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Does the root to shoot ratio show a hormetic response to stress? An ecological and environmental perspective

Evgenios Agathokleous^{1,2}  · Regina G. Belz³ · Mitsutoshi Kitao¹ · Takayoshi Koike² · Edward J. Calabrese⁴

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Abstract Root/shoot (R/S) ratio is an important index for assessing plant health, and has received increased attention in the last decades as a sensitive indicator of plant stress induced by chemical or physical agents. The R/S ratio has been discussed in the context of ecological theory and its potential importance in ecological succession, where species follow different strategies for above-ground growth for light or below-ground competition for water and nutrients. We present evidence showing the R/S ratio follows a biphasic dose–response relationship under stress, typical of hormesis. The R/S ratio in response to stress has been widely compared among species and ecological succession classes. It is constrained by a variety of factors such as

ontogeny. Furthermore, the current literature lacks dose–response studies incorporating the full dose–response continuum, hence limiting scientific understanding and possible valuable application. The data presented provide an important perspective for new-generation studies that can advance current ecological understanding and improve carbon storage estimates by R/S ratio considerations. Hormetic response of the R/S ratio can have an important role in forestry for producing seedlings with desired characteristics to achieve maximum health/productivity and resilience under plantation conditions.

Keywords Biological plasticity · Biphasic response · Hormesis · Plant stress · Root/shoot ratio

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Introduction

In a world of changing environments where plants are dealing with stress, dose–response studies serve as a tool for assessing and modelling plant stress at various levels. A wide range of scientific disciplines are concerned with plant stress induced by chemical or environmental stressors. Likewise, policy making faces the challenge to set environmental standards and derive critical levels/loads for protecting vegetation and ecosystems against environmental stress such as surface ozone and nitrogen deposition (Payne et al. 2013; Anav et al. 2016; Sicard et al. 2017; Agathokleous et al. 2019). At the same time, the field of dose–response studies is more and more suggesting hormesis as a fundamental dose–response phenomenon (Fig. 1). While hormetic dose–responses of animals received particular attention from the early 2000s, this was not the case for plants. However, in recent years hormetic dose–responses of plants have been shown for a variety of

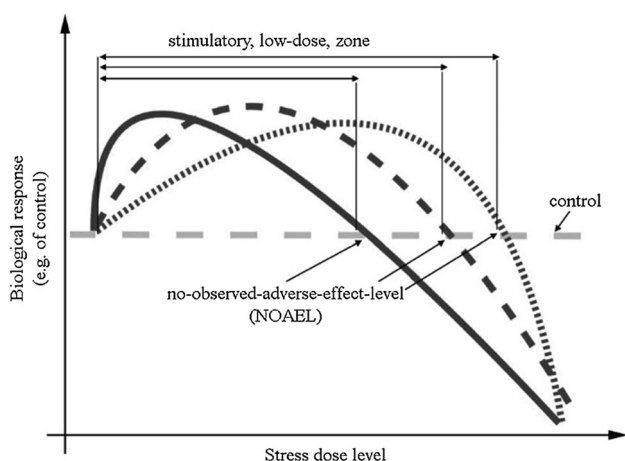


Fig. 1 Hypothetical examples of hormetic dose–response relationships. *Note:* Exposure of organisms to a wide range of narrowly-spaced stress doses/concentrations generates biphasic dose–response relationships with biological stimulation in response to low doses and inhibition by high doses. The stimulatory zone spans from the lowest, stimulatory dose to the dose where the no-observed-adverse-effect-level (NOAEL) occurs. The width of the stimulatory dose varies, e.g., with the experimental design (e.g., number of doses incorporated). Inhibition of biological response begins after (to the right) of the NOAEL

stressors and endpoints (Cedergreen et al. 2007; Calabrese and Blain 2009; Cedergreen et al. 2009; Belz and Duke 2017; Belz and Piepho 2017; Agathokleous et al. 2018a, b, c; Agathokleous and Kitao 2018; Sugai et al. 2018). Of particular importance to the field of hormesis is the recent action of the US Environmental Protection Agency examining the possibility to incorporate *U*-shaped, *J*-shaped, and bell-shaped models, typical examples of hormesis in the risk assessment process (US EPA 2018).

An important matter regarding plant health is whether an imbalance between the epigeous and hypogeous growth (root/shoot ratio, R/S) occurs under stress. Therefore, an important index for assessing plant health is the R/S ratio, estimated especially in the form of dry weight (R_{dw}/S_{dw} ratio), or to a lesser extent by length (R_{length}/S_{length} ratio). Changes in R_{dw}/S_{dw} ratios have been widely observed under stress, however the results are inconsistent and it remains uncertain if R_{dw}/S_{dw} ratios increase, decrease, or remain unaffected under certain conditions of stress (Wilson 1988; Agren and Franklin 2003; Koike et al. 2003; Grantz et al. 2006; Agathokleous et al. 2016). Despite extensive reviews of the topic, the R/S ratio has never been put into the context of dose–response studies incorporating the full dose–response continuum and thus hormesis. To this end, this commentary examines data from several peer-reviewed articles to illustrate R/S ratio responses to stress from a biphasic dose–response viewpoint including hormesis.

Hormetic response of root and shoot to stress

Root biomass/length and/or aboveground biomass/height have been found to display significant stimulation at low doses and inhibition at high doses upon exposure to several chemicals and physical agents in numerous independent experiments and with a variety of annual and perennial plant species (Table 1). However, a stimulatory response in one plant trait does not necessarily correlate or match with a stimulatory response in other plant traits (Duke et al. 2006), and this apparently also applies to the same trait measured on roots and shoots. For example, veterinary antibiotics induced hormetic responses in shoot and root elongation but root (Fig. 2a–d) and shoot (Fig. 2e–h) showed uncoupled low-dose responses, i.e., one endpoint showed significant stimulatory responses while the other might not (Pan and Chu 2016). Hormetic-like responses of shoot or root elongation were also observed for the antibiotic enrofloxacin affecting tamarillo plants (*Cyphomandra betacea* (Cav.) Sendtn.) or sulfadiazine sodium affecting wheat plants (*Triticum aestivum* L.) (Jin et al. 2009). Experiments with a variety of eastern tree species showing differential responses of R_{dw} and S_{dw} to atmospheric ozone exposure (Fig. 3a–d) (Kress and Skelly 1982) further support root and shoot imbalances. Hence, there is accumulated evidence from several independent experiments suggesting that hormetic responses of root biomass/length and/or aboveground biomass/height to stress is a general, but partly uncoupled phenomenon, independent of species and stress-inducing agent (Calabrese and Blain 2011; Table 1). At low stress doses, increased photosynthetic carbon gain and increased carbon partitioning into roots can be apparent. At high stress doses, reduced photosynthetic carbon gain by stomatal closure can result in a decrease in root biomass/elongation. Thus, there can be two (or more) responses to stress with different directions, depending on the dose of the stress. Based on these imbalances, it is suggested that the R/S ratio is also changing in a dose-dependent manner, thus having potential to affect ecological risk assessment and carbon storage estimates (Durigan et al. 2012; Luo et al. 2013). Therefore, this discussion raises the question of whether the R/S ratio (R_{dw}/S_{dw} or R_{length}/S_{height}) displays a hormetic response to stress, a matter of biological, ecological, and environmental significance.

Hormetic response of R/S ratio to stress

A literature analysis revealed that the R/S ratio displays hormetic responses for a variety of stressors and species. For example, a hormetic-like response of R_{dw}/S_{dw} to

Table 1 Examples of empirical data suggesting biphasic dose–response relationships of root biomass/length and above-ground biomass/height

Empirical data	Reference
<i>Type of plants</i>	
Cereals	Jin et al. (2009), Wang et al. (2010), Xie et al. (2010, 2011), Minden et al. (2017)
Grasses	Liu et al. (2008), Minden et al. (2017), Agathokleous et al. (2019)
Legumes	Diatloff et al. (1995), Liang and Wang (2013)
Vegetables	Belz et al. (2008, 2018), Belz and Leberle (2012), Belz and Piepho (2013, 2017), Pan and Chu (2016), Minden et al. (2017), Bastien et al. (2018), Agathokleous et al. (2019)
Weeds	He and Loh (2000), Cedergreen (2008), Minden et al. (2017), Li et al. (2017), Agathokleous et al. (2018c)
Trees	Jin et al. (2009), Wu et al. (2014), Chen et al. (2018), Cap and Eşen (2018), Agathokleous et al. (2019)
Medicinal crops and trees	Gorni and Pacheco (2016), Ma et al. (2017), Waman et al. (2018)
<i>Inducing agents</i>	
Herbicides	Belz et al. (2008, 2018), Cedergreen (2008), Belz and Leberle (2012), Belz and Piepho (2017), Cap and Eşen (2018)
Anthropogenic environmental contaminants (soil and air contaminants)	Diatloff et al. (1995), He and Loh (2000), Liu et al. (2008), Jin et al. (2009), Migliore et al. (2010a, 2010b), Xie et al. (2010, 2011), Liang and Wang (2013), Pan and Chu (2016), Minden et al. (2017), Ma et al. (2017), Agathokleous (2018), Agathokleous et al. (2018b, d, 2019), Bastien et al. (2018)
Nutrients	Wu et al. (2014), Chen et al. (2018)
Other natural and synthetic chemicals	Belz et al. (2008, 2018), Belz and Piepho (2013, 2017), Gorni and Pacheco (2016), Li et al. (2017), Agathokleous et al. (2018c), Waman et al. (2018)

lanthanum (La) was found in soybean (*Glycine max* L. cv. Kennong 18) (Fig. 4a) (Liang and Wang 2013), in tall fescue (*Festuca arundinacea* Schreb.) (Fig. 4b) (Liu et al. 2008), and in Chinese sage (*Salvia miltiorrhiza* Bunge) (Fig. 4c) (Zhou et al. 2011). Similar hormetic-like dose–response relationships of R_{dw}/S_{dw} were found in rapeseed (*Brassica napus* L.) and in common windgrass (*Apera spica-venti* (L.) P. Beauv.) in response to the veterinary antibiotic tetracycline (Fig. 5a) (Minden et al. 2017), in *Eucalyptus urophylla* × *E. camaldulensis* in response to phosphorus availability (Fig. 5b) (Wu et al. 2014), in yarrow (*Achillea millefolium* L.) exposed to salicylic acid (Fig. 5c) (Gorni and Pacheco 2016), in ryegrass (*Lolium perenne* L.) in response to soil moisture in two different growing conditions (Fig. 5d) and in clover (*Trifolium repens* L.) in response to soil nitrogen availability in four different growing conditions (Fig. 5e and f) (Davidson 1969b).

In most of the examples, an inverse *U*-shaped dose–response relationship was found for R_{dw}/S_{dw} (Figs. 4, 5a–d, f), suggesting higher root biomass relative to shoot biomass under low-dose stress and higher shoot biomass relative to root biomass under high-dose stress. However, in some examples, a non-inverse *U*-shaped hormetic dose–response relationship was found for R_{dw}/S_{dw} (Fig. 5e, f). Such non-inverse *U*-shaped dose–response relationships were also found in little seed canary grass (*Phalaris minor* Retz.) and

wild oat (*Avena fatua* L.) after spraying with the herbicide fenoxaprop-P-ethyl (Fig. 6a) (Abbas et al. 2016), and in tall fescue (*Festuca arundinacea* Schreb.), ryegrass and other grass species (*Vulpia* sp.) in response to soil temperatures (Fig. 6b) (Davidson 1969a).

The elongation ratio R_{length}/S_{height} can be interpreted in the same way. This is shown by Abbas et al. (2016) where R_{dw}/S_{dw} (Fig. 6a) is in full agreement with R_{length}/S_{height} (Fig. 7a). Additional examples of hormesis in R_{length}/S_{height} were found in durum wheat (*Triticum durum* Desf.) in response to KNO_3 (Fig. 7b), rare earth elements nitrate (Fig. 7c), and lanthanum nitrate (Fig. 7d) (d’Aquino et al. 2009). For all inverted-*U*-shaped hormetic findings presented here, the maximum stimulatory R/S response to low-dose stress was up to 2.4-fold of the control. This is in agreement with the plant Hormesis Database where the maximum stimulatory response to low-dose stress is commonly below twofold the control response across endpoints, species, and stress-inducing agents (Calabrese and Blain 2009).

If an optimal R/S ratio is defined as the equal growth limitation of root and shoot by stress (Aikio and Mari Markkola 2002), then hormetic R/S dose–responses suggest the paradox that optimal R/S occurs on the one hand before the threshold of the hormetic dose zone, i.e., where low-dose stimulatory response starts, and on the other hand at the no-observed-adverse-effect-level (NOAEL or else

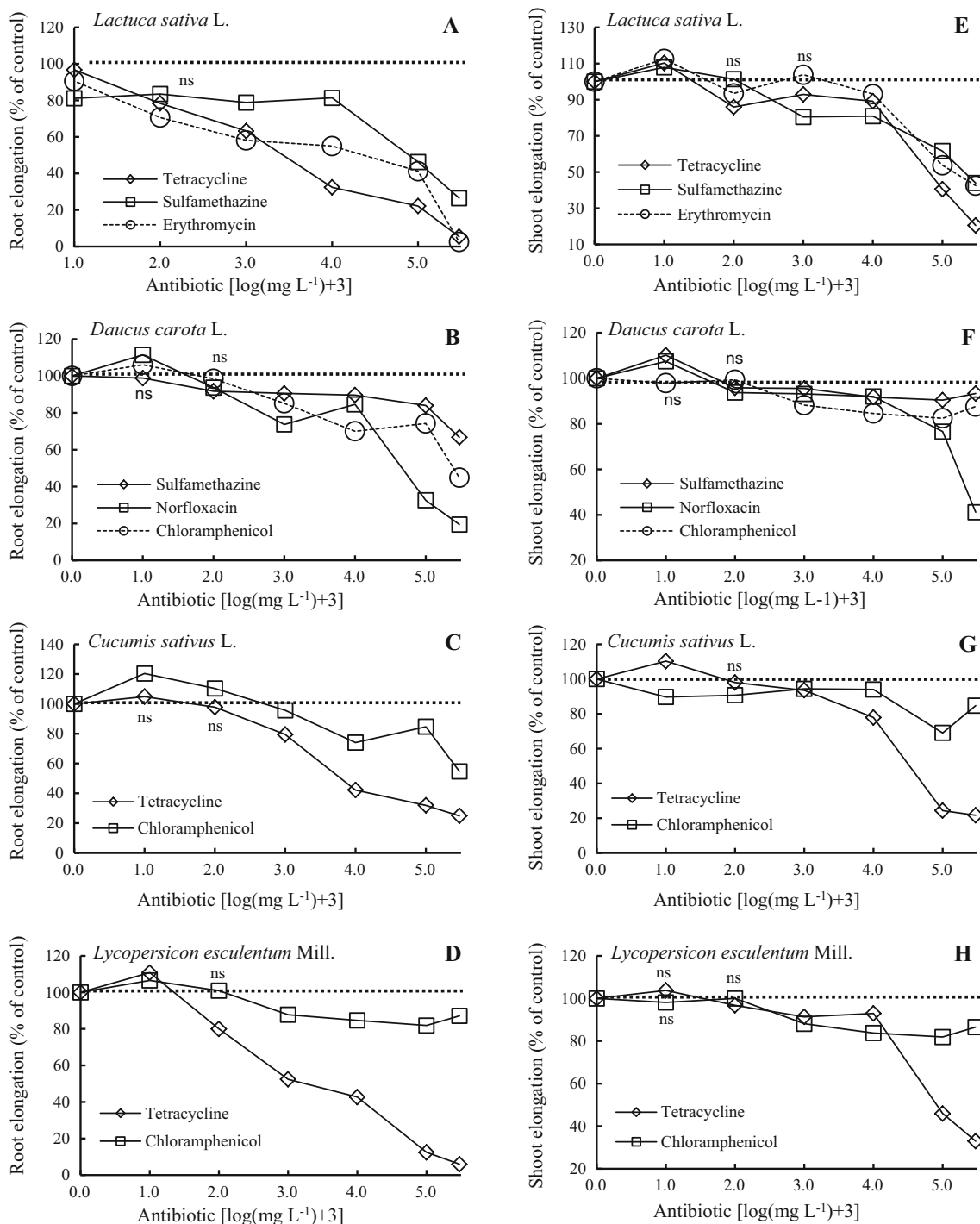


Fig. 2 Examples of antibiotic—induced hormesis: Root elongation (a–d) versus shoot elongation (e–h) (Pan and Chu 2016). “ns” above means indicate the difference from the control response is not statistically significant, whereas no sign indicates statistical

significance. For illustration purposes, in some cases with wide range of dose levels, the concentrations were transformed to logarithm (log) and when needed a constant was added

limited-dose-for-stimulation LDS), where hormesis ends and high-dose response starts. However, in order to derive these toxicological estimates from dose–response data, modeling of the hormetic curves is necessary. The next section introduces how hormetic curves can be modelled

and provides selected examples of significantly modelled hormetic curves for R, S, and R/S data.

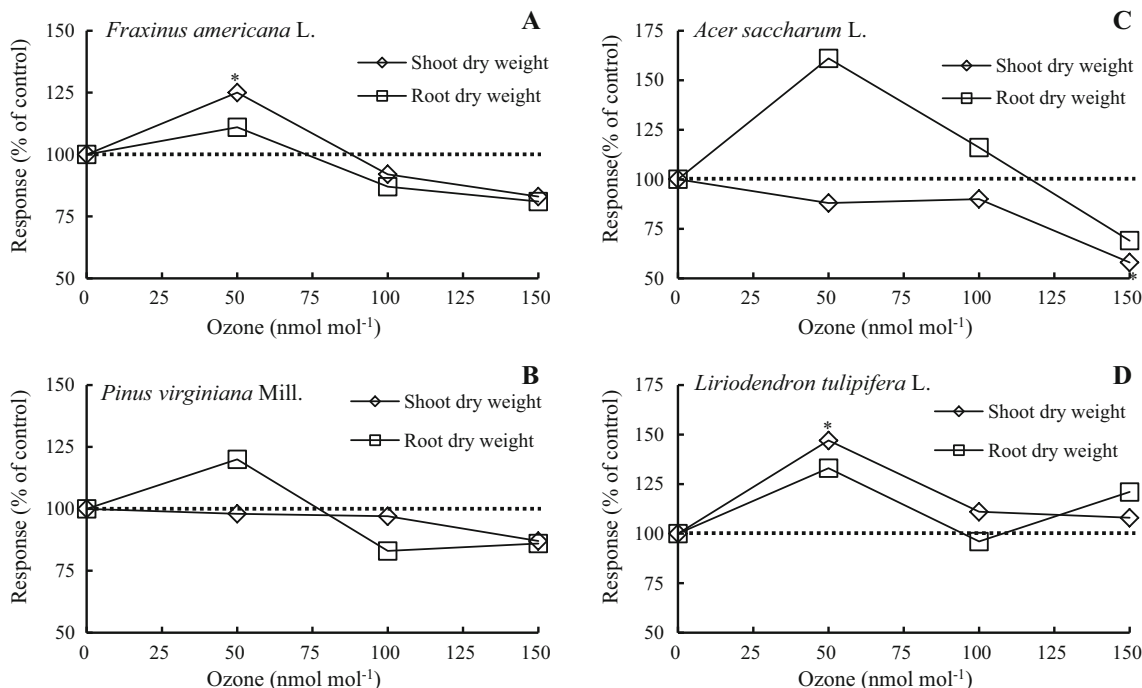


Fig. 3 Hormetic-like examples of uncoupled root dry weight and shoot dry weight responses to stress. Asterisks above or below means indicate the difference from the control response is statistically significant, whereas no sign indicates no statistical significance (Kress and Skelly 1982)

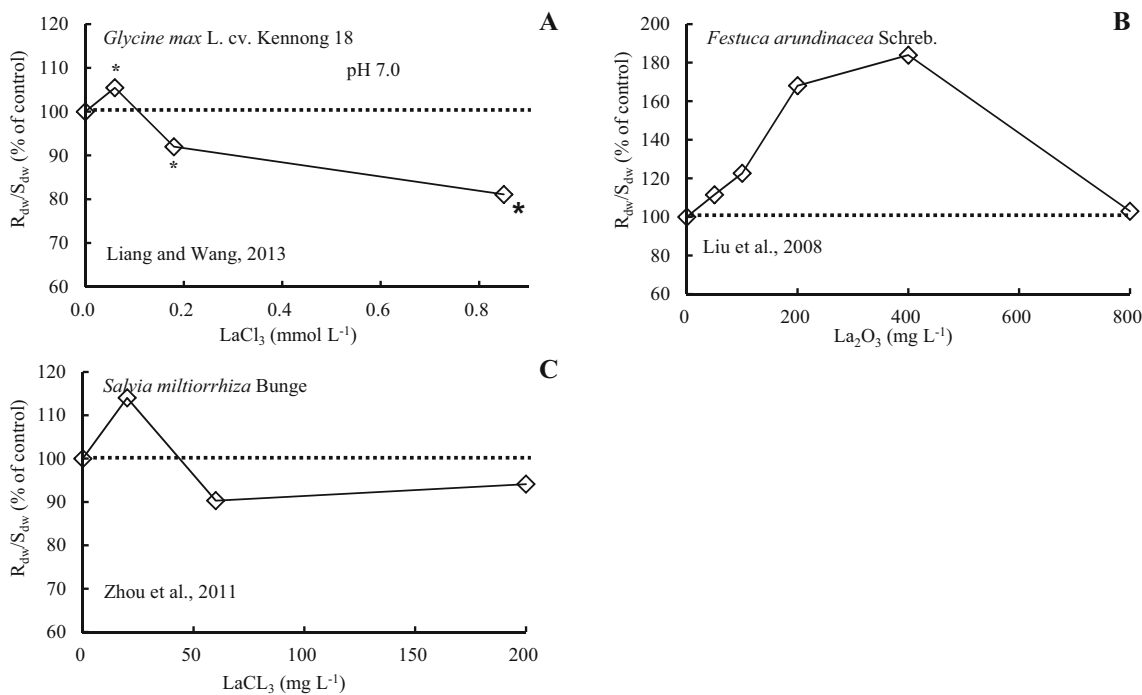


Fig. 4 Typical examples of hormetic-like responses of root dry weight to shoot dry weight ratio (R_{dw}/S_{dw}) to the rare earth element lanthanum. Asterisks above or below means indicate the difference from the control response is statistically significant, whereas no sign indicates no statistical significance after hypothesis testing or absence of statistical hypothesis testing. R_{dw}/S_{dw} data for the compartment

C were calculated based on R_{dw} and S_{dw} data displayed in the original paper. *Note:* For Figs. 4, 5, 6 and 7, when needed, dose–response data were estimated from figures of the reviewed articles using image analysis software (Adobe Photoshop CS4 Extended v.11, Adobe Systems Incorporated, CA, USA)

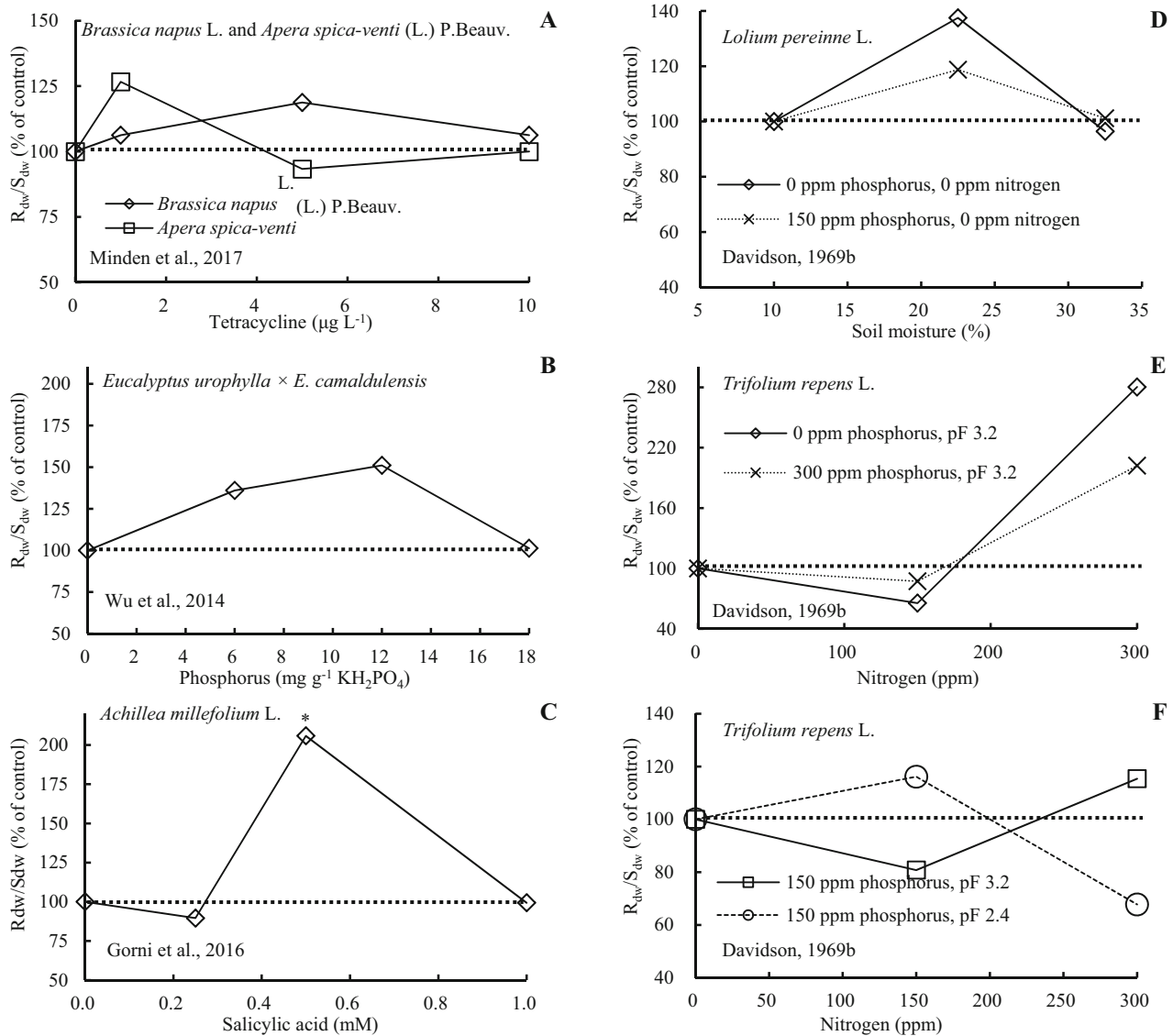


Fig. 5 Typical examples of hormetic-like responses of root dry weight to shoot dry weight ratio (R_{dw}/S_{dw}) to stress-inducing agents. Asterisks above or below means indicate the difference from the control response is statistically significant, whereas no sign indicates

no statistical significance after hypothesis testing or absence of statistical hypothesis testing. R_{length}/S_{length} data for the compartment *B* were calculated based on R_{length} and S_{length} data displayed in the original paper

Modeling hormetic response of R/S ratio to stress

There are mathematical models available that can quantitatively describe a hormetic dose–response curve, e.g., ecological-limiting-factor models (An et al. 1993; Liu et al. 2011), switching functions (Schabenberger and Birch 2001). However, only two are well-established in plant biology and directly include biologically meaningful parameters or allow to deduce such features: the four-parameter logistic model (Brain and Cousens 1989; Schabenberger et al. 1999), and its expansion in form of the five-parameter logistic Cedergreen model (Cedergreen et al. 2005) (Eqs. 1 and 2).

$$E[y|x] = c + \frac{d - c + fx}{1 + \exp[b \ln(x/e)]} \quad (1)$$

$$E[y|x] = c + \frac{d - c + f \exp(-1/x^a)}{1 + \exp[b \ln(x/e)]} \quad (2)$$

where c shows the response at indefinitely high doses; d the expected response of the control; f the rate of increase in the response at low-level doses; the size of a determines the steepness of the curve before the maximal hormetic effect, and the size of b does so thereafter. Parameter e has no straightforward biological meaning (Cedergreen et al. 2005).

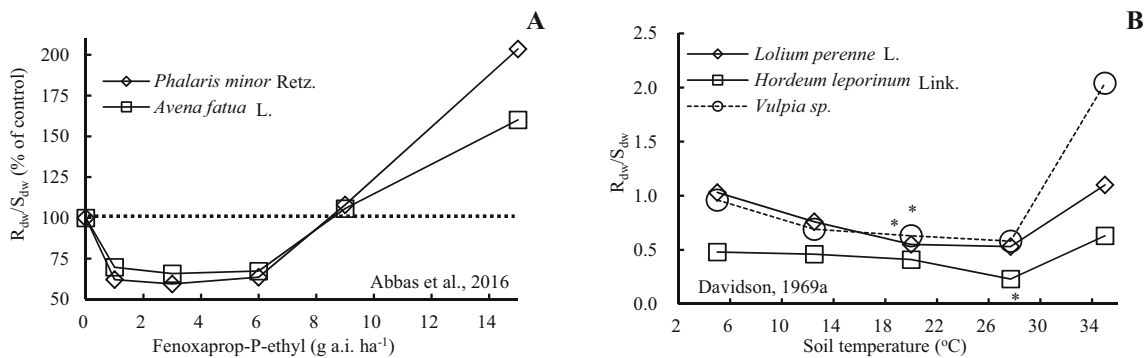


Fig. 6 Typical examples of hormetic-like responses of root dry weight to shoot dry weight ratio (R_{dw}/S_{dw}) to stress-inducing agents. Asterisks above or below means indicate the difference from the control response is statistically significant, whereas no sign indicates no statistical significance after hypothesis testing or absence of

statistical hypothesis testing. R_{length}/S_{length} data for the compartment A were calculated based on R_{length} and S_{length} data displayed in the original paper. The unit g a.i. ha⁻¹ stands for grams of active pharmaceutical ingredient dose per hectare

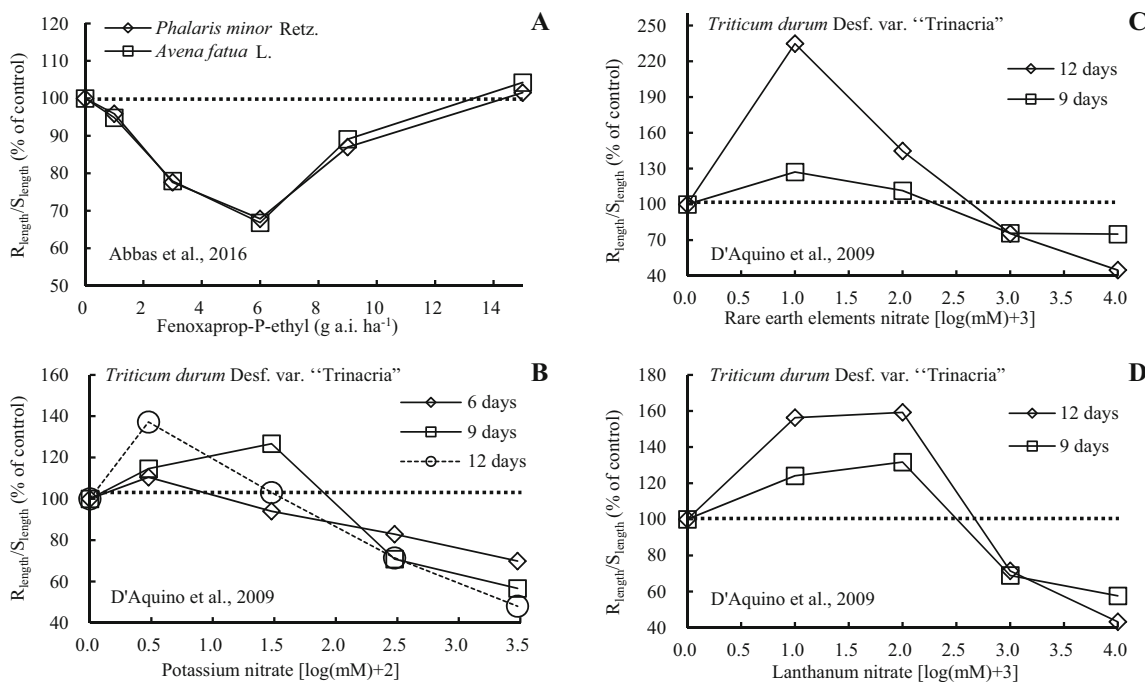


Fig. 7 Typical examples of hormetic-like responses of root length to above-ground height ratio (R_{length}/S_{length}) to stress-inducing agents. R_{length}/S_{length} data were calculated based on R_{length} and S_{length} data

displayed in the reference papers. The unit g a.i. ha⁻¹ stands for grams of active ingredient per hectare

The dose level where the response is inhibited by half (IC₅₀ or EC₅₀ or ED₅₀) and several other quantitative hormetic features (i.e., the dose where hormesis is maximum or the maximum amplitude of hormesis) cannot be directly derived from the original model equations, but can be modeled using re-parameterizations of the original functions (Schabenberger et al. 1999; Belz and Piepho 2012, 2015). Hormetic dose-responses can vary, especially

with respect to the width and location of the hormetic dose range, but also with the amplitude of stimulation (Belz and Piepho 2012). The two above functions are statistically eligible to model a wide range of different hormetic datasets, independent of species, endpoint, stressor or various levels of biological organization, but with the Cedergreen model (Cedergreen et al. 2005) showing a higher flexibility in modeling due to the second hormesis parameter α (Belz

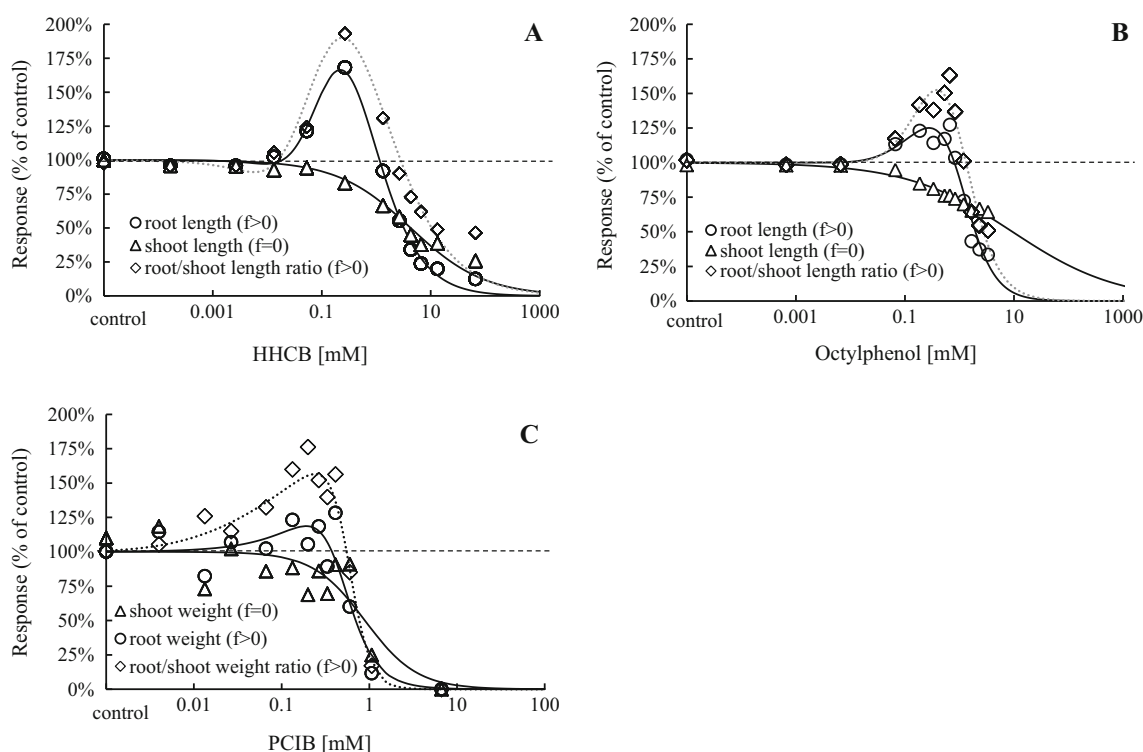


Fig. 8 Responses of *Lactuca sativa* to 1,3,4,6,7,8-hexahydro-4,6,6,7,8,8-hexamethylcyclopenta(g)-2-benzopyran (HHCB), 4-*tert*-octylphenol; 4-(1,1,3,3-tetramethylbutyl)phenol (octylphenol), and 2-(*p*-chlorophenoxy)-2-methylpropionic acid (PCIB). Dose–response

and Piepho 2012) (Fig. 8). Using the same models, we were able to model biphasic dose–response relationships also for R/S responses of *Lactuca sativa* L. to the environmental contaminants HHCB and octylphenol and the auxin inhibitor PCIB calculated from previous research (Belz et al. 2018) or from new experiments (Belz, unpublished data). The curves shown in Fig. 8 provide a preliminary, but illustrative example of significant hormesis in R/S ratio and substantiate the demand to consider R/S ratio hormesis in assessing above and belowground production/growth responses to stress.

Placing R/S ratio hormesis into an ecological/environmental context

Like shoots enable plants to reach required light, root plasticity is an evolution-acquired trait which assists plants in dealing with environmental pressures by foraging for nutrients and water in soil (Grossman and Rice 2012). The R/S ratio indicates the potential of supportive functions (water and nutrient uptake) relative to the potential of growth functions (light energy harvest).

The examples presented here show that hormetic R/S dose–response relationships exist and that they can be *U*-

relationships were modeled with Eqs. (1) or (2) for root length (R_{length}), shoot length (S_{height}), or their ratio ($R_{\text{length}}/S_{\text{height}}$). The parameter f indicates significant hormesis if $f > 0$ and no hormesis if $f = 0$. Data are from Belz et al. (2018) or Belz (unpublished)

shaped (Figs. 5e, f, 6, 7a) or inverted-*U*-shaped (Figs. 4, 5a–d, f, 7b–d, 8). At this stage, no conclusions can be drawn as to the reasons explaining this difference due to the lack of relevant dose–response data in the literature. It is also possible that a dose–response relationship for R/S ratio is triphasic, such that the non-inverted *U*-shaped curve goes down again at higher doses, (e.g., the weed control agent fenoxaprop-P-ethyl will, at a higher dose, kill the plant, Figs. 6a, 7a). This is a matter of utmost significance in the field of dose–response research which should be validated.

Below-ground competition capacity differs between early- and late-successional species (Xiang et al. 2013; Zangaro et al. 2016). It is generally believed that vegetation in early successional phases shows higher shoot productivity compared to root, whereas vegetation in climax phases shows higher root productivity compared to shoot, such as larch in non-permafrost regions (Kajimoto et al. 2006). Large-seeded species may have an advantage in asymmetric above-ground competition (Mašková and Herben 2018). For example, an old field succession may relate to increased root competitiveness and hence increased R/S ratios of successive dominants (Monk 1966). Although it was initially thought that fast-growing plants show higher phenotypic plasticity than slow-growing

plants which are not following a strategy for achieving maximum growth rate, this is not a universal case; R/S ratios can be independent of the maximum growth rate (Aikio and Mari Markkola 2002). However, there can be an indirect trade-off between R/S plasticity and maximum relative growth rate via a trade-off between maximum relative growth rate and a low-resource growing potential (Aikio and Mari Markkola 2002). After analysing data from 77 studies, no evidence was found for highest plasticity in fast-growing species adapted to high soil nutrient availability or for positive association of plasticity with competitive ability (Reynolds and D'Antonio 1996). These have not been studied in the context of a complete dose–response continuum, and this may have affected the results. Lack of a complete dose–response assessment may generate misleading results, mostly upon dose-specific sensitivity of each species or group that is compared, i.e., the stress dose levels used can be “low” for the one group but “neutral” (NOAEL) or “high” for the other group. Complete dose–response relationships are highly needed to understand R/S ratios from an ecological viewpoint and for selecting species for phytoremediation of specific environmental contaminants (with high R/S ratios at low doses for soil contaminants or with low R/S ratios at high doses for air contaminants).

Several factors drive the R/S ratio. Plasticity can occur in the context of the *optimal partitioning theory*, however being constrained by plant ontogeny (Gedroc et al. 1996; Lohier et al. 2014). For example, higher allocation to roots can occur early in ontogeny whereas higher relative shoot growth can occur later on (Gedroc et al. 1996; Lohier et al. 2014). The R/S ratio appears as a function of age/size due to different needs for carbon investment, e.g., with regard to canopy closure (Sanquetta et al. 2011). Furthermore, the plasticity of R/S ratios can be a function of different factors, i.e., mycorrhizal versus non-mycorrhizal species, woody perennials versus herbaceous perennials versus annuals, crops versus weeds (Monk 1966; Aikio and Mari Markkola 2002; Bonifas et al. 2005), or even ecotypes with different strategies of resource uptake (Xiang et al. 2013; Zangaro et al. 2016; Mašková and Herben 2018). The lack of a complete dose–response continuum while all constraints are not controlled will generate incomparable results.

Variation in R/S ratios is a common stress response driven by different plant strategies for coping with stress, and can have severe ecological consequences and implications to human welfare (Agathokleous et al. 2016), if this is not a temporary response in an effort to maintain homeostasis. Currently, the implications of the low-dose changes in R/S ratios are underexplored, and given the significance of this issue, priority should be given to understanding the low-dose stress effects on R/S ratios.

Furthermore, ecological risk assessment based on only a single biomass component is potentially misleading because R/S ratios differ across the complete dose–response continuum and are further driven by a series of factors. The R/S ratio could itself serve as an index of health because there can be competition consequences of R/S ratio changes at the community level (Luo et al. 2013).

Framed within a coordinated allocation to biological functions, the whole plant responds to stress and not certain organs (Kleyer and Minden 2015). Estimating carbon storage from either above- or below-ground components can under- or over-estimate the carbon stock (Durigan et al. 2012; Luo et al. 2013). Nowadays with global environmental changes, plants are likely continuously under some environmental pressure. Changes in R/S ratios due to both low and high doses of stress in the framework of hormesis suggest that estimates of carbon storage based on single components (above- or below-ground) are likely unrealistic and untrue [Sanquetta et al. 2011; see also the explanation by Zobel and Zobel (2002)]. As these findings suggest that root biomass cannot be realistically predicted from the above-ground biomass using allometric equations, forest tree biomass and carbon storage estimates should be based on both components and under both low and high doses of stress.

Conclusions and future opportunities

- Several collective examples of hormetic-like dose–response relationships of R_{dw}/S_{dw} and R_{length}/S_{height} ratios under stress are herein documented for the first time.
- Hormetic dose–response of R/S ratios may be a universal phenomenon, however, the plasticity framing the low-dose responses can be a function of plant-specific strategies of resource uptake.
- Hormetic dose–response of R/S ratios can provide an important perspective in forestry practice and should be considered in bioengineering of hybrids with desirable R/S characteristics.
- Hormetic dose–response of R/S ratios suggests that ecological risk assessment and carbon storage estimates should incorporate both above- and below-ground components for realistic and true estimates.
- Hormetic dose–response studies can provide a unique opportunity for assessing the ecological impacts of environmental contaminants, with potential incorporation of R/S ratios into the risk assessment as an integrated endpoint. R/S ratios can be also considered within a hormetic context for deriving more robust critical levels/loads for the protection of vegetation against environmental pollution.

- The current scientific literature of R/S response to stress suffers from dose–response limitations, with the major limitation being a lack of narrowly-spaced doses across the full dose–response continuum. This study provides a fundamental base for enhancing experimental design to understand R/S ratios in the context of dose–response relationship.

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