



Red-leafed species for urban “greening” in the age of global climate change

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Received: 22 March 2020 / Accepted: 10 April 2020
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Abstract Urban trees provide vital ecosystem services such as mitigating heat island, improving air quality by removing various air pollutants, capturing rainwater, and acting as topsoil carbon storage. The aesthetic value of urban trees is also another feature that has to be considered in the context of urban greening. Classical criteria for the selection of urban trees have to respond to new challenges imposed to the cities in a near future. Global climate change factors increase the harshness of our cities, and thereby the plant resilience to abiotic stresses has also to be seriously considered for planning the urban greening. Red-leafed species, characterized by the permanent presence of foliar anthocyanins, show a greater tolerance to different environmental cues than green-leafed species commonly used in our cities. In addition, red tree species own a great aesthetic value which has been underestimated in the context of urban areas, especially in the harsh Mediterranean cities. In this study, we emphasize the “privilege of being red” from different point of view, in order to drive the attention to the possibility to increase the use of red-leafed species for urban “greening”. Some possible negative aspects related to their use are rebutted and the direction of future researches are proposed.

Keywords Abiotic stress · Anthocyanin · Ecosystem service · Photoprotection · Urban forestry

Trees in urban environment: old and new challenges for urban greening

Beginning with the second industrial revolution, cities have gradually extended their green urban areas to mitigate the overbuilding, with their relative effects on climate and community (Tyrväinen et al. 2005). Nowadays, the terms “green building”, “green urbanism” or “green infrastructure” have become very popular and are usually used as a banner for the new urban planning.

Environmental sustainability, improvement of health and socio-psychological issues are only few aspects related to the green planning (Zuo and Zhao 2014; McDonnell and MacGregor-Fors 2016; Song et al. 2018). Some studies have demonstrated that the improvement of the green component in the urban environment can effectively: reduce the phenomenon of heat island, sequester atmospheric carbon dioxide (CO₂), capture rainwater and, improve the air quality (Berland et al. 2017; Song et al. 2018; Xing and Brimblecombe 2020).

Trees are the most important natural element in the urban environment (Tyrväinen et al. 2005); however, the common utilized term “element” is inadequate and completely detached from the concept of living organisms, leading to the idea that urban plants are mere ornamental elements that produce benefits, without thinking about the well-being of plants themselves. This erroneous idea very often leads to planning errors related to the incorrect choice of plants in urban environments, which, in turn, undermine the benefits of green areas to citizens, namely ecosystem services.

Project funding: No funding from projects.

The online version is available at <http://www.springerlink.com>.

Corresponding editor: Yu Lei.

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The strong efforts to “build in green” is in many cases not adequately supported by a correct management that takes into account the plant response to stress related to the urban environment (e.g. air pollution, water shortage, nutrient deficiency, soil pollution, high temperatures) (Watson et al. 2014; Allen et al. 2017). Moreover, the aforementioned stressful conditions of an urban environment to which tree species are normally exposed, could become a more serious limiting factor due to the harness imposed by global climate change (Yang 2009; Churkina et al. 2015; Ordóñez and Duinker 2015; Cotrozzi et al. 2016, 2017).

Only little information is available about trees, climate change and urban environment interactions if compared to data from studies conducted on forests or natural ecosystems (Ordóñez and Duinker 2015; Pretzsch et al. 2017). A study conducted in Philadelphia found that the predicted global climate change effects will result in suboptimal growth conditions for ten commonly used tree species, while others will thrive (Yang 2009). If the climate change factors have adverse effects for some tree species, for others they may exert the opposite result. A worldwide analysis conducted by Pretzsch et al. (2017) selected 10 metropolises around the world over four climate zones and found interesting results about climate change factors and plant interactions. The authors concluded that heat island, in concomitance with climate change factors contributed 14 and 21% in accelerating the tree growth compared to the rural counterparts. This assumption strengthens the idea that not all tree species are negatively affected by urban environmental conditions, but tree species with different degrees of susceptibility would show different responses to urban stressors (Cotrozzi et al. 2018; Araminiene et al. 2019; Sicard et al. 2018; Landi et al. 2019). However, an acceleration of growth could also accelerate the process of senescence itself, thereby shortening the tree lifetime and requiring a more dynamic management of green areas by municipalities (Pretzsch et al. 2017).

Many efforts have yet to be done for the selection of trees suitable for a specific urban area, in view of the actual lack of a large selection of plants for urban environment (usually non selected native species are used) and the lack of contextualization of each species to the planting area (microclimate, soil conditions, water supply, light and other factors) (Sjöman et al. 2012). These factors have contributed to create low tree species diversity in urban areas by choosing the most popular tree species, which in turn may not result the best solution in terms of plant resilience to the urban environment (e.g. insect pests or fungal disease outbreak) (Sjöman et al. 2012; Vogt et al. 2017). The selection of trees that demonstrate a marked resistance to abiotic stresses should therefore be encouraged to respond to actual and future challenges of urban greening (Yang 2009; Sicard et al. 2018).

From an ornamental point of view, tree species may differ in shape, size, habitus (deciduous or evergreen) and also in

crown color. All these macroscopic features translate into complex morpho-anatomical, allometric, physiological, and biochemical responses when plants sense a specific stress, and this can determine the success or the weakness of a specific tree species in a specific urban environment. Among others, recent studies have pointed the attention on trees species able to produce peculiar pigments in leaves, namely anthocyanins (ACNs), which confer them a well-appreciated red/purple coloration (Kyparissis et al. 2007; Hughes et al. 2007; Lo Piccolo et al. 2018). *Acer platanoides* L. var. *schwedleri nigrum*, *A. pseudoplatanus* L. var. *atropurpureum*, *A. palmatum* Thunb. var. *atropurpureum*, *Fagus sylvatica* L. var. *atropunicea*, *Corylus maxima* Mill. var. *purpurea*, *Prunus cerasifera* Ehrh. var. *pissardii*, *Cercis canadensis* L. var. forest pansy, *Cotinus coggygia* Scop. var. royal purple are the most widely used permanent red-leafed species for urban areas. These tree species have been selected by humans for their high ornamental value. However, besides their great aesthetic values, the constitutive presence of these colorful flavonoids on leaves, as shown in next sections, could also help these species to better accommodate some abiotic stressors, which is particularly advantageous for urban trees in the era of global climate change.

Chemistry and ecological roles of ACNs

ACNs are a conspicuous class of water-soluble pigments (ranging from pale pink, to red–purple and blue) which are responsible for the amazing color versatility of plant kingdom all around the world (Grotewold 2006). ACNs belong to the family of flavonoids, likely the most studied pathway of polyphenol metabolism *in planta* (Landi et al. 2015). ACNs are di- or tri-hydroxy B-ring-substituted flavonoids containing a flavylium cation which, owing to its conjugated double bonds, absorbs visible light with a peak in the 500–550 nm waveband (Fedenko et al. 2017). The wide range of anthocyanin-derived colors depends on the degree of hydroxylation and the number and/or type of substituted groups. To date, 17 anthocyanidins have been isolated, but most of these are found only in reproductive structures and only six aglycones (cyanidin, delphinidin, malvidin, pelargonidin, peonidin, and petunidin) have been identified in vegetative organs (Silva et al. 2016).

ACN pathway has been deeply studied in the last decades and this branch of phenylpropanoid metabolism has been extensively described, whereas their ecological roles is still a matter of argue. ACNs are synthesized in a wide range of plant tissues of different plant organs including leaves, flowers, fruits, roots, tubers and stems (Ellestad 2006; Winefield et al. 2009; Yoshida et al. 2009) and their possible ecological functions have puzzled scientists for well over a century. Mimicry, pollinator attraction, herbivory

repellence, and protection from abiotic stresses are the major ecological roles proposed for this widespread class of pigments (Winefield et al. 2009). Though the hypothesis that ACNs may have a protective role in plants date back to 1879 (Pringsheim 1879), the way through which they accommodated environmental cues is still highly debated.

In the next section, the possible ameliorative role(s) exerted by ACNs in a modern urban environment (Fig. 1), naturally exposed to multiple abiotic stressors, is depicted with the attempt to highlight ‘the privilege of being permanently red’ in our cities in the age of global climate change.

Benefits of foliar presence of ACNs for tree species in urban environment

Photoprotection

Sunscreen

The term “photoprotection” is widely used with different meanings by scientists dealing with plant physiology, biochemistry, genetics and ecology. We will refer to “photoprotection” in its broader meaning, intended as “protection from light-triggered damages at all physiological/biochemical/genetic level which induce depression of the photosynthetic process”. In this context, ACNs can serve multiple roles in photoprotecting the leaves from abiotic-stress-promoted photosynthesis impairment, acting as sunscreens, reactive oxygen species (ROS)-scavengers and sugar buffering compounds.

The excess of light burden to photosynthetic apparatus can undermine the chloroplast functionality and yield, as testimony by a rapid decline in the quantum efficiency of photosystem II (PSII), and a reduction in carbon fixation (Murata et al. 2007; Gururani et al. 2015). Abiotic stressors, which can affect the whole plant status, including chloroplast, lead

to an excess of excitation energy within photosynthetic apparatus (Murata et al. 2007) and trees in the urban environment are subjected to more abiotic stressors compared to trees grown in rural conditions (Sæbø et al. 2003). To avoid such an imbalance of light irradiance, plants have developed various morphological and physiological mechanisms, such as leaf or chloroplast movement, ROS scavenging systems, dissipation of absorbed light energy as heat, activation of cyclic electron flow and photorespiratory pathway (Takahashi and Badger 2011). Beside the aforementioned photoprotective mechanisms, ACNs, when localized in upper epidermis and mesophyll tissues, also constitute an effective sunblock, as reported for a different species, irrespectively to the fact that ACNs accumulate in the leaf mesophyll (Hughes and Smith 2007; Hughes et al. 2014) or in adaxial epidermis (Hughes et al. 2007; Landi et al. 2013a, b; Tattini et al. 2017).

The capacity of ACNs to absorb a proportion of the yellow/green and ultraviolet wavelengths (the latter especially when ACNs are acylated), may indeed significantly reduce the light-triggered damages to PSII, and in particular that related to D1 repair and the oxygen-evolving complex (Miyao et al. 1995; Antal et al. 2009; Takahashi and Badger 2011). Usually, under high irradiances, red-leafed individuals show lower level of other photoprotective pigments such as xanthophyll violaxanthin, antheraxanthin and zeaxanthin (VAZ), compared with green-leafed ones, which is consistent with the idea that ACNs might partially compensate for the photoprotective role of VAZ pool (Cavender-Bares et al. 1999; Verhoeven et al. 2005; Tattini et al. 2014; Logan et al. 2015; Lo Piccolo et al. 2018; Renner and Zohner 2019). In other cases, similar VAZ level were measured in both red and green leaves under optimal conditions, but when plants were subjected to high light, a stronger increment in VAZ de-epoxidation state in green than red leaves was observed, which is supportive for an alternative rather than compensatory role of ACNs (Hughes et al. 2012). Supportively to either an alternative or compensatory role of ACNs,

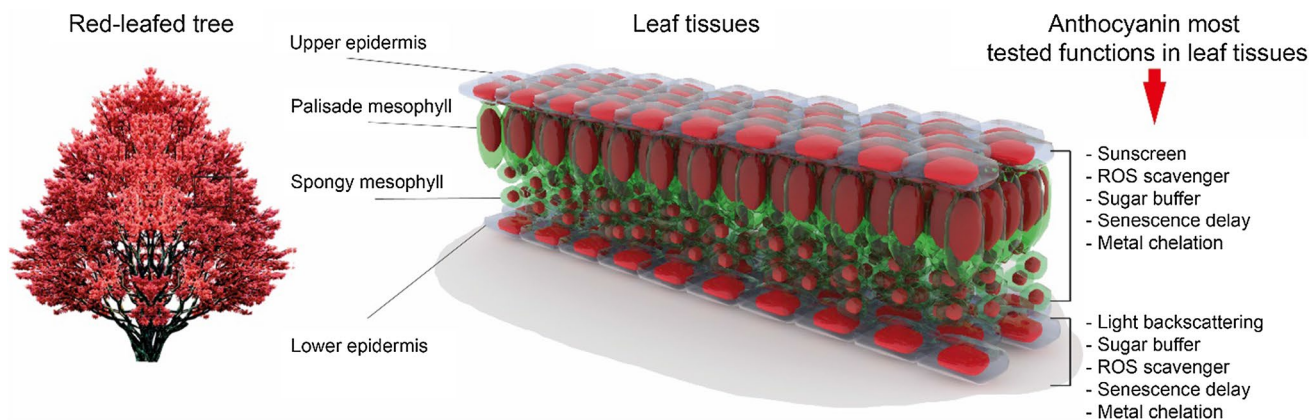


Fig. 1 Possible distribution of anthocyanins in leaf tissues of different plant species and their different role on the bases of their localization

when an extra amount of red light (able to overpass the ACN layer) was supplied, ACN-equipped and ACN-less leaves were similarly photoinhibited (Pietrini et al. 2002). When ACNs are localized in the lower epidermis, their possible sunscreen role appears inappropriate, leading to the hypothesis that ACNs localized in the lower epidermis may reflect adaxially-transmitted red light back to the mesophyll (Lee et al. 1979; Hughes et al. 2008). However, obtained results have failed to fully prove the functional significance of this trait, and further researches are needed (Hughes et al. 2008).

To date, only a few studies have investigated the performance of green- versus permanent red-leafed tree species in response to abiotic stresses which typically occur in cities, especially in the harsh Mediterranean area. However, these studies demonstrated the capacity of ACNs to protect the leaves from excessive light, thereby supporting ‘the privilege of being permanently red’, under condition of abiotic stress. For example, Lo Piccolo et al. (2018) and Vangelisti et al. (2020) observed that in vulnerable stages of leaves (young and senescent leaves), a red-leafed cv. of *Prunus cerasifera*, which is widely used in urban environment, was less susceptible to light excess than a green-leafed counterpart. In addition, Lo Piccolo et al. (2020a) observed that ACN presence ameliorates the performance of *Prunus* spp. in condition of limited water availability.

ROS prevention and scavenging

Abiotic stresses can consistently lead to an increase of ROS production over a physiological level in different cellular compartments, e.g., mitochondria and chloroplast, thereby promoting events of oxidative stress, oxidative burst and finally cell death (Foyer et al. 1994). Flavonoids, including ACNs, with poly-hydroxy B-ring substitutions, have been found to act as powerful ROS scavengers in in vitro experiments (Neill and Gould 2003; Juadjur et al. 2015). However, it is still under debate whether or not ACNs can serve as ROS scavenger in vivo, given that ACNs would only have the possibility to scavenge cytosolic and vacuolar ROS (whilst chloroplast and mitochondria with their electron transport chains are the primary sites for ROS production) before being shuttle to the vacuole (Hernández et al. 2009). In favor of their ROS scavenging role, the fact that ACNs can scavenge vacuolar H_2O_2 , which, produced in other sites, can easily pass lipid bilayers and reach the vacuole which normally occupied more than 70% of a total cell volume (Mittler et al. 2004). H_2O_2 is indeed more stable than other radical ROS, and therefore vacuolar ANCs are likely to have a pivotal role in counteracting the symplastic movement of ROS (Mittler et al. 2004), which is supportive for the theory of Yamasaki’s group (Yamasaki et al. 1996, 1997). Accordingly, lower levels of H_2O_2 were measured in red- than green-leafed *Prunus* during the last phase of leaf

ontogenesis (Lo Piccolo et al. 2018). Besides the opinion about the scavenging role of ACNs, it is undeniable that the previous role as sunscreen compounds also results in reducing the amount of ROS that could be otherwise produced being that amount of light not intercepted by ACNs. Therefore, accepting the definition of an antioxidant as “a substance that, when present at low concentrations compared to those of an oxidizable substrate, significantly delays or prevents oxidation of that substrate” (Gutteridge and Halliwell 1990), it emerges clearly the weak borderline between the classic dichotomy in ACN roles: sunscreens or antioxidants (Landi et al. 2015).

Sugar buffering

The perturbation of plant metabolism by abiotic stressors can result in sugar accumulation, which, in turn, induces the sugar-promoted feedback inhibition of photosynthesis (Krapp and Stitt 1995; Paul and Foyer 2001; Holland et al. 2016). In view of their nature, it has been proposed that ACN accumulation may represent an alternative sugar sink, thereby preventing or delaying the sugar-promoted inhibition of photosynthesis of plants subjected to abiotic stresses (Landi et al. 2015; Lo Piccolo et al. 2018, 2020a, b; Gould et al. 2018). Indeed, ACN and sugar metabolism are strictly interconnected, and sugar-promoted enhancement of ACN levels has been clearly demonstrated in previous experiments (Solfanelli et al. 2006; Das et al. 2012; Lo Piccolo et al. 2018). In order to test this hypothesis in tree species, it was recently demonstrated that ACN biosynthesis represents a relevant C-sink in conditions of imbalanced source-to-sink relationship induced by the effect of stem bark girdling (Lo Piccolo et al. 2020b). It has also been demonstrated that under drought, one of the main constrains for trees in Mediterranean cities (Sjöman et al. 2018), red-leafed *Prunus* plants were less affected than ACN-less individuals. The increase of ACNs in the first phase of water stress resulted in lower accumulation of soluble sugars in leaves of red than green individuals and correlated with a lower decline of PSII efficiency (Lo Piccolo et al. 2020a). The ACN enhancement was therefore proposed by the authors as a mean to both reduce the incident light and reduce the sugar-promoted feedback regulation of photosynthesis.

Senescence delay

Connected to the sugar-buffering role previously described, the C-sink exerted by ACNs may also offer the possibility to stressed plant to avoid the phenomenon of early senescence promoted by foliar sugar accumulation (Sami et al. 2016). The strict interconnection between sugar, ACNs and senescence has been well described in red versus green autumn leaves by different authors (Feild

et al. 2001; Hoch et al. 2003; Schaberg et al. 2003). In addition, a longer leaf life-span can increase the N resorption ability by the leaf, therefore reducing the loss of N due to earlier leaf fall (Feild et al. 2001; Hoch et al. 2003; Shi et al. 2017). Accordingly, Lo Piccolo et al. (2018) observed that accumulation of ACNs in older leaves of permanent red-leafed *Prunus* correlated with a delayed leaf senescence and a lower level of residual N into the leaves when compared to green-leafed individuals. This aspect can be particularly interesting in an urban environment, given that red species could maintain the leaves for longer than other green deciduous species at the end of autumn, thus further increasing the aesthetic value of ACN-rich tree species.

Metal chelation capacity

Metal accumulation and toxicity represent another hazardous risk for trees in an urban environment (Landi et al. 2020). Metal stress can induce ACN biosynthesis in a dose-dependent manner (Kumar et al. 1995; Chalker-Scott 1999), but it remains yet to be elucidated in which way ACN may help the plant to cope with metal toxicity. Besides the photoprotective roles described above, ACNs possess a 3',4'-O-dihydroxyl group in the B ring of their backbone, which have the capacity to form metal-ACN complexes (Fedenko et al. 2017). The occurrence of metal-ACN complexes has been reported for different metals including W, Al, Cd, Cu, Ga, Fe, Mo, Mg, Zn (Fedenko et al. 2017 and reference therein). However, only Hale et al. (2001, 2002) tested this ameliorative role in vivo and, in addition, this capacity was proved for W and Mo, which are not among the most common metal pollutants in urban environments. The capacity of ACNs to bind metal ions can expedite their cytosolic sequestration, boosting their shuttle to the vacuole in coordination with glutathione, glutathione S-transferase and phytochelatins, which are common carriers for both ACNs and metals into the vacuoles (Landi et al. 2015). This would result in lowering their toxic impact to the cytosolic environment and preventing the metal diffusion to other organelles. In addition, in case of epidermally-located ACNs, the sequestration of metal ions into the leaf epidermis represent a mean to avoid metal accumulation in more important tissues (e.g. mesophyll cells).

In view of the above discussion, permanent red-leafed species seem to be better equipped to survive in metal-enriched soils, even though future researches are needed to better understand whether the metal chelation ability of ACNs exerts a relevant role in metal tolerance of ACN-equipped tree species.

Possible argumentations against the use of red species in urban environment

Green means relax, red excitation

Besides the previous undeniable biochemical/physiological aspects which suggest red-leafed tree species as more suitable to counteract the stressful conditions of cities, there are, maybe, some possible argumentations and concerns related to the use of these species from different point of views.

Chromotherapy highlights that green, which represents the most present color in nature, is a restful color that inspires harmony. Green is associated with spiritual balance, can diffuse anxiety and helps us to keep calm and controlled (Garala et al. 2009). Conversely, red is often described as warm, vibrant, and intense. It is often seen as an exciting and even aggressive color able to stimulate blood pressure and nerves (Azeemi and Raza 2005). Based on the aforementioned statements, it seems conceivable that the use of red species should be limited. However, it should be considered that red can also evoke feelings of love and comfort. Red is often used to grab attention, particularly in advertising and traffic signage. In addition, purple color, which is more common in tree species than pure red, may evoke relaxation, comfort and calmness too (Kaya and Epps 2004).

The use of “red” or better anthocyanin-rich species has to be therefore carefully pondered with the typical green-leafed trees in order not to create an unfavorable effect. For example, the foliage that is typical of North America’s and Canada’s autumn, appears as an amazing alternation of yellow/red/purple tonalities. Conversely, the only use of monotone red species for an urban park would not be appreciable given that the aesthetic value of tree species is one of the most important ecosystem services exerted by urban trees. Anthocyanin-rich trees should be therefore used to alert the observer, using red trees to mark particular paths, or, alternatively, they should be carefully balanced to green species to confer a strongly appreciated dichromatic contrast to the scenery.

Constitutively red trees have been selected by humans; their use is against the natural plant evolution

Perhaps is sad to be admitted, but nowadays the most widely diffused plant species have been selected by humans for their own purposes. Trees species are not an exception, and especially in the context of the urban greening, the aesthetic value, rapid growth, and in some cases the stress tolerance should be key requisites for their selection. So that, besides many efforts which have been done, especially in the last decade, agriculture as well as urban greening are far to be oriented in maintaining the plant biodiversity and following the evolutionary criteria.

Constitutively permanent red-leafed tree species have been selected by humans for their high aesthetic value. However, if we consider the phylogenetic evolution of the ACN pathway, it emerges that ACNs are old pigments (the genes of the ACN pathway are thought to date back 450 million years to the first land plants) and this phenylpropanoid branch is present in all the angiosperm families (Campanella et al. 2014). Therefore, the human selection of red-leafed species have paralleled (and not contrasted) the evolution of ACNs and perhaps the leaf of the future will be transiently red for the majority of its ontogenetic cycle, especially in limiting environments.

The biosynthesis of ACNs is an expensive pathway and red species have consequently a reduced growth rate

As detailed above, ACN biosynthesis represents a relevant C-sink and requires energy investment by the plant to keep this pathway active (Lo Piccolo et al. 2020b). Under optimal conditions, a comparison of the growth rate of anthocyanin-rich versus ACN-less individuals would be in favor of the green ones (Landi et al. 2013a). However, when green and red plants were compared in stressful condition (the most common situation in an urban environment), usually red species are able to compensate for their apparent inability to compete with the growth rate of green-leafed individuals (Tattini et al. 2014), and in most cases they even exhibit superior performances (Landi et al. 2013a). Though the previous statements were derived from herbaceous species, due the lack of this kind of investigation in tree species, it is conceivable that the presence of foliar ACNs may also ameliorate tree performances under unfavorable environmental cues for all the reasons mentioned in the section “Benefits of foliar presence of ACNs for tree species in urban environment”, which can be considered valid to both herbaceous of arborous species. Tree species seem therefore more successful in a stressful and limiting environment as the city, especially in Mediterranean areas.

Conclusion and future perspectives

ACN-rich tree species represent a valid alternative, with an underestimated potential, to the most commonly used green species in urban environments. Future criteria for the selection of tree species should be improved in order to respond to the new challenges imposed by global climate change, which exacerbates the already harsh living conditions of our “leafed citizens”. The aesthetic value attributable to the presence of foliar ACNs, associated to capacity of these pigments to be helpful in accommodating

the common abiotic stress (typical of Mediterranean cities) should attract the attention of urban greening operators and promote their use, which is nowadays only marginally considered. New researches are still needed to deepen the pivotal aspects related to the ecophysiology of these permanently red-leafed species in relation to different urban environments, in order to wisely select the most suitable species in view of their peculiar features.

Acknowledgements The authors are thankful to Prof. Evgenios Agathokleous, who is the associate editor-in chief of Journal of Forestry Research, for the official invitation to publish the present review in Journal of Forestry Research.

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