Nitrogen cycles in terrestrial ecosystems: climate change impacts and mitigation

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Nitrogen cycles in terrestrial ecosystems: climate change impacts and mitigation

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Abstract

The nitrogen (N) cycle and N balance have primarily been modified by anthropogenic activities and environmental changes at various scales, including biological individual, ecosystem, local landscape, continental region and global scales. These modifications have drastically affected the structures and functions of natural and agricultural ecosystems in terrestrial and aquatic areas. In this manuscript, we first present a modified view of the global N cycle that includes N transport, conversion, and exchange processes. Second, several crucial issues concerning N balance, including N deposition and excessive addition and the dynamics of N and other nutrients, are reviewed. Third, the effects of climate change factors including water status, warming, and elevated CO₂ concentrations, on N balance and the N cycle and their interactions within and with other environmental factors are outlined. Finally, intervention strategies for improving N balance/cycling to address rapid continual climatic change and socio-economic development are presented and discussed. It is highlighted that the altered N balance and cycle between the geosphere, biosphere and atmosphere have produced the profoundly critical challenge of maintaining nitrogen levels within an appropriate range, which should be considered by relevant sectors and people, including researchers,

managers, and policy makers from ecological, environmental, and sustainable development aspects.

Key words: Nitrogen cycle, nitrogen deposition, excessive nitrogen addition, nitrogen management, terrestrial ecosystems, climate change.

1. Introduction

Nitrogen (N) is an important element in biogeochemical cycles and plays a pivotal role in regulating ecosystem structure and function (Vitousek et al. 1997; Fowler et al. 2013; Feng et al. 2015). However, great adverse impacts on the global N cycle have predominately resulted from anthropogenic activities, such as substantial fossil fuel combustion with rapid urbanization, excessive N application in intensive agricultural ecosystems with low N use efficiency (NUE), and enhanced N efflux from the rapid development of intensive livestock production systems (Galloway et al. 2008; Gruber and Galloway 2008; Ju et al. 2009; Paulot et al. 2013; Riha et al. 2014). Thus, this issue has become an important global concern (Sutton et al. 2012; Liu et al. 2013; Ciais et al. 2013; Fowler et al. 2013; Bechmann et al. 2014). Conversely, through a chain of chemical reactions and multi-transport processes, these emissions have resulted in the deposition of significant amounts of atmospheric N in terrestrial and aquatic ecosystems, which has led to ecosystem malfunction and environmental consequences, particularly with continual climatic change (Vitousek et al. 1997; Galloway et al. 2008; Gerber et al. 2010; Liu et al. 2013; Riha et al. 2014; Malik and Tauler 2015). Understanding the nitrogen cycle and its driving factors is important for evaluating the dynamics of N deposition and their effects on agricultural and natural ecosystems and for determining feasible and adaptable mitigation measures (Galloway et al. 2008; Liu et al. 2013; Dietze et al. 2013; Suddick et al. 2013; Rütting and Andresen 2015; Stevens et al. 2015). Here we review altered nitrogen cycle processes relative to the conventional cycle. The processes we review include the modified concepts of N dynamics, N deposition, N

contamination and, particularly, the environmental impacts on N cycle and its feedback across major N conversion and exchange processes (**Fig. 1**). Several critical concerns regarding N balance and the effects of climatic change are outlined. Finally, intervention management strategies for improving N balance/cycling to address rapid socio-economic development, continual climate change and other environmental pressures are presented and discussed.

2. Nitrogen deposition and dynamics in ecosystems

2.1. Atmospheric nitrogen deposition

Atmospheric N deposition (N_{dep}) is becoming an important component in the global N cycle and has led to severe issues regarding the imbalance of N in ecosystems (Galloway et al. 2008; Fowler et al. 2013), while anthropogenic N input (e.g. fertilizer and manure) is a dominant contributor to atmospheric N_{dep} at continental and regional scales (Galloway et al. 2008; Paulot et al. 2013). Generally, anthropogenic N components are emitted into the atmosphere in two forms, N oxides ($NO_x = NO + NO_2$), primarily due to fossil fuel combustion, and ammonia (NH_3) mainly from the agricultural sector; while N_2O mainly are emitted from soil during denitrification (Paulot et al. 2013, Bouwman et al. 2013; **Fig. 1**). Based on the report by Fowler et al. (2013), the annual emissions from land in the form of NO_x , NH_3 , and N_2O are about 35 Tg N, 60 Tg N, 13 Tg N, respectively. After chemical conversion and physical transport, NO_x and NH_3 are removed by wet scavenging and dry deposition in the earth's ecosystems. Reportedly, the portion of reactive N (N_r , all nitrogen forms other than N_2) that is returned to the land and ocean accounts for 60-80% of the total N_r emitted to atmosphere (Dentener and Crutzen 1994; Moffat 1998; Zhang et al. 2012; Jia et al. 2013). Globally, the total amount of N_r emitted to the atmosphere increased from 15 Tg N a^{-1} in 1860 to 187 Tg N a^{-1} in 2005, with a continued acceleration of N_r every year (Galloway et al. 2008). From another assessment report, the global annual mean atmospheric deposition rate has reached *c.* 180 Tg N a^{-1} , primarily in reduced

form from anthropogenic sources (Fowler et al. 2013).

For example, N deposition in China, a rapidly developing nation, has quickly increased in recent decades (Jia et al. 2013; Sheng et al. 2013). This increase likely resulted from large increases in both energy consumption and N fertilizer use, the two dominant human activities that affect N deposition (Sutton et al. 2011; Jia et al. 2013; Sheng et al. 2013). Based on data from 280 observational sites, national-scale inorganic N_{dep} patterns demonstrated a continual increase of *c.* 25% of the mean N_{dep} over China ($11.1 \text{ kg ha}^{-1} \text{ a}^{-1}$ in the 1990s vs $13.9 \text{ kg ha}^{-1} \text{ a}^{-1}$ in the 2000s, Jia et al. 2013). The highest N_{dep} of $30 \text{ kg ha}^{-1} \text{ a}^{-1}$ occurred in southern China and decreased to western and northern China (Jia et al. 2013). However, in Northern China, a N deposit of $80 \text{ kg ha}^{-1} \text{ a}^{-1}$ was recorded in an agro-ecosystem (He et al. 2007), which significantly exceeds the critical load of $10 \text{ kg N ha}^{-1} \text{ a}^{-1}$ (He et al. 2007). Exceeding the critical load has been known to have notable effects on native vegetation (e.g., Bobbink et al. 1998; Dentener et al. 2006). As suggested, the changes in N_{dep} depend on human activities, such as the application of N fertilizer, and climatic factors such as precipitation patterns (Jia et al. 2013). For example, Jia et al. (2013) indicated that a combination of anthropogenic sources, including the application of N fertilizer and energy consumption, and precipitation, accounts for 79% of the spatial variations of N_{dep} .

Nitrous oxide (N_2O), one of the six major greenhouse gases, has recently received great attention due to its significant greenhouse effect (Bouwman et al. 2013; Ciais et al. 2013). More N_2O could be produced as an intermediate or side-product in conventional biological nutrient removal (BNR) processes consisting of the two steps—nitrification and denitrification in wastewater treatment plants (Bouwman et al. 2013). A novel treatment technology with Anaerobic Ammonium Oxidation (Anammox) pathway can substantially remove N due to its low energy consumption and high removal efficiency with extremely low N_2O and CO_2 emissions. Thus, with Anammox microorganisms, in treating ammonium-rich wastewater, ammonium can be directly oxidized to nitrogen gas with the presence of nitrite as electron acceptor thereby circumventing

nitrification and denitrification (Meng 2012, and therein; **Fig. 1**).

2.2. Nitrogen dynamics in ecosystems

The major processes that N have participated in the ecosystems were depicted in **Fig. 1**. Briefly, atmospheric N is transformed by lighting process, biological N₂ fixation, N deposition, Haber-Bosch process, and through application N fertilizer, finally imported into terrestrial and aquatic ecosystems. In plants, N converts from NO₃⁻¹ into NH₄⁺ by nitrate reductase and nitrite reductase involvements, and continual conversions between crops, animal and people. In soil, N in organic matter is first mineralized to inorganic N forms such as NH₄⁺ and NO₃⁻, in which nitrification occurs with microbial involvements; some N components can be fixed in soil as an immobilized form. Thereafter, available inorganic N is absorbed by plant roots, again entering plant tissues. Nitrogen emission pathways mainly include denitrification in soil, Anammox reaction, gaseous N emission processes, and fossil fuel consumption (e.g., Lam et al. 1996; Aber et al. 1998; Galloway et al. 2008; Meng 2012; Fowler et al. 2013; Chen et al. 2014b). As early as 1989, Aber et al. (1989) indicated two major pathways by which N enters ecosystems: pulse fertilizer addition and chronic atmospheric deposition. The amount of N entering an ecosystem over several years may exceed the capacity of an ecosystem for uptaking and retaining N in soils, plants, and microbes, resulting in nitrogen saturation, and potentially N leaching (Aber et al. 1989, 1998; Kopáček et al. 2013; Bechmann et al. 2014). For instance, in temperate forest ecosystems, Aber et al. (1989, 1998) suggested that N levels could be described from nitrogen-limited to nitrogen-saturated processes. As suggested, the nitrogen level dynamic phase in any ecosystem can be separated into four stages: N limitation, N balance maintenance, N saturation, and N excessive stages (Aber et al. 1989, Kopáček et al. 2013). Bechmann et al. (2014) recently redefined nitrogen balances according to N inputs by atmospheric deposition, fertilizer and manure addition, and fixation minus N outputs with yields. The relationships between the annual N balances for the agricultural area in the catchments and the concentrations of N in the streams were volatile (Bechmann et al. 2014). In addition, positive relationships

between agricultural production intensity and N surplus were easily identified in these areas by monitoring data from the Nordic–Baltic region over 20 years (Bechmann et al. 2014). N deposition in Rocky Mountain National Park, Colorado, USA potentially resulted in a greater than 10% increase in vegetation in subalpine plant communities (McDonnell et al. 2014). A study of a semiarid grassland in north China by Wang et al. (2015) found that a modest addition of N may enhance both aboveground production and belowground microbial N transformation in soil including nitrification and mineralization. However, in some natural ecosystems, excessive N input may also result in soil acidification, that might offset the beneficial effects from N input fertilization (Wedin and Tilman 1996; Bai et al. et al. 2010). For instance, although N additions enhanced the total community production, plant community stability was negatively affected with the dominant native species being replaced by other secondary species (Wedin and Tilman 1996; Bai et al. et al. 2010). In addition, the belowground communities such as bacterial, fungal, and actinobacteria were also suppressed by soil acidification, indicating that abnormal N enrichment may decrease the linkage between aboveground and belowground components in semiarid grassland ecosystems (Bai et al. et al. 2010; Chen et al. 2015b). Soil acidification induced by N deposit may also limit forest ecosystem productivity and thus global-scale biodiversity (see a synthesis by Bobbink et al. 2010).

Land-use changes can alter the soil N status, and natural succession could enhance the N conservative capacities of terrestrial ecosystems (Deng et al. 2014). During vegetation growth in the central part of the Loess Plateau, China, N storage was observed to rapidly increase in the 0-60 cm soil layer before reaching a stable value after the emergence of the shrub community stage (50-60 years). This process resulted in the dramatic accumulation of long-term soil N storage (*c.* 150 years) in secondary forests (Deng et al. 2014). Although biodiversity in an ecosystem may be closely linked with N dynamics, it remains an area of controversy (Vitousek et al. 1997; Cardinale 2011; McDonnell et al. 2014). Bracken and Stachowicz (2006) observed that an increase in seaweed diversity may promote nitrogen uptake due to the complementary use

of nitrate and ammonium. Recently, a study provided evidence that increased species richness could provoke N accumulation in biological organisms in freshwater ecosystems (Cardinale 2011). Whether a high level of biodiversity can enhance the nitrate and ammonium uptake and storage and the feedback remains debatable, despite actual findings that the rapid accumulation of nitrate in terrestrial ecosystem has become a cause for global concern and potentially results in adverse feedback to ecosystem structure and function (Vitousek et al. 1997; Cardinale 2011). Additionally, NO emissions from a variety of different plant species have been observed, but further investigation is required (Chen et al. 2015c).

2.3. Nitrogen dynamics with other nutritious components

N, carbon (C) and sulphur (S) cycles may be associated with the biogeochemical cycle from a single ecosystem up to the global scale. For example, with N saturation, a transition from N to C limitation may appear (Kopáček et al. 2013)—available N exceeds plant and microbial demand in a vegetation ecosystem, consequently an increase in N would not increase, and may even decrease, plant and microbial biomass under saturating N conditions (Aber et al. 1998; Kardol et al. 2012; Wei et al. 2013). At N-saturated ecosystems, a sharp decline in C:N might appear, such as a decrease of ~20% in tree leaves in a temperate forest ecosystems (Aber et al. 1998), and a decrease of ~12% in a sagebrush-crested wheatgrass soil (Chen and Stark 2000). However, in coniferous forests, C:N ratio remained high in N-saturated soil (Gundersen et al. 1998), this trends needs to be better understood (Delgado-Baquerizo et al. 2013; Zhang et al. 2014). Moreover, in N-rich systems, lower amounts of bio-available dissolved organic C (DOC) may result in a C limitation for the microbial community. In these systems, the following three mechanisms have been hypothesized (Kopáček et al. 2013): (1) increased abundance of N for plant uptake, resulting in lower C allocation to plant roots; (2) chemical suppression of DOC solubility by soil acidification; and (3) enhanced mineralization of DOC due to an increase in the number of electron acceptors for SO_4^{2-} and NO_3^{-1} under anoxic soil conditions (Kopáček et al. 2013). However, the dynamics of available P may not be closely

associated with C and N (Smeck 1985). The availability of C and N is closely linked to the microbial mineralization primarily derived from organic matter, whereas the available P for plants and microorganisms could be mainly derived from mechanical rock weathering (Smeck 1985). However, P and iron limitations may play a predominant role in stabilizing the N inventory of marine ecosystem through the interactions of N_2 fixation and denitrification (Dietze et al. 2013), and current soil C, N and P status is linked to the long-term P weathering using a new model, N14CP (Davies et al. 2016). The balance between the major nutrients may be altered with environmental change, particularly under climatic change condition (Delgado-Baquerizo et al. 2013; Yuan and Chen 2015). For example, Delgado-Baquerizo et al. (2013) examined the effects of dryland aridity, which are expected to continue due to the great N deposit, and implied that a predicted increase in aridity may increase the available inorganic P concentration, mainly due to rock weathering, relative to C and N, possibly leading to an decoupling of the C, N and P cycles in drylands (Delgado-Baquerizo et al. 2013). Recently, Yuan and Chen (2015) reported that terrestrial plant N:P can decrease with elevated CO_2 and increased precipitation, but increases with climate warming, reduced precipitation, and N addition, indicating that a decoupling of N and P in terrestrial ecosystem may occur under global changes. Consequently, the biogeochemical processes that control key ecosystem functions and services, such as plant growth, community productivity, soil respiration, litter decomposition, and subsequent soil carbon storage, were changed, depending on the site, local, and regional to global scales (Finzi et al. 2011; Delgado-Baquerizo et al. 2013; Yuan and Chen 2015). A recent report from field-fertilizing experiments on typical temperate grasslands in China indicated that the addition of N with P and K treatments significantly enhanced N_2O emissions relative to N application alone (Zhang et al. 2014). This result implies that the other essential elements involved in soil microbial metabolism may also promote N turnover processes and accelerate soil N release. Furthermore, the nitrate production and mobility responses of an ecosystem to environmental change could be regulated by iron, which is involved in reduction

processes by serving as a catalyst when nitrate is reduced to nitrite (Aber et al. 1998; Davidson et al. 2003). However, this mechanism remains controversial (Li et al. 2012). In addition, land-use changes significantly affect N cycling features and stoichiometry (Davidson et al. 2007; Townsend et al. 2007). For example, conservative N-cycling properties appeared in young successional forests that were grown after agricultural abandonment. However, as secondary succession progresses, N-cycling properties may recover and a conservative P cycle may occur, which would lead to a shift in the N:P ratio (Davidson et al. 2007). This result indicates that the dynamic features and balance of N relative to other nutrition elements might be easily altered with land-use changes involving anthropogenic disturbance across the timescales.

3. Effects of N deposition and consequences of excessive N addition

Large increases in N_{dep} exerted dramatic beneficial and deleterious impacts on terrestrial ecosystems (Aber et al. 1998; Galloway et al. 2008; Sutton et al. 2012; Fowler et al. 2013; Wårlind et al. 2014). The advantageous aspect appears often in ecosystems that are frequently limited by N availability (Aber et al. 1998; Fowler et al. 2013; Davies et al. 2016). These aspects include increases in soil N availability; plant N uptake; plant foliar N concentrations in natural ecosystems, such as grasslands and forests (Rustad et al. 2001; Hyvönen et al. 2007); and crop N uptake and grain protein contents in agricultural ecosystems (Fowler et al. 2013; Liu et al. 2013). These processes positively alter soil nutrition status (Goulding et al. 1998), stimulate the development of the vegetation canopy (Reay et al. 2008; Fang et al. 2014), and result in an enhanced carbon sink (Wårlind et al. 2014; Fang et al. 2014). On the other hand, currently dramatic N deposition and excessive N fertilizer application can produce deleterious impacts, including severe soil acidification (Bowman et al. 2008; Yang et al. 2012; Fowler et al. 2013), loss of indigenous species and biodiversity (Goulding et al. 1998; Clark and Tilman 2008; Jia et al. 2013; Zhang et al. 2014) including the loss of soil microbial diversity (Zeng et al. 2016), un-linkage between aboveground biomass and belowground microbial

activities (mainly due to acidification) (Liu et al. 2014), decoupling of the C-N-P stoichiometric balance in surface soils over geographical regions (Yang et al. 2014; Yuan and Chen 2015), exacerbation of greenhouse gas imbalance (Galloway et al. 2008), and extra eutrophication and excessive N saturation in some ecosystems (Goulding et al. 1998; Bechmann et al. 2014). For instance, a major concern has emerged regarding soil acidification in intensive agricultural cropland systems in China, mainly due to the overuse of fertilizer application for pursuing high agricultural production to meet increasing demands for food (Guo et al. 2010; Yang et al. 2012). Soil acidification induced by N deposition also occurred in coniferous and mixed coniferous and broadleaved forests (Yang et al. 2015). In some intensive agricultural ecosystems, such as in wheat-maize cropping systems in a major grain production zone, excessive nitrogen application could decrease grain yield and could easily lead to nitrogen loss, which could result in environmental contamination (Wang et al. 2011; Xu et al. 2013; Lu et al. 2014). However, from a recent report by Chapman et al. (2015), the deciduous forest understory plant community of N-rich forested ecosystems can remain stable with excessively increasing N availability. Thus, there are arguments on N deposition issue.

Environmental changes and management practices may affect the N dynamics of ecosystems. For example, concentrated summer rainfall can increase ammonia volatilization by 19% - 24% (Ju et al. 2009). In wheat/maize systems in calcareous soils in the major grain production zone of China, N loss primarily occurred through nitrate leaching pathways (Ju et al. 2009). In these areas, a higher N loss rate was often observed in rice/wheat systems than in wheat/maize systems, and the ratios of ammonia volatilization loss to applied nitrogen were 16.6-18.4 % when different amounts of nitrogen were applied in a rice field (Chen et al. 2015a). These results indicated that different forms of N loss and different rates of N loss could occur for different vegetation types (Ju et al. 2009; Chen et al. 2014a). Based on a recent report from Northern Lithuania (Masilionytė et al. 2014), the lowest soil mineral nitrogen concentration (0–40 cm soil layer) was observed, and the risk of leaching into deeper layers was lower in organic cropping systems with catch crops

(e.g. winter wheat + catch crops), which suggested that the agro-ecosystems using organic cropping systems with catch crops resulted in lower diffuse nitrogen pollution in some areas (Masilionytė et al. 2014). Increased mineralization always enhances N uptake by crops and may increase the risk of N loss (Chen et al. 2014a). Plant residues can change the fate of inorganic N via three mechanisms: mineralization, immobilization–mineralization, and immobilization. For these mechanisms, plant residue characteristics and field soil properties may play a critical role. Recent reports by Chen et al. (2014) have indicated that N_r losses could be limited in integrated soil–crop systems in China based on the local environmental conditions, appropriate varieties, regulated planting dates and densities, and improved nutrient management, which could increase productivity while reducing the environmental costs of intensive agriculture (Chen et al. 2011a, 2014; Masilionytė et al. 2014). Through analyzing a set of results from simulations with two models, Durand et al. (2015) indicated that the reducing N input and increasing grassland would efficiently mitigate nitrogen pollution in farming catchments.

4. Effects of climate change on N balance/cycling

4.1. Water status effects

Climatic controls on biogeochemical cycles, including N balance, are more sensitive in arid and semi-arid areas because the biological activity in these areas is primarily driven by water deficit (Delgado-Baquerizo et al. 2013). In an acidic coniferous forest in Norway, the water deficit stress can reduce gross N turnover rates, including ammonification and nitrification processes (Chen et al. 2011b). In contrast, greater precipitation could enhance N₂O emissions. For example, the acceleration of the N cycling process under increased precipitation may lead to an increase in the release of N₂O in grazed grasslands in New Zealand (de Klein et al. 2015). Larsen et al. (2011) indicated that water deficit could weaken belowground gross N mineralization and decrease the mass of soil fauna N in Danish heathland ecosystems. The same scenario, i.e., limitations in

the N mineralization rate and nitrate production under water deficit conditions, was also found for farmlands (Wang et al. 2008). Nevertheless, whether nitrification is more sensitive to desiccation than ammonification and to what extent N turnover occurs depends on different soil horizons and the type of vegetation (Chen et al. 2011b; Larsen et al. 2011). However, an increased efflux of inorganic nitrogen was observed during a drought period in an annual grassland in California (Jackson et al. 1988). Drought can result in the allocation of more plant N in sink organs, such as roots (Xu and Yu 2005; Xu et al. 2007), and limit the absorption of soil N by plants (Yuan et al. 2006). Thus, relatively stable or high N levels remain in the soil during drought. Water stress can decrease nitrate reductase (NR) activity and other positive N anabolic processes in plants (Neeru et al. 1998; Xu and Zhou 2006a). Severe drought can decrease the protein contents of plant tissues and the ratio between protein N and total N (Xu and Zhou 2006ab), and waterlogging can decrease the N content and the amount of N accumulated in the plant roots in winter wheat by 12% - 39%. Furthermore, waterlogging can increase the C:N ratio by 80%, which would weaken synthetic N metabolism in the plant roots (Zhou et al. 2001; Xu and Zhou 2004, 2006b). In addition, the water status may also affect N₂ fixation processes in relative ecosystems. For instance, severe drought could constrain the N₂ fixation rate in common bean, in which droughts affect the transportation of ureides from the nodules and the accumulation of N in the stems and leaves (Coletto et al. 2014). Thus, water status may play an important role in regulating the N₂ fixation bioprocess (Vadez et al. 2000; Coletto et al. 2014).

4.2. Temperature effects

High temperatures affect belowground and aboveground N metabolic processes. Rustad et al. (2001) analyzed data from warming experiments in ecosystems at 32 research sites that represented four broadly defined biomes, including high and low tundra, grassland, and forest; and the result showed that temperature increases of 0.3–6.0°C significantly increased the net N mineralization rates in the soil by 46%. However, Gestel et al. (2011) reported reductions of 16-18% after 3 years of warming in the dissolved forms of soil N,

NO_3^- -N and NH_4^+ -N. Nitrate and ammonia are usually recognized as the two dominant forms of soil available N. Xia et al. (2009) indicated that a temperature increase of 1.8°C in the surface soil did not change the soil available N content according to the sum of the NH_4^+ and NO_3^- concentrations. However, in a Danish heathland, warming increased the N turnover based on the high rates of microbial NH_4^+ consumption, gross mineralization, potential nitrification, denitrification and N_2O emissions (Larsen et al. 2011). In addition, the decomposition in the soil was marginally accelerated by warming in a tidal marsh in Massachusetts, USA (Charles and Dukes 2009). Furthermore, N_2 fixation was promoted by warming in a subarctic moist heath in Northern Sweden (Sorensen and Michelsen 2011). N_2 fixation and N_2O emissions were enhanced as the temperature increased in a New Zealand grassland (de Klein et al. 2015). Within plants, heat stress limited the accumulation of leaf N and decreased nitrogen availability (Wollenweber et al. 2003). Decreases in N anabolic processes, such as decreases in NR and glutamine synthetase (GS) activities, and increasing catabolism, such as an increase in endopeptidase activity, were found at high temperature above optimum (Xu and Zhou 2006a). Modifications in molecular composition have been highlighted with warming based on higher levels of the expression of some genes and the enhanced synthesis of some heat-stress proteins (see a review by Penuelas et al. 2013). Furthermore, when the temperature is high, a decrease in the proportion of soluble protein to total leaf N may suppress the Rubisco activity and produce a negative effect on the photosynthetic capacity (Sicher and Bunce 1997; Xu and Zhou 2006a; Xu et al. 2013b). Thus, extremely high temperatures could lead to malfunctional effects within an individual or ecosystem belowground and aboveground.

4.3. Elevated CO_2 concentration effects

Elevated atmospheric CO_2 concentrations (elevated CO_2) may substantially affect terrestrial and aquatic ecosystems regarding their ecological processes, including ecosystem structure, plant physiological activity (e.g., photosynthesis and respiration), net primary production, nutrient cycle rate, C source-sink relationships,

and species successions (e.g., O'Neill 1995; Gutiérrez et al. 2013; Xu et al. 2014; Feng et al. 2015; Xu et al. 2015). Long-term elevated CO₂ can decrease the N contents of plant tissues, which are referred to as the N dilution effectiveness and/or progressive N limitation to plants (PNL)—this means that increased productivity from enhanced catalytic activity of Rubisco by elevated CO₂ does not necessarily match with enhanced N in plant tissue that results in N dilution (Farage et al. 1998; Davey et al. 1999; Gutiérrez et al. 2013). Thus, elevated CO₂ levels directly inhibit plant nitrogen metabolism and relevant physiological processes, particularly during long-term CO₂ enrichment (Conroy 1992; Luo et al. 2004; Larsen et al. 2011; Gutiérrez et al. 2013; Bloom et al. 2014). As suggested by Luo et al. (2004), in the presence of high CO₂ levels, the available N in soils, plants, and ecosystems becomes increasingly limiting as the net primary productivity (NPP) and soil organic matter (SOM) content continually increase. For instance, Gutiérrez et al. (2013) reported that elevated CO₂ could decrease the leaf N and Rubisco contents by 14% and 21%, respectively, in *Triticum aestivum* plants. This N dilution could lead to photosynthetic acclimation or the down-regulation of the photosynthetic capacity (Adachi et al. 2014), and reduce the protein grain concentrations in crops. For instance, there were decreases of 10–15% in the grain protein concentrations in wheat, barley and rice (Taub et al. 2008), and an average decrease of approximately 8% in wheat grain, rice grain, potato tuber and barley grain (Bloom et al. 2014), thereby decreasing product quality. On the other hand, when plant N contents are low, the plants may increase their NUE to counteract the N deficit, e.g., increasing their photosynthetic N use efficiency (PNUE) in green photosynthetic organs (Davey et al. 1999). A recent report by Feng et al. (2015) indicated that a significant positive relationship occurred between the stimulation of plant productivity and N acquisition when CO₂ concentrations were elevated for a long period in a Free-Air CO₂ Enrichment (FACE) experiment. In addition, this study indicated that an increase in N limitations relative to enhanced ecosystem productivity could result in a decrease in plant N acquisition (Feng et al. 2015), which implies that an adaptive response of N balance occurs in ecosystems. More N could

be allocated to belowground tissues under high CO₂ conditions (e.g., Cotrufo et al. 1998). Elevated CO₂ concentrations result in the transfer of more N into the roots than through the photosynthetic apparatus of green tissues to optimize energy costs and increase the NUE by regulating nitrogen transport and reallocation (Cotrufo et al. 1998; Luo et al. 2006; Yuan et al. 2006; Xu et al. 2007). C₄ plants were not affected by elevated CO₂ under ample water conditions (e.g., Leakey et al. 2006; Xu et al. 2014). Thus, PNL may not appear for the C₄ plants. For instance, Bloom et al. (2012) reported that nitrate assimilation into proteins in plant tissues was inhibited by elevated CO₂ in C₃ species rather than C₄ species. In this case, a marked suppression in leaf NO₃⁻ assimilation in field-grown wheat was observed under high [CO₂] (Bloom et al. 2012). In general, PNL in C₃ plants may be greater than in C₄ species, highlighting the species-specific and plant functional groups-specific responses of N conversions to CO₂ enrichment (Xu et al. 2015).

Soil nitrogen dynamics were also affected by CO₂ enrichment (O'Neill 1995). However, no general response of gross mineralization or gross nitrification to elevated CO₂ was found, which depends on ecosystems and experimental methods (Rütting and Andresen 2015). For example, in a grazed grassland, elevated CO₂ can accelerate N cycling, including increased N₂O emissions, because NPP, legume growth and biological nitrogen fixation (BNF) likely increase the amount of urine N deposition due to strengthened grazing (de Klein et al. 2015). N mineralization would be stimulated by elevated CO₂ in N limited ecosystems, but may decrease in N₂ fixing communities due to the increased N supply via BNF (Richter et al. 2003; Rütting and Andresen 2015). In P limited ecosystems, no N mineralization response to elevated CO₂ was observed because no association occurred between P mineralization and SOM decomposition (McGill and Cole 1981; Rütting and Andresen 2015).

Recently, van Groenigen (2014) reported that the stimulation of plant growth and carbon inputs into the soil from elevated CO₂ is expected to allow the microbial response to counteract the response by resulting in faster decomposition in the soil, which is closely associated with soil N availability (Cheng et al. 2012;

Carrillo et al. 2014; Hodge and Storer 2015). Under elevated CO₂ concentrations, high N concentrations and high C concentrations in root tissues may increase C efficiency, which indicates that elevated CO₂ may shift the stoichiometric balance and that N availability may become more important for regulating C efficiency at elevated CO₂ than at ambient CO₂ (Carrillo et al. 2014). In addition, a world with both high CO₂ and high N could result in greater carbon storage by soil microorganisms (Carrillo et al. 2014). In the soil, mycorrhizae, N-fixing bacteria and actinomycetes, microbiota, plant pathogens, and soil fauna could be altered under elevated CO₂ conditions (O'Neill 1995; Hu et al. 2001; Zhang et al. 2011). The diluted nitrogen concentrations in the plant litter could change the decomposition rates and expose an indirect effect on decomposer communities and their metabolic functions (O'Neill 1995; Hu et al. 2001). Hu et al. (2001) observed the effects of suppressed microbial decomposition and enhanced plant N uptake in an annual grassland under a long-term elevated CO₂ condition. Increases in soil microbial biomass C:N ratio and ¹⁵N content in plants were also found (Hu et al. 2001). In a soil microbial community in a grassland ecosystem, several N cycling genes, such as *nifH* and *nirS*, were significantly promoted in response to elevated CO₂ (Xu et al. 2013a). Under elevated CO₂, the ratio of ammonium oxidation to immobilization may decrease, which results in a tighter N cycle at a stable ecosystem N level (Rütting and Andresen 2015). Thus, under high CO₂ and with future climate change, nitrogen may be reallocated between aboveground and belowground parts, which would profoundly affect bioprocesses throughout the ecosystem at the regional or global scales (Cotrufo et al. 1998; Gruber and Galloway 2008; Xu et al. 2013b).

One hypothesis suggests that legume species may benefit more from CO₂ enrichment because they possess root nodules with high N-fixing capacities and potentially encounter N dilution effects (Newton et al. 2006; Rogers et al. 2009). However, in some legume species, N-fixing activities, such as symbiotic nitrogenase activity, were not enhanced by elevated CO₂ (Zhang et al. 2011). For some legumes species, N nutrient limitation also did not occur in response to elevated CO₂, mainly because of improved availability of C, N,

and water under elevated CO₂ (Cotrufo et al. 1998; Rogers et al. 2009). The growth of legume species does not outweigh the effects of growing plants without N-fixing bacteria under high CO₂ concentrations (Campbell et al. 2000; Zhang et al. 2011; Xu et al. 2014; Yan et al. 2014), which indicates that the deficits of other nutritious elements, such as a P, may limit the activity of N-fixing bacteria and their regulatory response to CO₂ enrichment (Rogers et al. 2009; Yoneyama et al. 2012; Rütting and Andresen 2015). The key responses of N processes in aboveground and belowground parts in vegetation ecosystems to climate change, such as elevated CO₂, are summarized in **Fig. 2**.

4.4. Multi-factor effects

Effects on N cycle processes in terrestrial ecosystems may not only derive from a single climate change variable, but multiple factors may play a complex role in the N cycle; the combined effects might reflect a changing environmental world. For example, decomposition was marginally accelerated by warming and was enhanced with increasing precipitation in a tidal marsh in Massachusetts, USA (Charles and Dukes 2009). However, the modest warming and altered precipitation did not significantly change the ammonium concentration in a marsh ecosystem (Charles and Dukes 2009) and in arid grassland (Liu et al. 2015). Although warming or increased precipitation did not change the microbial community structure, microbes-mediated soil C losses would increase under future climate change (Zhang et al. 2013). However, a combination of heat and drought would inhibit plant N fixation, leading to a higher C:N ratio in a savanna ecosystem in southern Africa (Dintwe et al. 2015). In plants, warming can exacerbate deleterious effects of drought stress on nitrogen metabolism, including decreasing the NR and GS activities and increasing the proteinase activities, which would reduce nitrogen anabolism and enhance protein catabolism (Xu and Zhou 2006a). In addition, the nitrogen absorption capacity of the plant could be weakened under the combination of drought and heat (Wollenweber et al. 2003; Xu and Zhou 2006a; Xu et al. 2007; Khan et al. 2014).

As recently reported, the down-regulation of photosynthesis in rice plants grown under CO₂ enrichment in

fields may be accelerated with soil warming (Adachi et al. 2014), potentially due to increasing N dilution at elevated CO₂ with warming. Elevated CO₂ could decrease plant leaf N content under well-watered conditions and remains nearly stable under water deficit conditions (Xu and Zhou 2004; Xu et al. 2007), which indicates that watering regimes could modify changes in N levels and N allocation due to CO₂ enrichment. Additionally, under high CO₂ concentrations, nitrogen deposition may have a beneficial effect on vegetation productivity when N is not saturated. For instance, a recent report highlighted this enhancement in Japanese forest vegetation growth that served as a carbon sink based on the long-term observation of data across a large regional range, which corresponded with both elevated CO₂ and substantial N_{dep} (Fang et al. 2014).

However, under low soil nutrition, CO₂ enrichment may not maintain enhanced plant growth and community productivity, particularly in the long-term CO₂ fumigation field, due to the dilution of key nutrients, such as N and P (Conroy 1992; Xu et al. 2013b; Reich et al. 2014). For instance, simultaneous limitations by water and nitrogen eliminated the stimulated response to elevated CO₂ in a perennial grassland (Reich et al. 2014). In a subtropical forest, a decrease in the N:P ratio due to elevated CO₂ was closely linked to an increase in P concentration, which indicated that P limitation could be alleviated in the subtropical ecosystems under elevated CO₂ (Liu et al. 2013), and highlighted the interactive effects of CO₂ enrichment with the other essential elements in the ecosystems (Yuan and Chen 2015).

Moreover, as considered under the context of the multifactor-driven effects of climate, elevated CO₂ may only have minor effects on belowground bioprocesses as warming increases and drought reduces soil N turnover in ecosystems (Larsen et al. 2011). Long-term multifactorial climate change could also affect mesofaunal activities related to soil N cycling. For example, in a dry grassland ecosystem in North Zealand, Denmark, the soil biomasses and N contents from mesofauna, such as oribatid and mesostigmatic mites, could increase at elevated CO₂. However, this process may be inhibited when the ecosystems were subjected

to acute heat and drought (Vestergård et al. 2015), which suggests that the soil mesofauna may be involved in the soil N cycling processes. Antagonistic effects may appear due to the effects of warming and drought on biological processes related to aboveground and belowground N metabolisms. Together, these effects may reduce N turnover with climate change and subsequently weaken the potential regulatory response of plant growth and productivity to elevated CO₂ (Larsen et al. 2011; Penuelas et al. 2013; Xu et al. 2014) (**Fig. 2**). Additionally, wildfires induced by heat and drought—the fire activities will be further exaggerated with global warming (Oris et al. 2014), may weaken N cycling rates such as N mineralization, mainly due to limitation to vegetation productivity in natural ecosystems such as forests and grasslands (Scholze et al. 2006; Reich et al. 2001; LeDuc et al. 2013; Oris et al. 2014; Pellegrini et al. 2015). Furthermore, climate change with human infrastructure, landscape, and the hydrologic residence might together control N denitrification based on a report in the aquatic ecosystems of the United States in USA (Baron et al. 2013). Nevertheless, unclear mechanisms regarding how global climatic change with terrestrial ecosystems control N availability and turnover, such as N fixation and organic matter decomposition, remain major challenges when assessing the N cycle with Earth system models (Thomas et al. 2015).

Using the climate model ARPEGE, Salmon-Monviola et al. (2013) reported that future climate change and elevated CO₂ could influence N cycling through significantly increasing N mineralization. Bernal et al. (2012) conducted both empirical data analyses and modelling on the forest N cycle in northeastern United States. Their results showed that climate change alone could not explain the occurrence of a dramatic nitrate decline over past 46 years, but about 50–60% of the N export could be explained by the long-lasting effect of the early forest cutting. Thus, climate change in combination with human activities may exert a complex effect on the forest nitrogen cycle (Bernal et al. 2012; Ciais et al. 2013). A recent report indicated that elevated O₃ could result in greater microbial biomass N and stabilize the soil N level, which suggests that a marked interaction between the pollutants may exist (Bassin et al. 2015). Additionally, anthropogenic NO_x emission

is closely associated with other climatic change factors including O₃ formation, a decrease in CH₄, and the formation of nitrate aerosols in the atmosphere, that collectively imposes a complementary feedback on climate warming (Ciais et al. 2013), that warrants further investigation.

4.5. Nitrogen–carbon cycle

Nitrogen–carbon cycles might interact significantly at regional and global scales (Ciais et al. 2013; Huang et al. 2016). The results of a study by Zaehle (2013) using a terrestrial biosphere model, showed that anthropogenic nitrogen from 1860 have contributed 1.3 Pg N to the terrestrial biosphere, simultaneously increasing the carbon sequestration by 11.2 Pg C. On the other hand, an increase in vegetation may enhance the N fixation in ecosystems. For example, a synthesis of published data by Elbert et al. (2012), estimated that global cryptogamic ecosystems may take up around 49 Tg N and 3.9 Pg carbon globally per year, indicating that N fixation by cryptogamic covers might be another crucial factor for carbon sequestration by plants, possibly playing an important role in combating with global warming. According to a recent report by Stevens et al. (2015), anthropogenic N deposition led to pronounced great carbon sequestration by herbaceous ecosystems worldwide. These results indicated that the interaction of N and C cycle may present a negative feedback to climatic change. However, at the same time, N deposition-enhanced vegetation ecosystem may also provoke nitrogen losses, consequently increasing the greenhouse gas N₂O in the atmosphere, partly compensating for the carbon sink-enlarged climate benefit (Zaehle 2013). In addition, in a mature tropical forest of southern China, soil carbon emission can be exacerbated based on the results of a field N addition experiment possibly because of a reduction in root biomass and a suppression in microbial community under N-enriched conditions (Mo et al. 2008). However, the mechanism underlying influence of N inputs on soil C cycle remained unclear in different types of ecosystems (Ciais et al. 2013; Du et al. 2014; Sun et al. 2014; Noormets et al. 2015). As suggested by Zaehle et al. (2015), these results caution that the full potential consequences of widespread terrestrial N limitation may be overlooked using the current coupled

carbon cycle–climate models and earth system model ensemble. Nevertheless, given the expected continued increases in CO₂ levels and anthropogenic Nr formation in the future, current observations and modelling results together show that low nitrogen availability will repress carbon sinks on land in this century (Ciais et al. 2013; Zaehle et al. 2015; Huang et al. 2016). Thus, the interaction of N–C cycle and its impact and feedback on climate change is complex, still remains poorly understood.

5. Intervention strategies to improve N balance/cycling

Abnormalities in the response and feedback of the nitrogen cycle have become an important environmental concern globally because Nr emissions could increase with adverse climate change and rapid socio-economic development (Galloway et al. 2008; Sutton et al. 2012; Liu et al. 2013; Suddick et al. 2013). More importantly, however, mitigation of excess Nr could both repress N₂O emissions and helpfully alleviate CO₂, CH₄, ozone effects in complex ways (Pinder et al. 2012; Ciais et al. 2013; Suddick et al. 2013). More efficient intervention pathways and methods should be found to mitigate the negative impacts of these abnormalities. Galloway et al. (2008) indicated four intervention pathways for alleviating excessive Nr emissions. First, the Nr emissions from fossil-fuel combustion may decrease by 72% (from 25 Tg N a⁻¹ to 7 Tg N a⁻¹) when the maximum feasible reduction pathways are chosen in controlling NO_x emissions from fossil-fuel combustion using reasonable currently available technologies (Galloway et al. 2008). Second, an increase in the nitrogen-uptake efficiency of crops by selecting species (Lu et al. 2014; Li et al. 2015) may reduce the Nr production of c. 15 Tg N a⁻¹. Third, the same reduction above may occur when appropriate animal management practices are applied. Fourth, 5 Tg N of Nr may be transformed into N₂ by using sewage treatment systems in cities. Together, approximately 28% of the total Nr produced in 2005 (187 Tg N a⁻¹) could be reduced by using these four intervention pathways (Galloway et al. 2008). Furthermore, more updated strategies and advanced methods are available for addressing urgent N management issues in

agricultural and natural ecosystems. These strategies mainly include the following: (1) Finding a better N application rate to solve the excessive use of N in intensive agricultural ecosystems for both environmental and farmer's profit (Ju et al. 2009; Wang et al. 2011). (2) Selecting appropriate cultivars with higher NUE, higher productive capacities, and better grain quality (Lu et al. 2014). (3) Using advanced field cultivation management that can substantially enhance sustainable N use and mitigate N contamination due to overuse. For example, returning plant residues to the soil to promote soil N turnover (Chen et al. 2014a); the addition of moderate N concentrations and the use of deep sub-soiling practices during fallow periods to improve the soil water status and grain quality (e.g., high protein concentration in grain) (Sun et al. 2014); the use of precision agriculture techniques, such as precision planting technologies, to attain higher yields when using moderate N fertilizer application rates in wheat fields (Xu et al. 2013c); the use of conservation tillage (Mueller et al. 2012), optimization of N, P and K fertilizer application ratios (Mueller et al. 2012; Sun and Huang 2012), application of slow release fertilizer (e.g. Shaviv and Mikkelsen 1993; Ni et al. 2011); and optimization of irrigation regimes to reduce inorganic N movement, including the movement of nitrate into deep soil layers, to mitigate N contamination in the most intensive agricultural ecosystems (Wang et al. 2008) where N_{dep} and the overuse of N fertilizers are substantial and common (Ju et al. 2009; Liu et al. 2013). (4) Extending more efficient cropping systems with low N use and decreased N pollution. For example, an agro-ecosystem that uses organic cropping systems with catch crops to decrease diffuse nitrogen pollution in some areas (Masilionytė et al. 2014); wheat/maize systems with lower N loss rates relative to rice/wheat systems (Ju et al. 2009); and an efficient integrated soil-crop management system for achieving sustainable intensification (Cui et al. 2014; Chen et al. 2014a). (5) Currently, biochemistry and genetic studies are alternative solutions for improving BNF in symbiotic systems, such as bean rhizobia, because they can employ biochemical technologies under climatic change conditions, such as elevated CO_2 and water deficits (Fowler et al. 2013; Coletto et al. 2014). These solutions may lead to the optimization of nitrogen fertilizer

application and subsequently maintain a positive N balance (Suddick et al. 2013). Finally, we should make great efforts to employ a feasible policy aiming at rising NUE to improve the nitrogen balance from regional to global scales. For instance, calculations of a nitrogen footprint would help one to track his contribution in the nitrogen balance of an ecosystem (N-Print 2016). Additionally, the creation of a network of experts from disciplines related to N dynamics and with the media can help us improve N management at regional and global scales such as the Research Coordination Network (RCN) or Reactive Nitrogen of North American Nitrogen Center (RCN 2016). Moreover, the use of some comprehensive environmental management methods, such as life cycle assessment (LCA), could help deal with N surplus issues in the ecosystem (Meier et al. 2015).

6. Challenging issues

There are several key issues that remain to be resolved including: (1) to explore underlying mechanisms of biochemical processes in N cycle driven by multiple climatic change factors such as warming, drought, and elevated CO₂; (2) to assess the different contributions across nations or regions and integrate their N deposition rates globally; (3) to integrate, estimate and predict the changes in natural ecosystem structures and functions that face continually increasing anthropogenic N deposition at different spatial-temporal scales (e.g., from local, regional to global scales, Stevens et al. 2015) using both integrated experimental data and modelling methods; (4) to elucidate the associations of biodiversity in a given natural ecosystem with the abnormal N cycle dynamics induced by climatic change (Cardinale 2011; McDonnell et al. 2014); (5) to deal with wildfire impacts on the global N cycle and sustaining long-term vegetation productivity by altering available N under ongoing climate warming with the increases in the frequency and strength of the ecological disturbances like fire (Scholze et al. 2006; LeDuc et al. 2013; Pellegrini et al. 2015); (6) to measure and classify the extent to which environmental contamination is derived from N-rich ecosystems,

and to assess the risks; (7) to find better intervention strategies to deal with N balance/cycling in the future (see above); (8) to compare processes of the N cycle between human managed (e.g. crop land) and natural ecosystems. Finally, how the N cycle interacts with biogeochemical cycle of other vital elements including C, P, and S remains elusive, particularly at regional and global scales, requiring to be investigated in the future. Thus, these crucial knowledge gaps remain to be filled urgently.

7. Conclusions

In most regions throughout the world, particularly in regions within developing nations, the environment is experiencing severe air pollution, which is partially caused by anthropogenic Nr emissions (Vitousek et al. 1997; Galloway et al. 2008; Liu et al. 2013, 2016). Consequently, the Nr level predominately created by human activities will continue to increase with climate change and rapid socio-economic development, especially in developing countries. Thus, Nr pollution is becoming a severe environmental issue (Liu et al. 2013; Bassin et al. 2015). The anthropogenic acidification primarily induced by N emissions has resulted in an abnormal balance in the natural biogeochemical cycles of terrestrial ecosystems, which has resulted in severe ecological management and agricultural sustainability problems (Hoegh-Guldberg 2007; Bechmann et al. 2014). Additionally, excessive nitrogen inputs into the land represent another major cause of water and soil pollution worldwide, further exaggerating the vulnerability of ecosystems, including rapid losses in biodiversity and severe degradation of ecosystem function (Goulding et al. 1998; Ju et al. 2009; Canfield et al. 2010; Bassin et al. 2015). Particularly, climatic change may substantially alter the N balance and cycle linking the geosphere, biosphere and atmosphere, and produce considerable challenges and raise new concerns that threaten environmental security. Overall, nitrogen is a critical element that primarily controls species composition, functions, and biological dynamics of many terrestrial and aquatic ecosystems (Vitousek et al. 1997). Thus, stabilizing nitrogen levels within an appropriate range in terrestrial ecosystems

and watersheds by mitigation pathways for the N management is one priority of ecological and environmental research, and management policies and practices (Masilionytė et al. 2014; Bechmann et al. 2014; Meier et al. 2015; Thomas et al. 2015).

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Legends of the figures:

Fig. 1. A modified conceptual model of the nitrogen biogeochemical cycle between atmosphere and terrestrial ecosystem – input, output, process, dynamics, and management. Atmospheric nitrogen (N) is transformed by lightning process (1), biological N₂ fixation (2), N deposition (3), Haber-Bosch process (4), and through application N fertilizer (5), finally imported into terrestrial and aquatic ecosystems; in plants, N converts from NO₃⁻ into NH₄⁺ by nitrate reductase (6) and nitrite reductase (7) involvements, and continual conversions between crops, animal and people (8). In soil, N in organic matter is first mineralized to inorganic N forms such as NH₄⁺ and NO₃⁻ (9-11), in which nitrification occurs with microbial involvements; some N components can be fixed in soil as a immobilized form(13). Thereafter, available inorganic N is absorbed by plant roots, again entering plant tissues (12). N emission paths mainly include denitrification in soil (13), Anammox reaction (14, Meng 2012), gaseous N emission processes (15), and fossil fuel consumption (16). N fluxes between atmosphere and terrestrial ecosystem are indicated by the red (output) and green (input) data (Tg N a⁻¹) (Lam *et al.* 1996; Vitousek *et al.* 1997; Aber *et al.* 1998; Galloway *et al.* 2008; Fowler *et al.* 2013; Chen *et al.* 2014b).

Fig. 2. A schematic representation of the major responses of nitrogen (N) bioprocesses in terrestrial ecosystems due to climate change (**a**, elevated CO₂; **b**, drought with heat). Notes: (**a**) elevated CO₂ concentrations affect plant biological processes (1), including decreased leaf N content (2), increased use efficiency (NUE) and photosynthetic N use efficiency (PNUE) (3), progressive N limitations to plants (PNL), and an decrease in net primary productivity (NPP) (e.g., Davey *et al.* 1999; Luo *et al.* 2004; Xu *et al.* 2007; Bloom *et al.* 2012; Gutiérrez *et al.* 2013). In soils under high CO₂ concentrations, the available N content decreases (4) while the soil organic matter (SOM) content increases (5), which results in more ammonia production (6, Groenigen 2014; Rütting and Andresen 2015). Furthermore, elevated CO₂ would enhance plant root systems (e.g., Xu *et al.* 2007) and potentially accelerate soil mineralization (7). However, the effects on soil microbiota and soil fauna depend on ecosystems and species (O'Neill 1995; Hu *et al.* 2001; Xu *et al.* 2013a), which result in complicated effects on N process underground (8, 9; Rütting and Andresen 2015; Vestergård *et al.* 2015). (**b**) A combination of drought and heat can affect plant biological processes (1), weaken N anabolism and promote N catabolism (2, 3: e.g., Xu and Zhou 2006a), limiting plant growth and NPP. In the soil, the two combined stresses may decrease, remain constant, or increase the soil available N level (4, Xu and Yu 2005; Xu *et al.* 2007; Yuan *et al.* 2006; Gestel *et al.* 2011; Rustad *et al.* 2001), depending

1047 on the severity of heating (Gestel et al. 2011; Rustad et al. 2001). However, drought may result in lower
1048 SOM contents (5) and gross N turnover rates (including the ammonification process) (6, Chen et al. 2011b;
1049 Larsen et al. 2011), potentially due to limited root growth due to drought (7, Xu et al. 2007). Finally,
1050 microbiota activity, including the N₂ fixation bioprocess, may be inhibited by drought (8, Vadez et al. 2000;
1051 Coletto et al. 2014). The activity of soil fauna may be constrained by negative climatic change factors, such
1052 as drought and heat, subsequently, the soil N process was negatively affected (9, Vestergård et al. 2015).
1053 Elevated CO₂, drought and heat may interact (10, 11). For example, drought with heat can limit the
1054 enhancement of plant biological processes due to CO₂ enrichment (Larsen et al. 2011; Penuelas et al. 2013;
1055 Xu et al. 2014). The soil microbial biomass N pool and litter C:N ratio could increase under elevated CO₂ but
1056 decrease when subjected to heat and drought (Vestergård et al. 2015), whereas N:P has opposite responses to
1057 elevated CO₂, heat and drought (11, Yuan and Chen 2015).

Draft

1058 **Figure 1**

1059

1060 **Figure 2**

1061