



The rise and fall of photosynthesis: hormetic dose response in plants

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Abstract The recent recognition that low doses of herbicides, human and veterinary antibiotics, metallic elements, micro/nano-plastics, and various other types of environmental pollutants widely enhance chlorophylls in the framework of hormesis created the need to further evaluate the response of photosynthetic pigments and gas exchange to low doses of stresses. An analysis of about 370 values of maximum stimulatory response (MAX; percentage of control response, %) of chlorophylls in higher plants, algae and duckweeds, and other photosynthesizing organisms, mined from published literatures, revealed a greater MAX for higher plants (median = 139.2%) compared to algae and duckweeds (median = 119.6%). However, an analysis of about 50

mined values of MAX of carotenoids revealed no significant difference in the median MAX between higher plants (median = 133.0%) and algae-duckweeds (median = 138.1%). About 70 mined values of MAX were also concentrated for photosynthetic rate (median MAX = 129.2%) and stomatal conductance (median MAX = 124.7%) in higher plants. Within higher plants, there was no significant difference in the median MAX among chlorophylls, carotenoids, photosynthetic rate, and stomatal conductance. Similarly, there was no significant difference in the median MAX between chlorophylls and carotenoids of pooled algae and duckweeds. The results suggest that the MAX is typically below 160% and as a rule below 200% of control response, and does not differ among chlorophylls, carotenoids, photosynthetic rate, and stomatal conductance. New research programs with improved experimental designs, in terms of number and spacing of doses within the “low-dose zone” of the hormetic dose–response relationship, are needed to study the molecular/genetic mechanisms underpinning the low-dose stimulation of photosynthesis and its ecological implications.

Four original papers traced after this paper was accepted for publication report data supporting the views presented herein (Adamakis et al. 2020; de Alkimin et al. 2020; dos Santos et al. 2020; Sharma et al. 2020).

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Introduction

Photosynthesis converts sunlight into energy, thus driving plant growth and productivity, and contributes in sustaining life on the planet as it uses water to release oxygen in the atmosphere. Because improving photosynthesis can also contribute to ensuring food security, photosynthesis has been a key target of bioengineering manipulations for a long time (Evans 2013; South et al. 2019; Simkin et al. 2019; Sinclair

et al. 2019). Such manipulations aiming at improving photosynthesis have targeted various physiological functions, such as photorespiration, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the Calvin–Benson cycle, and electron transport (Evans 2013; South et al. 2019; Simkin et al. 2019). However, a vast literature demonstrates that various abiotic stresses (including environmental pollutants) cause over-reduction of the electron transport chain and photo-oxidation, and extensively discusses the underpinning mechanisms of these adverse effects on photosynthesis (Heath 1994; Gururani et al. 2015; Li et al. 2017).

To understand how photosynthesis responds to environmental stresses, predict the effects of specific levels of pollutants, and derive critical levels of pollutants above which photosynthesis is adversely affected, dose–response relationships should be studied. Hormesis is a dose¹–response phenomenon where low doses of stress stimulate and high doses of stress adversely affect plants, producing biphasic dose–response relationships (Cedergreen et al. 2007; Belz 2008; Calabrese and Blain 2009). This dose–response relationship indicates that (1) biologically significant effects can occur at stress doses multi-fold smaller than the dose where the traditional toxicological threshold appears (i.e. no-observed-adverse-effect-level, NOAEL), and (2) prediction of effects by extrapolating from considerably higher doses to lower doses based on a linear-no-threshold perspective can generate incorrect estimates of inhibition at doses where even stimulation might occur (Calabrese and Blain 2009; Agathokleous et al. 2020c). However, there is no integrated documentation of hormetic response of photosynthesis to various environmental stresses.

The recent years have witnessed the widespread occurrence of hormesis in numerous plant species exposed to an array of environmental stresses, including contemporary emerging contaminants (Calabrese and Blain 2009; Hadacek et al. 2010; Erofeeva 2014; Morkunas et al. 2018; Agathokleous et al. 2020c; Macias-Bobadilla et al. 2020). Well-documented stresses inducing hormesis in plants are active pharmaceuticals (Agathokleous et al. 2018), air pollutants (Agathokleous et al. 2019a; Erofeeva and Yakimov 2020; Erofeeva 2020), hydrocarbons (Agathokleous et al. 2020a), metals, toxic ions and trace elements (Poschenrieder et al. 2013; Carvalho et al. 2020; Shahid et al. 2020), nanomaterials (Iavicoli et al. 2014; Agathokleous et al. 2019b), and pesticides and other agrochemicals (Garzon and Flores 2013; Brito et al. 2018; Agathokleous et al. 2019c, d; Jalal et al. 2021). These studies indicated that hormesis is a widely occurring phenomenon in plants exposed to single or combined stresses, with generalized quantitative characteristics; the maximum low-dose stimulation is modest, and as

a rule less than two-fold the control response (Agathokleous et al. 2020c).

As the basis of photosynthesis is chlorophyll whose response to increasing doses of stress has been widely found to be biphasic (i.e. typical of hormesis), and because photosynthesis is regulated by other functions displaying biphasic dose responses (Poschenrieder et al. 2013; Agathokleous et al. 2019e, 2020b; Jalal et al. 2021), photosynthetic rate may also show biphasic dose–response relationships (Cedergreen and Olesen 2010; Jia et al. 2015; Deng et al. 2017; Di Baccio et al. 2017; Wu et al. 2018; Hussain et al. 2019; Gohari et al. 2020a, b). To this end, this study aimed at collating evidence documenting biphasic dose–responses of photosynthetic rate and stomatal conductance to various stresses (Fig. 1), and examining whether the maximum stimulatory response (MAX) to low doses of environmental stresses differs among groups of photosynthesizing organisms, among photosynthetic pigments (chlorophylls and carotenoids) and gas exchange (photosynthetic rate and stomatal conductance) traits.

Analysis

Chlorophylls in higher plants

The methodology of data extraction, response calculation, and data analysis used in this section was same as described previously (Agathokleous et al. 2020b). Briefly, MAX was considered the greatest stimulation (% of control response) induced by stress in each dose–response evaluation. The raw data were extracted (with six decimals) from the original articles using Adobe Photoshop CS4 Extended v.11 (Adobe Systems Incorporated, CA, USA), and the maximum stimulatory responses were calculated as the percent difference from the response of control group.

To assess whether the dose–response samples of 2 or more groups were from different distributions, the dose–response data were subjected to Kruskal–Wallis tests by ranks (Figs. 2–5); the level of significance was predefined at $\alpha=0.05$. The level of α was corrected against inflation of the rate of false positive with a Bonferroni correction for significant Kruskal–Wallis tests with independent variables including 3 or more groups, with at least a sample stochastically dominating another sample. Data were processed and analyzed using EXCEL 2010 and STATISTICA v.10 (Stat-Soft Inc.).

A study conducted in late 2019 identified 177 dose responses of chlorophylls to over 20 stress-inducing agents, in 33 higher plant species and 43 experimental setups (Agathokleous et al. 2020b). In the framework of this paper, the earlier database (Agathokleous et al. 2020b) was extended by adding 121 dose responses of chlorophylls to

¹ Dose refers to both concentration and dose hereafter.

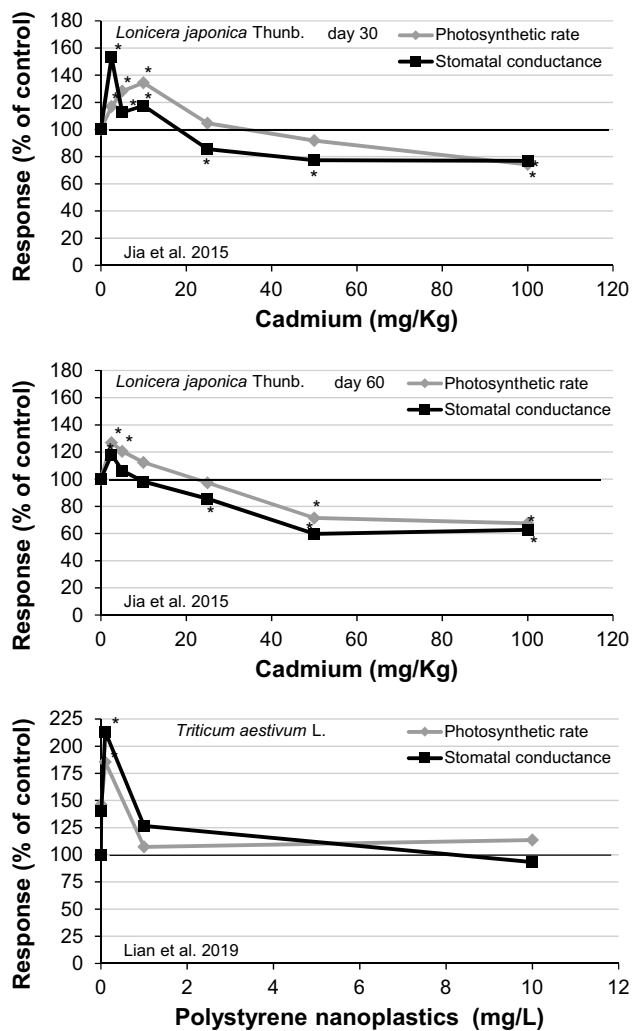


Fig. 1 Examples of biphasic dose–response relationships, typical of hormesis in plants. Asterisk above or below a mean response indicates statistical significance compared to the control group, according to the statistical analyses in the original paper. The raw data were extracted from the original articles using Adobe Photoshop CS4 Extended v.11 (Adobe Systems Incorporated, CA, USA)

22 stresses, mined from 25 published studies (of which 67% were published in 2020) with 24 species of higher plants, including tree and other perennial plants (Table S1). The 22 stresses included herbicides (Liu et al. 2019; Meseldžija et al. 2020), human and veterinary antibiotics (Guo et al. 2020; Liu et al. 2020a), metallic elements (Seth et al. 2008; Tang et al. 2009; Jia et al. 2015; Apodaca et al. 2017; Wu et al. 2018; Li et al. 2020a; Małkowski et al. 2020; Mo et al. 2020; Yang et al. 2020), micro/nano-plastics (Dong et al. 2020; Li et al. 2020c; Lian et al. 2020; Pignattelli et al. 2020), and various other types (Mostofa et al. 2015; Wang et al. 2016; Soliman et al. 2019; Kutty et al. 2020; He et al. 2020; Gohari et al. 2020b, a; Trejo-Téllez et al.

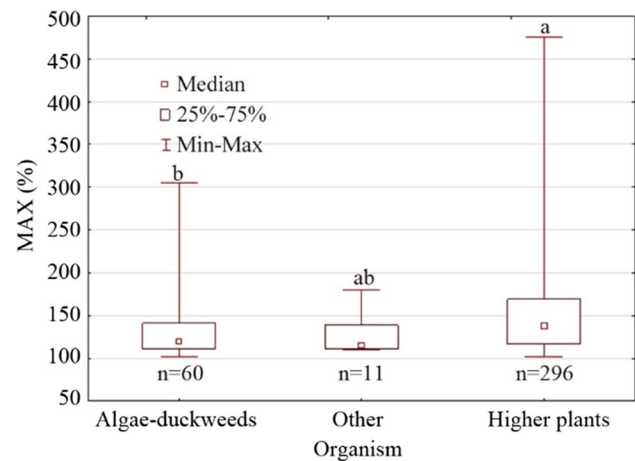


Fig. 2 The maximum stimulatory response (MAX, % of control response) of chlorophylls for different groups of organisms. Different letters above the min–max bars indicate samples of organism groups were from different distributions, after Kruskal–Wallis tests by ranks. The alpha level was pre-set at a value of 0.05. Note: Kruskal–Wallis tests by ranks was significant ($H=14.17$, $P<0.001$). As explained before (Agathokleous et al. 2020b), two entries of the old database of higher plants were extreme, and not in accordance with hormesis understandings (e.g. 5938.7% and 1235.5%). Therefore, the analysis was repeated after excluding these two values to test how they might have affected the results (this figure does not include the two extreme values for presentation purposes). The result ($H=13.68$, $P<0.01$) was similar with the first analysis (and multiple comparisons same), suggesting that the two extreme values did not affect the analysis

2020). More than half (57.0%) of the new dose responses were statistically significant compared with the control group (typically a zero dose of the same stressor), according to the original analysis (many of them did not report statistics). Kruskal–Wallis Test was not significant ($H=0.11$, $P=0.738$) between the old and the new databases (Fig. S1), and the databases were merged for analysis. The median MAX was 139.2% (geometric mean = 150.7%), and as many as 68.8% and 83.9% of the 298 entries had a MAX smaller than 160% and 200% of the control response, respectively, estimates that are in agreement with the broad plant hormesis literature (Calabrese et al. 2019; Agathokleous et al. 2020c; Shahid et al. 2020).

Chlorophylls in organisms other than higher plants

Making one step further, 20 studies with photosynthetic organisms other than higher plants were found to report dose–response data potentially suggestive of hormesis. An assessment of these studies revealed 71 dose responses (Table S2) of chlorophylls to herbicides (Wong and Chang 1988; Rioboo et al. 2002; Zaltauskaite and Kaciene 2020), human and veterinary antibiotics (Hu et al. 2019; Jiang et al. 2020; Tong et al. 2020), metallic elements (Zhou et al. 2018;

Li et al. 2020b), micro/nano-plastics (Tang et al. 2018; Chae et al. 2019; Zhao et al. 2019; Su et al. 2020; Song et al. 2020; Zhang et al. 2020), and other types of stresses (Zhou et al. 2016; Deng et al. 2017; Zhang et al. 2018, 2020; Cai et al. 2020; Liu et al. 2020b; Xue et al. 2020). These dose responses come from 16 species (one non-identified), and 31% were statistically significant compared with the control group, according to the original analysis (some papers did not report statistics). The median MAX was 120.5% (geometric mean = 137.4%), while 85.9% and 90.1% of the 71 entries had a MAX smaller than 160% and 200% of the control response, respectively. These suggest that the MAX is restricted below 200% of control response, in agreement with the chlorophyll response of higher plants as well as the broad hormesis literature (Calabrese et al. 2019; Agathokleous et al. 2020c; Shahid et al. 2020).

Comparing chlorophylls MAX among groups of photosynthesizing organisms

In order to understand whether chlorophyll MAX differs among groups of organisms, a further analysis was carried out. Three groups were created: (1) higher plants, (2) (micro) algae and duckweed, and (3) other organisms (cyanobacteria, dinoflagellates, and symbiotic zooxanthellae, i.e. scleractinian corals). This analysis revealed that samples of groups 1 and 2 were from different distributions (Fig. 2), which is in agreement with an analysis of nanomaterial-induced MAX, according to which the median MAX was 119.7% ($n=46$) and significantly lower in algae than in plants (125.2%, $n=453$) across all traits and plant species (Agathokleous et al. 2019b). While these may arise from differences in the stress biology between vascular plants and algae (Pinnola and Griffiths 2019) or a potentially more efficient light utilization and gas exchange in terrestrial systems compared to aquatic systems (Sand-Jensen 1997), the sample size of algae/duckweeds was considerably small in both analyses, not permitting any concrete conclusions at this stage. However, these findings indicate a need for more studies in order to better understand the biological responses of vascular and non-vascular plants to low doses of environmental stresses.

Carotenoids in higher plants and algae/duckweeds.

Carotenoids are the second most abundant pigments occurring naturally. They also serve as precursors of certain volatiles, abscisic acid, various apocarotenoids, and strigolactone, and play important roles as accessory light-harvesting photosynthetic pigments, antioxidants, and attractants for pollinators and seed dispersers (Havaux 2014; Nisar et al. 2015; Alós et al. 2016). Hence, not only chlorophylls (Agathokleous et al. 2020b) but also carotenoids have a multitude of roles in plant-plant competition, plant interaction

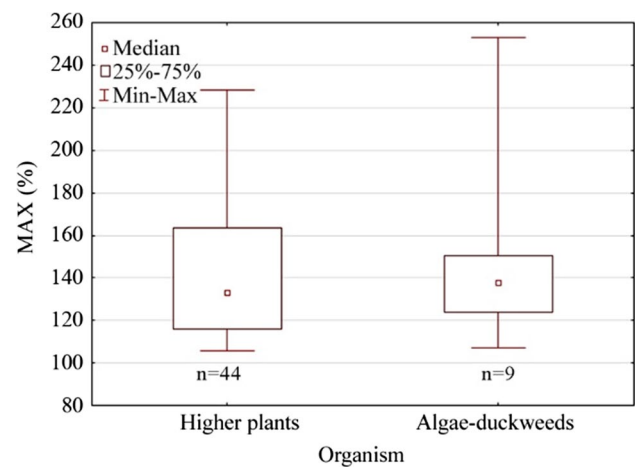


Fig. 3 The maximum stimulatory response (MAX, % of control response) of carotenoids for different groups of organisms. Carotenoids are involved in the light-harvesting complex during photosynthesis as well as the protection against photo-oxidation. Kruskal–Wallis test by ranks was non-significant ($H=0.20$, $P=0.653$)

with other organisms (e.g. insects), and plants success in the environment. Therefore, potential enhancement of carotenoids by low doses of pollutants might have unpredicted ecological consequences. For these reasons, carotenoids are an important trait for studying the effects of low doses of pollutants.

In a number of studies reporting responses of leaf photosynthetic pigments to stresses, data of carotenoids response were also included ($n=16$ studies with higher plants and $n=5$ studies with algae and duckweeds). These data were collected and further analyzed; 45.5% of the mined dose responses with higher plants and 44.4% of the mined dose responses with algae and duckweeds were statistically significant according to the original analyses of authors (Supplementary Information, Tables S3–S4). The median MAX was 133.0% for higher plants (geometric mean = 140.8%) and 138.1% for algae and duckweeds (geometric mean = 145.2%) exposed to human and veterinary antibiotics (Liu et al. 2020a), herbicides (Rioboo et al. 2002; Liu et al. 2019; Zaltauskaite and Kaciene 2020), metallic elements (Jia et al. 2015; Zhou et al. 2018; Wu et al. 2018; Hussain et al. 2019; Liu et al. 2019), micro/nano-plastics (Li et al., 2020c, d; Pignattelli et al. 2020; Song et al. 2020), and other stress-inducing agents (Mostofa et al. 2015; Farzana and Tam 2018; Dawood and Azooz 2019; Lassalle et al. 2019; Li et al. 2019; Soliman et al. 2019; Tombuloglu et al. 2019; Gohari et al. 2020b, a). The median MAX did not differ significantly between the two groups of organisms, although the sample size was small (Fig. 3).

Photosynthetic rate and stomatal conductance in higher plants.

Sixteen studies with data suggestive of biphasic responses of higher plants photosynthesis were traced. These included responses to herbicides (Cedergreen and Olesen 2010; de Carvalho et al. 2012; Adams et al. 2017; Nascentes et al. 2018; Khan et al. 2020), metallic elements (Jia et al. 2015; Chandra and Kang 2016; Wu et al. 2018; Gelioli Salgado et al. 2019; Małkowski et al. 2020; Mendonça et al. 2019; Yang et al. 2020), micro/nano-plastics (Dong et al. 2020; Lian et al. 2020), and other types of stresses (Sugai et al. 2018; Soliman et al. 2019). Low-dose stimulation of photosynthetic rate by various stresses appeared in various taxa of trees, shrubs, and vines (de Carvalho et al. 2012; Jia et al. 2015; Chandra and Kang 2016; Adams et al. 2017; Nascentes et al. 2018; Mendonça et al. 2019; Yang et al. 2020). Furthermore, biphasic dose-responses of photosynthetic rate to stresses were observed not only in C3 plants but also in C4 plants (*Zea mays* L.) (Małkowski et al. 2020). While some studies report data suggestive of hormetic responses of algae and duckweeds to stresses, in terms of biphasic responses of photosynthesis (Wong and Chang 1988; Di Baccio et al. 2017), their number is small and, thus, only the dose responses of higher plants were further analyzed. From the 16 traced studies with higher plants, 65 dose responses were mined, of which 38 concerned photosynthetic rate and 27 concerned stomatal conductance (Supplementary Information, Table S5). From the mined dose responses, 64.6% were statistically significant compared to the control group (as a rule a theoretically zero exposure), according to the original statistics (Table S5). The median MAX was 129.2% for photosynthesis (geometric mean = 134.1%) and 124.7% for stomatal conductance (geometric mean = 133.4%).

Comparing MAX among physiological traits

The present results raised the curiosity of this author to further evaluate whether MAX differs among physiological traits. To this end, an analysis of the MAX among chlorophyll content/concentration, carotenoid content/concentration, photosynthetic rate, and stomatal conductance in higher plants was carried out. According to the statistical results, the four traits shared a similar median MAX (Fig. 4). A similar analysis was also conducted for the MAX of chlorophyll content/concentration and carotenoid content/concentration of algae and duckweeds. This analysis also suggests that the median MAX was similar between chlorophylls and carotenoids (Fig. 5).

Different groups of organisms were subjected to different types of stresses, so comparison of MAX might be influenced in cases where the sample size (number of dose

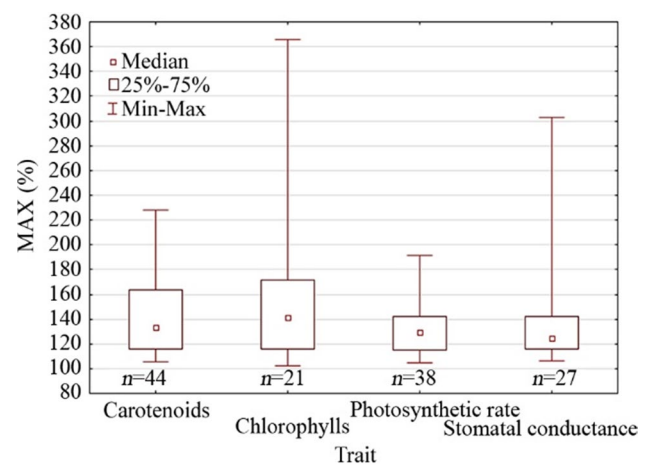


Fig. 4 The maximum stimulatory response (MAX, % of control response) of higher plants per physiological trait. Kruskal–Wallis test by ranks was non-significant ($H=5.23$, $P=0.156$)

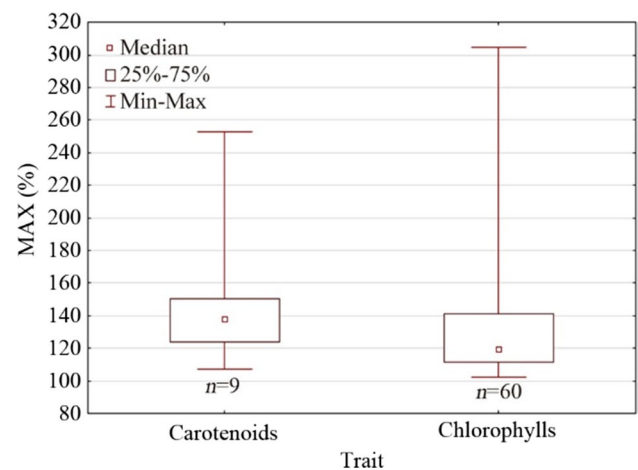


Fig. 5 The maximum stimulatory response (MAX, % of control response) of algae and duckweeds per physiological trait. Kruskal–Wallis test by ranks was non-significant ($H=2.60$, $P=0.107$)

responses) is small, such as for carotenoids in algae and duckweeds (Fig. 5). This shortcoming suggests that such results should be interpreted with caution. However, extensive databases including > 10 000 dose responses suggest that the median MAX does not differ significantly, or the difference (if any) is negligible, among types of pollutants (Calabrese and Blain 2009; Agathokleous et al. 2018, 2019a,b,c,d; Agathokleous et al. 2020a, b,c; Shahid et al. 2020). This phenomenon holds true for specific traits as well, i.e. chlorophylls (Agathokleous et al. 2020b), permitting the analyses of MAXs across different groups of organisms or photosynthesis-related traits with response data pooled together across stresses.

Discussion

Studies with multifactorial experimental designs including different levels of co-occurring stresses suggest that low-dose stimulation of photosynthetic pigments and photosynthesis is more likely to occur under “disease conditions” in the framework of conditioning hormesis, i.e. when plants are under adverse stress induced by other factors, but the stimulation also ceases as the dose of the concurrent stresses exceeds a specific threshold of adversity (Mostofa et al. 2015; Gelioli Salgado et al. 2019; Liu et al. 2019; Soliman et al. 2019; Agathokleous et al. 2020b; Dong et al. 2020; Gohari et al. 2020b; Gohari et al. 2020a; Li et al. 2020c; Yang et al. 2020;). These suggest that the magnitude of the low-dose stimulation by an environmental stressor significantly depends on the intensity of co-occurring environmental stresses.

The low-dose enhancement of chlorophylls and gas exchange (Seth et al. 2008; de Carvalho et al. 2012; Tang et al. 2018; Zhou et al. 2018; Zhao et al. 2019; Hu et al. 2019; Liu et al. 2020a) in higher plants and other photosynthetic organisms may be transient. However, this may indicate that the doses applied may become higher or smaller than those needed to induce MAX (as they accumulate or decline over time) because considerable research designed to study hormesis shows that the low-dose stimulation of chlorophylls and photosynthesis can persist throughout the plant growing season (Jia et al. 2015; Nascentes et al. 2018; Yang et al. 2020), yet it is known that the maximum stimulation occurs over a defined time window, after which it declines (Agathokleous et al. 2020b, c). Ceasing of the exposure is also expected to lead to returning to the control/background levels of chlorophylls to allow for recovery and maintenance of a homeostatic state (Zaltauskaite and Kaciene 2020). These suggest that research programs designed to study hormetic interventions directed to enhance plant photosynthesis should consider the temporal component to identify optimum intervention intervals.

The modest and generalized degree of MAX, typically 130–160% (as a rule < 200%) of control response, indicates that the low-dose stimulation is restricted by the limits of biological plasticity (Calabrese and Blain 2009; Calabrese et al. 2019; Agathokleous et al. 2020c; Shahid et al. 2020). Interestingly, the degree of enhancement of photosynthesis (e.g. \approx 130%–150%) and other traits by elevated concentrations of atmospheric CO₂ (Fajer and Bazzaz 1992; Kirschbaum 2011) presents an excellent agreement with the degree of enhancement by various environmental pollutants as analyzed here for photosynthetic pigments and photosynthesis as well as across traits and species (Calabrese and Blain 2009; Calabrese et al. 2019; Agathokleous et al. 2020c; Shahid et al. 2020). The enhancement of plants by CO₂ may be seen as a fertilizing effect of CO₂ where the rate of

photosynthesis increases with increasing concentrations of CO₂ in the atmosphere (so called carbon fertilization), while the enhancement of plants by other environmental stresses causing oxidative stress (discussed in Sect. 2) appears to occur in the framework of an ecological strategy of plants to prepare for forthcoming ‘life-threatening’ stress. The underlying molecular mechanisms of hormesis induced in plants by environmental pollutants remain poorly understood, but it may be hypothesized that plants may increase their photosynthetic rate so to increase carbon availability and potentially enhance the carbon-based defense system, including enhanced secondary metabolites as well as other defensive molecules. However, while some evidence of these speculations exists (explained later in the text), further studies are needed to examine these from the perspective of hormesis.

An inverted U-shaped dose–response relationship of chlorophylls and photosynthesis response to stresses was found to be consistent with biomass response pattern of higher terrestrial plants (Tang et al. 2009; Jia et al. 2015; Nascentes et al. 2018; Li et al. 2019; Lassalle et al. 2019; Gohari et al. 2020b; Khan et al. 2020; Lian et al. 2020) and aquatic duckweed (Zaltauskaite and Kaciene 2020) microalgae (Zhou et al. 2016). However, it should be highlighted that increased photosynthetic rate may not necessarily translate to increased photosynthetic efficiency or growth; e.g. a 30% average enhancement of photosynthesis over the course of the day under elevated CO₂ may increase relative growth rate by only \approx 10% (Kirschbaum 2011).

The underlying mechanisms of the stimulation of photosynthesis by environmental pollutants in the framework of hormesis remain underexplored (de Carvalho et al. 2012). The stimulation of chlorophylls by low-dose stress was found to co-occur with inhibition of chlorophyllase and Mg-dechelataase (Yang et al. 2020). Hormetic-like (inverted U-shaped) dose–response relationship was also found for defensive compounds such as α -tocopherol, ascorbic acid, phenolic compounds, flavonoids, and phytochelatin; it was similar to chlorophylls dose–response relationship (Dawood and Azooz 2019; Gohari et al. 2020b). Nitric oxide appeared to have a similar dose response (Dawood and Azooz 2019). Other molecules related to anti-oxidant properties with similar hormetic-like responses were reduced glutathione, superoxide dismutase, catalase, ascorbate peroxidase, and glutathione peroxidase (Dawood and Azooz 2019; Gohari et al. 2020b, a). It is noteworthy that hormetic-like (inverted U-shaped) dose–response relationship similar to chlorophylls was also found for xanthophylls (Hu et al. 2019). A major knowledge gap, however, exists with regard to the production and fate of unproductive by-products (Simkin et al. 2019) of increased photosynthesis due to low doses of environmental pollutants.

An increase in the rates of carbon fixation and/or their efficiency can result from increasing light harvesting and/

or stomatal and mesophyll conductance (de Carvalho et al. 2012). Coupled stimulation of photosynthesis and stomatal conductance under low-dose stress and coupled inverted U-shaped dose–response relationships were revealed (de Carvalho et al. 2012; Jia et al. 2015; Nascentes et al. 2018; Mendonça et al. 2019; Soliman et al. 2019; Lian et al. 2020; Małkowski et al. 2020; Yang et al. 2020). In some other cases, however, the stimulation of photosynthesis and stomatal conductance was uncoupled as to the magnitude and inducing dose, with shifts in the dose–response relationship (Nascentes et al. 2018; Wu et al. 2018; Małkowski et al. 2020). These suggest that the increase in photosynthesis due to low doses of environmental pollutants is not exclusively or primarily driven by increased stomatal conductance, a phenomenon indicating that other biochemical mechanisms (e.g. Rubisco, Ribulose 1,5-bisphosphate, triose phosphate utilization) may primarily drive the low-dose stimulation of photosynthesis. Within the low-dose zone, photosynthesis response was also found to correlate with respiration response (Cedergreen and Olesen 2010) (Fig. S2). It was also observed that in several of the examined cases of gas exchange response to stresses transpiration was also enhanced by low doses, a phenomenon that may indicate increased nutrient absorption efficiency with a potential for greater nutrient supply to aboveground tissues.

Conclusion

The herein analysis represents the first integrated documentation of plant hormesis as reflected to biphasic dose–response of gas exchange to various stresses. Preliminary but significant evidence suggests the widespread stimulation of photosynthesis by low doses of environmental pollutants. However, stimulation of photosynthesis by low doses of stress is also known to occur in response to non-essential elements that are not environmental pollutants, such as silicon that may also induce U-shaped dose–response relationships (Cooke and Leishman 2016; Li et al. 2018; Xu et al. 2020), signifying the importance of low-dose effects on photosynthesis.

While this may be seen as a preliminary analysis, it substantiates that enhanced awareness of researchers about these hormetic responses of plants would help in identifying such responses and facilitating cumulative science for a more complete and enhanced understanding of low-dose effects on plant photosynthesis, as well as improved toxicological estimates and risk assessment.

New studies directed to study hormetic responses of plants to environmental pollutants should consider to identify a ‘true’ MAX by studying dose–response relationships incorporating increased number of doses (> 6 doses), with narrower spacing, below the NOAEL (Calabrese et al. 2019).

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