

Review

The 'Edge Effect' Phenomenon in Plants: Morphological, Biochemical and Mineral Characteristics of Border Tissues

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Abstract: The 'edge' effect is considered one of the fundamental ecological phenomena essential for maintaining ecosystem integrity. The properties of plant outer tissues (root, tuber, bulb and fruit peel, tree and shrub bark, leaf and stem trichomes) mimic to a great extent the 'edge' effect properties of different ecosystems, which suggests the possibility of the 'edge' effect being applicable to individual plant organisms. The most important characteristics of plant border tissues are intensive oxidant stress, high variability and biodiversity of protection mechanisms and high adsorption capacity. Wide variations in morphological, biochemical and mineral components of border tissues play an important role in the characteristics of plant adaptability values, storage duration of roots, fruit, tubers and bulbs, and the diversity of outer tissue practical application. The significance of outer tissue antioxidant status and the accumulation of polyphenols, essential oil, lipids and minerals, and the artificial improvement of such accumulation is described in connection with plant tolerance to unfavorable environmental conditions. Methods of plant 'edge' effect utilization in agricultural crop breeding, production of specific preparations with powerful antioxidant value and green nanoparticle synthesis of different elements have been developed. Extending the 'edge' effect phenomenon from ecosystems to individual organisms is of fundamental importance in agriculture, pharmacology, food industry and wastewater treatment processes.

Keywords: plant wastes; outer tissues; bark; antioxidants; minerals



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1. Introduction

From the viewpoint of classical ecology, the 'edge' effect extends to the border areas between two or more habitats and is characterized by significant changes in populations or communities [1,2]. Such areas show increased biodiversity and high oxidant stress connected with changes in insolation, imbalance of light cycles, great fluctuations in temperature and water access, and complex interactions between the different components [3]. The relationship between the environment and an individual organism, particularly a plant, has not been previously considered as an example of the 'edge' effect. Nevertheless, the universality of the 'edge' effect phenomenon is clearly reflected at both the macro- and micro-ecosystem (individual organisms, including plants) levels. In fact, it is known that plant organism preservation is determined to a large extent by the formation of symbiotic communities with soil rhizobacteria, fungi and microbes [4], and allelopathic interactions

with other plants [5–7] and insects [8]. For instance, plant–fungi–bacteria symbiosis is shown to promote plant biodiversity, nutrition and seedling recruitment [9].

The mentioned processes largely mimic the classical ‘edge’ effect, providing the integrity of plant organism and its development.

On the other hand, attention should be paid to the existence of a secondary defense level in plants against unfavorable environmental factors: the development of morphologically distinct external tissues (Figure 1). To date, how clearly the ‘edge’ effect manifests itself at this level of morphological and biochemical changes in plant tissues remains unexplored.

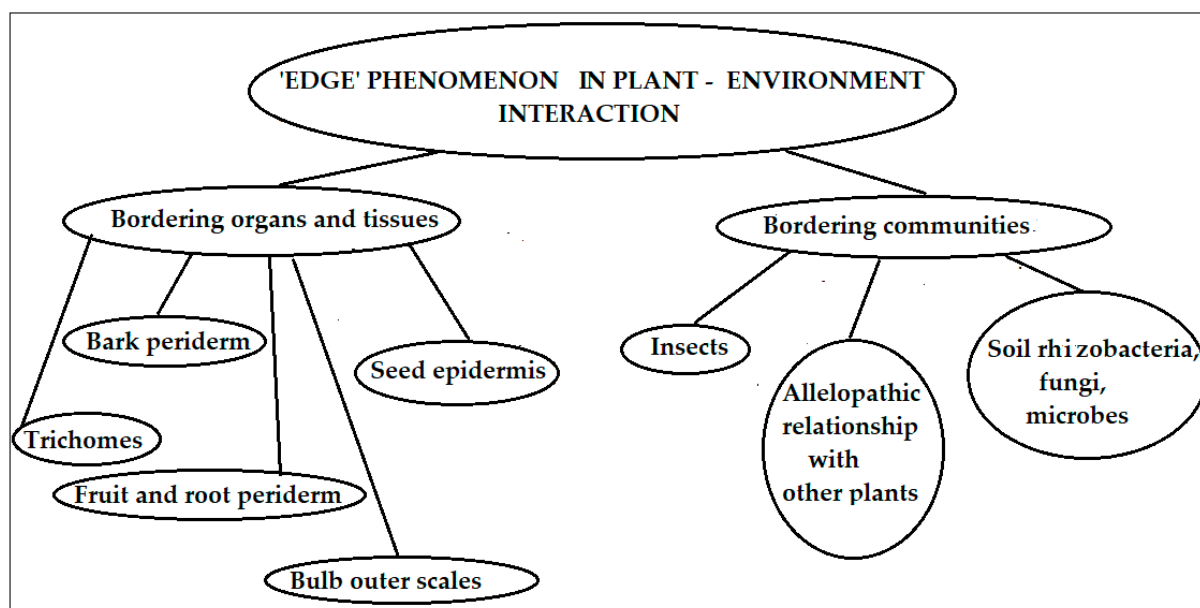


Figure 1. ‘Edge effect’ related to the interaction between plants and environment.

The comparison between macro-ecosystems and micro-systems of individual plant organisms enables the distinction of several resembling properties of the ‘edge effect’ in ecosystems and plants, including:

- (1) intensive oxidant stress;
- (2) high biodiversity of organisms in bordering areas and of biologically active compounds in plant border tissues;
- (3) damper effect of bordering areas/tissues necessary to withstand the unfavorable environmental conditions;
- (4) high adsorption capacity of plant bordering tissues and intensive energy accumulation in ecosystem bordering areas.

At present, many investigations address the bordering communities of ecosystems: bacteria, fungi, microorganisms and algae [10–13]. External plant parts have been discussed previously only in connection with the necessity of agricultural waste management [14,15], which hinders the identification of the general patterns of plant ‘edge’ effect and the successive development of their utilization.

The present review aims to reveal the peculiarities of plant bordering tissues as an example of the ‘edge’ effect and indicates new opportunities for its utilization. Among the external parts of plants, tree bark, leaf and stem trichomes, seed skin, tuber, bulb and fruit peel provide the most interesting objects of the plant ‘edge’ effect investigation. These parts differ greatly in biochemical composition, metabolism intensity and longevity value, with the highest longevity associated with tree bark [16]. Great variations in metabolism intensity have been recorded in onion outer scales [17] and seed shell [18] compared to beetroot [19] and young potato peel [20]. A decreased metabolism has been shown in pumpkin, squash [21] and tomato fruit [19] outer tissues. Leaf and stem trichomes have large surface areas and show intensive production of volatile derivatives [22].

This review combines both literature data of recent years and our own previously unpublished data.

2. Trichomes

Among the bordering plant parts that protect the integrity of an organism and enable tolerance to environmental stress factors, some of them should be mentioned. Multi- and mono-cellular trichomes (the so-called glandular and non-glandular forms) are situated at the surfaces of leaves, stems and buds and their formation and development are regulated predominantly via phytohormones [23]. Trichomes usually originate from epidermal cells and are typical in many plant species, showing significant diversity in morphology, cellular structure and function. While glandular trichomes provide mainly chemical protection for plants, non-glandular trichomes induce mostly physical protection (Figure 2), though these definitions are rather flexible [24–26].

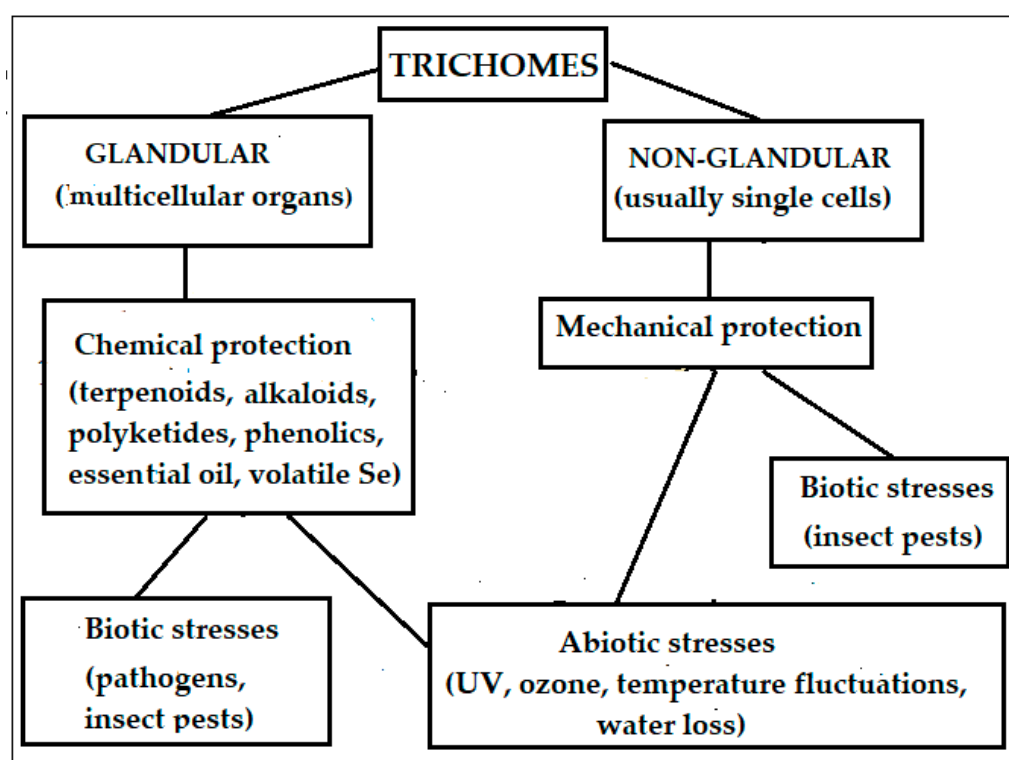


Figure 2. The role of trichomes in plant protection.

A great diversity of biologically active compounds is synthesized in trichomes: polyphenols, terpenoids, alkaloids and polyketides [26]. Among the different compounds of high medicinal value, it is worth mentioning the production of artemisinin by *Artemisia annua* L. trichomes, an antimalarial sesquiterpene [24], of essential oils [27,28] and of methylated forms of selenium (Se) containing amino acids (selenomethyl selenocysteine and gamma glutamyl selenomethyl selenocysteine) in the trichomes of Se hyperaccumulators (*Stanleya pinnata* (Pursh) Britton and *Astragalus bisulcatus* (Hook.) A. Gray), with powerful anti-carcinogen activity [29]. Essential oils may serve as a defense against arthropods [30] or as pollinator attractants [31]. Volatile Se derivatives of *Stanleya pinnata* (Pursh) Britton and *Astragalus bisulcatus* (Hook.) A. Gray along with high concentrations of toxic Se in trichomes protect plants against herbivory, providing additional advantages compared to non-Se accumulator plants. Flavonoids of non-glandular trichomes repel herbivory and protect against different pathogens [32]. The well-known halophyte tamarisk uses trichomes to secrete salt excess from tissues [33].

Furthermore, both glandular and non-glandular trichomes provide valuable defenses against different forms of abiotic stresses, including atmospheric oxidants, such as

ozone [34], and increase plant resistance to UV radiation [35], high temperature and water loss [32]. Notably, phenolics in the trichome cell walls act as optical filters, excluding light waves harmful to sensitive plant tissues.

One of the resistance mechanisms that develop in response to environmental stress in aromatic plants is an increase in essential oil component diversity, which was recorded in *Artemisia annua* L. grown in Nikitsky Botanic Gardens during 2016–2022 [36]. The results demonstrated a positive correlation between the number of essential oil components and of solar flares ($r = +0.996$, $p < 0.0001$). The investigated period was characterized by a 2 to 1530 solar flare range and 46 to 72 essential oil components. Furthermore, the essential oil yield negatively correlated with the number of spotless days ($r = -0.829$; $p < 0.01$). These results indicate that plant adaptability and the variation in the number of chemical compounds participating in plant defense is closely connected with solar activity. It seems doubtless that the diversity of trichome protection mechanisms stimulates the formation of ecological niches for different plant species and suggests multiple relationships between different organisms.

3. Seed Epidermis

One of the most evident examples of the ‘edge effect’ in plants is represented by the seed epidermis, which provides mechanical, antioxidant and anti-viral protection of the embryo, prevents water losses during dormancy, promotes active accumulation of nutrients during seed germination [37] and induces seed distribution along significant territories. These properties are determined by both the biochemical and mineral composition of the seed epidermis and by the peculiarities of its morphological structure. The great diversity of seed coat morphology [38] indicates the importance of the ‘edge’ effect in plant development.

The main components of the seed epidermis are soluble and insoluble fiber [18], polyphenols, [37], terpenoids [17] and wax. The biochemical protection of the embryo is achieved via the predominant accumulation of antioxidants in the seed coat [39]. These compounds provide a valuable defense against pathogens and an improvement in the nutritional quality of the seeds, which is highly valuable in the food industry and pharmaceuticals [40,41].

A seed epidermis predominately accumulates Zn, Se, K, Ca and S [42]. Se accumulation particularly in the aleurone layer of cereal grains was indicated by Moore et al. [43]. Selenium, a well-known natural antioxidant, was shown to be accumulated almost exclusively 1–2 mm below the surface of *Bertholletia excelsa* Humb. & Bonpl. (selenium_hyperaccumulator), while Zn and Ca provide the enrichment of the outer layer [44]. It is well known that the aleurone layer actively participates in seed development via the maintenance of low pH and the release of nitrites, α -amylase necessary for starch hydrolysis, proteases and storage proteins in endosperm [45]. The germination is accompanied by a significant increase in biologically active water-soluble compound content, able to stimulate seedling development and photosynthetic pigments accumulation [46]. The importance of seed epidermis Se content in seed germination is proved by the existence of a positive correlation between this parameter and seedling length [46]. In this respect, investigations of the seed collection of *Brassica chinensis* Jusl. and perennial onion at the Federal Scientific Vegetable Center revealed positive correlations between seedling length and seed epidermis Se content both in *Brassica chinensis* Jusl. and *Allium* species ($r = +0.722$, $n = 12$; $p < 0.01$ $r = +0.895$; $n = 10$; $p < 0.01$, respectively).

Compared to the embryo, the grain coat of wheat contains significantly higher levels of Se, and seed polishing during flour production promotes a decreased level of this essential microelement for humans in the resulting product [47].

Notably, the phenomenon of embryo protection and improvement of seed germination by the seed epidermis may be enhanced artificially via seed priming alone or in combination with low dosages of fungicides [48], nano-Si coating [49] and Se biofortification. Indeed, according to our data, the foliar application to bean plants of sodium selenate

or selenocystin at the dose of 0.265 mM resulted in a significant increase in the seed wax hexane extract absorption of mature plants (Figure 3). The waxy layer of the seed epidermis is known to increase seed viability and improve resistance to reactive oxygen species, and contributes to maintaining their dormant state [50,51]. Epicuticular wax is characterized by the ability to decrease surface wetting and moisture loss, the reflection of harmful UV light waves and the formation of a self-cleaning surface. On the other hand, the beginning of germination is accompanied by a decrease in wax biosynthesis [40].

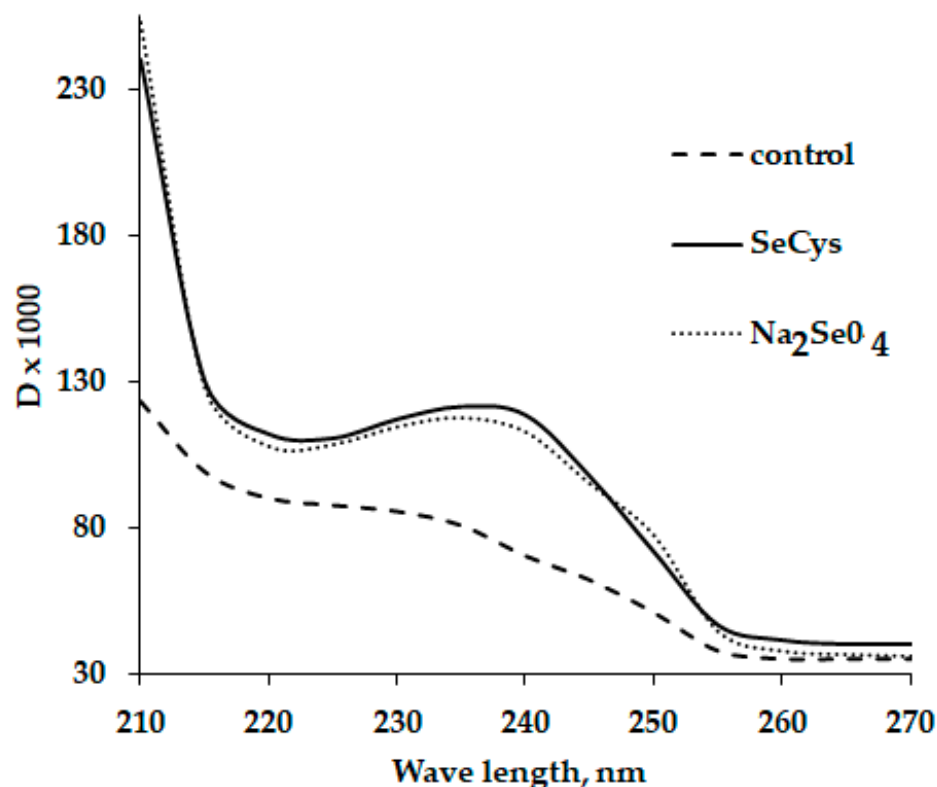


Figure 3. Effect of foliar sodium selenate and SeCys supply on wax accumulation on the surface of bean seeds, cv Uliasha (0.26 mM solution) (Supplement S1).

In practice, both whole seed and seed epidermis proved to be adsorbent and highly valuable as important sources of natural antioxidants [41,52–56]. In this respect, seed epidermis may act as a powerful water purification agent against organic dyes, antibiotics and heavy metals (Table 1).

Table 1. Several examples of seed coat absorption capacity.

Species	Pollutant	References
<i>Lupinus albus</i> L.	Malachite green dye	[57]
<i>Cucurbita</i> sp.	Pb	[58]
	Dyes	[59]
	Antibiotics	[60]
<i>Triticum</i> L. grain bran	Pb	[61]
	Dye from textile wastewater	[62]
<i>Cicer arietinum</i> L.	Dyes	[63]
<i>Sclerocarya birrea</i> (A.Rich.) Hochst.	Methylene blue	[64]
<i>Cucumis melo</i> L.	Methylene blue	[65]
<i>Bertholletia excelsa</i> Humb. & Bonpl. shells	Methylene blue, indigo carmine	[66]
<i>Helianthus</i> L.	Dyes	[67]

4. Tree Bark

Tree bark is one of the most typical examples of the ‘edge’ effect in plants. The outer tissues of bark are characterized by great morphological diversity, thickness [68–70] and biochemical peculiarities [71], which are directly connected with the different strategies of plant adaptation to the environment (for instance, protection against herbivory attack, drought, forest fires, etc.) [72]. Nevertheless, to date, the reasons for such diversities have been poorly understood [73]. According to the intensity of metabolic processes, the inner bark tissues (living phloem) and outer tissues (dead phloem and periderm) determine their main physiological functions. Inner tissues participate in the transport and storage of photosynthesis products and in carbon fixation, while the outer tissues (periderm) protect trees from water loss and provide a protection against pathogens and herbivory attack, mechanical injuries and anomalously high and low temperatures, providing a valuable insulation [74].

The values of bark tissue antioxidant activity are in accordance with the intensity of metabolic processes increasing from the periderm to phloem and to immature phloem and vascular cambium. Indeed, outer bark (periderm) and cork cambium (inner bark; phellem) are composed of nonliving cells and provide a mechanical protection for trees, demonstrating relatively low levels of antioxidants, while the middle phloem part and especially the vascular cambium actively metabolize tissues which show levels of total antioxidant activity 1.4–2 times higher, than the periderm [75]. It is also worth mentioning that the levels of total AOA and total polyphenol content in tree bark, though they show a wide range of values, are often equal to or even higher, than the levels recorded for most agricultural crops.

Similarly to other bordering tissues, tree bark periderm is characterized by a high capacity for environmental pollutant absorption, absorbing heavy metals, dyes and pesticides [76–78]. Bark is known to accumulate Na [79], Ca, Zn, Fe, Al, Pb and Sr, and the amount of accumulation correlates with the level of environmental pollution [80]. Relatively high levels of Ca and Zn were also recorded in poplar bark [81]. Species differences in adsorption capacity and total antioxidant activity have been recorded [75,76].

Tree adaptability to environmental factors reflects the effects of genetic peculiarities, place of growth, temperature, seashore vicinity, altitude and age [75,82,83]. Investigations relevant to the quantitative and qualitative composition of *Abies alba* Mill. bark extracts revealed an increase in the total polyphenol extract yield and a significant decrease in phenolics diversity from the base to the top of the tree [83]. The relationship between tree age and bark antioxidant status was also reported for *Acacia confusa* Merr. [84] and *Cinnamomum loureirii* Nees [85]. The differences in the bark and wood extractive levels vary between different species from 1.5 to 16. The extractives content increases with increasing age [86]. According to Dogan et al. [86], tannin content in the tree bark of different species varied from 2% to 54%.

ICP-MS analysis of elements in periderm, phloem and cambium of white willow (*Salix alba* L.) bark, gathered in Moscow region (55°39.51' N, 37°12.23' E), showed the highest macro-element concentrations in metabolically active tissue cambium (Figure 4) and the highest levels of toxic elements in periderm (Figure 5).

Among the micro-elements, the highest concentrations in periderm were recorded for B, Co, Cu, Fe, I, Mn, Mo and Zn, while no differences were detected for Se accumulation among the tissues tested, which may be connected with the low levels of this element (Figure 6). These results are in accordance with the work of Aoyama et al. [87], who demonstrated a higher Fe, Mn and Zn adsorption capacity in periderm compared to phloem in *Cryptomeria japonica* (L.f.) D. Don bark.

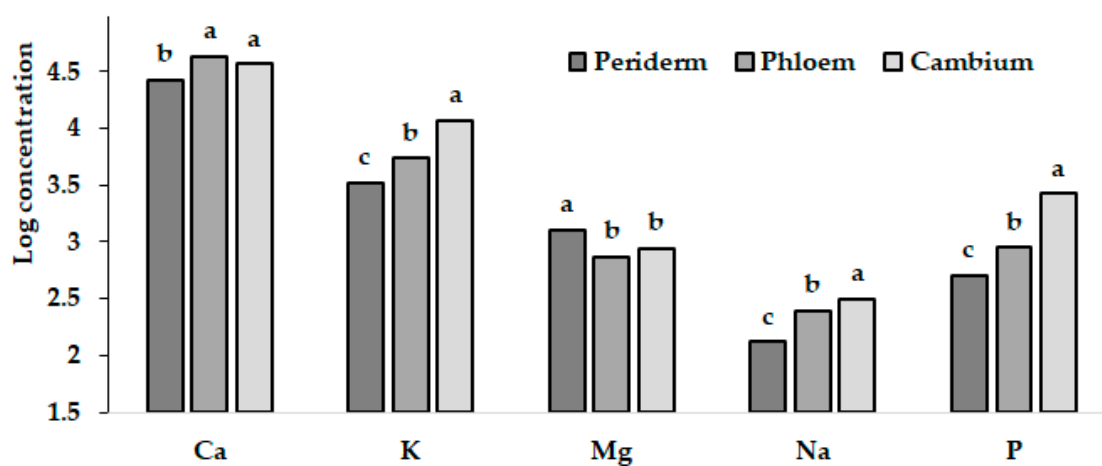


Figure 4. Distribution of macro-elements between periderm, phloem and cambium of white willow. For each element, values with the same letters do not differ statistically according to Duncan test at $p < 0.05$.

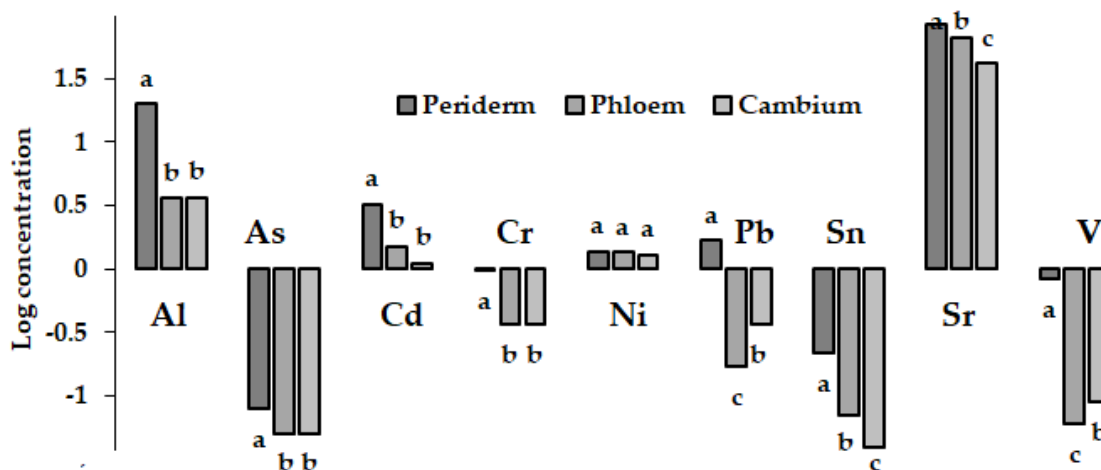


Figure 5. Distribution of Al, As and heavy metals between periderm, phloem and cambium of white willow. For each element, values with the same letters do not differ statistically according to Duncan test at $p < 0.05$.

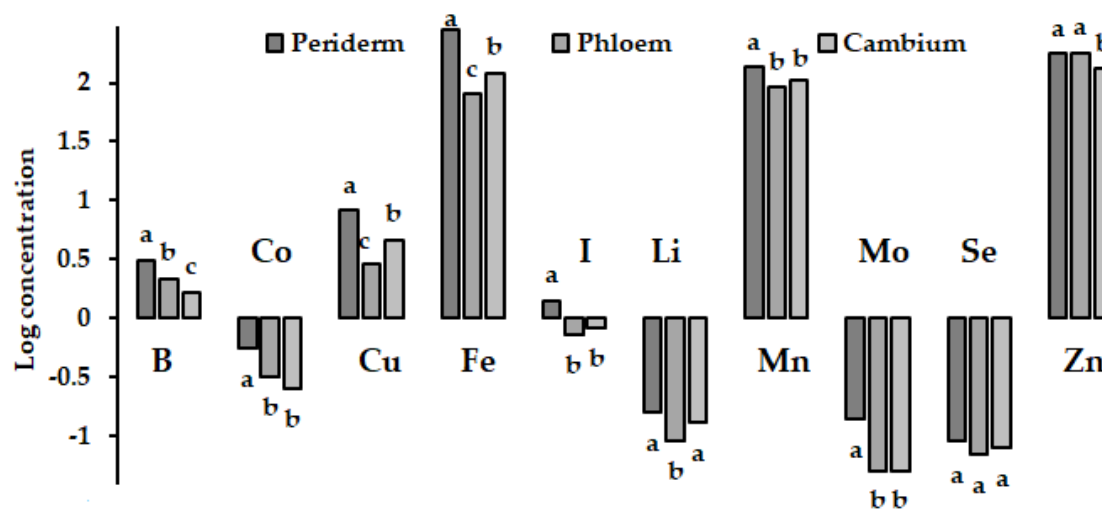


Figure 6. Distribution of micro-elements between periderm, phloem and cambium of white willow. For each element, values with the same letters do not differ statistically according to Duncan test at $p < 0.05$.

Furthermore, bark is rich in polysaccharides and polyphenols, including tannins and lignin. A high polyphenol content suggests a potential for bark utilization in the food industry, cosmetics and herbal medicine [88,89]. In this respect, there is a group of trees/shrubs with unusually high bark antioxidant activity, such as willow *Salix alba* L. (134 mg GAE g⁻¹ d.w.), deren shrubs *Cornus sanguinea* L. and *Cornus alba* L. (165–170 mg GAE g⁻¹ d.w.), and *Calligonum polygonoides* L. shrub of semi-desert (172 mg GAE g⁻¹ d.w.) [75].

The medicinal importance of tree bark is documented for many tree species, revealing its anti-inflammatory, chemo-preventive, neuro-protective, cardio-protective, anti-carcinogenic, antiviral, antibacterial and antidiabetic effects connected predominantly with its high antioxidant properties [90–93].

The high adsorption levels of bark periderm make it valuable for use in wastewater purification, and especially effective against Cr, Ni [94,95] and organic pollutants [96] (Table 2).

Table 2. Examples of bark utilization for water purification.

Active Ingredient	Pollutant	Reference
<i>Eucalyptus</i> L'Hér. bark	Cr, oil	[94]
<i>Platanus orientalis</i> L. bark	Cr, Ni	[95]
<i>Pinus</i> L. bark	Pentachlorophenol	[96]
<i>Pinus durangensis</i> Martínez sawdust	Methylene blue	[97]
<i>Juglans regia</i> L. sawdust	Methylene blue	[98]
<i>Pseudotsuga menziesii</i> (Mirb.) Franco bark	Uranium	[99]
<i>Pinophyta</i> Cronquist, Takht. & Zimmerm. ex Reveal bark	Hydrocarbons, Al, Ca, Fe, Mg, S	[100]
<i>Quercus cerris</i> L. cork	Cr ⁶⁺	[101]

5. Vegetable Root Periderm

The peel of fruit and vegetable roots is characterized by relatively high humidity, and as a result, by rather active metabolic processes. In this respect, changes in its biochemical characteristics as a consequence of oxidative stress during vegetation or storage may become highly valuable both for the evaluation of plant adaptability degree and plant breeding.

5.1. Potato (*Solanum tuberosum* L.)

Potato periderm is considered one of the most important waste products in the food industry, with an annual volume of 70–140 thousand tons [20,102,103]. It is rich in phenolics, with a predominance of chlorogenic acid [102], and demonstrates high biological activity [20,103–105]. Potato periderm is known to protect tubers against bacteria, fungi, viruses, insects [106] and phytopathogens [107]. Almost 50% of the phenolics in potato are located in the peel and adjoining tissues [108,109].

The protective effect of potato periderm has been recorded in peel morphology and the differences in the total antioxidant activity of the peel and pulp of tubers before and after 6 months of storage (Figure 7). Indeed, a significant decrease in AOA value occurred in potato peel after storage, which resulted in a simultaneous increase in pulp AOA. Similar changes were recorded in total phenolic content (TP) in potato peel and pulp. Notably, the peel/pulp AOA and TP values after storage became similar to each other. The rather large sample (18 cultivars) indicated the significance of such changes, valuable both for plants and humans. The results were consistent with the investigation of Külen et al. [110] who demonstrated that the total phenolic content (TP) of potato tubers was high at harvest, declined after two months of cold storage, increased after four months of cold storage, and finally returned to values similar to harvest levels after seven months of cold storage.

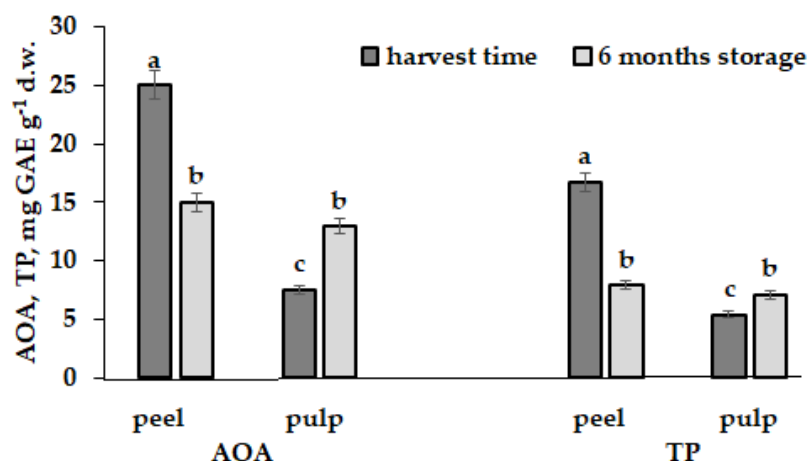


Figure 7. Changes in potato tuber total antioxidant activity (AOA) and total polyphenol content (TP) during storage (18 cultivars, Supplement S2). Values with the same letters do not differ statistically according to Duncan test at $p < 0.05$.

The powerful antioxidant status of potato periderm, which contains phenolics [111], anthocyanins, glycoalkaloids and polysaccharides [112] indicates the great potential for potato peel utilization.

The presented examples of potato periderm utilization combine cases based on its high antioxidant activity [113]; antibacterial properties; anti-inflammatory and anti-cancer properties; protection against pests; preservation of oil [114], fish [115,116] and meat [117]; wound healing [118] properties; high adsorption capacity (biosorbent, wound healing); high nutritional value (food additive, animal feed) [20]; biofertilizer [119] and mechanical protection of tubers. Table 3 also demonstrates several examples of potato periderm utilization for water purification, which is in accordance with the high adsorption capacity of the outer tissues [120].

Table 3. Prospects for potato peel utilization.

Active Ingredient	Utilization Efficiency	References
Antioxidant and antiviral properties		
Peel powder	Preservative in fish processing	[115,116]
	Preservative in meat storage and processing	[117]
	Oil preservation	[114]
	Wound healing	[118]
	Food additive and animal feed	[20]
Peel extracts	Anti-cancer, anti-inflammatory	[113]
Adsorption capacity for water purification		
Potato peel + HCl	Cr^{6+}	[121,122]
Potato peel ash	As^- , F^-	[123]
Potato peel dry powder; pH 5	Cu^{2+}	[124]
Potato peel	Ni^{2+}	[125]
Potato peel	Methylene blue, malachite green	[126]
Banana, orange, potato peel	Heavy metals	[127]
Potato raw and burned peel	Cd^{2+} , Co^{2+} , Cu^{2+} , Fe^{2+} , Ni^{2+} , Pb^{2+}	[128]
Potato peel	Mn^{2+} , Fe^{3+} , Zn^{2+} , Ni^{2+} , Cu^{2+} , Cd^{2+}	[129]
Others		
Potato peel	biofertilizer	[119]

5.2. *Beta vulgaris* L.

Beetroot periderm is another example of the ‘edge’ effect. *Beta vulgaris* L. is a popular plant food with high nutritional benefits. The high biological activity of beetroot is directly connected to its significant fiber content, both soluble and insoluble, which is highly important for the food industry, with uses such as the enrichment of pasta, cakes and cookies. Another beetroot attribute is its betalain content, which is a natural water-soluble pigment of the class of nitrogen compounds that consists of betacyanins, which are responsible for red–violet color, and betaxanthins, accounting for yellow–orange color [130]. Furthermore, the antioxidant activity of betalains, which is associated with protection against degenerative diseases [131], has been demonstrated [132].

The significance of biochemical changes in beetroot periderm during storage reflects cultivar adaptability. Indeed, the data in Figure 8 indicate that such changes are species-dependent and are accompanied by significant decreases in peel AOA.

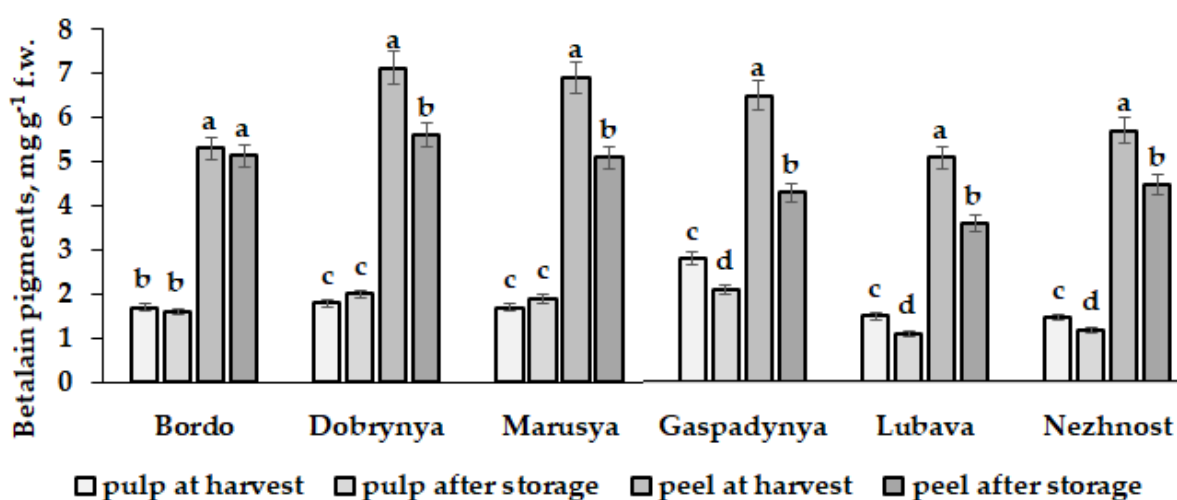


Figure 8. Effect of storage on peel/pulp betalain pigment levels of 6 cultivars with high (cvs. Bordo, Dobrynya and Marusya) and moderate adaptability (Gaspadynya, Lybava, Nezhnost). For each cultivar, values with the same letters do not differ statistically according to Duncan test at $p < 0.05$. (Supplement S3).

As far as pulp is concerned, the stability of its AOA is a good characteristic of plant adaptability. Among the cultivars tested, the highest adaptability was recorded in Bordo and to a lesser extent in the cultivars Dobrynya and Marusya. The significant decrease in the antioxidant defense of both peel and pulp during storage indicates the lower tolerance of the cultivars Gaspadynya, Lubava and Nezhnost to environmental factors. The main natural antioxidants of beetroot are phenolic acids (ferulic, vanillic, caffeic, protocatechuic, p-hydroxybenzoic), flavonoids (catechin, epicatechin, rutin) and betalain pigments (betacyanin, betaxanthin). The latter are of special importance as a unique natural pigment with high antioxidant activity and powerful biological effect, including hepatoprotective [133], anti-inflammatory, anti-aging, antidiabetic, cardioprotective and anti-cancer activity [134]. In this respect, the importance of root periderm is due to the 3–4 times higher levels of betalain pigment content compared to those of beetroot pulp. The utilization of beetroot betalains, as a natural colorant, stable at pH 3–7 [134], for the production of tomato paste, sauces, desserts, soups, jams, jellies, ice cream, sweets and snacks, as a food preservative due to its high antioxidant activity and as a supplement in the treatment of various diseases has been widely reported in literature (Table 4). The high adsorption capacity of beetroot periderm should also be highlighted, as it provides a great opportunity to extract uranium from wastewater [135]. Most of the biologically active compounds of beetroot (phenols, betalain pigments, organic acids, bioflavonoids) contain polar chemical groups (hydroxyl, carboxylic, carbonyl and amino), which form potential binding sites for uranium (VI).

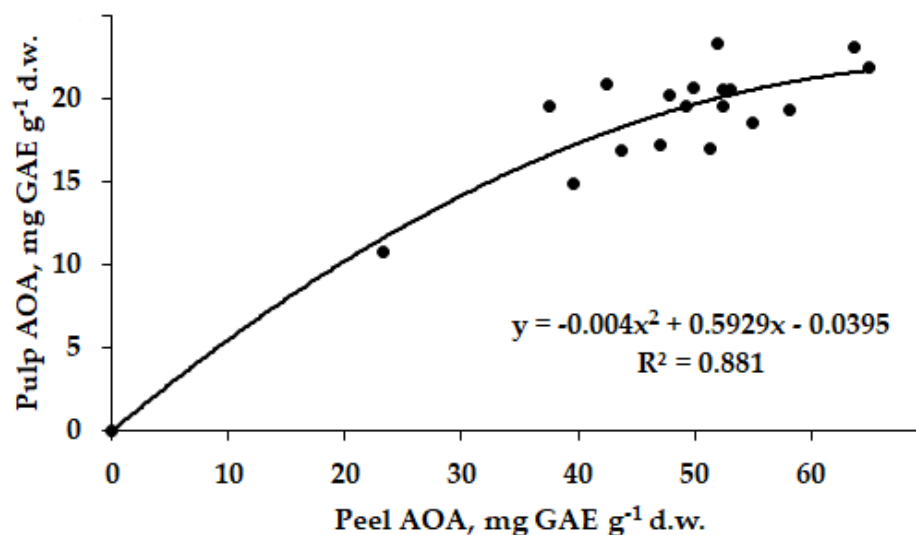
Table 4. Utilization of beetroot periderm.

	Active Ingredient	Properties	Ref.
Adsorption capacity	0.125 mm fraction of peel powder	U ⁶⁺	[135]
Antioxidant and antiviral effect	Peel powder	Improvement of Nile Tilapia storage	[136]
	Peel extract	Improvement of <i>Deccan mahseer</i> (Tor khudree) steaks storage	[137]
Medicine	Betain pigments, fiber, polyphenols	Degenerative diseases, anti-inflammatory, anti-aging, cancer prevention	[131,132]
		Hepatoprotective	[133]
Functional food, food additive and colorant	Peel powder	Food colorant, functional bread	[134]
		Mayonnaise	[138]
Others	Fresh peel	Mosquito attractant	[139]

Furthermore, geosmin from beetroot periderm was shown to be an excellent mosquito attractant. All the mentioned properties clearly reflect the exclusive properties of bordering tissues as examples of the ‘edge’ effect.

5.3. *Raphanus sativus* L.

In contrast to beetroot, radish roots accumulate pigments (anthocyanins) exclusively in the periderm, providing a powerful antioxidant defense via water-soluble antioxidants. This defense is enhanced by fat-soluble polyphenols, whose concentrations in radish periderm are almost three times higher than the corresponding concentrations in the pulp (Figure 9).

**Figure 9.** Relationship between peel/pulp AOA of radish roots (18 cultivars) (Supplement S4).

The statistically significant correlation between radish peel and pulp antioxidant activity presented in Figure 9 is a good example of the universal character of this phenomenon. Indeed, similar relationships were recorded for peel/pulp AOA of *A. cepa* L. and shallot bulbs, tomato fruit and beet (Table 5).

The general character of this phenomenon is proved by numerous examples of peel/pulp AOA relationship presented in Table 5.

Table 5. Correlation between peel and pulp antioxidant activity in different agricultural crops and betalain pigments in beetroot.

Species	N **	Mean Peel AOA ***	Parameter	Regression Equation ****	r
<i>A. cepa</i> L. red bulbs *	10	128	AOA	$Y = -0.009X^2 + 0.3756X$	+0.960
<i>Allium cepa</i> gr. <i>aggregatum</i>	8	123.4	AOA	$Y = -0.0012X^2 + 0.3548X$	+0.994
<i>Raphanus sativus</i> L.	18	50	AOA	$Y = -0.004X^2 + 0.5929X + 0.0395$	+0.939
<i>Solanum tuberosum</i> L.	8	15	AOA	$Y = -0.0127X^2 + 1.0921X - 0.0064$	+0.996
<i>Beta vulgaris</i> L.	6	30	Betacyanins	$Y = -0.0128X^2 + 0.5894X$	+0.968
	6		Betaxanthins	$Y = -0.02581X^2 + 0.5961X$	+0.991

* Nemtinov et al., 2019; ** number of varieties; *** in mg GAE g⁻¹ d.w.; **** Y: pulp AOA; X: peel AOA.

5.4. *Daucus carota* subsp. *sativus*

Carrot periderm is only 11% of the total carrot root weight, but is known to contain the highest levels of total polyphenols (54.1%) compared to the phloem (39.5%) and especially to the xylem (6.4%) [140]. Furthermore, carrot periderm accumulates significantly higher amounts of biologically active compounds, including carotenoids (+42%), organic acids (+103%), cations (+92%) and phenolic acids (seven times) than the root flesh [141]. However, a similar antioxidant distribution (periderm > phloem > xylem) has been recorded in other root vegetables [141].

The investigations of Hellström et al. [142] showed that mechanically stressed carrot roots (caused by washing, peeling, polishing or grating) may increase phenolic content, turning the inner tissues into the bordering ones. Nevertheless, the phenomenon of carrot root storage at reduced temperature may be applied to other vegetables. The efficiency of the antioxidant content increase depends greatly on the plant's genetic peculiarities. Great differences in the antioxidant status changes have been demonstrated in potatoes, broccoli, onion, celery and lettuce, and the effect is positively connected with the surface area of slices [143]. Lower levels of dry matter in root pulp compared to peel promote a more intensive increase in the total antioxidant activity (AOA) and polyphenol content (TP) in root pulp compared to peel as a consequence of root crushing and storage (Figure 10). Indeed, while a 1.5-fold increase in the AOA of celery root pulp was registered a week after root crushing, changes in periderm AOA and TP were not significant.

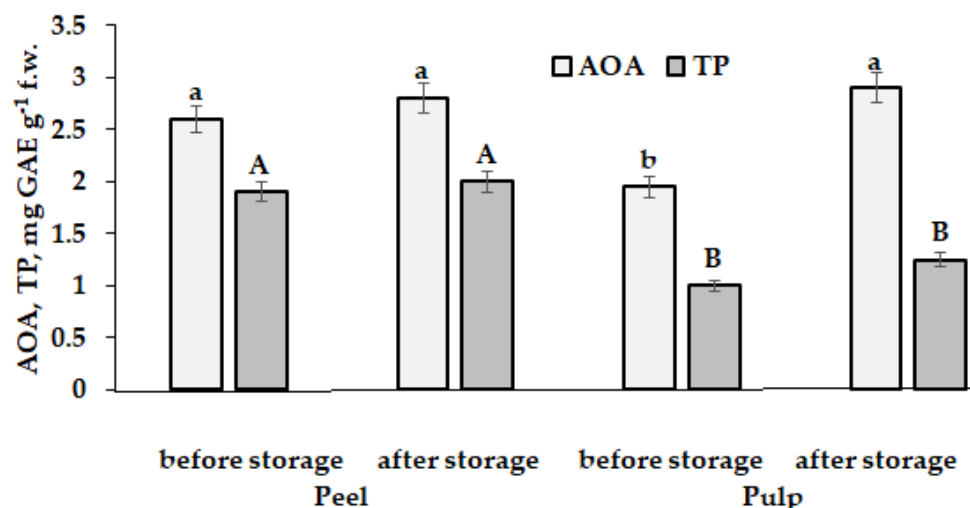


Figure 10. Changes in AOA and TP in crushed celery peel and pulp before and after storage at +4 °C during a week. Values with the same letters do not differ statistically according to Duncan test at $p < 0.05$.

A similar mechanism of secondary metabolite synthesis intensification due to oxidant stress takes place as a response to plant damage by herbivores and harmful insects [144].

5.5. *Allium* Species

Onion outer scales are among the most important agricultural by-products in the world, being highly valuable in medicine due to their antimicrobial, cardioprotective, antidiabetic, anticancer, neuroprotective and anti-obesity properties [145]. The outer scales have a physiological role in onion bulb growth, development and storage, because they provide mechanical, pathogen and antioxidant defense and water loss prevention during storage [146]. They are composed of dead cells, lacking active metabolism. The phenolic content of outer scales from different colored onions (pearl, red, yellow and white) was approximately six times higher than that of their fleshy edible parts [108]. Extracts from edible onion parts showed lower activity in all antioxidant tests carried out. Onion outer scales are known to predominantly accumulate quercetin aglucone, which is more bioavailable to the human organism than the quercetin glucosides present in the inner scales [147]. In this respect, the maximum plasma quercetin concentration of $1.02 \mu\text{mol L}^{-1}$ was reached 2.33 h after shallot flesh consumption, compared with $3.95 \mu\text{mol L}^{-1}$ recorded 2.78 h after dry outer scale consumption [147].

Data presented in Figure 11 a and b indicate species differences in AOA and TP content in the inner and outer scales of *Allium* plants, demonstrating the highest occurrence of polyphenols with reference to inner scale AOA and the absolute predominance of TP within the total antioxidant activity of *A. sativum* outer scales and bulb.

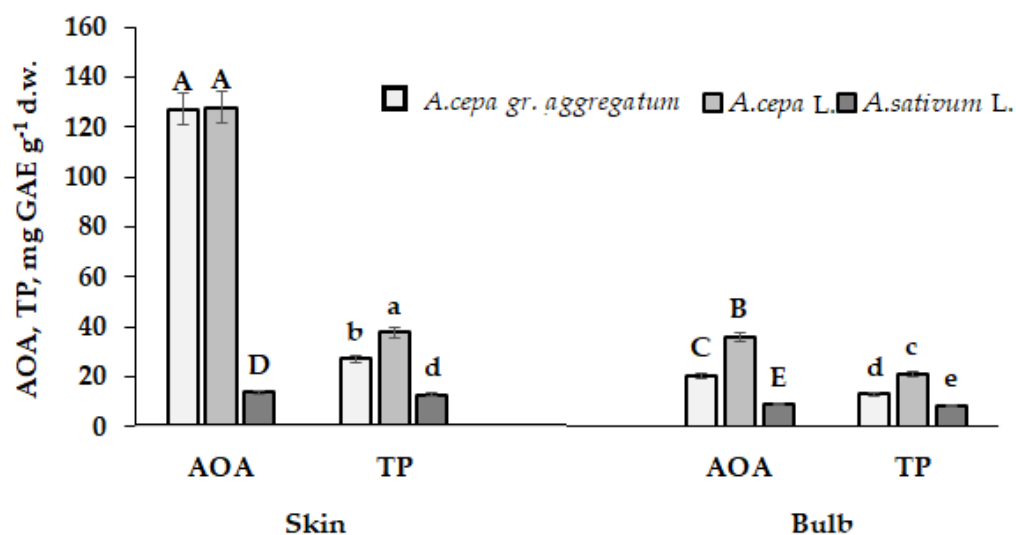


Figure 11. AOA and TP accumulation in outer and inner scales of *A. cepa L.*, *A. cepa gr. aggregatum* and *A. sativum L.* [148]. Values with the same letters do not differ statistically according to Duncan test at $p < 0.05$.

The comparison of lipid accumulation in the inner and outer scales of *A. cepa* in conditions of water stress against that occurring with adequate water supply indicates the high stability of this parameter in the outer scales under different vegetation conditions (Figure 12). However, a significant increase in the ratio between the outer and inner scale lipids was recorded as a consequence of a stress in cultivars with relatively low adaptability, compared to those tolerant to environmental stress (Figure 13). On the other hand, it may be supposed that the high adaptability of *A. cepa* cultivars is associated with the lower level of lipid outer/inner scale ratio, compared to cultivars with lower adaptability. Further investigations are necessary to disclose the significance of lipid accumulation for *A. cepa* breeding.

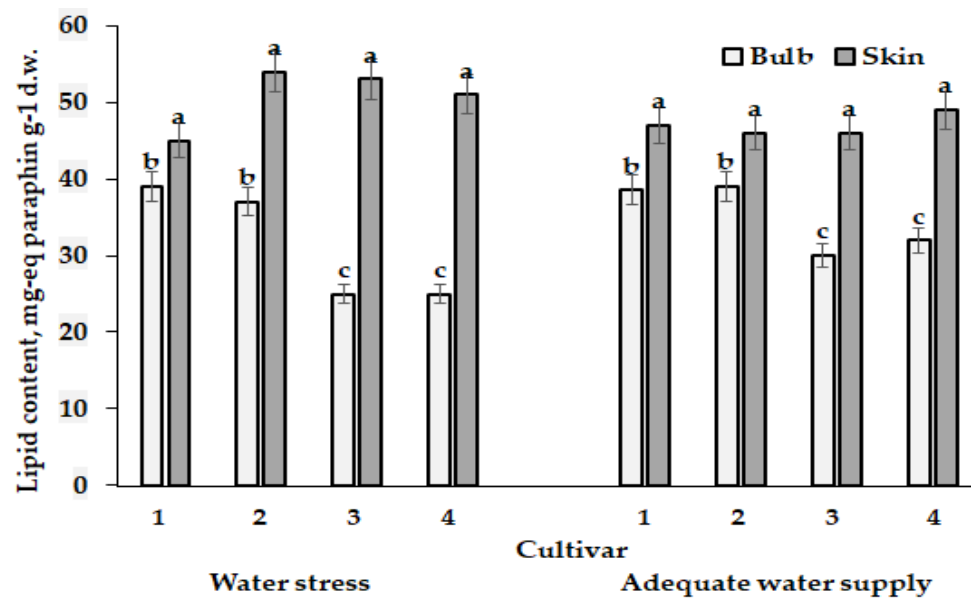


Figure 12. Lipid accumulation in outer and inner scales of *A. cepa* bulbs in conditions of water stress and adequate water supply (1-Zolotnichok, 2-Zolotie cupola, 3-Globus, 4-Myachkovski cvs.) (2021: high precipitation in the Amur region and adequate water supply in Moscow region). Values with the same letters do not differ statistically according to Duncan test at $p < 0.05$ (Supplement S5).

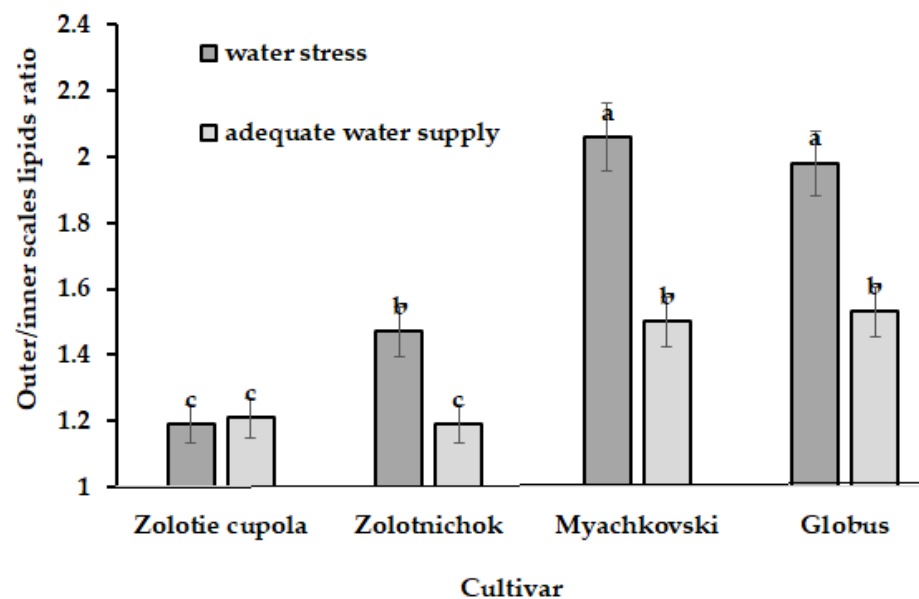


Figure 13. Effect of high humidity on lipid outer/inner scale ratio in *A. cepa* cultivars with high (Zolotie cupola and Zolotnichok) and moderate (Globus, Myachkovski) levels of adaptability. Values with the same letters do not differ statistically according to Duncan test at $p < 0.05$. (Supplement S5).

A. cepa outer scale utilization is closely connected with its high antioxidant activity, adsorption capacity and nutritional value [149] (Table 6).

Table 6. Utilization of onion outer scales.

Active Ingredient	Utilization Efficiency	Ref.
Adsorption capacity		
Anthocyanin containing onion peel	Removal of radioactive iodine	[150]

Table 6. Cont.

Active Ingredient	Utilization Efficiency	Ref.
Antioxidant effect		
Peel extracts	Cardioprotective, antidiabetic, anticancer, immunomodulatory, neuroprotective properties	[17,145]
Peel powder extract	Food preservative, pork sausages	[151]
Food additive and colorant		
Peel powder	Food colorant, functional bread	[152]

5.6. Cucurbita Species

Great species and varietal differences in antioxidant status of *Cucurbita moschata* Lindl., *C. maxima* Lindl., *C. pepo* L. and *C. ficifolia* Bouché (18 cultivars) were reported by Kostecka-Gugala et al. [153], although no data about exocarp/mesocarp differences have been presented. Investigations of *C. maxima* and *C. moschata* cvs. demonstrated small exocarp/mesocarp differences in total antioxidant activity and polyphenol accumulation [154]. By contrast, exocarp and mesocarp of *Cucurbita* plants were characterized by significant variations in macro- and micro-element distribution, suggesting the importance of mineral distribution in the ‘edge’ phenomenon (Figure 14).

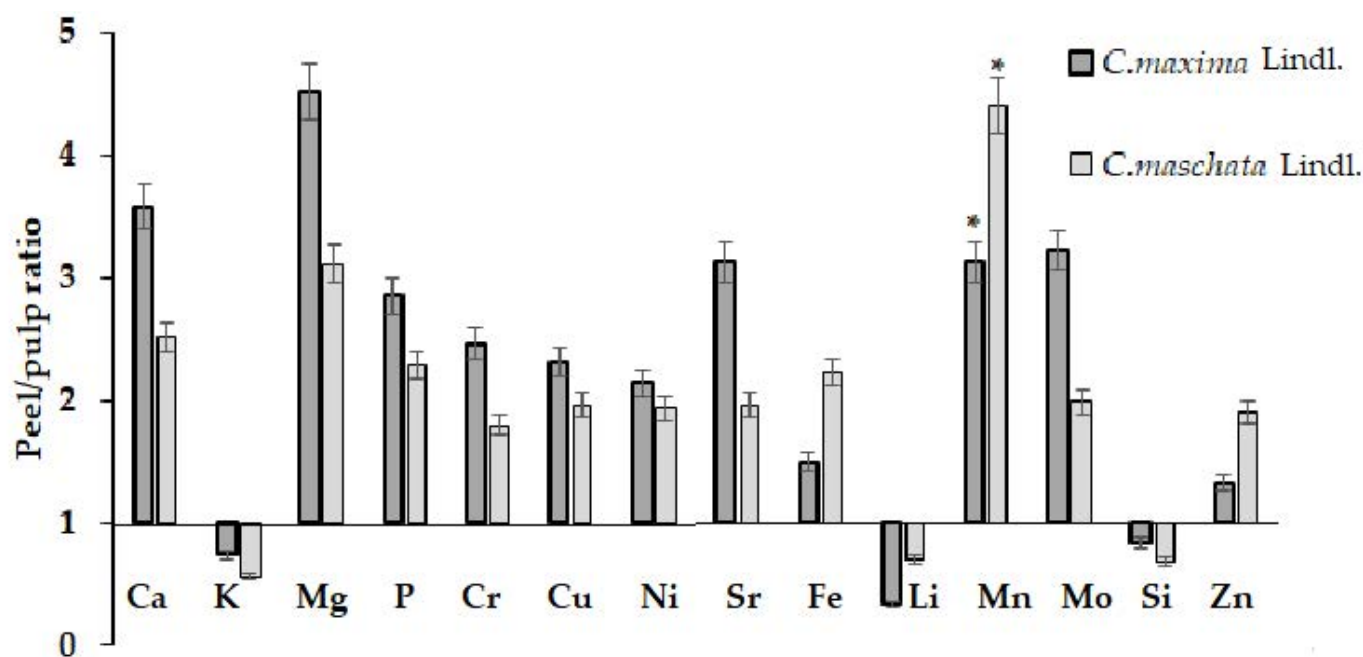


Figure 14. Exocarp/mesocarp differences in minerals accumulation. (* values are halved).

Notably, the biodiversity effect in the ‘bordering tissues’ has been clearly shown in the exocarp/mesocarp mineral distribution of *Cucurbita maxima* Lindl. and *Cucurbita moschata* Lindl. fruit (Figure 14) [154]. Only K, Li and Si predominate in fruit mesocarp, while other element concentrations were significantly higher in exocarp, especially Mn. The analysis of the relationship between elements in *Cucurbita* fruit revealed the highest correlations ($r = 0.85$ – 0.98) between Ca, Sr, Cr and Ni [154]. The variations in pumpkin exocarp utilization are closely connected with the main characteristics of the bordering plant parts, combining high antioxidant and adsorption activity (Table 7).

Table 7. Utilization of pumpkin exocarp.

Active Ingredient	Utilization Efficiency	References
Absorption capacity		
pulverized <i>C. pepo</i> L. peel	Cd, Co, Cr, Fe, Mn, Ni, and Pb removal	[155]
<i>Cucurbita</i> sp. Biocar	Methylene blue removal	[156]
activated carbon	Methylene blue removal	[157]
Antioxidant effect		
Peel extract	Oxidative stability of canola oil	[158]
	Antifungal activity against anthracnose in banana	[159]
Food additive and colorant		
<i>Helianthus annuus</i> L. oil extract	β-carotene enriched mayonnaise production	[160]
<i>C. maxima</i> Lindl., peel	Pectin, polysaccharides and fiber production	[161]
<i>C. maxima</i> Lindl., peel	Bread baking	[21]
<i>C. maxima</i> Lindl.	Carotenoids extraction	[162]

6. Other Agricultural Crops and Nanoparticle Production

The utilization of the peel of different vegetables proves the exclusive character of the outer tissues. In this respect, tomato fruit periderm is a good source of pectin, polyphenols and fatty acids and a tin corrosion inhibitor [163,164]. Fruit peel is also used to produce biodegradable packaging material [165].

Recent investigations show the interesting utilization prospects of plant outer tissues in the green synthesis of nanoparticles (Table 8), due to their powerful antioxidant properties and the high diversity of their biologically active compounds [166,167]. In this respect, periderm extracts provide not only chemically active reductants, but also a broad number of nanoparticle stabilizers, such as polysaccharides, proteins, etc. Furthermore, the high diversity of biologically active compounds in plant outer tissues raises the opportunity to valorize the effect of their synergism to enhance the benefits from single compounds to human organism.

Table 8. Examples of periderm extract utilization for production of nanoparticles.

Nanoparticles	Species Waste	Size, nm	Ref.
Au	<i>Beta vulgaris</i> L. waste	50–65	[168]
	<i>Salix alba</i> L. bark	15	[169]
	<i>Allium cepa</i> L. peel ethyl acetate extracts	<20 nm	[170]
Ag	<i>Ziziphus xylopyrus</i> B.Heyne ex Roth (Rhamnaceae)	60–70	[171]
	<i>Juglans regia</i> L. shell		[172]
	<i>Cucurbita pepo</i> L. and <i>Trichosanthes cucumerina</i> L.		[173]
	<i>Lagenaria siceraria</i> (Molina) Standl., <i>Luffa cylindrica</i> (L.), <i>Solanum lycopersicum</i> L., <i>Solanum melongena</i> L. and <i>Cucumis sativus</i> L.	20	[174]
	<i>Pinus sativum</i> L. and <i>Lagenaria siceraria</i> (Molina) Standl.		[175]
	<i>Pinus eldarica</i> (Medw.) Silba (Pinaceae)—Eldarica pine	10–40	[176]
	<i>Allium cepa</i> L. peel		[177]
Se	<i>Diospyros montana</i> Roxb.	120–200	[178]
	<i>Butea monosperma</i> (Lam.) Taub.	35	[179]
CuO	<i>Brassica oleracea</i> var. botrytis L. waste, <i>Solanum tuberosum</i> L. and <i>Pisum sativum</i> L. peel		[180]
ZnO	<i>Moringa oleifera</i> Lam. peel	40–45	[181]
	<i>Allium cepa</i> L. peel	20–80	[182]
Fe ₂ O ₃	<i>Salvadora persica</i> L. bark		[183,184]

7. Conclusions

The presented data indicate important peculiarities of the ‘edge’ effect in plant outer tissues: (i) high diversity in the morphological, biochemical and mineral characteristics of bordering tissues, which improve plant adaptability to different environmental factors; (ii) great possibilities for plant outer tissue utilization based on its enhanced antioxidant status and high adsorption abilities; (iii) the opportunity to improve plant defenses via mechanical or biochemical changes to plant outer tissues and (iv) the importance of outer tissue biochemical characteristics in plant breeding. The revealed patterns are important for the implementation of the plant ‘edge’ effect in agricultural crop production, food and pharmaceutical industries and non-waste production. Further investigations are needed to elicit new prospects for the use of the ‘edge’ effect in agricultural crop breeding and protection methods against environmental stresses.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15010123/s1>, Supplement S1: Effect of foliar sodium selenate and selenocystin supply on wax accumulation at the surface of bean seeds, Uliasha cv (0.26 mM solution); Supplement S2: Determination of potato peel, pulp antioxidant status; Supplement S3. Determination of betalain pigments in beet peel and pulp; Supplement S4. Radish antioxidant activity; Supplement S5 Effect of water stress on lipids accumulation in inner and outer scales of *A. cepa*. References [185,186] are cited in the supplementary materials.

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