The role of CAM ecophysiology in the Anthropocene

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Abstract

Human impact on the planet is such that geologists have acknowledged the start of a new geological epoch, the Anthropocene, which is characterized by an environmental emergency with multiple open fronts such as climate change, biodiversity loss, decreased fresh water availability, alterations to the nitrogen cycle, and chemical pollution. Activities such as food production and the increasing aggregation of people in urban areas are simultaneously major drivers and vulnerable points of such environmental change. For example, climate change represents a major threat to food production, considering that a reduction of annual precipitation, in addition to temperature increases, is likely to occur especially in tropical agricultural regions. The use of CAM crops has been recognized as a useful strategy for climate change adaptation, owing to their tolerance of high temperatures and their inherently high water use efficiency. The potential performance of *Opuntia ficus-indica* and *Agave tequilana* is modeled as an application of the environmental productivity index for identifying potential areas for cultivation under climate change. Regarding alterations to the nitrogen biogeochemical cycle, CAM epiphytes can be useful to characterize environmental pollution in tropical environments, especially when electrochemical monitoring networks are lacking. Indeed, CAM epiphytes are particularly promising to characterize the prevalent levels of heavy metals, persistent organic pollutants and, especially, nitrogen deposition. This is illustrated with the use of the orchid *Laelia speciosa* and the bromeliad *Tillandsia recurvata* as biomonitors of atmospheric nitrogen deposition. From fundamental research on the mechanisms behind plant responses to environmental change to applications in agriculture and biomonitoring, CAM ecophysiology will be essential in the Anthropocene.

Keywords: arid agriculture, atmospheric pollution, biomonitors, climate change, environmental productivity index (EPI), food security, nitrogen deposition

INTRODUCTION

Over recent decades the study of plant physiological ecology has improved our understanding of plant responses to a changing and often stressful environment (De la Barrera and Andrade, 2005; Nobel, 2009; Cooke et al., 2021). For the particular case of CAM plants, the study of their adaptations and performance in usually warm, dry, and often oligotrophic environments has allowed the elucidation of fundamental mechanisms of temperature, water, and nutrient utilization by plants (Nobel, 1988; De la Barrera and Andrade, 2005; Yang et al., 2015; Inglese et al., 2017). For example, it is now possible to engineer succulence in plant tissues utilizing molecular tools (Cushman and Lim, 2021). As a result, the study of CAM ecophysiology has also allowed the development of vigorous arid and semi-arid horticultural activities and the development of new crops that are better suited to grow in stressful environments than traditional crops (Nobel, 2000). This is of particular importance considering that ongoing environmental change poses a substantial risk to global food security, particularly in tropical regions where rainfed agriculture is estimated to have a decrease in productivity during the present century as a direct consequence of higher air temperatures, lower annual precipitation, and an increase in the frequency and severity of

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extreme weather events, such as frosts, droughts, hail events, or floods (McDonald, 2010; Intergovernmental Panel on Climate Change, 2012, 2021).

This work considers some of the potential contributions of CAM ecophysiology in a human dominated world. First, we will review the origin and current status of the Anthropocene, as a backdrop for global environmental change. We will then consider the "planetary boundaries" framework (Rockström et al., 2009) as a group of parameters by which human effects on the planet can be quantified and kept at levels that allow the persistence of human civilization. The general introduction to planetary boundaries will be followed by an in-depth discussion of two of the boundaries whose thresholds have been crossed, for which CAM plants can be a useful tool. For the case of climate change, we will revisit the environmental productivity index (Nobel, 1984), which can be a useful tool for estimating the productivity of CAM crops under different climate change scenarios, which we will illustrate with the potential cultivation of *Opuntia ficus-indica* in California, USA, and *Agave tequilana* in Jalisco, Mexico. The second planetary boundary under consideration is the removal of large amounts of nitrogen from the atmosphere and its release into the biosphere as reactive chemical forms. The case will be made for the use of two succulent CAM epiphytes, the orchid *Laelia speciosa* and the bromeliad *Tillandsia recurvata*, as biomonitors of such atmospheric nitrogen deposition.

ANTHROPOCENE

The term Anthropocene was coined at the start of this century by the atmospheric chemist Paul Crutzen while attending a scientific meeting in Cuernavaca, Mexico (Steffen, 2013). As presenters kept referring to the Holocene in their talks in a business-as-usual manner, Prof. Crutzen became increasingly uneasy, until finally interjecting that people should stop referring to the Holocene as the current geological period, because we already were in the Anthropocene. The term was formally proposed shortly after, arguing that the human impact on the planet is such that we have effectively changed various biogeochemical processes, from the loss of biodiversity directly caused by land use change, to the thinning of the stratospheric ozone layer by the action of chlorofluorocarbons and an impending global warming resulting from the release of greenhouse gases to the atmosphere (Crutzen and Stoermer, 2000). The year 1784 was originally proposed as the starting point for the Anthropocene to coincide with the invention of the steam engine, although the authors acknowledged that human influence on terrestrial systems can be traced throughout the Holocene. During the following two decades, the term Anthropocene became a convenient heuristic for discussing and teaching about the human impact on the planet (Trischler, 2016). Its use has become controversial in various scientific disciplines, partly owing to its utilization without a formal definition nor scientific rigor and many cases with an activism connotation (Zalasiewicz et al., 2019; Gibbard et al., 2021).

As the Anthropocene became an increasingly prevalent concept in the academic literature, a formal evaluation was undertaken by the Anthropocene Working Group, a part of the International Commission on Stratigraphy, which concluded that the impact of human activities on various planetary systems is such that its magnitude is equivalent to that of an Epoch (Zalasiewicz et al., 2019; Working Group on the Anthropocene, 2021). The Anthropocene is now proposed to have begun in the mid-20th century, although the actual geological indicator, or "golden spike", still remains under debate, including the accumulation of plastics or electronic waste, and even the enormous amounts of broiler chicken that make up a substantial part of various global diets (Bennett et al., 2018; Zalasiewicz et al., 2019). The most favored indicator for the start of the Anthropocene, however, is the increase in radioactive material resulting from thermonuclear explosions. In any case, the Anthropocene Working Group has explicitly recognized that the two conditions required for the acceptance of a distinct geological time term have been met. First, that the geological signal needs to be sufficiently large and distinct so that its accumulation is possible in the strata that are currently under formation. Second, that the term utilized, i.e., Anthropocene, is actually useful to various scientific communities. They point out, however, that a distinction should be made between the formal geological Anthropocene and the increasingly frequent use by various scientists and non-scientists in a non-chronostratigraphic way, but that these two uses can be complementary.

PLANETARY BOUNDARIES

With a human-influenced geological period underway, indicators are required to monitor our impacts on the various planetary systems. To this end, a “planetary boundaries” framework has been proposed that considers nine environmental subsystems that are essential for maintaining (human) life on Earth and which are under severe anthropic pressure: climate change, interference with the nitrogen and phosphorus biogeochemical cycles, biodiversity loss, land use change, ocean acidification, freshwater availability, chemical pollution, atmospheric aerosol loading, and stratospheric ozone depletion (Rockström et al., 2009). For each dimension a quantitative threshold can be identified, at least in theory, beyond which anthropogenic pressure may lead to an irreversible and abrupt environmental change that will deteriorate human wellbeing. In this case, a “safe operating space for humanity” is expected to prevail if the boundaries are not crossed for all nine dimensions.

The thresholds for three of the planetary boundaries have already been exceeded, i.e., climate change, the nitrogen cycle, and the rate of biodiversity loss. Given their importance for food production, we shall focus on climate change and nitrogen. For the first case, an atmospheric CO_2 concentration of 350 ppm has been proposed as the critical threshold because the resulting air temperatures are compatible with a rather stable existence of the polar ice sheets, which only appeared on the planet after the CO_2 concentration of the primitive atmosphere was driven down by photosynthetic organisms (Rockström et al., 2009). Considering that the current atmospheric concentration of carbon dioxide has already exceeded 400 ppm, multinational efforts are now required to remove carbon from the atmosphere in addition to avoiding future emissions of greenhouse gases (Intergovernmental Panel on Climate Change, 2021; Global Monitoring Laboratory, 2021). For the case of nitrogen, a proposed boundary of 34 Tg year^{-1} of nitrogen removed from the atmosphere for human utilization matches the approximate amount of reactive nitrogen that is produced by natural processes (Fowler et al., 2004). The current annual rate of reactive nitrogen emissions of ca. 124 Tg exceeds the historical availability of reactive nitrogen, leading to biodiversity loss, contributing to climate change, and constituting a main component of environmental pollution.

Climate change

Climate change is driven by the accumulation of the greenhouse gases that are released to the atmosphere by various human activities. Given their optical properties – i.e., absorbing electromagnetic radiation at certain wavelengths (Platt et al., 2007) – these gases retain the solar energy that reaches the surface of the Earth instead of allowing its rapid dissipation back to space. While this mechanism maintains atmospheric temperatures in a range that is compatible with life, the utilization of fossil fuels over the past 150 years is releasing back to the atmosphere substantial amounts of the carbon that had been captured and immobilized over the course of evolutionary history, at a rate that exceeds the buffering capacity of existing photosynthetic organisms (Intergovernmental Panel on Climate Change, 2021).

Climate change has been extensively studied and its linkage to anthropic activities, once a matter of debate, is clear (Intergovernmental Panel on Climate Change, 2021; Lynas et al., 2021). Its imminence and severity have led to numerous calls to action, effectively forcing governments to commit to the implementation of policies that decrease the release of greenhouse gases. However, from the Rio de Janeiro Earth Summit in 1992 to the 2021 COP-26 in Glasgow, governments have been negligent in implementing the required changes that could reduce greenhouse gas emissions at the required pace. It is no longer sufficient to reduce the rate of greenhouse gas emissions to stay within the 1.5°C increase in air temperature required to minimize the climate risk facing human populations (Intergovernmental Panel on Climate Change, 2018, 2021). At this point, the development and implementation of new technologies that can remove carbon from the atmosphere at a rapid pace are required in addition to limiting new emissions.

Agricultural production is a major source of direct and indirect greenhouse gas emissions, contributing about one quarter of the greenhouse gases that are released to the atmosphere each year (Intergovernmental Panel on Climate Change, 2019). Unfortunately, agriculture is also one of the most vulnerable economic sectors to environmental change, precisely because it relies on a relatively stable and benign climate (McDonald, 2010). The optimal areas for the cultivation of various tropical crops are likely to shift during the present century toward higher altitudes and latitudes (Intergovernmental Panel on Climate Change, 2021). At the same time, the frequency and severity of extreme weather events, such as droughts, are likely to increase (Intergovernmental Panel on Climate Change, 2012). Under this ongoing climatic threat to rural livelihoods, and food security in general, the study and utilization of CAM crops has been proposed as an alternative (Nobel, 1988; García-Moya et al., 2011).

The performance of CAM plants under different climatological conditions, including climate change scenarios, can be modeled by means of the Environmental Productivity Index (EPI), which was originally developed for *Agave deserti*, a relatively small plant from the Mohave Desert, USA (Nobel, 1984). Briefly, CO_2 uptake rates are measured in the laboratory in response to changes of a single environmental factor, e.g., air temperature, soil water potential, photosynthetic photon flux (PPF), while the rest are kept at optimal levels (Nobel, 1988, 2009). An equation can be created for plant responses to each individual factor and expressed as a proportion of the maximum. Such individual indices can thus have a maximum value of 1.0 when the condition leads to the maximum rate of gas exchange, and it decreases as the condition departs from the optimum. The minimum value is zero when the environmental condition leads to the interruption of gas exchange. The EPI is then calculated by the multiplication of the individual index values that result from a particular set of environmental conditions. Once the EPI has been created experimentally for a given plant species, its field validation can be conducted in two parts. First, a growth parameter that correlates with gas exchange is identified so that the plant's productivity can be monitored in a non-destructive way, such as measuring cladode area for opuntias, the formation of new areolas for columnar and barrel cacti, or the unfolding of new leaves for agaves. The second step is to gather environmental information in the field, i.e., air temperature, soil water potential, PPF, and verify whether the estimated values for the individual indices and the combined EPI effectively predict the plant's productivity.

The EPI approach has been useful over the past four decades for predicting the field performance of various CAM plants, especially for crops, such as *Opuntia ficus-indica*, *Hylocereus undatus*, and different agaves cultivated either for fiber or liquor production (Nobel, 1984, 1988, 2009; Nobel and Hartsock, 1984; Nobel and Valenzuela, 1987; Nobel and de la Barrera, 2004; Nobel et al., 2002; Cervera et al., 2007). Facing the Anthropocene, the EPI can be utilized in combination with climate change models to estimate future plant performance. Let us consider two examples focusing on temperature, the environmental factor that is most difficult to control. Indeed, the amount of light reaching the photosynthetic tissues of plants can be manipulated by means of plant spacing and training, as well as with the use of shade-cloth or trees. In turn, the amount of soil water available for the plants can be increased by irrigation.

The first example considers the potential cultivation of *Opuntia ficus-indica* in the Central Valley basin, California, USA (Figure 1A, top left). This region is considered to be the most valuable agricultural region in the United States, owing primarily to the cultivation of high-value crops, usually under irrigation. However, multi-annual droughts over the past two decades have affected the entire state of California, posing a threat to the economic viability of water-intensive crops such as rice and almonds (Howitt et al., 2014). In some instances, farmers are opting to sell their annual water quotas and abandoning agricultural activities altogether. *Opuntia ficus-indica* can be a convenient alternative for cultivation in this region, considering that about one third of the area of the state of California is already very suitable for its cultivation, especially in the Central Valley (Nobel et al., 2002). Indeed, a temperature index of 0.83±0.03 is representative for *Opuntia ficus-indica* in this region (Figure 1B). However, this can decrease by up to 28% over the course of the century as a result of the air warming estimated under two moderate climate change scenarios.

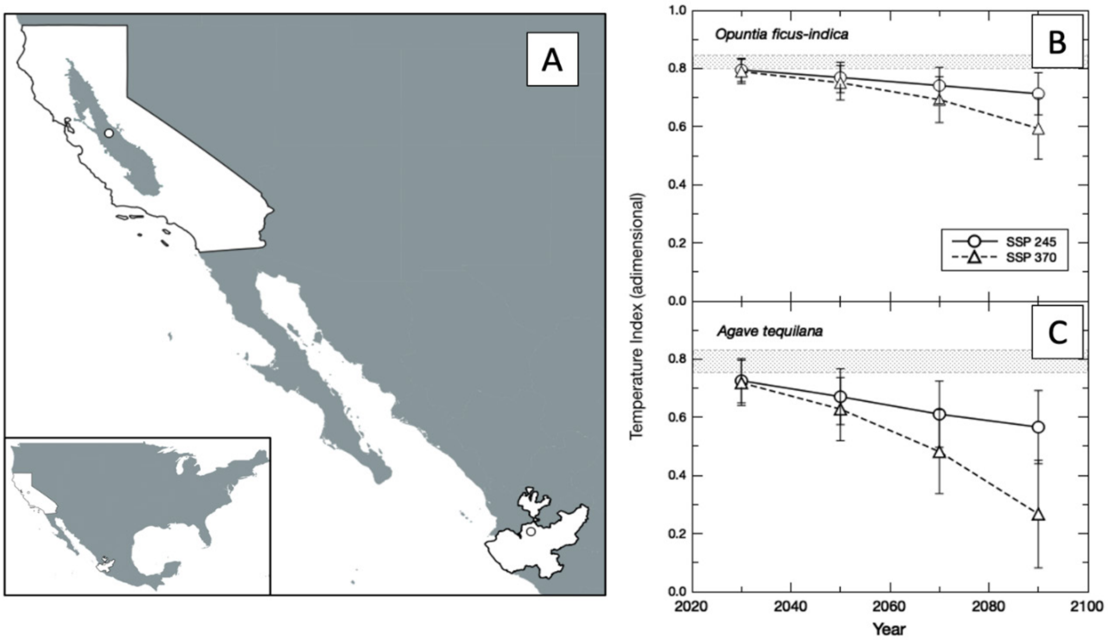

Figure 1. Responses of the temperature index (TI) to climate change for two CAM crops in North America (A), *Opuntia ficus-indica* (B) in the Central Valley, California, and *Agave tequilana* (C) in Tequila, Jalisco. In panel A the inset shows the location of the states of California, USA and Jalisco, Mexico, along the Pacific coast. The shaded area in California indicates the Central Valley basin and the circle in either state indicates the location utilized for the TI calculations. For panels B and C the shaded band indicates the "current" mean TI ±1 S.E. (*n*=12 months) based on the 1970-2000 climate normals. Symbols indicate the mean TI ±1 S.E. (*n*=12 months) under the SSP25 (circles) and SSP370 (triangles) emissions scenarios from the CanESM5 global climate model. The temperature indices were calculated from Nobel and Hartsock (1984) and Nobel and Valenzuela (1987), with climate scenarios were obtained from WorldClim 2.0 (Fick and Hijmans, 2017).

The second example under consideration is *Agave tequilana* in Jalisco, México (Figure 1A, bottom right). The sugars accumulated by this plant over multiple years are utilized in the production of tequila, a distilled liquor that is protected under the first geographic indication issued by the Mexican government in 1976. Because the geographical region where tequila can be produced is legally constrained, climate change can pose a risk for the economic viability of what has become a multi-million dollar transnational industry. Indeed, the temperature index for *A. tequilana* is 0.79±0.04 near Tequila, Jalisco, the municipality of west-central Mexico that gave origin and name to the drink (Figure 1C). Temperature increases are likely to drive a regional reduction of this plant's productivity of up to 66% over the course of the century.

When projected on a geographic space, the temperature index can help identify suitable areas for cultivation, including under different scenarios of climate change. For instance, the air temperature at the Central Valley, which is currently optimal for the cultivation of *Opuntia ficus-indica* (Figure 2A), is likely to increase driving a reduction of the crop's productivity in the entire basin, while the optimum temperatures will shift in elevation toward the surrounding mountains that are currently too cold for the cultivation of the cactus (Figure 2B). For the case of *A. tequilana*, the optimal thermal region within the state of Jalisco, which represents the bulk of the protected region for the production of tequila, is precisely the central portion of the state, including tequila (Figure 2C). However, temperature increases over the course of the century are likely to displace the optimal regions for the cultivation of the plant to higher elevations toward the north-eastern portion of the state (Figure 2D).

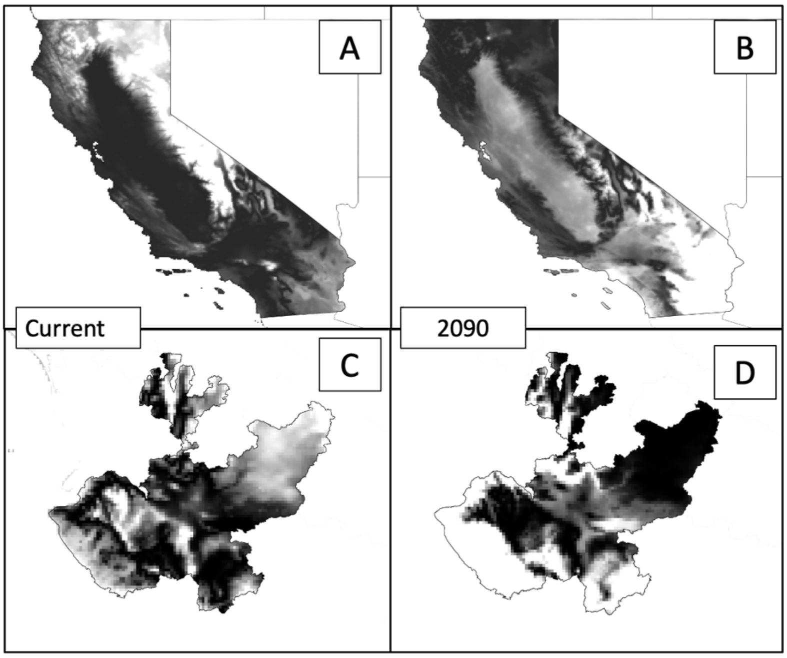

Figure 2. Potential productivity of two CAM crops in North America. The temperature index for *Opuntia ficus-indica* is shown for sites of California, USA, where it is higher than 0.5 (A) under "current" climate (based on normals of 1970-2000) and (B) under future potential climate centered in 2090 under the SSP370 emissions scenario from the CanESM5 global climate model. Similarly, the temperature index for *Agave tequilana* is shown in sites in the state of Jalisco, Mexico, where it exceeds 0.5 for (C) current and (D) future conditions. A darker shading indicates a higher temperature index under the environmental condition, while white areas are deemed unsuitable. Data sources are the same as for Figure 1.

As ongoing climate change exerts pressure on conventional agricultural production, the importance of CAM crops as sources for food, forage, fiber, energy, etc., is likely to increase during the current century.

Nitrogen deposition

Despite the abundance of nitrogen in the planet's atmosphere, this essential element has remained mostly unavailable to organisms throughout evolutionary history given the chemical stability of the N_2 molecule. Indeed, large amounts of energy are required to break the triple bond holding molecular nitrogen together, so that only ca. 34 Tg are fixed annually by the energy of lightning and through the action of certain soil microbes (Fowler et al., 2004). With the invention of the Haber-Bosch process at the start of the 20th century, through which ammonia is produced from the reaction of molecular nitrogen and hydrogen under elevated hydrostatic pressures and temperatures, it became possible to produce essentially unlimited amounts of synthetic fertilizers, although at very high energy and carbon costs (Galloway et al., 2017, 2021; Martínez et al., 2021). This artificial nitrogen fixation pathway has become the primary source of reactive nitrogen entering the biosphere. The ability to produce fertilizers from "thin air" has allowed the increase of food production driving our accelerated population growth (McDonald, 2010). However, the massive release of reactive nitrogen to the environment, which currently exceeds 124 Tg year^{-1}, has also been identified as the cause of severe environmental problems, including the eutrophication of water bodies, the proliferation of nitrophilous invasive species, and the loss of sensitive native organisms (Sala et al., 2000; Fowler et al., 2004; Rockström et al., 2009).

As our understanding of the role of nitrogen improves, efforts are necessary to limit the amount of reactive species that are released to the environment, while increasing agricultural productivity to meet the challenge of accelerating food production at a rate that matches the requirements of our increasing population (McDonald, 2010; Galloway et al., 2017). For example, a higher nitrogen use efficiency in agriculture, either by cultivar selection or by controlling nutrient application, will certainly reduce the utilization of synthetic fertilizers. However, an additional source of reactive nitrogen needs to be addressed if the planetary boundary of nitrogen is to be met. The controlled explosions of internal combustion engines, most prevalent in cities, release sufficient energy to break down the molecular nitrogen from the air, producing nitrogen oxides (NOx), which are directly harmful and are precursors of other noxious pollutants, such as particulate matter and tropospheric ozone (Galloway et al., 2021).

In addition to being a principal cause of biodiversity loss, environmental pollution has become a major threat to public health globally; it is in fact the main cause of premature mortality (Landrigan et al., 2018). It is thus necessary to control the release of pollutants and measure the levels to which the population is exposed. In fact, most countries have implemented legislation in this sense and the UN has recently recognized access to a clean and healthy environment as a basic human right. However, the deployment, operation, and maintenance of monitoring stations, usually an obligation of local governments, can be excessively costly so that the fulfilment of environmental mandates becomes unenforced. In these cases, the utilization of biomonitors has been proposed as an economically viable alternative for regions where electrochemical monitoring networks are not available (Díaz-Álvarez et al., 2018; Martínez et al., 2021). Most biomonitoring studies have been conducted in temperate regions of Europe, the USA, and China, with bryophytes (Martínez et al., 2021). The lack of cuticle of these plants allows the ready diffusion into plant cells and rapid assimilation of nitrogen deposition. In addition, their lack of proper organs, particularly functional roots, allows these plants to grow on inert surfaces, such as rocks, tree branches, rooftops, etc., where their mineral nutrition depends on atmospheric sources.

A large proportion of biodiversity occurs in tropical regions where an accelerated urban growth is also prevalent, usually in countries with emerging economies, whose local governments are often unable or unwilling to implement environmental monitoring. Thus, the development and utilization of biomonitors in these regions could help characterize the prevailing atmospheric pollution in different regions of interest. However, the use of bryophytic biomonitors is not always possible in seasonally dry regions. Under this situation, a lack of cuticle makes plants prone desiccation, while they require continuous humidity to remain physiologically active. In these circumstances, succulent CAM epiphytes can be a viable alternative. Let us consider two examples of epiphytic CAM succulents that can be particularly useful as biomonitors of nitrogen deposition, given their adaptation to the environmentally taxing epiphytic habit, including a predominantly atmospheric origin of their mineral nutrition.

The first example is the epiphytic CAM orchid *Laelia speciosa*, an emblematic plant of the state of Michoacán, Mexico, along with various local maizes, the *cempasúchil* (a yellow *Asteraceae* utilized for day of the dead decorations), and the controversial avocado. This plant not only produces beautiful flowers during the spring – hence its common name of *flor de mayo*, May flower –, but it is also utilized to make religious art pieces in the vicinity of Lake Pátzcuaro. In particular, the juice of the pseudobulbs of *L. speciosa* is mixed as a mordant with the pith of cornstalks to create a paste used for sculpting life-sized figures that are displayed in catholic churches. For this plant, rates of nitrogen deposition of up to 20 kg ha^{-1} year^{-1} actually have a fertilizing effect, as revealed by dose-response experiments (Díaz-Álvarez et al., 2015). At such levels of exposure to reactive nitrogen, the production of new leaves and pseudobulbs are maximum but decrease at higher doses, as do various parameters related with photosynthesis. In contrast, the tissue nitrogen content for this plant increases proportionally with the rate of nitrogen deposition and their ∂^{15}N becomes increasingly negative, in response to the isotopic composition of the ammonium nitrogen utilized in the experiments. Tolerance to nitrogen deposition by *L. speciosa* is substantial, considering that many plant species suffer physiological damage with rates as low as 10 kg ha^{-1} year^{-1} (Díaz-Álvarez et al., 2018).

The amount and origin of the reactive nitrogen that *L. speciosa* takes up from atmospheric deposition determine the nitrogen status of the plants. For example, a comparison of plants from a natural population from a remote location and unfertilized individuals from a peri-urban shadehouse suggest that the rate of nitrogen deposition at the experimental location is relatively low, as indicated by their very similar leaf nitrogen content (Díaz-Álvarez et al., 2016). However, isotopic analyses indicate that the sources of nitrogen available to either group are different. Indeed, the positive ∂^{15}N measured for the plants from the peri-urban shadehouse are characteristic of reactive nitrogen species originated from industrial and vehicular combustion (Xiao and Liu, 2002), contrasting with the negative values for the plants from the remote location, which are common for rural environments (Redling et al., 2013).

The morphological characteristics of orchids such as *L. speciosa* also allow for the tracking of nitrogen deposition over multiple years, in a similar way as tree rings can record the environmental and developmental history. Indeed, these plants produce a pseudobulb during each growing season, which remains attached to the plant and physiologically active over multiple years, even after its leaves have abscised (Figure 3A). The ∂^{15}N for a decadal chronosequence of *L. speciosa* pseudobulbs remains negative and relatively stable for plants growing in the remote location discussed above (Figure 3B). In contrast, the isotopic values for the pseudobulbs of transplanted individuals from the peri-urban shadehouse becomes increasingly positive over the years following their transplantation to the periurban site.

As illustrated by the case of *L. speciosa*, epiphytic CAM orchids can be useful biomonitors, especially in sites where urbanization is underway and the rates of nitrogen depositin are not excessively high (Díaz-Álvarez et al., 2019). Considering that the rates of atmospheric nitrogen deposition are likely to increase during the present century and already exceed 50 kg ha^{-1} year^{-1} in certain regions (Phoenix et al., 2006; Díaz-Álvarez et al., 2018), the utilization of orchid biomonitors may not become widespread. Additionally, despite the fact that the *Orchidaceae* is among the most diverse botanical families and that there are several invasive species, the fact that several orchids are under some degree of conservation risk, mainly from habitat loss or collection from the wild for ornamental purposes, their utilization can be difficult from legal and ethical standpoints.

The second example of a CAM succulent biomonitor is *Tillandsia recurvata* (common name is ball moss), which is amply distributed in the Americas and has been reported to become a plague in forests and plantations under certain circumstances (Benzing, 1980; Rodríguez-Robles and Arredondo, 2022). This plant is tolerant of urban atmospheric pollution, as can be deduced from its presence in many cities, where it often grows on the power lines along roads. In fact, it has proven to be an excellent monitor of several atmospheric pollutants, from carbon emissions of internal combustion engines to the deposition of heavy metals (Schrimpff, 1984; Zambrano García et al., 2009; Felix et al., 2016; Díaz-Álvarez and de la Barrera, 2020). The anatomical characteristics that allow *T. recurvata* to survive the very dry microenvironment where it lives, leading to a relatively slow growth, make it insensitive to different forms of wet nitrogen deposition (Díaz-Álvarez et al., 2020). However, both the tissue nitrogen content and the isotopic signature of this plant are most responsive to the atmospheric concentration of NOx (Díaz-Álvarez and de la Barrera, 2018). In particular, it has been documented in Mexico City, where an extensive electrochemical atmospheric monitoring network is in place, that the tissue nitrogen content of *T. recurvata* responds linearly to increasing concentrations of NOx of up to 80 ppb, which appears to become toxic at higher concentrations (Figure 4A). In turn, the ∂^{15}N of the plant becomes increasingly negative at higher atmospheric concentrations of NOx (Figure 4B). Following the “calibration” of *T. recurvata* conducted in the laboratory and its assessment in the field in Mexico City, work is underway to characterize atmospheric nitrogen deposition in other cities of Mexico lacking monitoring networks.

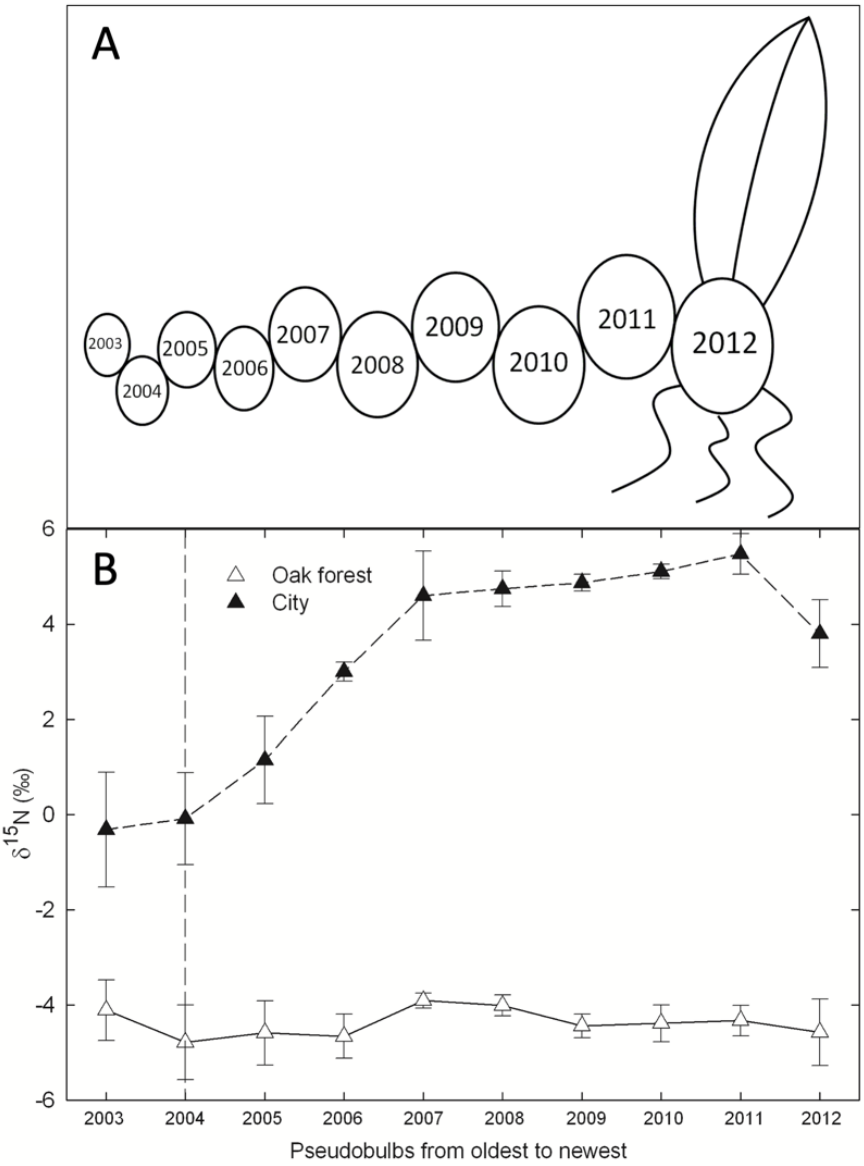

Figure 3. (A) Morphology of *Laelia speciosa* showing a series of then consecutive produced pseudobulbs. The most recent pseudobulb was formed during the 2012 growing season and is displayed having functional roots. As the carbon, water, and nutrient reserves are utilized, the older pseudobulbs become progressively smaller. (B) The $\partial^{15}N$ for individuals of *L. speciosa* from a remote forest and a periurban shadehouse over the course of a decade. Data are shown as mean ±1 S.E. (*n*=4 individuals per site). The vertical dashed line indicates the time when the "city" plants were transplanted from the field.

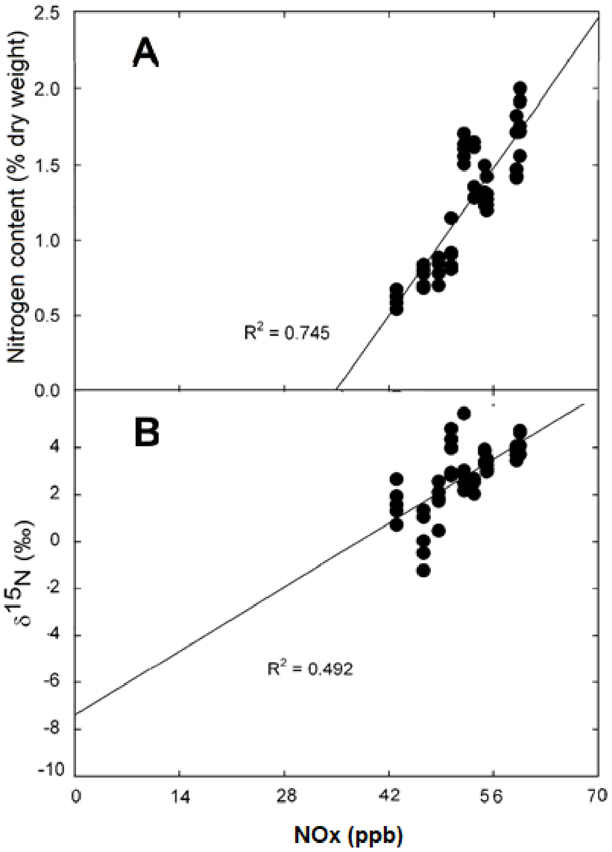

Figure 4. Relationship between NOx concentration in Mexico City and the nitrogen content (A) and $\partial^{15}N$ values (B) of *Tillandsia recurvata*. Modified from Díaz-Álvarez and de la Barrera (2018).

PERSPECTIVES

Among the different economic activities with important environmental impacts, food production is particularly problematic, considering that it is a major source for environmental degradation. Indeed, the clearing of natural vegetation for establishing new croplands is the main contributor to land-use change and biodiversity loss (Sala et al., 2000; Rockström et al., 2009). In addition, humans have appropriated one quarter of the terrestrial net primary productivity, 70% of which is related to the harvest of a few crops (Haberl et al., 2007; Krausmann et al., 2013). In consequence, agricultural operations also mobilize and transport large volumes of embedded water and nutrients, which may pose a threat to future water and food security in food-exporting regions (Dalin et al., 2017; Alcántara-Plazola and de la Barrera, 2021). As emerging economies become consolidated and increasingly urban, the demand for meat has increased in an accelerated way, creating even more pressure on various planetary systems (Tilman et al., 2011). However, food production will be required to double in order to meet the demand of our growing population, which is expected to reach 10 billion by mid-century (McDonald, 2010). As a result, the human appropriation of the biosphere and impacts on other planetary functions are likely to increase during the present century.

Simultaneously, food production is particularly vulnerable to environmental change, considering that agriculture relies on a relatively stable and benign climate with rather predictable seasons (Intergovernmental Panel on Climate Change, 2019). Unfortunately, climate change scenarios for the current century anticipate an increase of aridity, driven both by higher air temperatures and a decrease in precipitation, which will be particularly severe in tropical regions, where different peoples still rely substantially on nature for food, water, and energy (Fedele et al., 2022). Considering that most agricultural operations are rainfed, a decrease in yield in response to climate change, which has already been documented in various regions, is likely to pose an important threat to food security (Intergovernmental Panel on Climate Change, 2021). The utilization of CAM crops can represent an important alternative for increasing adaptation capacities for communities where rainfed agriculture of cereals becomes unfeasible. This is especially true for a versatile crop such as *Opuntia ficus-indica*.

The recent acceleration of food production that has sustained our civilization was allowed by the invention of the Haber-Bosch process that enables the production of synthetic fertilizer from ammonium derived from the molecular nitrogen that constitutes the bulk of the atmosphere (Galloway et al., 2021). Such large amounts of anthropogenic reactive nitrogen introduced to the biosphere not only represent a major threat to biodiversity but is also noxious to public health (Sala et al., 2000; Landrigan et al., 2018; Martínez et al., 2021). Although most countries have issued legislation to reduce the emissions of environmental pollutants and to monitor the levels of exposure of their citizens, the cost of deploying and maintaining monitoring networks can be excessively onerous. For these sites, the use of epiphytic photosynthetic organisms can help in the characterization of the pollution environment. Moreover, under impending scenarios of climate change, epiphytic CAM biomonitors can be especially suited to help characterize atmospheric pollution in seasonally dry neotropical regions.

Humans have become the dominant species on the planet, such that there is no place remaining that we have not impacted (Bazzaz et al., 1998). As it becomes increasingly clear that the effects of our combined actions actually have consequences on various planetary systems, our understanding of the drivers and connections of such systems also has improved. This lends the opportunity to develop and implement societal changes that reduce the ongoing environmental degradation (Chapin et al., 2010; De la Barrera, 2016). The study of CAM ecophysiology, either to improve food security, for biomonitoring environmental pollution, or for mitigating the pressure on other planetary boundaries, will undoubtedly realize its potential as a useful scientific tool for the Anthropocene.

CONCLUSIONS

- Human actions have impacted the planet in such a magnitude that a new geological epoch, the Anthropocene, has been proposed to have begun during the 20th century;
- Out of the nine planetary boundaries that have been identified that for maintaining a "safe operating space for humanity", three have been exceeded: biodiversity loss, climate change, and alterations to the nitrogen biogeochemical cycle;
- CAM crops, such as *Opuntia ficus-indica* and *Agave tequilana*, can be an adaptation tool for reducing the threat to food security posed by climate change, especially in tropical regions where aridity is likely to increase;
- While the gold standard for characterizing atmospheric pollution is the instrumentation of electrochemical monitoring networks, their use is often cost-prohibitive, especially in tropical regions with high biodiversity. In these sites, local species can be screened to develop biomonitors, bearing in mind that the species need to be tolerant to the pollutant of interest but sensitive such that that an ecophysiological parameter can be identified that reliably responds to the prevailing levels of pollution;
- *Laelia speciosa*, *Tillandsia recurvata*, and other epiphytic CAM succulents are most adequate biomonitors of atmospheric nitrogen deposition, especially for characterizing gaseous pollutants in cities. Their use as a complement to electrochemical monitoring is especially useful in seasonally dry tropical regions.

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