The effect of excessive nitrogen on the development of trees

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Abstract

Nitrogen deposition is an increasing problem for nature and biodiversity. Since forests are a large carbon storage, it is important to know what effect nitrogen has on seeds and young trees, since those are important for renewal and establishment. Increasing nitrogen has a net negative effect on oak recruitment of 3-29%. For conifers there seems to be a net positive effect, but more research has to be done on other species. For young trees mortality increases, but if a young tree survives, nitrogen has a positive effect on growth up to a certain threshold, after which there is no significant increase, or even a decrease. Most of the results found were species specific, so there should be more research done on different species. Also, since nitrogen deposition may have combined effects with factors like carbon dioxide concentration, there should be research done on natural differences.

Introduction

Nitrogen deposition has an increasing influence on nature, due to anthropogenic additions. Human activities, such as intensified agriculture, have resulted in an increase of reactive nitrogen to a level of twice as much in the last decade (Fowler et al. 2013, Vitousek et al. 1997). This increase has lead to a decrease in biodiversity in, among other things, plants (Clark et al. 2013). This is a problem, because losses in biodiversity lead to more unstable ecosystems, due to a loss of trophic links. Forests are also an important source of carbon uptake, taking up a large proportion of earths terrestrial surface. The carbon stock is mostly regulated through trees, so it is important to see to what extent trees are effected by nitrogen.

Trees are most vulnerable when they are young, since there is a large pressure from both competition and herbivory. Seeds and young trees are vital for both renewal of old tree stocks in forests and establishment in new areas. Therefore it is interesting to look specifically at how excessive nitrogen affects trees in a young stadium. To do this, both aspects from seeds and young trees (seedlings/saplings) are discussed. If more nitrogen is added to the nitrogen cycle, it is expected that plants will show a morphological adaptation, since their growth is no longer or less limited by nitrogen. The main question is: How does excessive nitrogen affect the development of trees? To understand this we first look at seed production, since that is where the life of a tree starts. Then comes seed size and shape, seed dispersal, seed predation and seed germination and establishment, followed by the net effect of all these factors. Next is the young tree stage, where biomass, leaves, shoots, roots and mortality are discussed, with again a section on the net effect of these. There are also aspects that are important, but are not discussed here. Firstly there is soil acidification. Excessive nitrogen can affect soils by lowering pH levels. This in turn can also affect trees, but the reason it is not discussed here is that soil acidification is not solely caused by nitrogen. Sulphur, for example, can also acidify soils, so it would be hard to disentangle the source of acidification, and it would be best to study acidification in a separate research. Another aspect is aluminium toxicity, which is a result of soil acidification, so the same reason is applied here to not delve deeper into this. Aluminium toxicity is important, since aluminium is toxic for plants. The last aspect that is relevant and not discussed is competition with other species, like grasses. This is because it is important to first establish what direct effects nitrogen has on trees before studying indirect effects such as interspecies competition.

It is important to know nitrogen is often a limiting resource for plants. This is partly because plants can often only take up nitrogen in the forms NO_{3^-} and NH_{4^+} , or nitrate and ammonium, from the soil. Another important aspect of studies on how nitrogen affects development is the difference between low and high nitrogen addition. Low and high nitrogen concentrations differ a bit per species, but high nitrogen addition is used for concentrations ranging from 75 to 150 kg ha⁻¹ year⁻¹. Low concentrations are often under 75 kg ha⁻¹ year⁻¹.

Seed production

Every tree starts its life as a seed on a tree, in some form. As nitrogen deposition affects adult trees, seed production can also be affected. This has a direct influence on the reproductive effect of trees, and an influence on the renewal of old tree stocks in forests. An example of why renewal is important is *Juniperus communis* (Clifton et al. 1997), since the species has low seed viability, which endangers it as a whole.

Red oaks produce 2 to 7 times more acorns under low nitrogen addition (50 kg ha⁻¹ year⁻¹) and 4 to 9 times more acorns under high nitrogen addition (150 kg ha⁻¹ year⁻¹) compared to no addition (Bogdziewicz et al. 2017, Lovett et al. 2013). When looking at red oaks and black oaks combined, similar effects are found (Callahan et al. 2008).

However, in conifer species there is no effect of nitrogen on cone production. An example is white spruce, which did not show a significant response in cone production as reaction to increasing nitrogen concentration (Leeper et al. 2020).

There are also deciduous species in which no significant change in seed production is found as response to nitrogen addition. Examples of this are sugar maple, American beech, yellow birch, and eastern hemlock (Lovett et al. 2013). Similarly in black beech (*Nothofagus solandri*), it was found that no significant effect of nitrogen fertilisation was found on total seed mass over 10 years (Smaill et al. 2011). When looking at separate years however, there were increases in seed production, so it was possible for nitrogen addition to increase seed production.

Overall, there seems to be species-specific reactions to nitrogen addition. This might be explained due to the fact that, since some species have more resources available in the form of nitrogen, they can invest more in reproduction. Why some species do not show a change might be because they are not limited in nitrogen before addition, so an increase will not affect the trees. This can for example be found as explanation in the research done by Lovett et al. (2013). Another explanation for why no difference might be found is that trees might simply decide to invest in growth instead of reproduction.

Seed size and shape

The size of seeds is an indication of quality and both size and shape may influence predation behaviour (Muñoz et al. 2012). Seed size of acorns from red oaks decreases under low nitrogen additions (50 kg ha⁻¹ year⁻¹) but does not decrease significantly under high nitrogen additions (150 kg ha⁻¹ year⁻¹) (Bogdziewicz et al. 2017).

Another study on oaks found similar results, with no increase in acorn size when treated with high nitrogen concentrations (168 kg ha⁻¹) (Brooke et al. 2019).

In a study by Callahan et al. (2008) on red and black oaks, however, an increase of acorn size was still found at a concentration of 150 kg ha⁻¹ year⁻¹, as well as in concentrations of both 50 and 100 kg ha⁻¹ year⁻¹.

A study done on spruce, fir and pine data also showed an increase in seed mass as response to increasing nitrogen deposition (Liu & El-Kassaby 2020).

The shape of acorns is also altered by nitrogen addition. Acorns become more spherical when treated with nitrogen (both high and low), which means they have a smaller length to width ratio when compared to acorns with no nitrogen treatment (Bogdziewicz et al. 2017).

Overall an increase in seed size is found, both in deciduous and coniferous species. This might once again be due to the fact that a tree has more nitrogen resources, which it can invest in reproduction. For seed shape there is not enough research done to draw definitive conclusions.

The seed size and shape have an effect on seed dispersal, as we will see next.

Seed dispersal

Seed dispersal is a way for trees to reduce the mortality of their offspring by increasing the distance between seeds, to avoid competition or density-dependent mortality. It can also be used to try to reduce predation or the spread of pathogens (Howe & Smallwood 1982). This means that a reduction in seed dispersal may be detrimental to seed survival.

For red oak, dispersal of seeds is mediated by rodents, like squirrels and chipmunks. These rodents can cache (store) the seeds underground to eat at a later date. They may for various reasons cache seeds that they do not retrieve later. This gives the acorns a higher chance to germinate successfully, since the acorn is no longer predated, has better access to nutrients etc. Nitrogen addition reduces the rate of caching and not retrieving of acorns by rodents, from a normal rate of 6.3% to a rate of 1.7% under low nitrogen addition and only 0.008% under high nitrogen addition (Bogdziewicz et al. 2017). This is due to the smaller size of the acorns, since rodents tend to pick larger seeds to cache.

The shape of the acorns also played a role, which partly explains why the high nitrogen acorns were dispersed so little, since their size was not significantly lower compared to control seeds. The nitrogen influenced seeds were more spherical, as said before, which might influence the mechanical cost of transport for the rodents.

For Korean pines, however, the opposite is true. Nitrogen addition results in more hoarding by small rodents (Yi et al. 2016). This has been explained by the fact that nitrogen addition changes physical and chemical traits, in this case changes in volatile compounds due to shifted seed coat to seed meat ratios. Since this is an indication of higher quality, this in turn has an effect on the behaviour of rodents, since they tend to hoard higher quality seeds rather than immediately consume them.

As already suggested by Bogdziewicz et al. (2017), it seems likely that the effect of nitrogen on seed dispersal is species specific as well.

Seed predation

Seed predation can drastically reduce plant reproductive success. Infection by weevils in acorns can occur in 26% up to 68% of total acorn stocks in a mast year (Lombardo et al. 2008). Nitrogen addition results in an increase in total infection by weevils. In low nitrogen concentrations, 49% of acorns got infected by weevils and in high concentrations this percentage rose to 59%, compared to 38% infection found in control acorns (Bogdziewicz et al. 2017).

In another study by Callahan et al. (2008) however, no significant increase in infestation was found. There was however a significant increase in a post-mast year, which was declared as being caused by higher abundance of acorns. This is a result of increasing nitrogen, as we saw before.

Infection does however not mean that seeds cannot germinate anymore. This is also dependent on seed size, with bigger acorns having a higher survival probability after infection. Accounting for this leads to survival odds of 3.03 times higher for control compared to low nitrogen acorns and 2.22 times higher for control compared to high nitrogen acorns (Bogdziewicz et al. 2017).

Predation can also occur by rodents. For this nitrogen addition leads to a decrease in predation. Predation by rodents occurred was significantly higher in control acorns than in both high and low nitrogen treated acorns, with the amount of acorns being consumed not being significantly different between treatments (Bogdziewicz et al. 2017).

Seed germination and establishment

After being dispersed and surviving predation, seeds need to germinate to survive. The timing of germination is important, as earlier germination can lead to increased growth time combined with a higher availability of local resources (Varma et al. 2016). For several tropical tree species (*Sapin-dus emarginatus, Shorea robusta, Terminalia arjuna, Ziziphus jujuba*) a delay in germination of up to 13% was found when treated with nitrogen compared to control situations (Varma et al. 2016).

Besides timing of germination, the probability of germination is also important, since a higher probability of germination means more seedlings survive. Nitrogen addition reduces the probability that seeds can germinate significantly in oaks, with a reduction in germination probability of two to three times compared to control situations where no nitrogen was added (Bogdziewicz et al. 2017).

However, in another experiment with oaks, there was a slightly higher, but not significant, increase of probability of germination for acorns of trees that received high nitrogen addition compared to control or low nitrogen addition acorns (Callahan et al. 2008).

Total seed influences

In total there seems to be a positive or no effect of nitrogen on seed production. However, there seems to be a negative effect on seed size and shape under low nitrogen conditions, with no effect on size under high nitrogen conditions. This in turn has a negative effect on dispersal for oaks, a deciduous species and a positive effect on dispersal for Korean pines, a coniferous species. There is also more predation on nitrogen acorns, which leads to reduced survival odds. In total this leads to oaks having a 3-29% reduction in recruitment (Bogdziewicz et al. 2017). For coniferous species there has not been enough research done to say whether nitrogen affects seeds negatively or positively, but the research that has been done seems to indicate a net positive effect.

Young tree biomass

After a tree seed successfully germinates, it becomes a seedling. This stadium is vital for trees, since it is one of the last stages where a tree is still in high danger of competition and herbivory. An indication of growth is total biomass, with a higher total biomass indicating faster growth.

Nitrogen addition affects tree species *Schima superba* and *Pinus massioniana*, respectively a deciduous and coniferous species, significantly (Wu et al. 2019). For *S. Superba* a significant effect was found only when nitrogen was added in medium concentration to the soil (156 kg ha⁻¹ yr⁻¹), which lead to an increase in biomass (Wu et al. 2019), and in other research a significant increase of biomass was found in response to an addition of 10 g m⁻² year⁻¹ nitrogen (Mo et al. 2008). For *P. massioniana* however, a significant decrease in biomass was measured when nitrogen was added in both medium and high concentration to the soil (206 kg ha⁻¹ yr⁻¹). When nitrogen was added to the canopy however, there was a significant increase in biomass under high concentration nitrogen addition. In other research done by Wang et al. (2019), a significant in-

crease in biomass of 58% compared to control plants was measured in response to nitrogen in the soil with a concentration of 40 kg ha⁻¹ year⁻¹. So in total for *P. massioniana* there seems to be an increase in biomass when a low concentration of nitrogen is added to soil or a high concentration of nitrogen is added to the canopy, but a decrease when medium or high concentrations of nitrogen are added to the soil.

However, for Norway spruce, which is a coniferous species, nitrogen addition does not affect biomass significantly (Lumme & Smolander 1996).

In a tropical species, *Poutera torta*, similar to the Norway spruce, there was no effect of nitrogen addition on total biomass (Cárate-Tandalla et al. 2015).

For the tropical species *Cryptocarya concinna*, however, a significant increase of biomass was found in C. concinna in response to 15 g m⁻² year⁻¹ (Mo et al. 2008). At higher concentrations however, there was no significant effect of nitrogen on biomass for both species.

Young tree leaves

For a sapling to grow, it needs to produce carbohydrates through photosynthesis. Since photosynthesis relies on chlorophyll, and chlorophyll contains nitrogen, it is important to know how nitrogen addition affects leaves, since they contain most of the chlorophyll in a plant.

In *Eucalyptus grandis* nitrogen increased total leaf area and increased leaf nitrogen levels (when comparing all nitrogen treated trees as one group) which in turn increased the light-saturated photosynthetic rate (Clearwater & Meinzer 2001). There was however, no effect on the stomatal conductance of the leaves and the hydraulic capacity.

For the tree species from Wu et al. (2019), nitrogen addition also lead to a higher leaf nitrogen concentration in all species.

Bethers et al. (2009) also found an increase in nitrogen concentration, but there might also have been an effect of sulphur, since both sulphur and nitrogen were added to the soil to acidify it. Therefore it becomes hard to disentangle the cause of the increase, since the research did not include a site with only sulphur or nitrogen.

In other species (*M. hyporeuca, C. cordata, P. ssiori* and *Q. mongolica*) nitrogen addition resulted in an increase in leaf nitrogen content in both *M. hyporeuca* and *Q. mongolica,* but there was no significant effect on *C. cordata* and *P. ssiori* (Kitaoka et al. 2009). The light-saturated photosynthetic rate also increased in both *Q. mongolica* and *C. cordata*, but no significant change was found in the other two trees.

In the tropical species Alseis blackiana, Desmopsis panamensis, Heisteria concinna, Sorocea affinis and Tetragastris panamensis, nitrogen addition also caused an increase in nitrogen levels in both young and old leaves (Santiago et al. 2012). Interesting is that nitrogen addition did not significantly increase leaf damage through herbivory compared to control situations.

In other tropical species (*S. superba* and *C. concinna*), nitrogen addition lead to a significant increase of the nitrogen concentration in leaves, for *S. superba* only at a concentration of 30 g m⁻² year⁻¹ and for *C. concinna* from 10 g m⁻² year⁻¹ up to 30 g m⁻² year⁻¹ (Mo et al. 2008). Also photosynthesis was altered, with *S. superba* only having a significantly higher photosynthetic rate at 10 g m⁻² year⁻¹ nitrogen and *C. concinna* having a significantly higher rate from 5 to 15 g m⁻² year⁻¹ nitrogen. Interesting to note is that at a higher nitrogen concentration of 30 g m⁻² year⁻¹ the photosynthetic rate of both species was not significantly different from control plants.

Young tree shoot

Trees rely on their shoots for both length and support, through both composition and thickness. Length is important since it allows saplings to outcompete their rivals, and strength is a requirement for growing tall. However, since seedlings are discussed, strength is not that relevant yet.

Santiago et al. (2012) found an increase in nitrogen content in the stem after nitrogen addition compared to control plants. Nitrogen addition did however not affect stem growth, but this was explained by the fact that the soil in the study site already had a relatively high nitrogen concentration, whilst normally trees are often mostly limited by nitrogen.

For the tropical species *S. superba* and *C. concinna* nitrogen addition lead to an increase in shoot height (Mo et al. 2008). For *S. superba* this increase was only significant when a concentration of 10 g m⁻² year⁻¹ nitrogen was added. For *C. concinna* however, there was an increase of height with increasing nitrogen concentrations up to 15 g m⁻² year⁻¹. At a concentration of 30 g m⁻² year⁻¹ nitrogen however, a significantly lower height was observed compared to control plants. This might have been caused by an excess of nitrogen in the soil causing nutrient leaching and soil acidification.

For *Eucalyptus grandis,* shoot length increased significantly under nitrogen addition ranging from 112 to 336 kg ha⁻¹ compared to control plants (Clearwater & Meinzer 2001).

Young tree roots

Roots regulate most of the uptake of nutrients for trees. If trees have more nutrients available which are normally limiting, like nitrogen, it is expected that they can afford to invest less into their root systems.

For the species *J. mandshurica, F. mandschurica, P. amurense, L. gmelinii, P. koraiensis* and *P. koraiensis*, which are all temperate species, nitrogen fertilization lead to an increase in stele radius, ranging from a 13 to a 22% increase (Liu et al. 2018). Cortical thickness only significantly increased in *L. gmelinii*, with no significant difference in the other species. This lead to a decrease in cortical thickness to stele radius ratios, which in turn may facilitate a higher nutrient transport.

In *Pinus tabuliformis*, a significantly higher stele radius as response to nitrogen addition was also found in coarse roots (Wang et al. 2017). However, fine root number, biomass, length and mycorrhizal colonisation rates decreased under increasing nitrogen conditions. Mycorrhizal colonisation rates are important for plants, since it improves the trees' capacity to take up nutrients. Root hydraulic conductance did significantly increase for fine roots, which means that the seedlings have a better ability to transport water. For the fine roots, root respiration rates increased as well, meaning that the roots could better exchange carbon dioxide with their environment.

Another interesting aspect is whether nitrogen is added to the soil or the canopy. For the species *Acacia magnium* and *Pinus massoniana* an increase in nitrogen to the canopy lead to an increase in fine root biomass, while there was no significant increase in both *Ormosia pinnata* and *Schima superba* (Wu et al. 2019). When nitrogen was added to the soil however, an increase in fine root biomass was found under medium nitrogen addition (2.5 g m⁻² year⁻¹), but a decrease was found under high nitrogen addition (7.5 g m⁻² year⁻¹) in *A. magnium*. For *O. pinnata* this was only a decrease under high nitrogen addition. For *S. superba* there was no effect of nitrogen on fine root biomass.

Young tree mortality

Nitrogen may have an effect on the survival of saplings. For example, in *Pouteria torta,* when given 50 kg ha⁻¹ nitrogen, mortality significantly increased, from $54\pm5\%$ in control to $70\pm3\%$ (Cárate-Tandalla et al. 2015). Similar results were found in species *S. superba* and *C. concinna,* where there was no difference in survival up to 15 g m⁻² year⁻¹ nitrogen addition, but a significant decrease in survival was found when 30 g m⁻² year⁻¹ nitrogen was added (Mo et al. 2008).

In red oaks, white pines and red spruces, a similar significant decrease in survival was found in response to nitrogen addition, up to 7.5 g m⁻² year⁻¹ (Catovsky & Bazzaz 2002).

In a research by McWhirter and Henry (2015), in *E. umbellata* a significant increase in survival was found in the first year of the experiment in response to nitrogen addition (6 g nitrogen m⁻²). In the second year of the experiment however, the survival percentage was not significantly altered by nitrogen addition. For the other species in the experiment (*F. americana, M. coronaria* and *R. typhina*) no effect of nitrogen addition was found on survival percentage in either year.

Total young tree influences

In total there seems to be a positive effect of nitrogen on stem growth up to a certain concentration, after which it turns into a negative effect. This is possibly due to nutrient leaching or soil acidification. Roots seem to become thicker, but the amount of fine root biomass seems to become lower, with exceptions, when nitrogen addition gets higher. Because of this, a lower root shoot ratio might be expected, but research has shown that the root:shoot ratio is not significantly altered (Santiago et al. 2012, Cárate-Tandalla et al. 2015, Wang et al. 2019). This might be explained by the fact that root:shoot ratio is measured in dry weight instead of length, and roots do become thicker, which alleviates the decrease in weight from a decrease in fine root biomass. Leaves also can to contain more nitrogen in reaction to higher nitrogen concentration, which allows a higher rate of photosynthesis. This also decreases to control levels again when too much nitrogen is added. This might partly explain why the shoot of the plants can grow higher under higher nitrogen conditions, with the decrease at a too high nitrogen concentration. Sapling mortality seems to be determined species specific.

Main conclusions

For seeds in total there seems to be a net neutral or negative effect of nitrogen addition for deciduous species. For coniferous species there seems to be a net positive effect. However, there is still a lack of research which can be used as comparison. For some aspects, like seed predation, very little research has been done. This in turn gives us little basis to draw general conclusions on the ways nitrogen affects both tree seeds and saplings and limits us to drawing conclusions for separate species. Whilst it is also important to have knowledge of individual species, it gives us doubt when trying to reason about other species. For example, research on the effect of nitrogen on seed predation has only been done in oaks, so it would be difficult to know if we should fix it for every tree species. At the same time, nitrogen does affect more species than oaks and the other trees mentioned here due to the increased anthropogenic nitrogen deposition. Because this lack of knowledge exists, it is advised that more research is done on the influence of nitrogen on seed aspects in other species. This should preferably be both deciduous and coniferous species, since we already observed a difference in results between the two.

A significant difference in the reaction of different species to nitrogen addition was also observed. This furthermore confirms the need for more research on different species.

For saplings we see positive effects for the separate parts (roots, shoots, leaves), but an increase in mortality in most species observed. This indicates that if a tree does survive as sapling, it has an advantage compared to other saplings which are not affected by nitrogen. However, since nitrogen deposition affects forests as a whole, these differences within species would not matter, as every tree is affected by increased nitrogen levels. This in turn can lead to a loss of biodiversity, since the mortality chances differ per species.

A more positive aspect is the fact that roots in saplings seem to have a higher hydraulic conductance, which might allow better establishment of trees in dry areas when aided by either human or natural nitrogen addition.

Another positive aspect is that, although seeds are often negatively affected by nitrogen, young trees are not, so it could be beneficial for trees to germinate in low nitrogen conditions, before being put in high nitrogen areas, where they might grow very well.

Overall, it should also be noted that nitrogen is not the sole influence on the different aspects mentioned. There are always other aspects which play a role, which might also be dynamic, such as carbon dioxide concentrations, temperature, or sulphur deposition. It would be too complex to create a solution for all these intertwined problems when you only know what effect nitrogen has on trees. Therefore another proposal for future research would be to look at natural situations, so without adding nitrogen, and check soil nutrient concentrations, air nutrient concentrations, air temperature, etc. and correlate that with all seed and young tree characteristics. This could for example be done besides agricultural landscapes, since those areas are a good example of an affected area, since fertiliser, which contains nitrogen compounds, can get washed out to nearby forests. This is also not a counterargument for the need to do more research on the effect of nitrogen addition, since, as also said earlier, nitrogen addition through fertilisation might help in developing new establishment methods for, for example, dry areas.

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