Hormesis in plants, rather a rule then exception

Abstract

Hormesis is a positive effect after introducing a small dose of a toxin to all kinds of organisms. This article focuses only on the hormetic effects on plants and tries to find out if it really exists and what kind of mechanism is behind the effect by doing a literature study. Looking at different chemicals and elements gives a good insight on the effect on hormesis. By reviewing articles that found hormesis, it can be said it is rather a rule then exception and there still needs to be more research to be done for better understanding how the mechanism is behind hormesis. While it does occur researchers still need to acknowledge and realise its appearance.

Introduction

When a stress factor such as a toxin is introduced to an organism, it will perform better at low dosage or sub lethal concentration. This phenomenon is called hormesis. The term hormesis means in Greek "excite". In science the term hormesis is used for about 65 years, however the concept is even older with term embodied used by Hugo Schulz in 1885 (Calabrese 2009). Alternative name for hormesis is also dose response, which means "exact amount of medicine or extend of some other treatment to be given or taken at one or at stated intervals" (Jäger and Krupa 2009).

When an experiment is done, hormesis could be recognised with first a stimulation on the organism then the expected decline of performance of a stress factor as variable. When plotted as a graph it can be recognised as typical inverted "U" shape (fig.1). The common explanation to this phenomena is possibly due the organism is overcompensating for the stress factor that has been introduced (Calabrese 1999). This effect will be gone as soon the dosage gets to higher and the stress factor is stronger then the generalised positive effect.

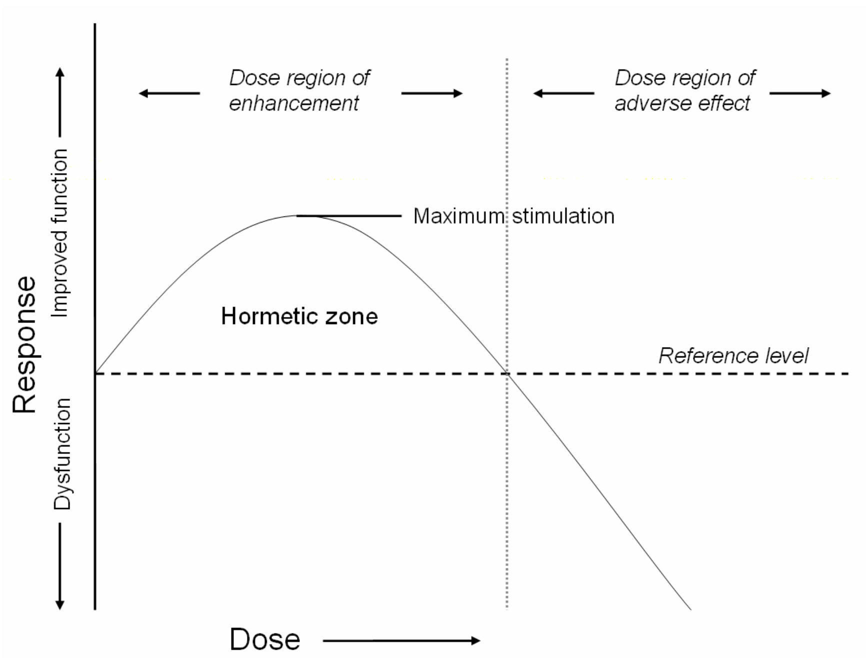


Fig. 1. Theoretical representation of hormetic dose response curve (inverter U shape). Y-axis is the response effect such as growth rate. X-axis is concentration or time given of the stress factor to the organism. Adapted from: (Calabrese et al 1999; Jäger and Krupa 2009).

Even though the term hormesis is rather old, not much is known about the process and there for not very well understood or accepted. One of the reasons is; it is hard to prove the slight improvement is caused by hormesis and is also hard to determine the required dosage that is needed to get the maximum stimulated effect. Small increases require strong statistical power to proof whether it is not a random effect. None the less, research is still done for possible potentials (Calabrese et al. 1999). The potential usage for hormesis could be for (human) health care or things like enhanced crop growth.

Hormesis is observed widespread in all kinds of organisms and different stress factors and could be therefore seen as a generalised effect. Despite it can be observed so widespread it does not always occur and the stimulated effect can vary from 10-60 % in compare to the control (Jäger and Krupa 2009; Calabrese and Blain 2009). This raises the question whether it really exists.

Although there has been studies done on mice, fungus, algae and humans and radiation hormesis, this paper only focuses on the effect of a-biotic hormesis on plants.

Hormesis on plants is often found and there for it could be said it is rather a rule then exception (Calabrese and Blain 2009). It is found with air pollution, heavy metals, salt and herbicides. All these stress factors contain totally different chemical components and yet they share stimulated effect at low dosage. This paper is going to look if there is indeed a hormetic effect on different chemicals and what kinds of hormetic effect induce on plants and see whether there is any process given to this effect.

To find if hormetic effects occurs an experiment can be done, but there already has been a lot of studies done on growth on plants with different chemicals. To see whether hormesis is indeed a general effect different chemicals (heavy metals, air pollution, herbicides, and salinity) literature study has been done and discussed below.

A-biotic stress factors

Heavy metals

Soil contains heavy metals such as cadmium, nickel and lead. These metals could be toxic at a certain dosage which can be very low. It is toxic because it could bind to organic acids and could cause oxidative stress. Some trace elements have the potential to cause extensive oxidative damage to plant tissue (Taiz and Zeiger 2006). In some cases these metals could cause a wide spread problems, such as with aluminium where deforest occur due acidification (Barceló and Poschenrieder 2002). Even though the plant doesn't need such metal there is still a small range that induces hormesis. Metals like aluminium are present in the soil almost everywhere but it only becomes available to plants with a certain pH (Taiz and Zeiger 2006).

In the article of (Barceló and Poschenrieder 2002) they have taken a look on how plants cope with the toxic concentration and what kind of process plays a role in detoxification, such as root length. Although they never had intention to look for hormesis, the process still occurred. They found a small increase of relative root elongation of about 12 % after exposing plants to a small amount of time (fig. 2) with an aluminium concentration of 50 µM. Similar graph is found when they introduce different low concentration of aluminium. This could indicate time plays also a role in hormesis instead of only concentration.

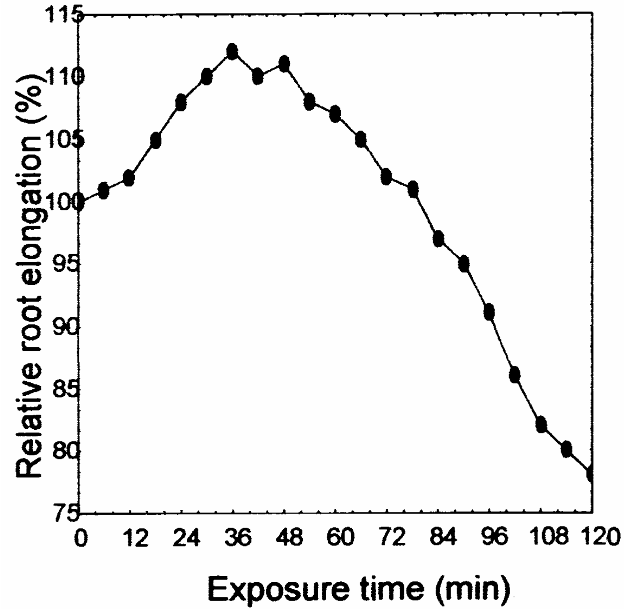


Fig. 2. Root elongation of maize plants that has been exposed to 50 µM aluminium at pH 4.3. X-axis shows the time the plants have been exposed and the Y-asis shows the relative growth of the roots compare to the control. A classic hormetic effect is between 0 and 72 minutes with its maximum effect around 40 minutes.
(Barceló and Poschenrieder 2002).

Another example is from (Pinto et al. 2004) where they tested uptake and the growth of plants with different concentration of cadmium, zinc, copper and iron in the soil.
They took cadmium as main focus to see what the effect is on the plants and found a small increase of biomass at low concentration. They found at 0.1 mg L^{-1} cadmium an increase of 19 % of biomass (root and shoot) after 5 days of exposure, while a concentration of 10 mg Cd L^{-1} causes plants to die. After 20 days they even found an increase of biomass of 77 %. Note that these numbers are biomass increase and not relative growth rate. Just like with aluminium there has been no mechanism given to the hormesis effect

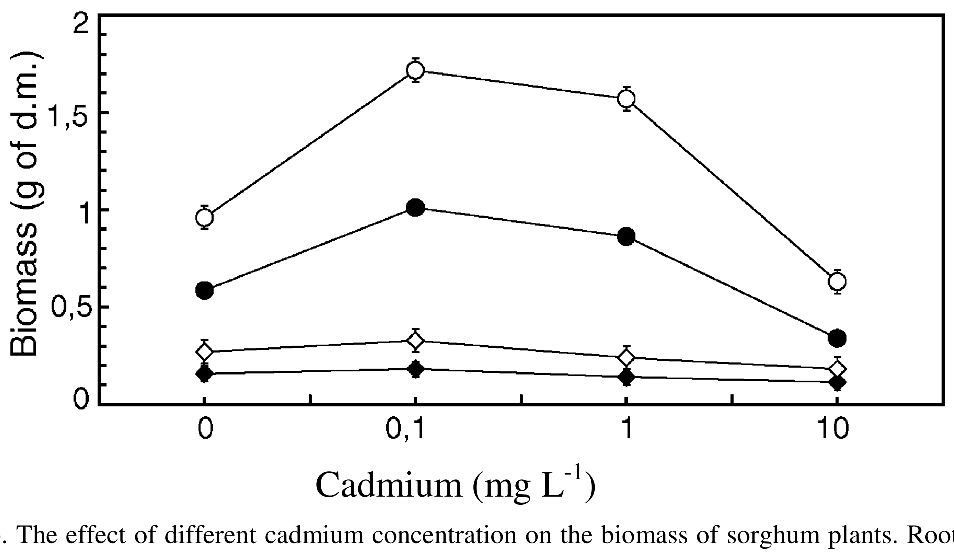


Fig. 3. The effect of different cadmium concentration on the biomass of sorghum plants. Roots are indicated as black dots and shoot open dots. Diamonds are 5 days after exposure and circles are 20 days after exposure. Hormetic effect is somewhere between 0.05 and 8 mg L^{-1} cadmium with its optimum effect around 0.1 mg L^{-1}.
(Pinto et al. 2004).

In (Allender et al. 1997) they have taken a look on the effect of lithium and lanthanum on herbicide induced hormesis on cotton and corn plants. Both plants got treated with both metals separately as variable. They have found that hormetic corn plants have an increase of leaf area up to 40-50 %. For cotton there is a less clear picture, probably due they didn't take the right dosage, as they started with their concentration just before retardation. However it looks like on both plants and heavy metals there is hormesis induced, only they also used herbicides which makes it hard to predict what actually caused the hormesis (fig. 4). This paper shows indirect evidence that Ca^{2+} is involved with hormesis. This is because both lithium and lanthanum interferes with the calcium channels and regulation and reducing the Ca^{2+} influx and activity. Lithium shares the same physiochemical properties with Ca^{2+} and lanthanum is a calcium channel blocking agent. By combining with an herbicide that also induces hormesis, compare can be made upon the uptake of Ca^{2+}.

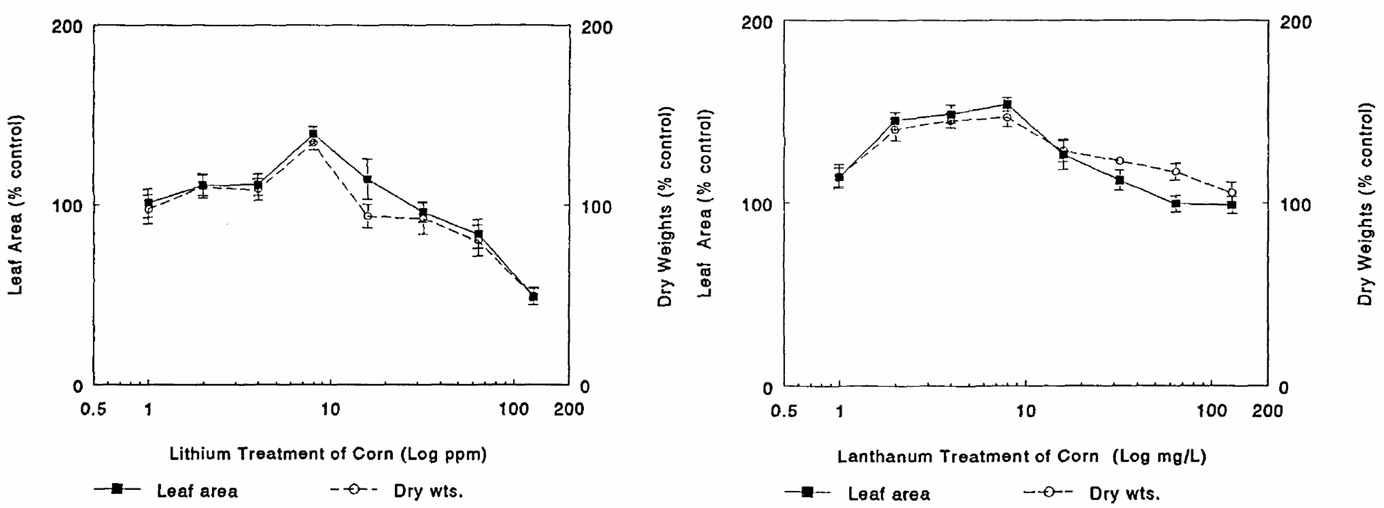


Fig. 4. The effect of lanthanum (a) and lithium (b) on hydroponically-grown corn plants. The y-axes show the relative growth rate of leaf area (left axis) and the dry weights tops (right axis), the x-axis is the concentration of the metals in log scale. Hormetic effect can be observed between the concentrations of 1 and 20 mg L^{-1} with an optimal around 10 mg L^{-1} (Allender et al. 1997).

Salinity

Salt can be toxic for most plants and can be common in soils at certain regions such as arid places and near sea shores. Therefore most common plants can not grow in such area's accept for halophytic plants. Salt is toxic because it changes the electric conductivity and therefore changes the osmotic potential. The result is similar to water deficit such as loss of turgor. Salt can also induce ion toxicity. Specific ions accumulate in the cytosol and exchanging for other ions such as Na^+ and K^+ resulting in inactivation of enzymes and disturbing ion homeostasis (Taiz and Zeiger 2006).

In (Khan et al. 200) they tested a halophyte plant and several salt concentration and see what the growth effect will have. Only at one concentration hormetic effect is observed. There is a growth increase of 50 % at 200 mM of NaCl. Testing a halophyte on salinity also causes a problem showing if there is hormesis. The plants are adapted to grow under a certain salt concentration in the soil. The same article also indicates that some halophytic plants species grow better with some salt in the soil. In (Jeschke et al.1986) they have tested the effect of salinity on *Lupinus albus* L. cv. Ultra. This is no halophyte and cannot tolerate salt very well and growth increase is still shown. Due it is not a halophyte the concentration for the optimal hormesis effect was much lower between 5-15 mM of NaCl.

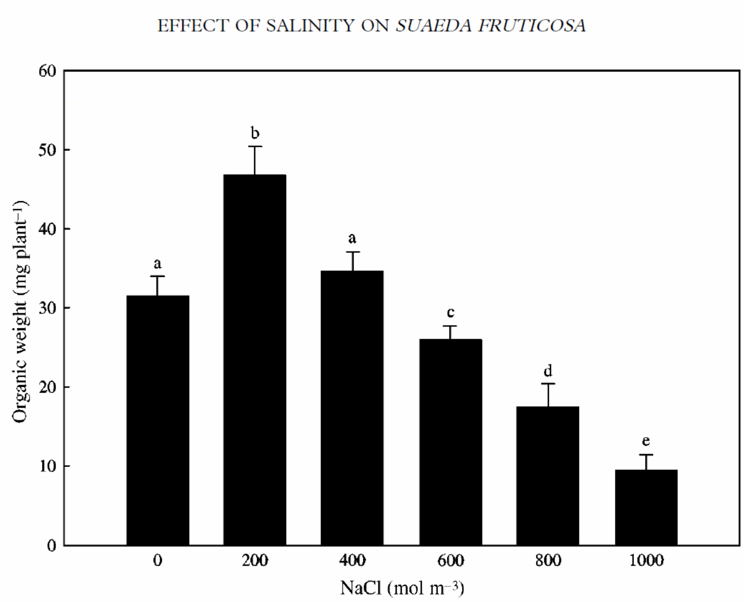


fig. 5. Effect of NaCl (0, 200, 400, 600, 800 and 1000 mM) on organic (ash-free dry weight) and ash weight of *Suaeda fruticosa* shoots. Bars represent mean S.E. Different letters above bars represent significant differences ($p<0.05$) among treatments. (Khan et al. 200).

A different example of salinity is (Stuiver et al. 1984). Different concentration of Na_2SO_4 on sugar beet plants has been tested. they found an increase at low dosage, only it was not found significant (fig. 6). However the article also shows that the same experiment was reproduced and shows the same growth curve. It occurred with also Na_2SO_4 around the concentration of 40 mM, this could still indicate for the effect hormesis.

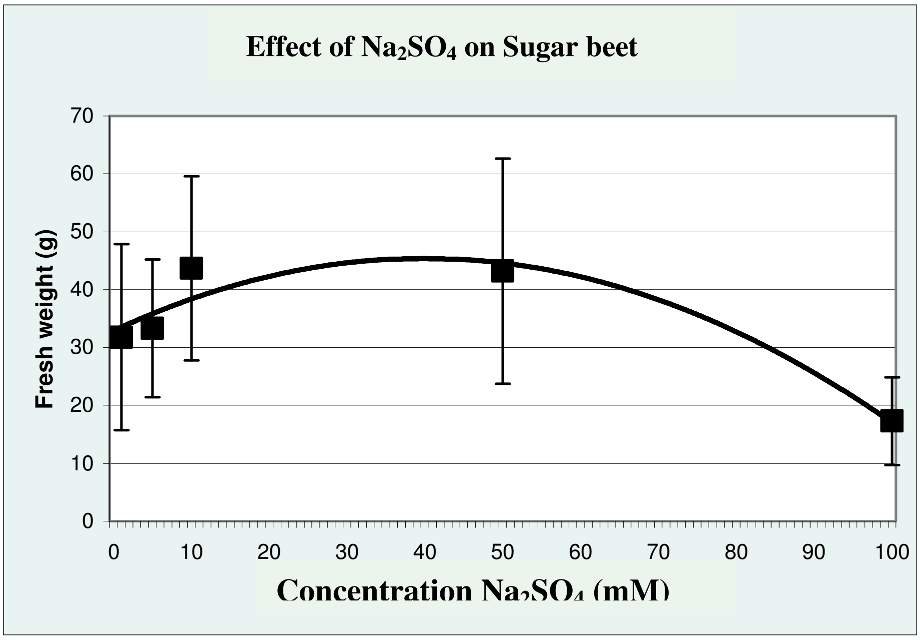


Fig. 6. Effect of different concentration Na_2SO_4 on the fresh weight on *Beta vulgaris* (sugar beet plants). X-axis is the concentration of Na_2SO_4 in mM and Y-axis is the fresh weight in gram. Possible hormesis effect shown between the concentration 10 and 50 mM Na_2SO_4. Graph drawn from data from table in (Stuiver et al.).

Air pollution

Less studied effect of hormesis is air pollution, such as the effect of ozone to plant. In various experiments has shown that ozone at low concentrations resulted in positive effects on growth rate even if the plants were ozone sensitive (Jäger and Krupa 2009). Ozone is toxic in several ways. It causes hydroxyl radical (OH) once it breaks down under aqueous condition and interferes with the C-C double bound in various hydrocarbons such as in cell membranes. This could cause direct damage to plant cell tissues (Hewitt and Tery 1992).

An example study done on ozone is (Flowers et al 2007). They tested the effect of ozone on the yield of beans with different genotypes. Two genotypes are ozone resistant and one sensitive. All the genotypes give an indication of hormesis including the sensitive genotype only the seed yield is different among the genotypes (fig. 7).

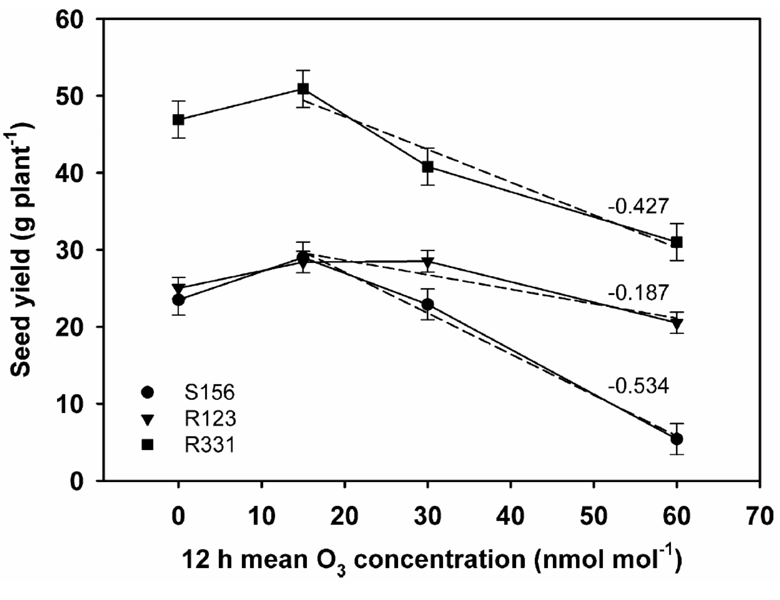


Fig. 7. The effect of different concentration of ozone to the yield of a bean, *Phaseolus vulgaris L.* R123, R331 are the resistant genotypes to ozone, S156 is the sensitive genotype. Hormetic effect is found at the concentration of 15 nmol mol^{-1} for all the genotypes, only R123 shows a longer hormetic effect up to 60 nmol mol^{-1}. (Flowers et al. 2007).

Herbicides and phytotoxic

Herbicides are a different kind of a group. They are man made for specific target plants to inhibit growth. But it doesn't say the non targeted group does not go unaffected. Because of this herbicides should be taken separately then the other a-biotic factors. But still it should not be ignored because it still occurs and a large number of hormesis is tested with herbicides. (Calabrese and Blain 2009)

Most studies investigate only one type of herbicide and what effect it will have on one type of plant. In (Cedergreen 2008) they have taken a look on one type of plant (barley) and eight different herbicides. This gives a nice overview of different herbicides. Their experiment was designed to see also if there is any trade-off for increased growth rate. This idea is because there has been trade-offs been found on animals, and therefore also expected to be found on plants. They found that not all herbicide induce hormesis. But what's remarkable is since they done their experiment twice they can compare the effects with the same treatment. They found that not all herbicides show consistent hormesis effect and the growth increase is also not consistent (fig. 8).

One of the problems of herbicides is that it is often a complex substance or it can be a mixture of more then one chemical. This makes it extra hard to determine what causes the hormesis. But the fact hormesis does occur it is important for those who use it to take in account with hormesis to calculate the right dosage.

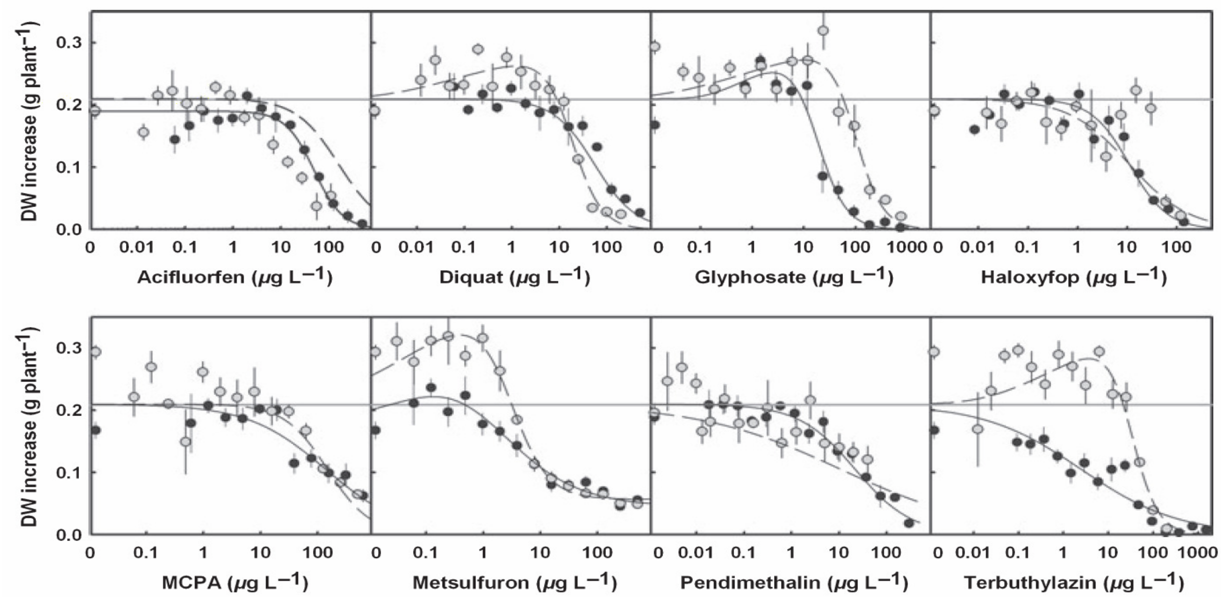
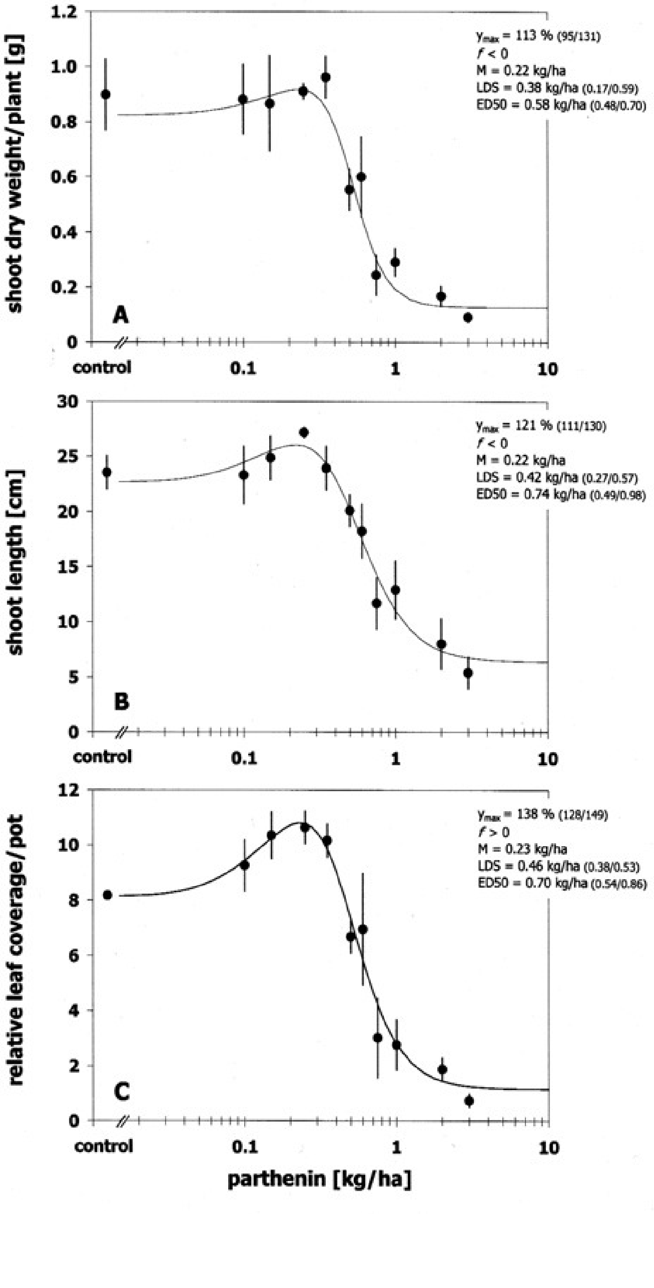


Fig. 8. Effect of eight different herbicides (acifluorfen, diquat, glyphosate, haloxyfop, MCPA, mestsulfuron, pendimethalin, terbuthylazin) with different concentration on barley. X-axis is the concentration in log scale and the Y-axis shows the dry weight increase. Black dots indicate the first experiment and grey dots the second experiment. The average of the control is given with a straight line on each graph. (Cedergreen 2008).

Most of the research that has been done on hormesis is herbicides (Calabrese and Blain 2009), yet plants can also create toxic substances that resembles herbicides. It is created by the plant to kill or reduce growth of surrounding competitive plants. In (Belz 2008) they have taken a look on the effect of a phytotoxic called parthenin. In this research they show growth increase on shoot weight (fig. 9a) shoot length (fig. 9b) and relative leaf coverage (fig. 9c). All these growth increase occur at the same concentration of parthenin with a growth increase between 15 and 30 %.



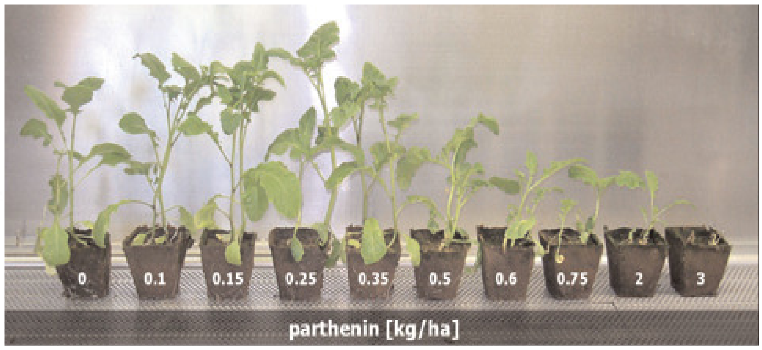


Fig. 9a,b,c,d. The effect of different concentration of parthenin on *Sinapis arvensis* after 13/14 days of exposure. X-axis indicates the concentration of patherin in kg/ha in log scale and the y- axis show the shoot dry weight (a), shoot length (b) and relative leaf coverage (c). Highest hormetic effect occurs near 0.25 kg/ha. The photo image shows how hormesis looks like on the plant itself with different concentration of parthenin (Belz 2008).

Discussion.

Neither of these articles shown above reveals any clear mechanism how hormesis is induced. One of the reasons is that researchers never were looking for hormesis but it was just an effect that occurred (Cedergreen 2008). However some give a suggestion what might be part of the mechanism.

Indirectly there has been proven that Ca^{2+} channels got something to do with hormesis effect (Allender et al. 1997). This is because both lithium and lanthanum interferes with Ca^{2+} metabolism and regulation and reducing the Ca^{2+} influx and activity. More investigation is required to understand it fully. There is also an indication that hormesis is not only induced on concentration but also time effect (Barceló and Poschenrieder 2002). No other article is to be found about hormesis and the effect of time, whether hormesis is induced for a very limited time or whether it is a consisted effect. Also there is no indication about long term effect of hormesis on plants, like a life time span. It is possible that time can also play an important role on the hormesis effect rather then just concentration.

A different idea of hormesis is a trade off between growth rate and something else like in insects, where there is a lower offspring survival (Cedergreen 2008). As it is found in animals a trade-off on plants could be also expected. However although it has been tested on a trade-off for plants no growth differences is found (Cedergreen 2008). To find if there is a trade-off for hormesis several treatments could be required. Most articles however look at one aspect of one treatment or they just measure the shoot (Cedergreen 2008). This gives not so much information for explaining the hormesis effect. There have been some studies who tried to find the mechanism, but they are inconclusive (Cedergreen 2008). There is also another problem on hormesis that is how you define it. Toxic element like aluminium is not known to be a necessary metal for growth, but copper is. Both can induce growth rate, but when do you call it hormesis. A similar problem is with salinity. Halophyte plants are known to grow better with some salt in the soil, but in the example given in this article non halophyte plants also grow better with some salt, only it is a lower concentration then with halophyte plants.

Another idea is that hormesis is a generalised effect between all plants due a stress response from an interruption in homeostasis. This would lead to overcompensation (Calabrese 1999; Calabrese et al 1999). But when looking at the salt example it is also possible that the little amount of sodium can help the plant with their potential differences. Since there is so little known about the mechanism, a generalised effect could be still possible, however it does not exclude there is also specific effects that also occur at the same time.

Conclusion

All the examples in this article show hormetic effect. Of course not all studies show an indication of hormesis (Calabrese and Blain 2009). One of the reasons is that they do not show how they calculated the right dosage or they have problems making it significant. It is hard to show significant since the controls may vary in data size and they have taken a small sample size (Calabrese 2008). Thus looking for hormesis requires strong statistical power, especially when the hormetic effect is rather low. Therefore it is required to have a large sample size and also the treatment requires enough concentration steps in the right range where hormesis occurs.

There are also articles that show no hormetic effect on herbicides. But herbicide gives the problem as they can be complex molecules or exist of a mixture. Herbicides may require even more attention how the mechanism works or how to determine the right dosage to get hormetic effect. But still there so many articles that claim to find hormesis with all kinds of chemicals that it can be said it is a rule rather then exception. But if hormesis is also a generalised effect that might be still right, but there is no evidence yet, simply because there is too little known about the process and mechanism of hormesis. There have been some studies who tried to find the mechanism, but they are inconclusive (Cedergreen 2008).

Also when researchers look for hormesis they often use one treatment and only look at few measurements such as biomass. This does not really help to understand the mechanism how hormesis work. To find the real mechanism of hormesis, specific research needs to be done, rather be only able to confirm whether it exists or not.

Since hormesis does occur it should be taken in account. It could cause problems with standard logistic model, making it hard to determine the right dosage (what ever the use could be). Researchers should also take in account that hormesis effect can interfere with results when fitting a model.

References

Allender W. J., Cresswell G. C., Kaldor J. and Kennedy I. R. 1997. Effect of lithium and Lanthum on Herbicide induced Hormesis in Hydroponically-Grown Cotton and Corn. Journal of Plant Nutrition, 20, 81-95.

Barceló J., Poschenrieder C. 2002. Fast root growth responses, root exudates, and internal detoxification as clues to the mechanisms of aluminium toxicity and resistance: a review. Environmental and Experimental Botany 48, 75-92.

Belz R. G. 2008. Stimulation versus inhibition-bioactivity of parthenin, a phytochemical from parthenium hysterophorus l. Dose-Response 6:80-96.

Calabrese E. J. 1999. Evidence that hormesis represents an "Overcompensation" Response to a Disruption in Hormeostasis. Ecotoxicology and Environmental Safety 42, 135-137.

Calabrese E. J. 2009. Getting the dose-response wrong: why hormesis became marginalized and the threshold model accepted. Arch toxicol 83:277-247.

Calabrese E. J. 2008. Hormesis: why it is important to toxicology and toxicologists. Environmental toxicology and Chemistry vol. 27, No 7 1451-1474.

Calabrese E. J., Blain R. B. 2009. Hormesis and plant biology. Environmental Pollution 157, 42-48.

Calabrese E. J.,Baldwin L. A. , and Holland C. D. 1999. Hormesis: A highly Generalizeble and Reproducible Phenomenon With Important Implications for Risk Assessment. Risk Analysis, Vol. 19, No 2.

Cedergreen N. 2008. Herbicides can stimulate plant growth. Weed Research 48, 429-438.

Hewitt N., Tery G. 1992. Understanding Ozone Plant chermistry. Environmental Science Technology, Vol 26, No. 10.

Flowers M. D., Fiscus E. L., Burkey K. O., Booker F. L., Dubois J. B. 2007. Photosynthesis, chlorophyll fluorescence, and yield of snap bean (Phaseolus vulgarisL.) genotypes differing in sensitivity to ozone. Environmental and Experimental Botany 61, 190-198.

Jäger H. and Krupa S. V. 2009. Hormesis-Its Relevance in Phytotoxicology. Developments in Environmental Science, volume 9, 137-152.

Jeschke, W.D., Pate J.S., Atkins C.A. 1986. Effects of NaCL salinity on growth, development, ion transport and ion storage in white lupin. Journal of Plant Physiology, 257-274.

Khan A. M., Ungar I. A., Showalter A. M. 2000. The effect of salinity on the growth, water status, and ion content of a leaf succulent perennial halophyte, Suaeda fructicosa (L.) Forssk. Journal of Arid Environments 45: 73-84.

Pinto A. P., Mota A.M., Varennes A. de, Pinto F.C. 2004. Influence of organic matter on the uptake of cadmium, zinc, copper and iron by sorghum plants. Science of the Total Environment 326, 239-247.

Stuiver C.E.E., Kok de L.J., Santens J.M.O., Kuiper P.J.C. 1984. The effect of Na_2SO_4 on the lipid Composition of Sugar Beet Plants. Zeitschrift für Pflanzenphysiologie. Band 114, 187-191.

Taiz L. and Zeiger E. 2006. Plant Physiology 4th ed. Sunderland Massachusetts: Sinauer Associates, Inc., Publishers.

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Bachelor Scriptie

Hormesis in plants, rather a rule then exception

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