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OPINION PAPER

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Belowground plant traits and their ecosystem functions along aridity gradients in grasslands

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Abstract Ecosystem responses to environmental change are usually studied solely using aboveground (usually leaf) traits. However, belowground plant traits, such as fine roots and coarse belowground organs, likely play a crucial role in ecosystem response, especially under aridifcation. We conducted a literature survey on belowground plant traits along aridity gradients in temperate grasslands to propose which effect traits might be connected with abrupt vegetation changes that would occur with aridification due to environmental change. With increasing aridity, seasonal regeneration decreasingly relies on recruitment from the belowground bud bank and increasingly relies on regeneration from seeds. This leads to greater inter-annual variability in biomass production. Other belowground traits, such as bud bearing organs and fine root distribution in the soil, also shifts along the aridity gradient. As aridifcation begins, we propose that plants would become more conservative in their belowground traits producing lower amounts of belowground litter. Increasing aridifcation would lead to the loss of rhizomatous plants from the community and a prevalence of deep rooting plants leading to changes in soil resource utilization and increasing susceptibility to soil erosion. Under extreme aridification, perennial plants, except those with bulbs, would be lost from the community and replaced by annuals which produce low amounts of litter and use only ephemeral water resources in the upper soil layers. Belowground plant traits, such as belowground clonal growth organs, bud banks, and fine root distributions, may provide a more mechanistic understanding behind shifts in ecosystem functioning due to environmental change.

Keywords Aridity · Belowground plant organs · Ecosystem functions · Fine roots · Grasslands · Rhizomes

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Introduction

Plant traits are characteristics that affect not only plant fitness (Violle et al. 2007) but they may also affect ecosystem functions (response versus effect traits; Lavorel and Garnier 2002). For example, thin, nitrogen-rich leaves photosynthesize effectively and are favorable for a plant growing in a surplus of water and nutrients. At the same time, thin nitrogen-rich leaves are short-lived and easily decompose, thereby speeding up nutrient cycles in an ecosystem (Lavorel and Garnier 2002). While aboveground traits (e.g. leaf traits) are extensively studied, our understanding of belowground plant traits, such as those of roots, rhizomes, tubers or bulbs, lags behind (Freschet and Roumet 2017). Therefore we still have limited knowledge not only about the response of traits on belowground organs to environmental gradients (e.g., Klimešová et al. 2016; Weemstra et al. 2021) but especially about their possible effect on ecosystem properties and services (Jackson et al. 2000; Cornelissen et al. 2014).

Belowground plant parts encompass fine roots and also bud-bearing and storage organs such as coarse roots, rhizomes, bulbs and tubers. These organs provide plants with key functions concerning their response to the environment such as acquiring water and nutrients, storing carbohydrates for growth and regeneration, enabling clonal multiplication and lateral spread, and providing belowground connections between fine roots and aboveground parts as well as between neighboring ramets (Klimešová et al. 2018a). The same organs and their traits affect ecosystem functions. The horizontal growth of rhizomes versus the vertical growth of coarse roots determines the distribution of fine roots in the soil and subsequently the system's resistance to soil erosion (Yu et al. 2008; Vannoppen et al. 2017) and the portion of the soil profile that is accessible for nutrient and water uptake (Bayala and Prieto 2020; Querejeta et al. 2021; Klimešová and Herben 2023). The connection of individual shoots into clones by the rhizome system allows homogenization of the environment by redistribution of resources and signals (Stuefer et al. 1996). Rhizodeposition and root and rhizome litter affect microbial communities and nutrient cycling (Kaštovská et al. 2015).

Our current understanding of how belowground plant traits affect ecosystem functions is based mainly on case studies examining individual species or processes and a systematic exploration at the ecosystem level is missing. Nevertheless, we think that increased consideration of belowground plant organ traits would improve our mechanistic understanding of changes in ecosystem functions due to land use or global change. To outline a framework for systematic exploration of effect traits of belowground plant organs, we present an example focusing on aridification in temperate grasslands. Due to aridification resulting from climate change, dryland ecosystems worldwide are experiencing abrupt changes in function leading to loss of biodiversity, reduction of primary productivity, and soil degradation (Berdugo et al. 2020). Recently, the possible mechanisms behind the collapse of dryland ecosystem functions along an aridity gradient were proposed by Berdugo et al. (2022) and focused on soil biology, rooting depth and aboveground plant characteristics, such as spatial distribution of vegetation, leaf traits, and aboveground productivity (Fig. 1). As the cited work aspires to be a basis for developing future research and monitoring strategies as aridification intensifies, we see an opportunity to incorporate belowground plant parts and their functions into the conceptual model to fully understand the mechanisms driving abrupt changes along aridity gradients and provide more robust hypotheses for testing mechanisms underlying aridity thresholds.

First, we aim to review available literature about belowground plant traits along aridity gradients that align with the three parameters of biotic processes mentioned by Berdugo et al. (2022): decreasing biomass production, loss of perennial plants and the dominance of annuals, and changing root structure and decrease in leaf nitrogen content. Then, we will propose how traits of belowground organs may be indicative of aridification in each of three aridity thresholds by Berdugo et al. (2022): Vegetation decline phase, Soil disruption phase, and Systemic breakdown phase.

Biotic processes along an aridity gradient

Decreasing biomass production

Grasslands represent a majority of global drylands where herbs dominate (Maestre et al. 2021). Herbaceous plants maintain the pool of dormant meristems and carbohydrate storage enabling regrowth after an unfavorable season or following a disturbance. In such herb-dominated systems, the pool of dormant meristems (bud bank sensu Harper 1977) is mainly located very close to the soil surface or belowground where it is protected by litter, snow, or soil and remains out of reach of most ecosystem disturbances, such as grazing and fire (Clarke et al. 2013; Ott et al. 2019; Lubbe et al. 2021). The bud bank provides populations with

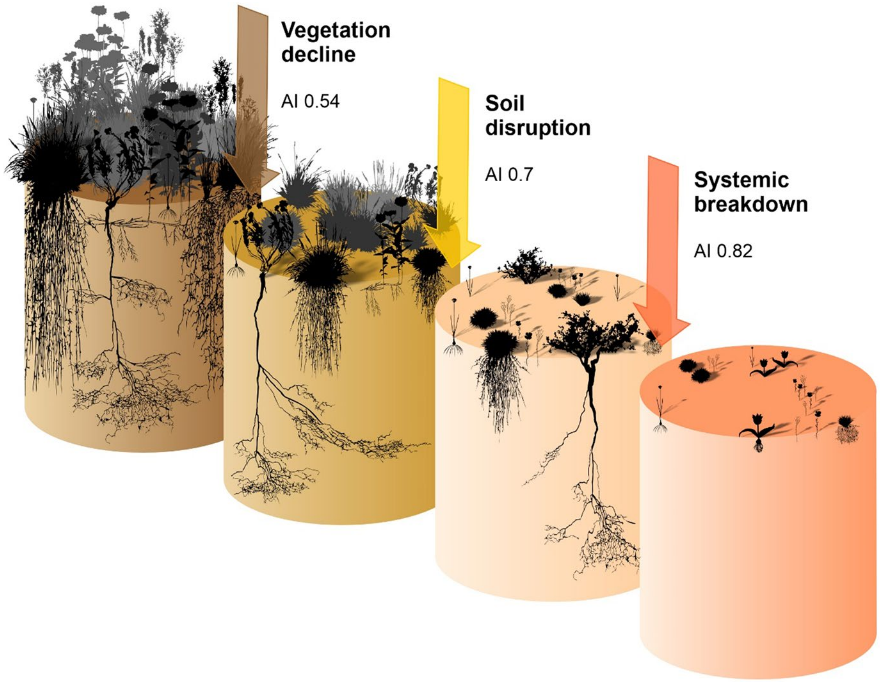

Fig. 1 Abrupt changes in vegetation composition and cover along an aridity gradient in grasslands. Thresholds are marked by arrows: According to Berdugo et al. 2022 the phases are described as follows: Vegetation decline phase (aridity index cca 0.54) is characterized by decreasing biomass production and increased drought adaptation; Soil disruption phase (aridity index cca 0.7) is characterized by changing root structure and decrease in leaf nitrogen content; Systemic breakdown phase (aridity index cca 0.82) is characterized by loss of perennial plants, dominance of annuals and high danger of soil erosion. The phases are illustrated by diagrams showing distribution of aboveground and belowground biomass and growth forms in grasslands along aridity gradient described in the paper. Inspiration for depicting belowground organs was taken from Weaver (1919)

a long-term buffer to environmental intra- and inter-annual climatic perturbations and ensures steady biomass production thanks to an established root system accompanied by carbohydrate storage and lower dependence on environmental triggering factors than germination from the seed bank (Ott and Hartnett 2012; Ott et al. 2019). With decreasing precipitation across herbaceous ecosystems, biomass production decreases while year-to-year variability increases (Knapp and Smith 2001; Berdugo et al. 2020). This was proposed to result in more vegetation cover and a larger pool of reserve meristems along the wetter portion of the gradient occupied by grasslands in contrast to deserts at the dry end of the gradient (Knapp and Smith 2001). The biomass of a herbaceous community and its variability over years is therfore expected to be closely related to the density of bud bank.

The hypothesis that bud bank density in grasslands decreases with aridity was tested in large grassland systems on two continents by looking at bud bank density along mesic to arid grassland gradients in North American Prairie and Inner Mongolian Steppe (Dalgleish and Hartnett 2006; Qian et al. 2017). The studied gradients spanned aridity from an Aridity Index (AI) of 0.36 to 0.91 and crossed all 3 AI thresholds (0.54, 0.70, and 0.80) recognized by Berdugo et al. (2020, 2022). On both North American and Asian continents, bud density ranged from hundreds to thousands per square meter (Fig. 2). The North American bud densities sharply declined after Berdugo et al.'s first proposed threshold (Fig. 2A), while the Inner Mongolian bud densities sharply declined after the second proposed threshold (Fig. 2B). Differences between continents could be due to differences in species composition and/or grazing pressure (higher in Inner Mongolia). Bud bank and bud bearing organs filled with carbohydrates might be considered as important

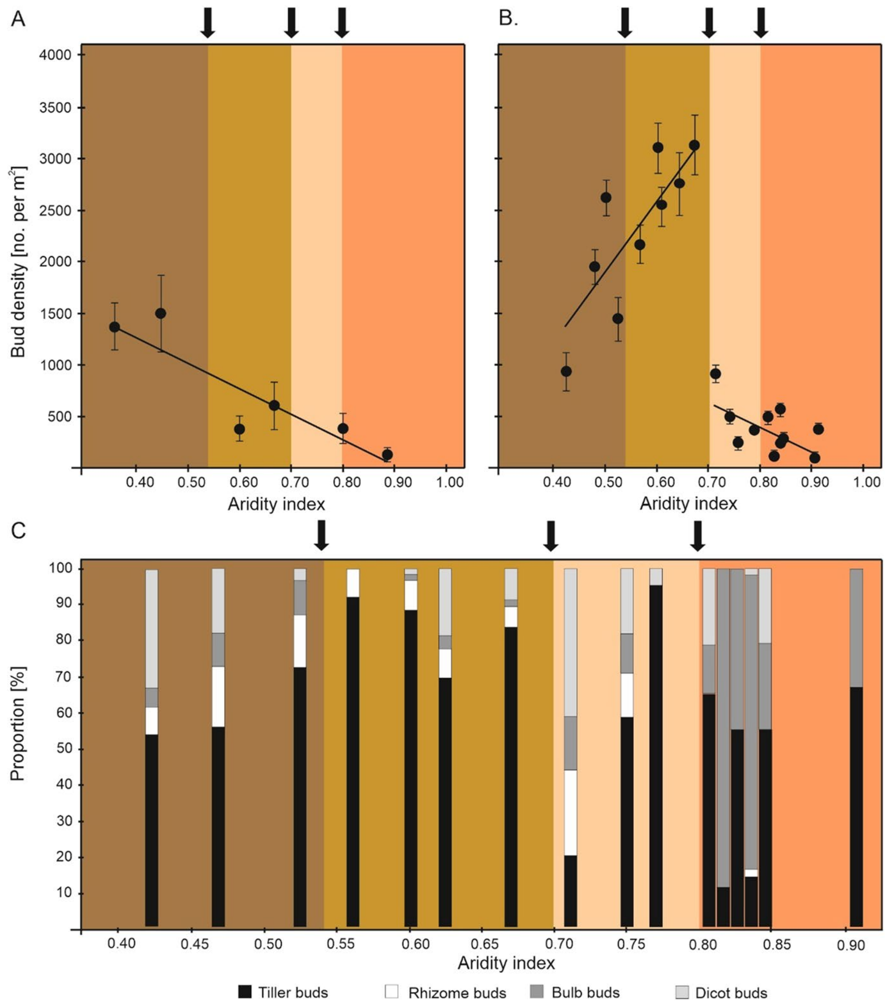

Fig. 2 Bud bank density (**A**, **B**) and relative representation of buds according to bud-bearing organs (**C**) along aridity gradients in North American Prairies (**A**) and Inner Mongolian steppes (**B**, **C**). Color background and arrows denote aridity thresholds recognized by Berdugo et al. (2022). Data from Dalgleish and Hartnett (2006) and University of Montana Numerical Terradynamic Simulation Group (2015) (**A**) and Qian et al. (2017) (**B**, **C**)

characteristics enabling resistance of dryland community to perturbations and ensuring steady biomass production.

The composition of bud-bearing belowground organs also differed along an aridity gradient (studied only by Qian et al. 2017 in Inner Mongolia) (Fig. 2C). The majority of buds were located on grass tiller bases in tussock grasses along the whole gradient. Grass rhizome buds and dicot buds were absent above the third aridity threshold, while bulbs dominated the most arid sites (Fig. 1C). Bud protection by the grass stem leaf sheaths at the base of the tiller and by storage leaves in bulbous species becomes more important with increasing aridity as both growth forms occurred at the highest aridity sites where annual plants prevailed. The absence of rhizomes at the most arid sites was likely caused by a lack of resources and coarse soil limiting rhizome growth. This supports Berdugo's view of systemic breakdown as rhizomes are critical for preventing soil erosion (Yu et al. 2008).

Loss of perennial plants, dominance of annuals

The bud bank is typical for perennial herbs in temperate grasslands and is the source of the majority of aboveground shoots rather than the seed bank (Benson and Hartnett 2006; Vítová et al. 2017). Vegetative regeneration from the bud bank prevails over generative regeneration from the seed bank in grasslands because, under competition with neighboring vegetation, it is easier to rebuild an individual supported by a bud-bearing organ with storage carbohydrates and an established root system rather than establish a new individuum from a small seed. Nevertheless, with increasing aridity, the bud bank is decreasing in density and perennial plants that are not able to support their bud-bearing organs anymore are replaced by annuals relying on a seed bank and generative regeneration (Qian et al. 2017). Regrowth from the seed bank, however, is much more dependent on triggering factors for germination than regrowth from the bud bank. If the signals do not occur, germination is poor and biomass production is low.

Typical disturbances of arid grasslands are fire and grazing – both disturbance types support germination from the seed bank by creating gaps in the vegetation (Benson et al. 2004). Overgrazing could initially increase bud banks at intermediate aridities as plants may mitigate the dual stressors by increasing bud production. At higher aridities, overgazing could accelerate grassland degradation by causing shifts from perennial grasses to annual species (Jiang et al. 2006). The dramatic shift in belowground bud bank densities observed at AI = 0.70 in Inner Mongolia (Fig. 2B) could demonstrate how the interaction of aridity and overgrazing creates an abrupt systemic breakdown. Low productivity, low plant cover in the growing season and bare soil in winter are responsible for wind erosion vulnerability in the most arid sites.

Changing root structure and decrease in leaf nitrogen content

Decreasing productivity and lower leaf nitrogen content along the aridity gradient results in decreasing input of litter quantity and quality into the soil (Berdugo et al. 2022). The decline in litter quality is due to the more conservative growth of plants in arid conditions as plants invest into long-lived plant organs and reutilize nutrients when those organs senesce rather than investing in short-lived organs. This strategy is not limited to leaves but also to belowground organs, e.g. roots and rhizomes, which also contribute to litter inputs following their death. As conservation of acquired resources becomes the dominant strategy with increasing aridity, short-lived belowground structures are lost from the community. This mainly concerns rhizomatous plants that produce new rhizome increments with new roots each year and, at the same time, lose old increments bearing old roots (Klimešová and Herben 2022). This type of growth is connected with the relatively shallow rooting of rhizomatous plants (Klimešová and Herben 2023), which is also not an advantageous plant trait under increasing drought. First, with increasing aridity, only rhizomatous plants with persistent and slowly growing rhizomes prevail (Jónsdóttir and Watson 1997; Klimeš 2008), later majority of rhizomatous plants are lost from the community (Qian et al. 2017). When a community loses its rhizomatous plants, it is losing a growth form that typically occupies a large horizontal spatial extent and shares resources within its clones promoting community homogeneity (Klimešová et al. 2018b).

Aridity thresholds in grasslands

On the base of available literature reviewed in the previous section, we can outline which belowground traits are indicative of the aridity gradient and may be used for understanding the mechanism behind aridification or for monitoring.

The vegetation decline phase

In this phase (Tables 1 and 2; Fig. 1), we see an increase in the proportion of long-lived bud-bearing organs and an associated increase in bud number and bud longevity (Fig. 2B). Increased belowground bud and organ longevity leads to a decreased input of belowground litter into the soil. Belowground plant traits shift (e.g., more long-lived plant parts with lower lateral spread) and parallel the change in aboveground plant traits (e.g., increasing leaf dry matter content, decreasing leaf nitrogen content) to more conservative strategies (Berdugo et al. 2022). Fine roots are still abundant.

The soil disruption phase

The soil disruption phase (Tables 1 and 2; Fig. 1) is connected with a loss of rhizomatous species and their substitution by short-lived plants (bulbous perennials and annuals) and by perennials with deep root systems. Loss of rhizomatous species causes a decline in water and nutrient redistribution across the community via the rhizome network and also increases vulnerability to soil erosion. A change toward deep rooting plants and shrubs with an integrated modular hydraulic system also occurs at this stage (Schenk et al. 2008). The transition from rhizomatous to non-rhizomatous vegetation

Table 1 Ecosystem functions and relevant effect traits of individual growth forms occurring along an aridity gradient in grasslands

	Source of annual aboveground production/Regeneration	Redistribution of water; Water niche	Erosion protection	Carbon cycle (litter addition to the soil during plant lifespan)	Threshold in abundance
Rhizomatous grasses	Large belowground bud bank[1,2] buds are not protected; poor seed bank	Shallow rooting and redistribution of water in horizontal dimension[3,4,5,6]	High: substrate is kept by network of rhizomes[7]	Large: old parts of rhizomes together with their roots are dying off and new are produced [8,9]	Soil Disruption (large decrease)
Tussock grasses	Small belowground bud bank[2]; buds protected by leaf bases; poor seed bank [10]	Intermediately deep rooting	Intermediate: substrate is kept by perennial root system	Intermediate: dependent on lifespan of roots	Systemic Breakdown (large decrease)
Deep rooting and root sprouting forbs	Small belowground bud bank[2,6]; buds are not protected; seed bank [10]	Deep rooting and redistribution of water in vertical dimension [11]	Intermediate: substrate is kept by perennial root system	Small: dependent on lifespan of fine roots	Soil Disruption (large decrease)
Bulbous perennial herbs	Small belowground bud bank[2,12]; buds protected by leaf bases; poor seed bank	Shallow rooting and reliance on short seasonal water availability	None: small and short-lived root system	Intermediate: dependent on lifespan of roots	Occur along the whole gradient
Shrubs	Aboveground bud bank or bud bank on roots; seed bank	Change from integrated to modular hydraulic system towards dry conditions; deep rooting and redistribution of water in vertical dimension [11,13,14]	Intermediate: substrate is kept by perennial root system	Small: dependent on lifespan of fine roots	Soil Disruption (increases)
Annual herbs	No bud bank[12]; large seed bank	Shallow rooting and reliance on short seasonal water availability[6]	None in winter and small in the growing season: small and short-lived root system	None	Systemic Breakdown (large increase)

References in the Table: 1 – Qian et al. (2022); 2 – Herben and Klimešová (2020); 3 - Weaver (1919); 4 - Dong and Alaten (1999); 5 – Ye et al. (2016); 6 - Klimešová and Herben (2023); 7 - Yu et al. (2008); 8 - Janeček et al. (2008); 9 - Bartušková et al. (2022); 10 - Mudrák et al. (2012); 11 – Prieto and Ryel (2014); 12 - Klimešová et al. (2017); 13 – Schenk and Jackson (2005); 14 - Schenk et al. (2008)

Table 2 Ecosystem functions and relevant vegetation/plant characteristics along an aridity gradient in grasslands

Aridity thresholds	Vegetation decline phase	Soil disruption phase	Systematic breakdown phase
Driver	Water shortage but water still available in shallow as well as deep soil horizons	Water only in deep soil horizons, shallow water ephemeral and unpredictable	Water too deep for herbs, shallow water ephemeral and unpredictable
Vegetation composition changes	Advantage for plants adapted to water scarcity that are using deep as well as shallow water	Advantage for plants with deep rooting	Advantage for short-lived (annual) or shortly active (summer dormant) plants dependent on ephemeral precipitation
Regeneration after seasonal rest or disturbance	Regeneraton from bud bank prevails; regeneration from seed bank is hindered by competition	Regeneration from bud bank in which buds are protected from desiccation prevails; but regeneration from seed bank is possible due to facilitation	Regeneration is possible from well protected bud bank or seed bank; presence of complex triggers for releasing from seed dormancy
Growth forms (with stress on bud- bearing organ type)	Co-occurrence of all growth forms: rhizomatous and tussock grasses, deep rooting and root-sprouting forbs, bulbous plants, shrubs	Co-occurrence of deep rooting and root-sprouting forbs, shrubs, tussock grasses, bulbous plants and annuals	Co-occurrence of bulbous plants and annuals
Biomass production	Decreasing productivity (quantity and quality)	Decreasing productivity (quantity and quality)	Low productivity and low interannual stability of biomass production
Plant-soil feedback	Increasing longevity of plant organs (leaves, rhizomes, roots); resorption of nutrients from dead organs – poor quality of litter	Plants use water from deep soil horizons that are poor in nutrients and this leads to decreasing amount of litter of poor quality	Plants are small and have shallow roots, their growth depends on unpredictable precipitation, they produce a low amount of high quality litter
Plant-plant interactions	Competition; intraclonal translocation of limiting resources via system of rhizomes	Facilitation (shading and hydraulic uplift)	Density independent processes
Major Disturbances	Fire and grazing	Fire and grazing	Grazing and wind erosion
Alternative steady stages and risks	When fire is excluded, the grassland may change to shrubland	When overgrazed, perennial plants may be lost and system enters systematic breakdown phase	Encroaching of deep rooting shrubs that may facilitate germination of annuals
Consequence for ecosystem functions	Slowing down nutrient cycling	Decreasing soil fertility	Increasing wind erosion

also leads to a further decline in root and rhizome litter input into the soil which contributes to altered soil nutrient cycling. Decreasing amounts of fine roots would lead to a reduction of root surface area that is important in maintaining belowground mycorrhizal associations. This is a key shift in soil disruption (Berdugo et al. 2022), and further makes the soil prone to erosion as mycorrhizal fungi are soil stabilizers (Bearden and Petersen 2000). An alternative steady state may be annual vegetation in a case of overgrazing and loss of perennial plants.

The systemic breakdown phase

This phase (Tables 1 and 2; Fig. 1) is characterized by further reduction of the belowground bud bank and bud-bearing organs, leaving only those with well-protected buds (bulbs) capable of prolonged dormancy while utilizing temporary surface water. The dominant vegetation becomes annual plants that depend on unpredictable conditions for germination. Their biomass production, therefore, highly varies from year to year. Loss of perennial plants results in overall unprotected soil that may be easily eroded by wind or rare heavy rainfall events (Li et al. 2005; Su et al. 2005; Xu et al. 2021). Sparse plant cover also further reduces litter inputs from above and belowground plant organs. Litter of annuals and bulbs may more easily decompose than the litter of perennials due to their shorter lifespan. However, water scarcity would prohibit effective utilization of the litter in nutrient cycling in the system. An alternative steady state might be a dominance of shrubs with deep rooting.

Conclusion

Belowground plant organs are of immense importance for plants in arid environments. Consideration of them along with aboveground plant parts substantially contributes to a mechanistic understanding of vegetation processes under land use or climate change.

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Declarations

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