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On the Nonmonotonic, Hormetic Photoprotective Response of Plants to Stress

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Abstract

Accumulated evidence show that reactive species play a dual role in plants as well, with likely biphasic responses. This suggests that photoprotective mechanisms may also show similar patterns because they are highly related to reactive species. The nonphotochemical quenching (NPQ) is an index of heat dissipation of excitation energy in the antenna system. We present here preliminary evidence from some published studies showing significant biphasic response of NPQ to increasing doses of stress, with U-shaped or inverted U-shaped dose–response relationships, typical of hormesis. This evidence provides a remarkable perspective for designing novel studies where the fate of light energy will be seen through the lens of hormesis.

Keywords

biphasic, chlorophyll fluorescence, electron transport rate, homeostasis disruption, hormesis, nonphotochemical quenching, plant stress

Background

The fields of dose–response and stress biology noted a remarkable progress over the last 2 decades. Among the notable advancements in the last few years was the recognition that the reactive species, which were previously considered as harmful byproducts of plant aerobic metabolism, are rather signaling molecules with dual functions characterized by disease preventing and health protection effects at modest elevation in their levels and harmful effects at excessive elevation in their levels.[1] This suggests that the nonphotochemical quenching (NPQ), a major component of the systemic acquired acclimation and systemic acquired resistance which is tightly related to reactive species, may follow a similar dose–time–response pattern.[1]

Survival of green plants depends on the light. Photons absorbed by photosynthetic molecules of green plants drive photosynthesis. Some of them are emitted as fluorescence, while others are dissipated as heat. Heat dissipation of excitation energy in the antenna system is indicated by the NPQ, a photoprotective mechanism.[2] Nonphotochemical quenching can be assessed nondestructively and cost-effectively using portable chlorophyll *a* fluorescence instruments; thus, it can be measured *in situ* as a valuable biomarker of stress. For these reasons, chlorophyll *a* fluorescence has been widely used for assessing plant response to changing environments.[3]

There is no researcher studying dose–response who is unaware of the issue with insufficient spacing of low doses in dose–response studies. The lack of dose–response studies designed to assess dose–response relationships across the full dose–response spectrum did not permit to understand if the NPQ shows a biphasic dose–response relationship, typical of hormesis, across different experimental setups and conditions. In this commentary, we point out that this theory is valid by collating data from a series of independent dose–response studies.

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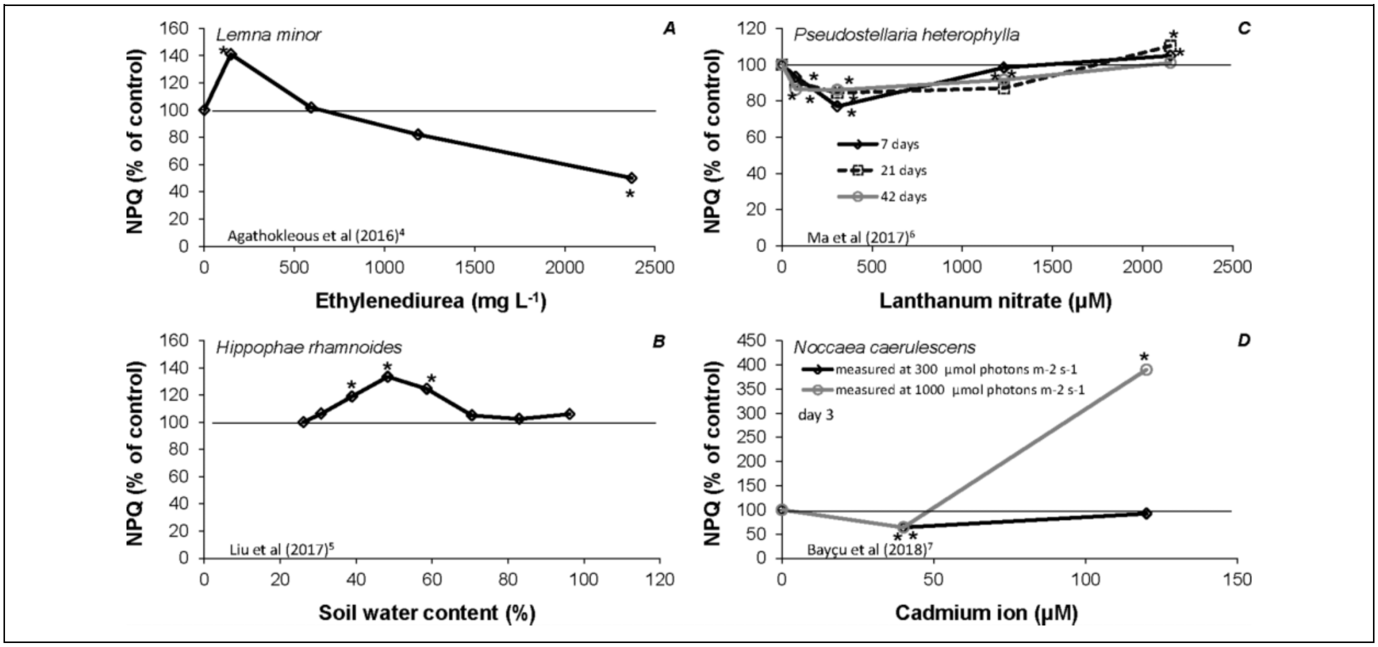

Figure 1. Typical examples of hormetic responses of nonphotochemical quenching (NPQ) to stress from published literature. Nonphotochemical quenching response data were estimated from figures of the original articles using image analysis software (Adobe Photoshop CS4 Extended v.11; Adobe Systems Incorporated, San Jose, California). The response to stress was calculated as percentage of control response. Asterisk indicates statistically significant difference from the control.

Preliminary Evidence for Hormetic Response of NPQ to Stress

Case I

When NPQ was assessed in *Arabidopsis thaliana* (L.) Heynh. treated with paraquat, a herbicide, significant biphasic responses of NPQ as a function of time were observed, with peak in values at 1 hour after exposure or even earlier (for the kinetics formation).[2]

Case II

In a study with the hydrophyte *Lemna minor* L., NPQ showed a biphasic response (inverted U-shaped dose–response relationship) to increasing concentrations of ethylene diurea, an antiozonant, in the first day after exposure; however, the maximum induction was dropped to a more or less homeostatic state when assessed 3 and 5 days after exposure (Figure 1A).[4] Only NPQ and NPQ of fluorescence (qN) displayed similar biphasic responses, from 6 chlorophyll *a* fluorescence parameters assessed (maximal efficiency of PSII photochemistry [F_v/F_m], effective efficiency of PSII photochemistry [F_v'/F_m'], qP, NPQ of fluorescence [qN], electron transport rate [ETR], and NPQ).

Case III

In a different study, the response of the deciduous shrub *Hippophae rhamnoides* L. was studied after subjection to different levels of soil water content ranging between 26.1% and 96.2%.[5] A significant biphasic response of NPQ appeared in the form of inverted U-shaped relationship, with the value reaching a maximum when the soil water content dropped to 48.3% (Figure 1B). Interestingly, among 6 chlorophyll *a* fluorescence parameters that were assessed (minimal fluorescence [F_o], maximal fluorescence [F_m], F_v/F_m, actual photochemical efficiency of PSII [Φ_{PSII}], and qP), only NPQ showed a significant biphasic response, and only NPQ showed a stress–response pattern similar to that of the activity of superoxide dismutase, peroxidase, and catalase.

Case IV

An additional study investigated the effects of different concentrations of lanthanum nitrate (0, 25, 100, 400, and 700 $mg \cdot L^{-1}$) on the adaptogen *Pseudostellaria heterophylla* Rupr. & Maxim. weekly, for 42 days after exposure.[6] All the chlorophyll *a* fluorescence parameters that were assessed (F_v'/F_m', F_v/F_m, Φ_{PSII}, qP, and NPQ) showed significant biphasic dose–response relationships which were maintained for 42 days. However, only NPQ showed a U-shaped dose–response relationship (Figure 1C), while the other 4 parameters displayed inverted U-shaped dose–response relationships; the maximum low-dose response commonly occurred at 100 $mg \cdot L^{-1}$.[6] In this experiment, chlorophyll and carotenoid content in leaves, ground diameter, seedling height, root tuber length and diameter, fresh and dry mass of root tuber, and root tuber yield per unit area displayed significant biphasic dose–responses with maximum stimulation commonly at 100 $mg \cdot L^{-1}$, similarly to chlorophyll *a* fluorescence parameters.

Case V

Furthermore, when the responses of the zinc–cadmium–nickel hyperaccumulator *Noccaea caerulescens* (J.Presl & C.Presl) F.K.Mey. to 0, 40, and 120 μM cadmium ion were evaluated, the NPQ displayed clear U-shaped dose–response relationships after 3 days of exposure (Figure 1D).[7] This response was similar to that of F_v/F_m, Φ_{PSII}, qP, and ETR.

Conclusions and Future Directions

Biphasic kinetics of NPQ have been widely shown in the literature and for a wide array of plant species and experimental conditions. The herein evidence further depicts hormetic responses of NPQ and related chlorophyll *a* fluorescence parameters to increasing doses of stress. This evidence comes from species with different taxonomical and botanical characteristics and different stressors and experimental setups. These responses of NPQ took the form of U-shaped or inverted U-shaped dose–response relationships, a difference which may be upon (i) the exposure duration,[2-7] (ii) failure of the experimental design to depict responses that would normally be triphasic rather than biphasic, and (iii) potentially different responses between NPQ components,[8] for example, inverse U-shaped responses may reflect the regulated component of NPQ with a decrease due to damage arising from damaged membrane (proton gradient difference), whereas inverted U-shaped responses may reflect the unregulated component of NPQ.

It may be postulated that the NPQ, and the photobiology, is executed within a hormetic framework, a hypothesis warranting further validation. The hormetic response of NPQ is of utmost importance and should be better understood as the life on Earth depends on the harvesting of light energy through photosynthesis and its fate after harvesting. Therefore, further and appropriately designed research should be directed toward the hormetic response of NPQ to stress, across plant systems and conditions.

The evidence presented here also suggests that chlorophyll fluorescence imaging analysis can be used as a low-cost and easy-to-use tool for assessing plant stress in response not only to high doses but also to low doses within the hormetic zone (below the classic toxicological threshold).

Declaration of Conflicting Interests

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References

1. Czarnocka W, Karpiński S. Friend or foe? Reactive oxygen species production, scavenging and signaling in plant response to environmental stresses. *Free Radic Biol Med*. 2018;122:4-20.
2. Moustaka J, Tanou G, Adamakis ID, Eleftheriou E, Moustakas M. Leaf age-dependent photoprotective and antioxidative response mechanisms to paraquat-induced oxidative stress in *Arabidopsis thaliana*. *Int J Mol Sci*. 2015;16(6):13989-14006.
3. Bussotti F, Desotgiu R, Cascio C, et al. Ozone stress in woody plants assessed with chlorophyll a fluorescence. A critical reassessment of existing data. *Environ Exp Bot*. 2011;73:19-30.
4. Agathokleous E, Mouzaki-Paxinou AC, Saitanis CJ, Paoletti E, Manning WJ. The first toxicological study of the antiozonant and research tool ethylene diurea (EDU) using a *Lemna minor* L. bioassay: hints to its mode of action. *Environ Pollut*. 2016;213:996-1006.
5. Liu J, Zhang R, Zhang G, Guo J, Dong Z. Effects of soil drought on photosynthetic traits and antioxidant enzyme activities in *Hippophae rhamnoides* seedlings. *J For Res*. 2017;28(2):255-263.
6. Ma Y, Zou H, Gu H, et al. Stimulatory effect of lanthanum nitrate on the root tuber yield of *Pseudostellaria heterophylla* via improved photosynthetic characteristics. *J Rare Earths*. 2017;35(6):610-620.
7. Bayçu G, Moustaka J, Gevrek N, Moustakas M. Chlorophyll fluorescence imaging analysis for elucidating the mechanism of photosystem II acclimation to cadmium exposure in the hyperaccumulating plant *Noccaea caerulescens*. *Materials (Basel)*. 2018;11(12):2580.
8. Klughammer C, Schreiber U. Complementary PS II quantum yields calculated from simple fluorescence parameters measured by PAM fluorometry and the Saturation Pulse method. *PAM Appl Notes*. 2008;1:27-35.