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Original Articles

The antioxidation-related functional structure of plant communities: Understanding antioxidation at the plant community level

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ABSTRACT

In the case of ecological stresses, reactive oxygen species (ROS) can be overproduced in plant cells, leading to lipid peroxidation that causes damage or death to cells. To prevent damage, plant tissues contain several antioxidants that scavenge ROS. However, antioxidation at the plant community level still remains unknown and may provide an insight into ecosystem functioning regarding stress resistance. To understand the property, we established the antioxidation-related functional structure based on the concept of the functional structure and the activities of superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), reduced glutathione (GSH), carotenoid (Car) and proline (Pro) and the relative abundance of component species in natural plant communities on the Chinese hilly-gullied Loess Plateau. An information-theoretic (I-T) approach was used to infer the effects of antioxidation-related functional components and stresses that we investigated on lipid peroxidation at the plant community level quantified by the community-weighted mean of malondialdehyde (MDA). We found that the induction of lipid peroxidation was more closely associated with a soil available nitrogen deficiency than it was with an available phosphorus deficiency. However, the inducing effect of soil available nitrogen was finite. The prevention of lipid peroxidation was more closely associated with the community-weighted means of GSH and Pro (CWM GSH and CWM Pro) than it was with other antioxidation-related functional components. However, the efficiency of CWM Pro was quite low; CWM GSH exhibited inefficiency. In addition, antioxidation-related functional components were affected by neither soil available nitrogen nor available phosphorus. Furthermore, by estimating the relative weights of the antioxidants and considering the feasibility of community assemblages, we proposed that *Stipa grandis*, *Leymus secalinus*, *Stipa bungeana*, *Phragmites australis*, *Potentilla tanacetifolia*, *Artemisia gmelinii*, *Artemisia scoparia*, *Heteropappus altaicus* and *Syringa oblata* could be utilized in community assemblages to achieve an antioxidation-functional target. Additionally, appropriate phosphorus application for *A. gmelinii* and *H. altaicus* might contribute to maintaining their antioxidation.

1. Introduction

There is often disequilibrium between pro-oxidation and antioxidation in plants, which is imposed by the overproduction of reactive oxygen species (ROS) and can cause lipid peroxidation that poses disturbance to cellular metabolism, individual growth and even ecosystem functioning (Blokhina et al., 2003; Kaur et al., 2014). To prevent the disturbance, plants contain several antioxidants that scavenge ROS. Ecologically, the overproduction of ROS can be provoked by numerous abiotic and biotic stresses, such as drought, salinity, infertility, radiation, extreme temperatures, pathogen infestation, or other regimes (De Gara et al., 2003; Huang et al., 2004; Anjum et al., 2015). At present, a variety of stresses and stress interactions have been simulated to study the production of ROS, induction of lipid peroxidation, responses of antioxidants and expression of relevant genes in different plants (Keles and Oncel, 2002; Reddy et al., 2004; Herbinger et al., 2005; Shi et al., 2010;

Abbreviations: AN, available nitrogen; AP, available phosphorus; SM, soil moisture; ND, niche differentiation; D, dominance; NB, niche breadth; MNO, mean niche overlap; I-T, information-theoretic; MMI, multimodel inference.

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Zhang et al., 2016). However, in natural ecosystems, especially degraded ones, there are ecological stresses that are too complicated to be stimulated. In addition, the research in this field has remained at or below the level of plant individuals (De Gara et al., 2003; Myouga et al., 2008; Cartes et al., 2012). However, studying antioxidation at the plant community level should be of equal importance from the perspective of plant sociology and ecosystem functioning.

The concept of the functional structure of communities has been proposed to provide multidimensional insights into ecosystem functioning (Mouillot et al., 2011; de Bello et al., 2013). The functional structure is composed of functional identity and functional diversity. The former component is often quantified by the community-weighted mean (CWM) that represents the trait value in a community weighted by species relative abundance (Garnier et al., 2004). Functional diversity is increasingly identified as an important driver of ecosystem functioning (Hooper et al., 2005). We often quantify it based on three metrics: functional richness (FRic), reflecting the volume of functional space occupied by a community; functional divergence (FDiv), reflecting the divergence of abundance distribution in this space; and functional evenness (FEve), reflecting the regularity of abundance distribution in this space (Mason et al., 2005). At present, various aspects of ecosystem functioning—such as water use, light interception, biomass dynamics, litter decomposition, soil carbon and nitrogen storage and reduced soil erosion—have been closely associated with these functional components of plant communities based on relevant functional traits (Garnier et al., 2004; Mokany et al., 2008; Zhu et al., 2015). For example, the reduction of soil erosion could be explained by FDiv integrated by relevant root and leaf traits, CWM root diameter and CWM root tensile strength (Zhu et al., 2015). Thus, establishing the antioxidation-related functional structure of plant communities can improve the understanding of antioxidation at the plant community level and may supplement the knowledge of ecosystem functioning regarding stress resistance.

Destruction of vegetation on the Chinese Loess Plateau because of long-term human activities has resulted in severe soil erosion and ecological degradation (Zhao et al., 2015). To address this issue, the improvement of vegetation cover is critical (Zucca et al., 2015). For example, the “Grain for Green” program was initiated by Chinese government in 1999. In particular, afforestation was considered as a key technique in the past fifteen years (Li et al., 2008). However, we ignored the climatic, pedologic, hydrologic and topographic conditions that made a site unsuitable for afforestation on the one hand (Piao et al., 2010; Cao et al., 2011), and failed by introducing inappropriate species that caused more deteriorative outcomes in terms of increased soil erosion, exacerbated water shortages and deep soil desiccation on the other hand (Cao et al., 2009; Cao, 2011). Excessive afforestation and arbitrary species introduction should thus be avoided, and the use of herbaceous and native plants is wise because of their long-term adaptability (Cao et al., 2011; Jiang et al., 2013). Therefore, a prerequisite for present vegetation restoration is to study different aspects of ecosystem functioning based on plant functional traits and the functional structure of natural plant communities, especially grassland communities. According to the relationship between functional components and ecosystem functioning, functional species can be selected from the natural plant species pool to assemble functional communities, enabling us to apply these trait-based studies to practical vegetation restoration. However, the functioning of ecosystems on the Loess Plateau has not been studied from very many aspects (Zhu et al., 2015). Ecological stresses on the Loess plateau are characterized by drought, infertility, radiation, and soil erosion, all of which are often definitive control of ecosystem functioning (Li et al., 2008; Gelaw et al., 2015; de Oliveira et al., 2015; Roa-Fuentes et al., 2015; Liu et al., 2016). It should be noted that antioxidation, reflecting long-term resistance to complicated ecological stresses, is necessary to be utilized in community assemblages to achieve an antioxidation-functional target while restoring the functioning of degraded ecosystems on the Loess Plateau.

Therefore, the objectives of our study were 1) to investigate, at the level of natural plant communities, how strongly lipid peroxidation was induced by stresses, how efficiently antioxidation-related functional components prevented lipid peroxidation and how negatively antioxidation-related functional components were affected by stresses; 2) to identify antioxidation-functional species and then select feasible species for community assemblages.

2. Materials and methods

2.1. Study area

This study was conducted in the Chenjiagua (36°49′–36°50′, 109°15′–109°19′), Wangjiagou (36°50′–36°52′, 109°10–109°11′) and Shiziwan watersheds (37°8′–37°10′, 109°3′–109°5′), located in the hilly-gullied region of the Loess Plateau in China. Within the studied watersheds, the climate is semi-arid characterized by low annual precipitation (450–490 mm) as well as a low annual mean temperature (8–9 °C) (Li et al., 2008). According to our watershed-wide investigation, the soils are mainly silt loams (approximately 23% sand, 55% silt and 22% clay; mass percent), Calcaric Cambisols (pH values are 7.85–8.29), less compact (bulk densities are 1.11–1.32 g/cm^3) and non-saline (soluble salt contents are less than 1 g/kg). The study area is distributed in the transition zone between forest and grassland. Natural shrubs are usually sparse, including *Syringa oblata*, *Sophora davidii*, *Periploca sepium*, and *Buddleja alternifolia*, among others. Natural subshrubs and perennial herbs are dominant in this area and are mainly mes-xerophytes and xerophytes, including *Artemisia gmelinii*, *Artemisia giraldii*, *Lespedeza daurica*, *Bothriochloa ischaemum*, and *Stipa bungeana*, among others.

2.2. Vegetation survey

Considering the fragmented landscape and common types of natural vegetation within the study area, a vegetation survey was conducted on sixteen plots (10 × 10 m) scattered on different hill-slopes that had similar altitudes, aspects, angles and species occurrences, but dissimilar species abundances (Table 1). We focused on sunny aspects for maximizing the identification of abiotic and biotic stresses and eliminating the differences in solar radiation and soil temperature. In each plot, we marked five transects (2 × 10 m) along the slope: three spaced transects were used to record vegetation information and sample plant biomass; the remaining two transects were used for soil and plant sampling. In detail, all plant species present in each transect were identified, the canopy height at maturity per species was measured, and the proportional biomass per species was sampled. The mean values of three transects were used to represent the quantitative character of each plot. Sixteen communities were defined based on the simplified importance value expressed by the species relative biomass (He et al., 2004).

2.3. Sampling and assays for antioxidants and malondialdehyde (MDA)

The chloroplast and mitochondrion are the main sites producing ROS. Thus, lipid peroxidation is likely to be induced in these two organelles. Hydroxyl radicals ($^\bullet OH$) can induce lipid peroxidation directly. Superoxide anion free radicals ($O_2{}^{\bullet -}$), hydrogen peroxide (H_2O_2) and singlet oxygen ($^1O_2$) can also induce lipid peroxidation by transforming into $^\bullet OH$. Superoxide dismutase (SOD; EC 1.15.1.1) can catalyze $O_2{}^{\bullet -}$ produced in mitochondria, chloroplasts