

# Temperature-induced hormesis in plants

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**Abstract** Environmental change attracts particular attention by biologists concerned with the performance of biological systems under stress. To investigate these, dose–response relationships should be clarified. It was previously assumed that the fundamental nature of biological dose–responses follows a linear model, either with no threshold or with a threshold below which no effects are expected to occur in biological endpoints. However, substantial literature, including widespread documentation in plants, has revealed that hormesis commonly occurs. Hormesis is highly generalized and can be utilized as a quantitative measure of biological plasticity. Conditioning induced by adaptive responses also occurs in the framework of hormesis and is of particular importance to environmental change biology with regards to evolutionary adaptations. This paper presents additional evidence for hormetic dose

responses induced by temperature in plants. The current understanding on hormesis provides a perspective for next generation environmental change research. Hormesis should have a central role in environmental change biology of vegetation.

**Keywords** Adaptive response · Biological plasticity · Dose response · Hormesis · Stress biology

## Introduction

Environmental change is the focus for biologists concerned with the functioning of biological systems under stress. How biological systems respond to environmental stressors, what capacity biological systems have to adapt, and what are “safe” levels of environmental change “stress” factors to not only avoid adverse effects but also to enhance productivity, are some of the many questions puzzling scientists dealing with environmental change biology, policy and decision makers, and governments.

At the center of these biological questions is the dose–response relationship, a pillar of toxicology and fundamental in biology which guides the assessment of environmental tolerances. Throughout the 20th century, it was assumed that the fundamental nature of dose–response relationships (Fig. 1) was either linear or a threshold below which no effects were expected (Calabrese 2016a, 2017a, b). Linear non-threshold (LNT) and threshold models have been widely applied and adopted by worldwide regulatory agencies for human cancer and non-cancer endpoints, (e.g., endocrine disruptor agents), but also for the effects of air pollutants on vegetation as in the case of ground-level ozone (Fuhrer et al. 1997; USEPA

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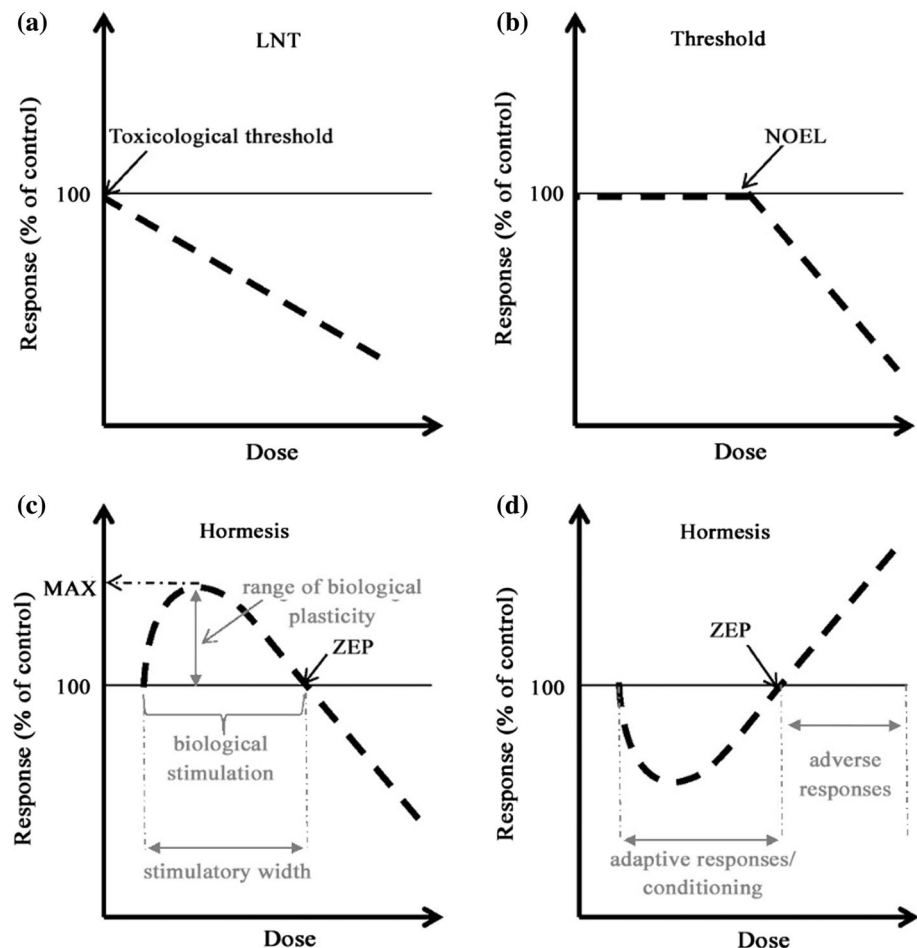
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**Fig. 1** Hypothetical linear non-threshold, LNT (a), threshold (b) and hormesis (c, d) dose–response models. Hormesis provides quantitative estimates on the limits of biological plasticity, and appears as inverse U-shape (c) or U-shape (d) dose–response curve, depending on the endpoint. For example, inverse U-shape curve would appear for net photosynthetic rate and biomass whereas a U-shape curve would appear for hydrogen peroxide and non-photochemical quenching. Notes: Toxicological threshold in the LNT model indicates a threshold of zero dose, i.e. practically no traditional threshold. NOEL and ZEP indicate no observed effect level and zero equivalent point (i.e., toxicological thresholds) for the threshold and hormesis models. MAX indicates the maximum stimulatory response in the hormesis model



1998, 2013; WHO 2000a, 2006; Enstrom 2005, 2017; Mills et al. 2007; Zoeller et al. 2015; Bogen 2016, 2017).

The problem with the adoption and use of these two dose–response models that regulatory agencies employ is that they are accompanied by thousands of exceptions (Calabrese 2016a, 2017a, b). The vast majority of these reflect biphasic dose responses commonly referred to as hormesis (Calabrese and Blain 2011; Calabrese 2017c; Calabrese and Mattson 2017; Agathokleous 2018; Agathokleous et al. 2018a, b; Kim et al. 2018).

In light of recent significant progress in the field of dose response, this paper examines the question of whether hormesis should have a central role in vegetation environmental change biology or be ignored or even marginalized. In the framework of this examination, plant response to air temperature is provided as a paradigm of the occurrence of hormesis in vegetation environmental change biology.

### The biological basis of the phenomenon of hormesis

Hormesis (Fig. 1) is a dose–response phenomenon where low doses induce stimulation and high doses induce inhibition (Stebbing 2003). The differentiation of the biological response between the low and high dose zones, as seen in the hormetic model, has generated considerable scientific curiosity about the biological mechanisms underpinning the response. Therefore, the biological mechanisms have been widely studied, and there is now available a large record documenting such processes (Calabrese 2013, 2016b, c; Calabrese and Mattson 2017).

These findings suggest that the concept of hormesis can be utilized as a quantitative measure of biological plasticity, i.e., the organism capacity to re-arrange biological functions via the activation of adaptive responses under the influence of stress (Calabrese and Blain 2011; Calabrese and Mattson 2017; Agathokleous 2018). By studying hormetic dose responses, the quantitative limits of biological plasticity can be clarified (Fig. 1). Meta-assessment of  $\approx 9000$  dose responses revealed that the maximum

stimulatory response is commonly less than two-fold the control response, and that the stimulatory width is within  $\approx 10$ – $20$ -fold of the estimated toxicological threshold (Calabrese and Blain 2011). These features of hormesis indicate its links to evolutionary processes and may provide an important perspective in environmental change biology.

When adaptive responses are activated by low-level stimuli they often elicit therapeutic properties, especially with regards to aging-related homeostasis disruptions and malfunctions (Calabrese et al. 2018; Son et al. 2008). The therapeutic properties of adaptive responses are now well recognized in medicine and find application in combating human diseases. Adaptive responses within a hormetic framework would have important implications to vegetation environmental change biology and could provide a further perspective for biosphere sustainability (Calabrese and Mattson 2017).

Conditioning is also a manifestation of hormesis (Calabrese 2016b, c). Pre- and post-conditioning are the phenomena, where a prior experience of low-level stress protects against a subsequent high-level stress, and where a low-level stress following closely after high-level stress may alleviate much of the induced injury (Calabrese 2016b, c). Pre- and post-conditioning occur in the framework of hormesis and are of particular importance to environmental change biology in terms of significant evolutionary adaptations. Conditioning that may naturally occur in the environment, i.e., via activation of adaptive responses by low-level stress, may mediate biological responses to environmental change. Current understandings about pre- and post-conditioning open new doors to the next generation of environmental change research.

## Hormesis in plants

While indications for hormesis existed from the late 1880s, including effects on plants (Calabrese and Baldwin 2000), the concept remained marginalized until recently. Numerous studies now exist showing that hundreds of chemicals and environmental pollutants and environmental change factors such as radiation, nitrogen deposition, ground-level ozone, and sulfur dioxide, induce hormesis in plants at various organizational (i.e., cell, organ, organism, and community) levels (Cedergreen et al. 2007; Son et al. 2008; Costantini et al. 2010; Calabrese and Blain 2011; Belz and Piepho 2013, 2015; Gressel and Dodds 2013; Poschenrieder et al. 2013; Hashmi et al. 2014; Agathokleous 2017, 2018; Belz and Duke 2017; Pagano 2017; Agathokleous et al. 2018a, b, c; Kim et al. 2018; Murakami 2018).

Hormetic effects of chemicals and radiation on plants have been extensively documented since the “rediscovery” of hormesis in the late 1970s. However, this was not the case with environmental factors on plants. Although there was evidence for hormesis induced by environmental factors (including pollutants) in plants, such as for ozone, nitrogen deposition, and sulfur dioxide via the documentation of low-dose stimulation and high-dose inhibition (Bennett et al. 1974; Roberts 1984; Darrall 1989), the possibility of hormesis was not considered for a long time. The concept of hormesis was proposed in a book chapter as a potential response of plants to ozone (Jaeger and Krupa 2009). Furthermore, in a book chapter of the World Health Organization (WHO) on the effects of nitrogen deposition, it was suggested that nitrogen deposition stimulates growth at lower levels and inhibits growth at higher levels, i.e., implying the occurrence of the phenomenon of hormesis (WHO 2000b). Recent literature reviews suggest that, when the experimental design permits testing the possibility of hormesis, environmental change factors, including ozone and nitrogen deposition, often induce hormesis in vegetation even at community or ecosystem levels (Agathokleous 2018; Agathokleous et al. 2018a, b).

Hormetic dose responses occur frequently, being independent of biological model (organism), endpoint, stressor and mechanism, suggesting widespread generality (Calabrese and Blain 2011; Calabrese 2013, 2014; Calabrese and Mattson 2017; Agathokleous 2018; Agathokleous et al. 2018a, b, c). The substantial evidence for non-linear biological/physiological processes produced endogenously or after a homeostatic disruption by exogenous agents, challenges the long-held belief that the fundamental nature of biological responses is some combination of threshold and non-threshold linear processes.

## Plant response to temperature: an interesting example of hormesis

Temperature holds a crucial role in global change biology as the average global surface temperature appears to have increased over the last decades (Wen et al. 2011; Shi et al. 2018). Therefore, it is important to understand how plants respond to temperature within a dose–response continuum.

Air temperature is a critical factor for organismal health, and biota have evolved complex biological mechanisms to regulate body temperature, including organisms which cannot move but still have evolved mechanisms for regulating internal temperature (Wigge 2013; Szymańska et al. 2017; Körner and Hiltbrunner 2018). A large amount of literature deals with the effects of air temperature on plants. A review study has suggested that a variety of tree species shows a positive response to elevated temperature (Saxe

et al. 2002). A recent meta-analysis also suggests that a temperature increase of 0.3–10 °C enhanced growth, productivity, and health overall of woody plants (Yuan et al. 2018).

In their Tansley review, Saxe et al. (2002), in the supplement to their findings for positive tree response to elevated temperature, have questioned “but how close are we to the optima?” This question would be answered by studying dose–response relationships. However, there is a lack of sufficiently high number of exposure levels in dose–response experiments and narrow spacing of exposure levels, especially when the stressor agent is an environmental factor such as temperature, ozone, and carbon dioxide due to technical difficulties compared to studies with chemical agents.

Here, we examine the literature and provide for the first time collective evidence for temperature-induced hormesis in plants (Fig. 2).

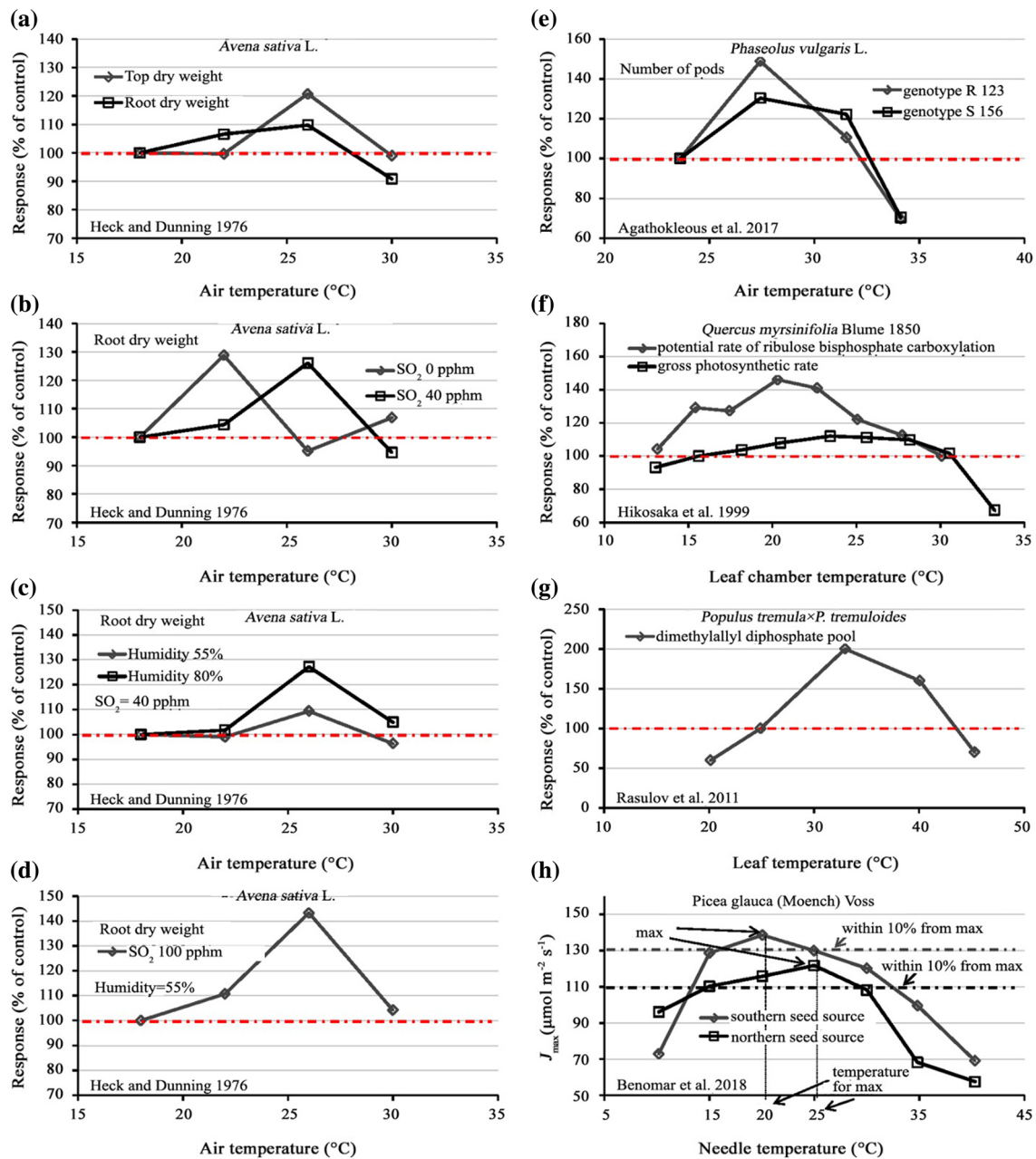
As early as the 1960s, hormesis was revealed for the foliage yield of warm temperate, cool temperate and winter annual species in response to soil temperature; the maximum stimulatory response was in the temperature range of 12.5–27.5 °C (Davidson 1969). In the 1970s, a report was published after an extensive experimentation on the effects of ozone and sulfur dioxide on oat (*Avena sativa* L.) varieties (Heck and Dunning 1976). This research was sponsored by the Agricultural Research Service (ARS), Environmental Protection Agency (EPA), and the North Carolina Agricultural Experiment Station of the U.S, and was prepared for the Office of Research and Development of the EPA. In this study, the response of oat plants to four temperature levels in the range 18–30 °C was studied under different sulfur dioxide levels and relative humidities. These results suggested the occurrence of hormesis in top and root dry weight of oat plants exposed four times, three hours per time, in each experiment (Heck and Dunning 1976). This was seen in controlled environments with modified temperatures only (Fig. 2a), under different sulfur dioxide levels (Fig. 2b), and under different sulfur dioxide exposures for two different relative humidity levels (Fig. 2c, d). The results also suggested that temperature-induced hormesis is modified/offset by other environmental conditions such as relative humidity and sulfur dioxide. Hormetic dose response was also found in the number of pods of snap bean (*Phaseolus vulgaris* L.) plants exposed to different levels of air temperature at 82 days after seeding (Fig. 2e) (Agathokleous et al. 2017).

Indications for hormesis were also observed in several biological/physiological endpoints of different plant species. One example was the response of gas exchange to growth temperatures investigated in the temperate evergreen tree species *Quercus myrsinaefolia* Blume (Hikosaka et al. 1999). Hormetic-like dose–response relationships

were observed for gross photosynthetic rate (net photosynthetic rate + dark respiration) and potential rate of ribulose biphosphate (RuBP) carboxylation (Fig. 2f). Hormetic-like dose–response relationships of net photosynthesis to leaf or mean monthly temperature has been also revealed in numerous species from a variety of families (Ishikawa et al. 2007; Vårhammar et al. 2015; Slot and Winter 2016, 2017; Slot et al. 2016; Benomar et al. 2018; Zhang et al. 2018). Another example is a hormetic-like response of dimethylallyl diphosphate (DMADP) pool, precursor of leaf-emitted isoprene, to leaf temperatures observed in hybrid aspen (*Populus tremula* × *P. tremuloides*) (Rasulov et al. 2011) (Fig. 2g). Likewise, a hormetic-like response in leaf anthocyanin content of *Betula* hybrid ‘Royal Frost’ (*Betula populifolia* ‘Whitespire’ × *B. populifolia* ‘Crimson Frost’) seedlings to temperature was found; maximum stimulatory response was observed at 20 °C (Yang et al. 2017). Interestingly, a U-shaped curve of litter decomposition in response to climate (cooler to warmer) was also hypothesized in a recent study on early stage litter decomposition across biomes (Djukic et al. 2018), which remains to be validated by narrow-spaced dose–response experiments.

Slot and Winter (2016) suggested that the temperature where the maximum response (Fig. 1) occurs reflects the optimum temperature at which optimum photosynthesis occurs in the short-term temperature response. They also proposed that the U-shaped curve moves to the right of the x-axis and up the y-axis with higher photosynthesis response when plants are grown under warmer or hot conditions with a constructive adjustment (both optimum temperature and optimum photosynthesis increase). Furthermore, they proposed that the U-shaped curve moves to the right of the x-axis but down the y-axis with a lower photosynthesis response when plants are grown under warmer or hot conditions with a detractive adjustment (optimum photosynthesis decreases with increasing temperature) (Slot and Winter 2016). This is an interesting proposal which falls within the concept of hormesis as it has been shown for various animal models, i.e., *conditioning* (Calabrese 2016c).

Using quantitative estimates of dose–response relationships, important information can be obtained as to the biological plasticity of plants. As an example, we use a dose–response relationship for the maximum potential electron transport rate ( $J_{\max}$ ) of white spruce (*Picea glauca* (Moench) Voss) to needle temperature (Benomar et al. 2018). Dose–response relationships were obtained for plants from either a southern seed source or a northern seed source (Fig. 2h). These relationships suggest that plants from a northern seed source show a maximum response of  $J_{\max}$  at 5 °C higher than plants from a southern seed source. In addition, temperature limits within which  $J_{\max}$  is



**Fig. 2** Preliminary examples of hormetic-like responses of plants to temperature. Dose and response data presented only in figures in the reviewed articles were estimated using image analysis software (Adobe Photoshop CS4 Extended v.11, Adobe Systems Incorporated, CA, USA).  $J_{max}$  is the maximum potential electron transport rate. Notes: In the experiment of Rasulov et al. (2011), control was considered the leaf temperature closer to the day temperature under

up to 10% lower than the maximum response of  $J_{max}$  may provide a range of temperatures within which an approximate maximum response of  $J_{max}$  occurs and a plasticity range of  $J_{max}$  values (Fig. 2h).

The discussion raises two ecologically important questions, the first one being whether a temperature-induced hormetic dose–response curve corresponds to the curve of

which plants were grown (26 °C). The values in Hikosaka et al. (1999) were averaged per target temperature, and the response data were corrected based on the group of control values to avoid overestimation. The control was 30 °C for the potential rate of ribulose biphosphate (RuBP) carboxylation and 15 °C for the gross photosynthetic rate

Shelford’s law of tolerance (Shelford 1931), and the second whether the hormetic zone corresponds to the optimal temperature range for plants. Indeed, the examples presented are in agreement with Shelford’s curve, where an organism has an optimum and a minimum and maximum level of a single stressor or mixture of stressors which determine success (Shelford 1931). Similarly, while the



optimal temperature range for plants varies with a variety of factors, with the stage in ontogeny being a major driver, the hormetic zone is expected to correspond to the optimal temperature range under certain conditions, i.e., at certain stages of ontogeny (Abrami 1972; Hatfield and Prueger 2015).

## Conclusion

We summarize, for the first time, examples of hormetic dose responses induced by temperature in plants. Temperature-induced hormesis is in agreement with extensive evidence from studies with insects, animals, and fungi (Rattan 2005; Sørensen et al. 2008; Vaiserman 2010). These research programs suggest that hormesis is independent of biological models and re-affirm the notion that hormesis is a fundamental biological phenomenon which occurs independently of stressor types, and not only upon agents which were previously considered “toxic”.

Recent developments in plant science, along with the examples presented in this Review, underline the possibility that hormesis should be implemented in the design of vegetation-environmental change dose–response studies. These developments are important in ecotoxicological studies for understanding the mechanisms and processes whereby chemicals exert their effects on ecosystems.

The latter suggestion does not imply that a hormetic dose–response model is more appropriate than the threshold or linear non-threshold model (LNT). Which model will be more appropriate will be decided upon the dose–response relationship; however, failure to incorporate the possibility of hormesis will result in failure to detect hormesis and eventually to misleading information for decision, policy, and regulation making.

Hormesis should have a central role in environmental vegetation change biology. The concept of environmental hormesis provides an important perspective for advancing the current scientific base of environmental change biology, ecology, and evolutionary biology research agendas.

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