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Nitrogen accumulation, rather than carbon: nitrogen stoichiometric variation, underlies carbon storage during forest succession

Junliang Zou 1, Juying Wu 1, Bruce Osborne 2, Brian Tobin 3 and Yiqi Luo 4

1 Beijing Research & Development Centre for Grass and Environment, Beijing Academy of Agriculture and Forestry Sciences, Beijing 100097, People’s Republic of China
2 UCD School of Biology and Environmental Science and UCD Earth Institute, University College Dublin, Belfield, Dublin 4, Ireland
3 UCD Forestry, School of Agriculture and Food Science and UCD Earth Institute, University College Dublin, Belfield, Dublin 4, Ireland
4 Center for Ecosystem Science and Society, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, United States of America

E-mail: jlzou@nwafu.edu.cn and wujuying@grass-env.com

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Abstract

Forest ecosystems play an important role in regulating global temperatures through their capability to take up and store CO₂ from the atmosphere, but the magnitude and sustainability of this carbon (C) sink is critically dependent on the availability of nutrients, particularly nitrogen (N). However, the extent to which the absolute amount of N or modifications in plant and soil C:N ratios controls long-term forest carbon sequestration (Cseq) remains uncertain. To assess this, we analyzed the results of 135 global field studies that investigated the dynamics of C and N availability during forest succession. The results showed that the accumulation of C and N in plant (including above- and below-ground vegetation) and litter pools decreased with forest age and approached an equilibrium value in the latter stages of stand development. Plant and litter C:N ratios increased during the first 10–20 years and remained relatively stable thereafter. The analysis further showed that the relative importance of a change in the total amount of N or modifications in the C:N ratio, to increases in Cseq, varied with forest age. Whilst the relative importance of a change in the total amount of N increased with forest age, the relative importance of a varied C:N stoichiometry decreased with forest age. Overall, a change in the total amount of N was the more important factor contributing to C storage during forest stand development and the C stored in vegetation dominated the total ecosystem C pool. These results show that ecosystem N availability is a key factor supporting long-term forest Cseq during forest succession. As most of the C is found in above-ground vegetation, this pool is particularly susceptible to abiotic or biotic factors and anthropogenically-related disturbances.

1. Introduction

Large scale anthropogenic activities, such as deforestation, land use conversion, and fossil fuel combustion have led to increased atmospheric carbon dioxide (CO₂) concentrations, which has accelerated global warming (Stocker et al 2013). In response to this, there have been many proposals about how atmospheric CO₂ concentrations might best be reduced and/or how carbon sequestration (Cseq) might be enhanced. Secondary forests are a globally important terrestrial carbon (C) sink (Kauppi et al 2006), and tree planting provides a potentially effective way to remove atmospheric CO₂ (Houghton et al 2009). Young forests have been shown to store large amounts of C in tree trunks, roots and soil over relatively short time periods due to their rapid regeneration rate (Chazdon et al 2016). However, whether this large capacity for Cseq can be maintained during the later stages of forest succession remains unclear.
Growing evidence suggests that nitrogen (N) availability can regulate C fixation by terrestrial ecosystems (Rastetter et al. 1997, Finzi et al. 2001, Hungate et al. 2003, Luo et al. 2006, Reich et al. 2006, Terrer et al. 2018). Increased N availability typically results in increased above- and below-ground plant productivity, due to enhanced photosynthesis, resulting in increased soil C$_{eq}$ through increased litter- and root-associated inputs, including labile C exudates (Lu et al. 2011, Niu et al. 2016, Yue et al. 2016). High levels of forest C accumulation can be sustained if the ecosystem is able to continuously acquire enough N to meet their potential growth requirements, and/or if any available N can be utilized more effectively within their tissues, or by actively recycling it within the ecosystem (Luo et al. 2004, Hungate et al. 2006). Changes in the efficiency of N-use will inevitably cause changes in C:N ratio, with any increase in efficiency reflected in a higher C:N ratio. In a simulation study (Rastetter et al. 1997) showed that the accumulation of N largely determined the long-term patterns of C gain by terrestrial ecosystems. If additional organic C inputs result in reduced N losses through increased N uptake, and/or there is enhanced biological fixation or increased atmospheric deposition, then progressive N limitation may not occur (Luo et al. 2004, 2006). Whilst the increased decomposition of organic matter would not increase the N capital, it could also reduce N limitation by converting more N into inorganic forms that may be more usable by the vegetation. In addition, the stoichiometric relationship between C and N is flexible due to the transient stimulation of NPP and the increased absorption of available N by deeper plant roots, which may be crucial for C$_{eq}$ during the early stages of forest succession (Comins and McMurtrie 1993, McMurtrie and Comins 1996, Rastetter et al. 1997). However, the magnitude and way in which N availability regulates forest C$_{eq}$ has not been well evaluated with observational data.

Elevated CO$_2$ experiments (e.g. Korner and Arnone 1992, Finzi et al. 2006, 2007, Hungate et al. 2006, 2013, Norby and Iversen 2006, Norby et al. 2010, Sun et al. 2018, Terrer et al. 2018) provide invaluable evidence of the importance of understanding the significance of C–N coupling for C$_{eq}$ by terrestrial ecosystems. However, it is still difficult to use these experiments to quantify the importance of N availability for long-term C$_{eq}$. In contrast, studies of forest succession over extended periods, including different stages of stand development, provides a way of assessing longer-term C and N dynamics and their relationship to C$_{eq}$ (Johnson and Miyaniishi 2008).

In the past decades, extensive research has been undertaken to examine how C–N stoichiometry varies along forest age gradients. For example, 115 years after the abandonment of agricultural areas in Rhode Island, USA, C:N ratios in different vegetation components and in mineral soils were reported to increase with forest age (Hooker and Compton 2003), Yang et al. (2014), in contrast, reported unchanged shoot C:N ratios but decreased soil C:N ratios, in a deciduous broadleaf forest over different stand ages on the eastern Tibetan Plateau. A synthesis of a number of studies showed generally increased root and shoot C:N ratios but unchanged soil and litter C:N ratios during forest stand development (Yang and Luo 2011). In general, due to large increases in C storage in vegetation, total ecosystem C storage increases with increasing forest age (Yang et al. 2011), although soil C may show variable responses (Zak et al. 1990, Pérez et al. 2004, Rothstein et al. 2004, O’Neill et al. 2006, Gough et al. 2007). Total ecosystem N amount may also increase with stand age through increased input from enhanced biological N fixation or atmospheric deposition, or through decreased losses due to reduced N leaching or gaseous emissions (Yang et al. 2011). In many field studies, the total N content of vegetation and litter has been reported to increase with stand age (Hooker and Compton 2003, Noh et al. 2010, Li et al. 2013, Yang et al. 2014, Jiang et al. 2017). In contrast, the N in mineral soil has been reported to increase (Morris et al. 2007, Sartori et al. 2007) or decrease (Hooker and Compton 2003, Mao et al. 2010) with stand age.

One way to examine any general patterns of C and N changes in secondary forests during forest succession is through the use of a meta-analysis approach that can quantitatively explore C–N interactions at time scales of decades or centuries (Borenstein et al. 2011, Yang and Luo 2011, Yang et al. 2011). This approach can also help to resolve interactions between different drivers from studies conducted in different regions or at smaller scales. In this study we synthesized published results from 135 individual studies aiming to resolve two major questions: (a) what is the temporal variation in C and N accumulation rates and C:N ratio changes in mineral soil, litter, and vegetation during forest succession? (b) what is the relationship between ecosystem C accumulation and changes in ecosystem N amount or variations in C:N ratio during forest succession? A major objective was to examine the hypothesis that variations in total ecosystem N amount is the dominant mechanism controlling long-term C$_{eq}$ during forest succession.

2. Materials and methods

Data was collected from recently published literature from 1970 to 2018 reporting field investigations on dynamics of C and N stocks during forest succession (appendix figure S1, reference S1, table S1 (available online at stacks.iop.org/ERL/16/024055/mmedia)) and is an update of the dataset of Yang et al. (2011). In order to maintain consistency with the study of Yang et al. (2011), we used similar criteria (note S1)
for selecting and collating data on C and N dynamics. In total, 135 published papers were included in this study to compile a dataset including 2850 rows of observations and some basic information (geographic location, climatic information, forest type, stand age) for each study. The 12 variables of primary interest describe the C and N stocks (mg ha\(^{-1}\)) and their stoichiometric ratios in above- and below-ground vegetation, litter and soil pools. More information on data extraction and processing, as well as the conversion of the original soil C and N values from various depths to a standardized depth of 100 cm, are detailed in note S1 and Yang et al (2011).

We partitioned the C increment during stand development between that related to an altered stoichiometric flexibility and a changed total N amount, following the approach used by Hungate et al (2006) with more detailed description in note S1.

The increment in C mass of ecosystem component \(i\) during forest stand development induced by changes in C:N ratio (\(\Delta C_{C:N,i}\)) was quantified using equation (1):

\[
\Delta C_{C:N,i} = \left( \frac{C}{N} \right)_{(t+1)i} - \left( \frac{C}{N} \right)_{ti} \times N_{ti}
\]  

(1)

where \(\left( \frac{C}{N} \right)_{(t+1)i}\) and \(\left( \frac{C}{N} \right)_{ti}\) are the C:N ratios of ecosystem component \(i\) at stand age \(t + 1\) and the previous stand age \(t\), and \(N_{ti}\) is the N amount of ecosystem \(i\) in a stand at age \(t\).

The increment in C mass of ecosystem component \(i\) during forest stand development due to changes in N amount (\(\Delta C_{TNi}\)) can be quantified using equation (2):

\[
\Delta C_{TNi} = [N_{(t+1)i} - N_{ti}] \times \left( \frac{C}{N} \right)_{ti}
\]  

(2)

where \(N_{(t+1)i}\) is the N amount of ecosystem component \(i\) in a stand at age \(t + 1\).

Finally, the increment in C mass of ecosystem component \(i\) during forest stand development due to changes in both N amount and C:N ratios (an interactive component, \(\Delta C_{\text{inter}}\)) can be expressed as

\[
\Delta C_{\text{inter}} = \left[ \left( \frac{C}{N} \right)_{(t+1)i} - \left( \frac{C}{N} \right)_{ti} \right] \times \left[ N_{(t+1)i} - N_{ti} \right].
\]  

(3)

We applied this analysis to individual pools comprising above-ground vegetation, below-ground vegetation and litter using N mass and C:N data as described above. We used the sum of the C and N accumulation in these pools to assess the relative importance of the two pathways for C accumulation in vegetation.

3. Results

3.1. Dynamics of C and N stocks and their stoichiometry along forest age gradient

The stocks of C and N in above- and below-ground components of the vegetation and litter increased during succession (figure S2), but no significant trends were noted in the C and N of soils (figure S3). The C and N accumulation rates (including rates of C:N change) in the three main ecosystem components exhibited similar decreasing patterns with stand age (figure 1). For instance, the C accumulation rate decreased markedly from \(\sim 4\) to \(\sim 2\) mg C ha\(^{-1}\) yr\(^{-1}\) in the above-ground vegetation (figure 1(a)), from \(~0.7\) to \(~0.3\) mg C ha\(^{-1}\) yr\(^{-1}\) in the below-ground vegetation (figure 1(b)), and from \(~0.3\) to \(~0.1\) mg C ha\(^{-1}\) yr\(^{-1}\) in litter (figure 1(c)), during the first 30–40 years. These reductions then stabilized during the later stages of forest succession. The N accumulation rates (figures 1(d)–(f)) and the rates of change in the C:N ratio (figures 1(g)–(i)) in these vegetation components showed similar patterns to the C accumulation rates. The relationships with stand age are best described by either an exponential or a logarithm function. Consequently, C and N storage and C:N ratio in plant biomass or necromass pools increased along the age gradient and tended to level off during the later stages of forest succession (figure S2).

3.2. Contributions of plant N accumulation and stoichiometric flexibility to plant C storage

As shown in figure 2, contribution of alterations in total N amount and stoichiometric flexibility to \(\Delta C\) across stand ages differed over time. In general, change in the amount of N was a more important contributor throughout all stages of forest stand development than any adjustments in C:N ratios, and its importance to C storage increased with forest age. In contrast, the importance of adjustments in C:N ratios to \(\Delta C\) decreased with forest age (figure 2). More specifically, after 10 years of stand development, adjustments in C:N ratios contributed \(\sim 40\%\) of \(\Delta C\) (\(\sim 1.2\) mg ha\(^{-1}\) yr\(^{-1}\)), whilst changes in the total amount of N contributed to \(\sim 60\%\) of \(\Delta C\) (\(\sim 2.0\) mg ha\(^{-1}\) yr\(^{-1}\)). After 30–40 years of stand development, adjustments in C:N ratio contributed less than 10% of \(\Delta C\) (<0.01 mg ha\(^{-1}\) yr\(^{-1}\)), whilst changes in total N contributed over 90% of \(\Delta C\) (>1.2 mg ha\(^{-1}\) yr\(^{-1}\)). During an even later stage of stand development (i.e. after \(60–70\) years), the importance of adjustments in C:N ratio was negligible, whilst the importance of changes in the amount of N became almost the sole driver for \(\Delta C\) (figure 2). The \(\Delta C\) induced by the interactive combination of the two mechanisms (\(\Delta C\)-inter) was of minor significance along the age gradient.
4. Discussion

The accumulation of ecosystem C during forest stand development was mainly associated with an increasing C accumulation in vegetation and litter (figure S2(a)) whilst C accumulation in mineral soil remained unchanged (figure S3(a)). Since N often limits forest productivity (Miller 1981, Magill et al 2000, Luo et al 2004, Yang et al 2011, Terrer et al 2018), long-term Cseq during forest stand development requires an input of N from soil or other sources or the more efficient use of N by the vegetation. The results of this analysis indicated that C accumulation during forest succession can be largely ascribed to changes in both total N amount and modification in C:N ratio (insert figure in figure 2). Increases in forest C stocks during the first 30 years of forest development was supported by a significant increase in N accumulation as well as by an expanded C:N ratio (figure 2), demonstrating a dependence on both N input and improvements in N use efficiency. At the latter stages of forest development (30–40 years), the average rate of N accumulation was ~4.0 kg N ha⁻¹ yr⁻¹, supporting over 90% of forest Cseq, which suggests that N availability over-rides stoichiometric flexibility in determining long-term forest Cseq. This provides important insights into how forests use N during the development of stands (Takeuchi et al 2001, Crous and Ellsworth 2004, Sholtis et al 2004, Calfapietra et al 2005) and suggests that flexibility in the use of N is limited to early forest growth with C:N ratios remaining relatively stable after 30 years (Sistla and Schimel 2012). In contrast, Cseq by more mature forests is dependent on significant inputs of N. Of course, other factors, such as P availability, in particular, may play a more important role in tropical forests. In addition, there could be climate-related effects, as well as differences in C and N dynamics between needleleaf and broadleaf trees. However, the data is very limited, so that we could not carry out any further meaningful analysis related to climate zone or to differences between needleleaf and broadleaf trees and these require further investigation.
Figure 2. Absolute (a) and relative (b) importance of alterations in total vegetation N amount ($\Delta C$-TN), modifications in the C:N ratios ($\Delta C$-C/N), and their interactions ($\Delta C$-inter), to the change in plant carbon ($\Delta TC$) during forest stand development. The insert figure shows that there is a good fit between the calculated (based on C–N relationships using equations (1)–(3) and reported (based on synthesized results from our dataset) changes in C stocks of various ecosystem pools (ACP, above-ground C pool; BCP, below-ground C pool; LCP, litter C pool; and Total, total plant C pool) during forest stand development.

The unchanged C content in mineral soils suggest that C accumulation in vegetation and litter largely determined the extent of ecosystem $C_{eq}$ during forest succession. Carbon accumulation in above-ground vegetation is largely associated with increases in stem/trunk height and girth. In the early stages of forest development, plant productivity is high due to high rates of photosynthesis and rapid increase in leaf area index, and then decreases until an equilibrium state is reached after canopy closure (Odum 1969, Gower et al 1996, Ryan et al 1997). Although a constant soil C content during forest succession may be somewhat surprising, this has also been reported in other studies (Gaudinski et al 2000, Yang et al 2011, Uri et al 2012). Whilst the increase in litter C (figure 1) may result in more C eventually being sequestered in soil (Chapin et al 2011), microbial decomposition is often observed to accelerate after reforestation and over the subsequent rotation because the higher availability of soil-based and above-ground decomposable debris supports a larger and more diverse population of microfauna (Covington 1981, Zak et al 1990). Clearly, further consideration of the woody debris pool and the processes that contribute to its decomposition is important as this could represent an additional source of C and N. Whilst increases in tree mortality with succession will reduce litterfall and the contribution of C and N from vegetation into the soil pool (see Karelin et al 2020 for an example from the boreal region), a corresponding increase in woody debris could have the opposite effect and this requires quantification. At the same time NPP and net mineralization also decline, so both factors are likely to contribute to an overall decrease in C and N as forests age.

In addition, C outputs associated with the transfer of dissolved organic carbon (DOC) and particulate organic carbon (POC) to river networks might increase during forest succession (Ball et al...
2010, Lajtha and Jones 2018). Thus, enhanced C input from plant litter could be offset by increased C losses through higher microbial activity and/or greater DOC or POC losses, resulting in a relatively unchanged soil C pool during forest succession. The variation in litter N accumulation seen in figure 1(f) may be a reflection of the differences in decomposition times found in studies like Kavvadias et al (2001) where turnover times vary from 1 to 3 decades. Material entering the woody debris pool are shifted into an altered trajectory of slow C-release and slower N accumulation (Pastore et al 2019), however, the woody debris pool could not be assessed due to lack of data. Recent evidence also suggests that most C accumulated in soil is derived from labile compounds produced by roots (Sokol et al 2019) and this may decrease with stand development due to reductions in photosynthesis, or because of a reduced root mass per unit area due to self-thinning as forests age. This could counteract any increases in C due to litter incorporation. Clearly, more work is required in quantifying C inputs and outputs in forest soils. It has been well recognized that the C:N ratio of above-ground vegetation and litter increases with stand age (Yang and Luo 2011), facilitating the accumulation of C without the need for additional N (Rastetter et al 1992, Luo et al 2004). Our results illustrate increased C:N ratio with forest age because C accumulates quicker than N during the first 20–30 years of stand development (figure 1). However, changes in C:N ratio stabilized during the latter stages (i.e. after 30 years) of forest succession (figure 1). Expansion of the C:N ratio in plant tissues may have been due to increases in structural woody tissues with larger C:N ratios than foliage (Ågren 2008, Janssens and Luysaert 2009), which increases substantially during the early stages of stand development (Sterner and Elser 2002, Ågren 2008). While the addition of more woody tissue would have little impact on the C:N ratio in older forests, where tree biomass is dominated by woody tissue with a high C:N ratio. The increased C:N ratio occurred mainly during the first 20–30 years of forest succession (figure 1) and is an important contributor to forest C\text{seq} during this period, though the proportion of C supported by adjustments in the C:N ratio is still less than that supported by changes in the total N amount (figure 2). However, as trees age relatively more woody biomass is produced and canopy closure occurs, the influence of N-use efficiency on C\text{seq} becomes greatly diminished and eventually becomes insignificant. Overall, changes in the total N amount outweighed the effects of any flexibility in the C:N ratio in determining forest C\text{seq} during stand development and largely become the sole contributor after 30–40 years of forest succession (figure 2). Therefore, increases in N availability are the more typical mechanism supporting high forest C storage rates, particularly during the latter stages of forest development. How long this lasts will depend on the availability of N to vegetation either through organic matter decomposition, the supply from other sources (e.g. atmospheric N deposition, biological N fixation), or the exploitation of formerly inaccessible resources through deeper or more extensive root systems. It is also important to recognize that by far the largest C store is in the above-ground vegetation where it is susceptible to the effects of biotic and abiotic factors as well as anthropogenic disturbances. This work emphasizes that continuous increases in C storage are only sustainable when there is an external N input into the ecosystem (Luo et al 2004, 2006, Hungate et al 2006, Reich et al 2006, Yang et al 2014). In this study, the annual N accumulation, on average, was $\sim 5.6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in above-ground vegetation, $\sim 1.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in below-ground vegetation, and $\sim 0.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in litter. Since the N content in mineral soil remained constant, the annual ecosystem N accumulation was approximately $8.0 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, falling well within the range (0 to $120 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) reported previously (Binkley et al 2000). The accumulation of N during forest succession might, in many cases, be mainly due to external inputs via biological N fixation and atmospheric N deposition (Bormann 1993, Davidson et al 2007). Biological N fixation rates were reported to be 2.2, 4.9 and 2.9 g N m$^{-2}$ yr$^{-1}$, respectively, for boreal, temperate and tropical forests (Houlton et al 2008), whilst atmospheric N deposition rates were reported to vary from $< 0.2 \text{ g N m}^{-2} \text{ yr}^{-1}$ to $> 5 \text{ g N m}^{-2} \text{ yr}^{-1}$, depending on the region (Dentener et al 2006). Clearly, any inputs from N fixation will depend on the presence and activity of biological N fixers and it is evident that this is often an unlikely source of N as many secondary forests are largely devoid of N fixing species. Similarly, any increases in N through atmospheric N deposition are likely to be site-specific and regionally variable. The availability of N during forest succession might also be influenced by legacies from past atmospheric N deposition, biological N fixation and previous land use history, including the afforestation of abandoned fertilized croplands (Kicklighter et al 2019). Also the exploitation of available soil N by roots from deeper soil reserves may increase with succession, resulting in the greater allocation of biomass to fine roots (Iversen 2010). A recent field investigation (Pastore et al 2019) suggests that the decomposition of litter and coarse woody debris can also lead to continuous N release, though this process is relatively slow. In addition, it has been suggested that the increased availability of N could be stimulated by rhizosphere interactions between plants and microorganisms (Phillips 2007, Frank and Groffman 2009). Subsequently, more N will become available for plant uptake in the mineral soil that could stimulate forest production over decades and centuries (Rastetter et al 1997). Nevertheless, a large
excess of N may down-regulate the fertilization effect of N on tree growth (Schulte-Ubbeling and de Vries 2018) or even prove to be detrimental to further growth (Aber et al. 1989). Like C, changes in the soil N stock are determined by both inputs (e.g. atmospheric N deposition, biological N fixation) and outputs (e.g. tree N uptake, gaseous or leaching loss of N). During forest development, the total N amount/capital in older forests is larger as they continue to accumulate N, although the accumulation rate declines with age due to a higher biomass than younger forests (Johnson 1992). If no external N can be supplied to trees, progressive N limitation may occur (Luo et al. 2004) due to increasing N uptake and accumulation in forest standing biomass during forest development. In addition, gaseous losses of N (Benanti et al. 2014) as well as dissolved organic N and particulate organic N leaching to river networks (Ball et al. 2010) might also increase with stand age. The outputs of N might offset any increase in N as detailed earlier leading to unchanged soil N stocks, thus limited N availability in late succession could drive increasing rates of biological N fixation in forest ecosystems (Vitousek et al. 2002, 2013, Zackrison et al. 2004). The N accumulation rates gradually decreased with forest age (figure 1), which may have been caused by more N being fixed in organic forms and a widened C:N ratio in the litter, thereby reducing the available N, as has been reported in many field studies (Hooker and Compton 2003, Noh et al. 2010, Li et al. 2013, Yang et al. 2014, Jiang et al. 2017).

Due to the N stoichiometric relationship between vegetation and soil, it is essential that N is acquired from external resources in order to match the accumulation of ecosystem C (Hungate et al. 2003). If an ecosystem is unable to accumulate enough N to support an increase in C storage capacity will be reduced and would not persist for extended periods of time (Hungate et al. 2003, Luo et al. 2004, Reich et al. 2006, Wang et al. 2020). As shown in this study, increases in both ecosystem N amount and C:N ratios supported a positive C increment during different phases of forest succession. This study also showed that N accumulated continuously during forest succession; whilst the C:N ratio increased dramatically in the early years of forest stand development they remained relatively constant during latter stages.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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ORCID iD

Junliang Zou  https://orcid.org/0000-0001-9635-0686

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