resistance to rust in *Eucaliptus grandis* (Masullo et al. 2020).

Calcium (Ca) is an important element for the formation of plant tissues and acts as a structural component of plant cells, especially pectin (Fig. 2B). Under stress conditions, the nutrient is characterized as an efficient plant defense signal, since proteins linked to calcium are responsible for the signal transduction mechanism (Verma et al. 2022). Furthermore, Ca plays a key role in mitigating abiotic stresses caused by salinity, water deficit, temperature and heavy metals, as it activates the defense system of plants, increasing the production of antioxidants and osmoprotectors (Shabbir et al. 2022).

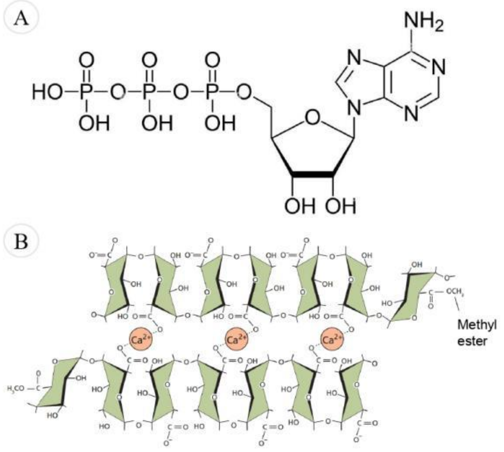

Figure 2. Function of phosphorus as a component of the ATP molecule (A), and of calcium ions connecting carboxyl groups and assisting in the structure of the pectin network (B). Source: Adapted from Furian (2022) and Taiz et al. (2017).

Magnesium (Mg) is one of the most important elements for the activation of these proteins (Mao et al. 2022), especially those involved in photosynthetic processes. That is because Mg is the central atom of the chlorophyll molecule (Fig. 3), consequently its deficiency is directly related to the decrease in photosynthetic rates (Cakmak and Kirkby 2008). However, excess Mg may inhibit the transport of K of cytosol (Guan et al. 2020), a study conducted with Hevea brasiliensis seedlings found a reduction in chlorophyll content and approximately 20% reduction in chloroplast length (Xue et al. 2019).

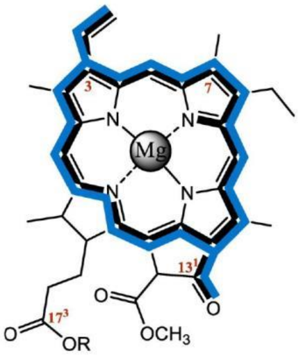

Figure 3. Structural function of magnesium as the central atom of the chlorophyll molecule. Source: Karcz et al. (2014).

Regarding micronutrients, the absence of iron (Fe) interferes with metabolic processes, hormonal regulation, and enzymatic reactions (Krohling et al. 2016). The deficiency of this nutrient leads to a synthesis of Abscisic Acid in the roots to regulate the distribution of Fe and reduce the impacts of stress (Zhang et al. 2020). Additionally, iron deficiency increases the enzymatic activity of ferric reductase, which is responsible for the reduction of iron in the roots (Jin et al. 2011). The impacts under this condition are also related to the inhibition of other macros (K, Ca, Mg and P) and micronutrients (Mn, Cu, Mo and Zn) (Lima et al. 2018). In the case of cobalt (Co), deficiency directly interferes with nitrogen fixation, since the component is part of cobalamin, a vitamin used in bacterial fixation enzymes (Akeel and Jahan 2020).

Heavy metals also result in physiological damage to the plant. In mulberry seedlings (*Morus alba* L.), for instance, the stress caused by lead (Pb) and cadmium (Cd) intensified the formation of reactive oxygen species (ROS), and consequently, caused the degradation of chlorophyll (Huihui et al. 2020). For other forest species native to Brazil, the increase in inc (Zn) concentration led to lipid peroxidation due to ROS (Souza et al. 2020).

Anatomical and morphological responses

Biochemical and physiological impacts result in anatomical (or morphological) reactions in plants. Decreases in height, biomass, and leaf area are characteristics of boron deficiency (Fig. 4A), while the toxicity caused by the excess of the nutrient causes scorching of leaves, but without significant impacts on the roots due to the lower concentration of the nutrient in this region (García-Sánchez et al. 2020). On the other hand, phosphorus deficiency in *Citrus* species showed an increase in the ratio between the root and the shoot due to the decrease in the leaf and stem area (Fig. 4B), which can be explained by the reduction in the chlorophyll content (Meng et al. 2021). Additionally, soils with high aluminum concentrations can result in P stress, as aluminum reduced phosphorus concentrations in the root, stem, and leaves of *Citrus grandis* (L.) Osbeck (pomelo) (Jiang et al. 2009).

For clones of *Prunus persica* Batsch (peach tree), symptoms of chlorosis, senescence, and necrosis (Fig. 4C) were observed as a response to calcium deficiency. Moreover, this element acts to mitigate the effects caused by the phosphorus deficiency in Chinese spruce trees (*Cunninghamia lanceolata* (Lamb.) Hook.) (Rashid et al. 2020). Under conditions of soil nitrogen limitation, forest species are more sensitive to drought due to reduced root biomass (Song et al. 2019). The exposure time to N showed a positive correlation with the degree of injury in *Carpinus putoensis* W.C.Cheng (Putuo hornbeam) leaves (Fig. 4D), where after 72 hours the impacts were irreversible and resulted in the death of the leaf (Sheng et al. 2021).

On the other hand, excess copper (Cu) is associated with increased susceptibility to attack from pathogens such as rust. The omission of this nutrient in fertilization accounted for 30% of the reduction in *Eucaliptus* leaf width (Masullo et al. 2020). In a study carried out with the *Salix babylonica* tree (Weeping willow) in China, dosages from 100 μM resulted in morphological alterations, with a reduction in the total height and number of leaves (Fig. 4E). With the application of 200 μM of Cu, there was a decrease in length and quantity of roots, and at dosages of 200 to 400 μM the plants gradually died (Wang et al. 2020).

In *Hevea brasiliensis* (rubber tree) seedlings, the omission of potassium and magnesium in the fertilization caused a reduction of approximately 12% and 16% in the total height and diameter of the stem of the plants, respectively (Fig. 4F) (Xue et al. 2019). The root biomass can also be reduced, that is because the reduction in the content of both nutrients increases the concentration of sugar (sucrose and starch) in leaves, as consequence of the reduction in transport of sucrose (Xue et al. 2019).

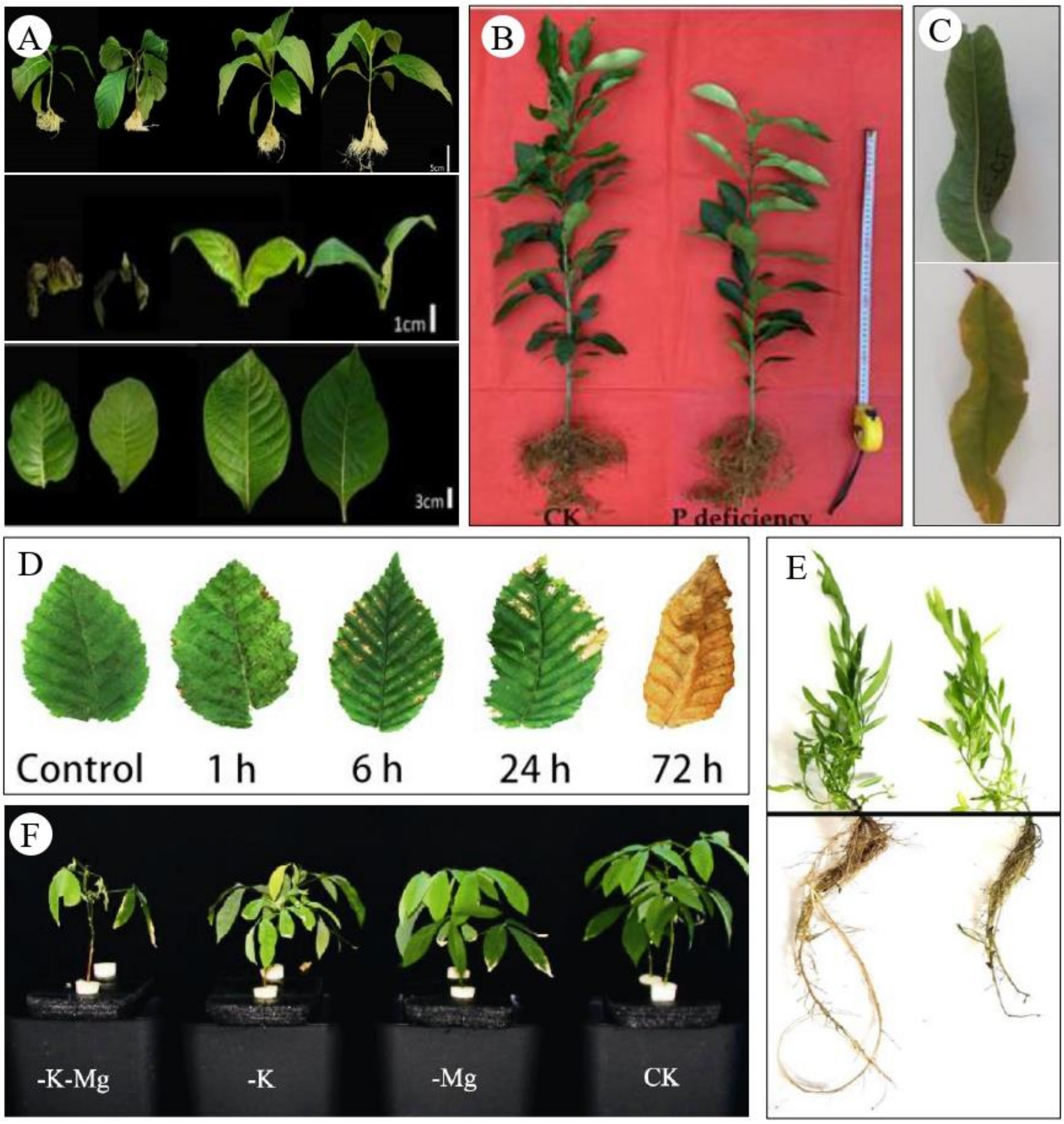

Figure 4. Morphological responses in leaves and/or roots of tree species subjected to nutritional stress. A = *Neolamarckia cadamba* (Roxb.) Bosser seedlings that did not receive boron dosages, on the left, and those that received 20 µM of boron, on the right (Yin et al. 2022). B = Effects of phosphorus deficiency on *Citrus grandis* (L.) Osbeck seedlings (Meng et al. 2021). C = Calcium deficiency on *Prunus persica* Batsch leaves (Aras et al. 2021). D = Effects of exposure time to NO2 ion *Carpinus putoensis* Cheng (Sheng et al. 2021). E = Responses of the application of 100 µM of cobalt in comparison with the non-application on *Salix babylonica* seedlings (Wang et al. 2020). F = Fertilization with the joint absence of K and Mg (-K-Mg), absence of K only (-K), absence of Mg only (-Mg) and control treatment in *Hevea brasiliensis* seedlings (Xue et al. 2019). Source: Adapted from Yin et al. (2022); Meng et al. (2021); Aras; Keles; Bozkurt (2021); Sheng et al. (2021); Wang et al. (2020b) and Xue et al (2019).

Visually, interveinal chlorosis is one of the characteristics of iron (Fe) deficiency which can be minimized by ABA production (Fig. 5). In an experiment conducted under controlled conditions, the application of abscisic acid helped in the increase of the root system, and the results indicated a gradual reduction of the action of this hormone in 7 days, allowing to infer the consumption of ABA by the roots in the circumstance of Fe deficiency (Zhang et al. 2020).

Figure 5. Influence of Abscisic Acid (ABA) and iron deficiency (Fe) in two-month-old Malus hupenensis seedlings for phenotypes (A), appearance of leaves from bottom to top (B), activity of ferric reductase enzyme (C) and root development (D). Intense purple represents high Fe2+ concentrations. Where the treatments are: -Fe = iron deficiency; +Fe = Addition of 50 µM Fe; -Fe + ABA = without addition of iron, and addition of 5 µM de ABA; + Fe + ABA = addition ofb50 µM Fe and 5 µM of ABA. Source: Adapted from Zhang et al. (2020).

Strategies used in forest restoration practices in the Amazon to minimize nutritional stress

In order to mitigate the impacts of nutritional limitations and enhance the results of restoration methods, strategies have been adopted by numerous researchers in the Amazon biome (Dias et al. 2012, Thomas and Gale 2015, Barbosa et al. 2022) (Fig. 6A). Among them, revegetation with seedling planting of native species is the most used one (Fig. 6B), being advantageous due to the possibility of choosing species suitable for the conditions of the ecosystem (Martins et al. 2022). In the Amazon, the specie *Mimosa acutistipula* var. ferrea Barneby (Mimosa of canga) is highly recommended for revegetation of areas with ferruginous outcrops, as it favors symbiotic associations with nitrogen-fixing bacteria (Costa et al. 2021).

Trees of the genus *Cecropia* and *Inga*, naturally regenerated in altered areas in the Amazon (Rezende and Vieira 2019), are generally characterized by low mortality and high contribution to restoration (Barbosa et al. 2021, Oliveira et al. 2022). Photosynthetic efficiency and nutrient use may be the main reasons for the successful establishment of these species (Santos Junior et al. 2006). Combined with revegetation, fertilization and remediation of soil acidity are the most common and widely used alternatives (Fig. 6C). Generally, after the application of nitrogen fertilizers (Martins et al. 2018) and dolomitic limestone (Oliveira et al. 2022), there are short-term and positive responses to tree seedling development, mainly due to reduced aluminum and increased availability of calcium and magnesium. On the other hand, it is costly and often not feasible strategy (Nunes et al. 2020), which may be replaced by organic fertilization methods that also supply the absence of these nutrients in the soil and are low cost and easy to acquire.

Used for decades, natural regeneration is a simple and generally efficient alternative that depends on the degree of degradation and propagules sources available (Poorter et al. 2016, Chazdon and Uriarte 2016), mainly due to the resilience of the Amazon ecosystems (Andrade et al. 2020). The technique consists of progressively recovering ecosystem functions, especially the nutrient cycle, without human interference (Chazdon and Uriarte 2016). A case study in the Amazon showed the return of edaphic attributes after 7 years of regeneration (Brasil Neto et al. 2021). However, in cases where propagules sources are exhausted, the method of spreading piles of organic waste called nucleation (Fig. 6D) intensifies the action of microorganisms and, consequently, the formation of organic matter in the soil, raising the pH (Barbosa et al. 2022).

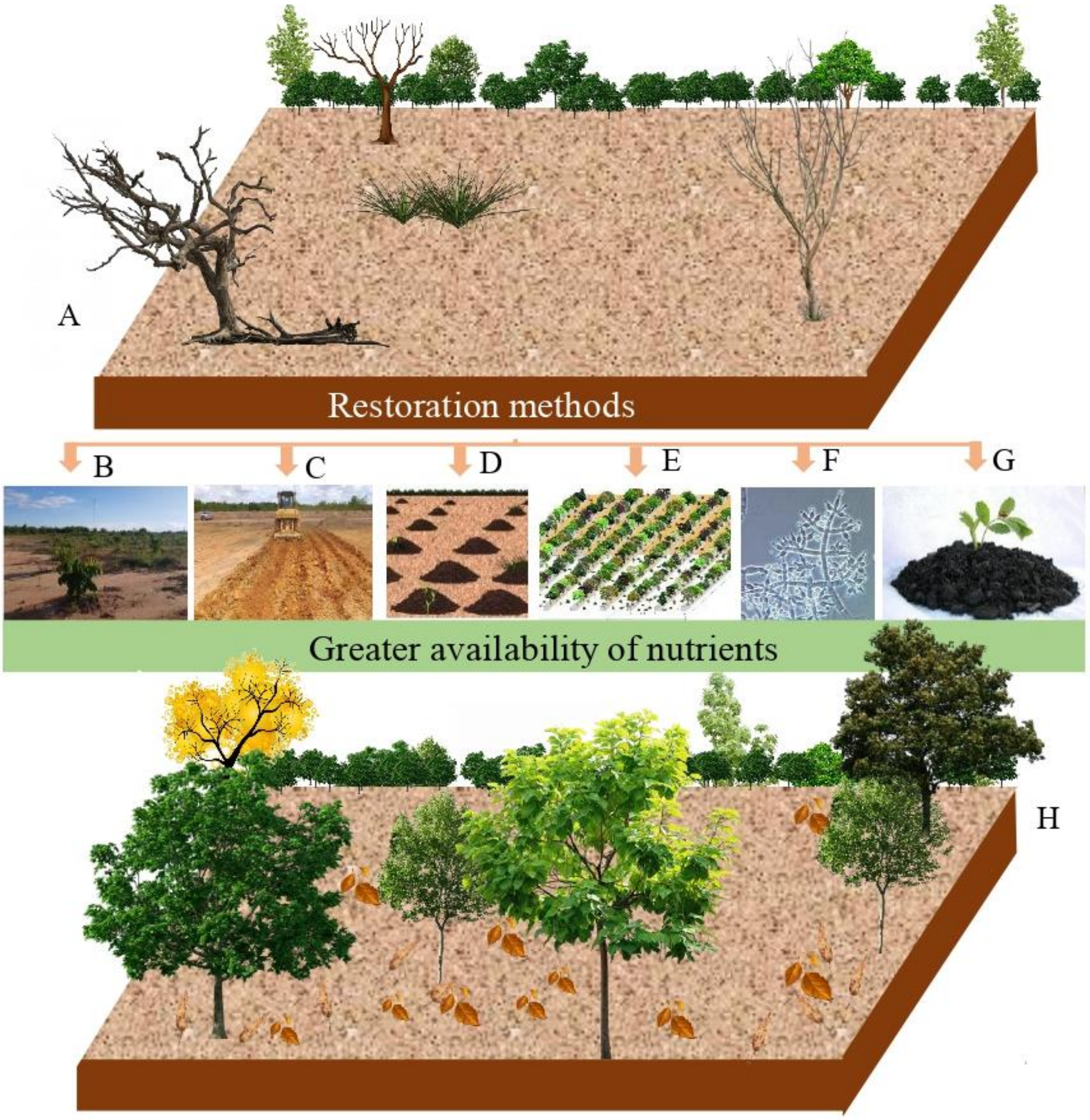

Figure 6. Strategies used in the Amazon to minimize the impacts of soil nutritional limitations and promote the restoration of degraded ecosystems (A). Where B = seedling planting; C = soil preparation with fertilizers (Oliveira et al., 2022); D = nucleation (Barbosa et al., 2022); E = soil cover with organic waste (Ribeiro et al., 2022); F = biostimulants application; G = biochar use. Source: Authors.

For shifting cultivation, researchers from the Brazilian Agricultural Research Corporation (Embrapa) have developed a “Chop-and-mulch” system, aiming to replace the use of fire by the shredding of vegetation of a secondary forest called "capoeira" with the aid of an adapted tractor (Embrapa, 2017). Another alternative to increase the sustainability and self-maintenance of this type of cultivation is the agroforestry systems (Suárez et al. 2021). Organic fertilization with sawdust (Fig. 6E) reduced soil acidity and increased the availability of nutrients in an area degraded by kaolin mining in the Eastern Amazon (Ribeiro et al. 2021), and can also be used for shifting cultivation.

In general, biofertilizers and biostimulants are increasingly required in both national and international scenarios (Kumar and Pandey 2020, Silva, Nascente, et al. 2020, Ligowe et al. 2020, Zin and Badaluddin 2020). Biofortification is an approach widely used in agricultural crops to reduce nutrient deficiencies in rural communities (Ligowe et al. 2020) but lately, it has been used to reverse nutrient deficiencies in soils, optimizing the growth of tree species (Younas et al. 2022). For instance, biofortification with selenium, which is an essential nutrient for the production of cell membrane protective enzymes, stimulates antioxidant activity, fighting ROS and minimizing the impacts of nutritional stress (Lanza and Reis 2021; Silva et al. 2020).

In other ways, inoculation of growth-promoting microorganisms such as Arbuscular Mycorrhizal Fungi (AMF) and nitrogen-fixing bacteria are effective biostimulants in plant growth (Vieira et al. 2017). Fungi of the genus *Trichoderma* sp. (Fig. 6F), for example, are phytopathogenic controllers and decomposition attenuators, increasing the availability of macro and micronutrients (López-Bucio et al. 2015). In the Brazilian Atlantic Forest biome, the fungus increased the survival rates and height of tree seedlings such as *Cedrela fissilis* Vell. (Cedro rosa), ensuring successful restoration (Griebeler et al. 2021). Added to this, inoculation of the fungus causes the root system to expand, allowing for increased absorption of nutrients (Zin and Badaluddin 2020).

Another strategy is the use of biochar (Fig. 6G), a natural, inexpensive, and effective remediation solution for contaminated soil (Lefebvre et al. 2019, Neogi et al. 2022), used to recover degraded areas in the Amazon, reusing açaí seeds (Ramos et al. 2021). In other biomes, biochar from *Eucalyptus* sp. promoted an increase in soil pH and a reduction in the availability of heavy metals such as cadmium, lead, and zinc (Penido et al. 2019).

Conclusions

Our research has demonstrated the impacts of nutritional limitations on the development of tree species and the efforts of the scientific community to minimize damage to restoration. Nutrient deficiencies in cell structures are closely linked to the reduction of plant structural variables, such as height and diameter. Damage to enzymatic activity and stomatal regulation was also observed. In contrast, oxidative stress can lead to phytotoxicity because of the formation of reactive oxygen species. Despite this, we noted in our review a limitation of scientific information related to the theme, particularly for forest species in the Amazon. In this way, we recommend the promotion of research for the biome, aiming to reduce existing gaps and maximize the potential of forest restoration.

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