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Elimination Processes in Higher Plants

A. FREY-WYSSLING

RÉSUMÉ

Les métabolites d'une plante qui ne sont plus soumis au "turn-over" sont éliminés. Comme les possibilités d'élimination externe sont restreintes, la plus grande partie s'accumule dans le végétal. Selon leur position dans le métabolisme on peut distinguer les substances résorbées (récrétions), assimilées (sécrétions) ou dissimilées (excrétions).

SUMMARY

Plant metabolites that are no longer under the submitted influence of the turn over are eliminated. As the possibilities of an external elimination are restricted, the greater part accumulates in the plant. In terms of their position in the metabolism these substances can be resorbed (recretions), assimilated (secretions) or dissimilated (excretions).

ZUSAMMENFASSUNG

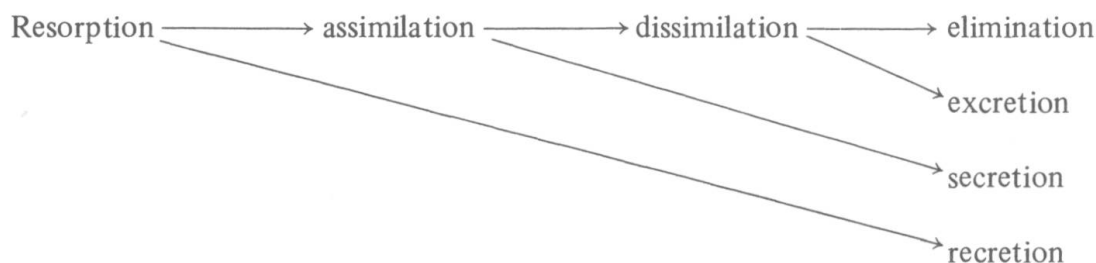
Die Stoffwechselprodukte einer Pflanze, die nicht mehr dem "turn-over" unterworfen sind, werden ausgeschieden. Da die Möglichkeiten der Ausscheidung nach aussen gering sind, wird der grösste Teil dieser Stoffe in der Pflanze abgelagert. Nach der Art ihrer Stellung im Stoffwechsel hat man zwischen resorbierten (Rekretion), assimilierten (Sekretion) oder dissimilierten (Exkretion) Substanzen zu unterscheiden.

Metabolism proceeds along the four steps: resorption, assimilation, dissimilation and elimination. In plants the CO₂ and inorganic ions resorbed are hydrogenated into assimilates. About one third of these is dissimilated by respiration for the production of ATP necessary for energy consuming life processes. The other two thirds are said to be used partly for growth and partly as reserve

material stored in special tissues (starch, oil, aleuron etc.). The substances stored can be brought back into metabolism by hydrolysis, in the same way as the organelles of differentiating cells which are constantly disintegrated by lysosomal hydrolases and reorganized in the so-called turnover.

As resorption goes on and on, it is evident that turnover and storage cycles would undergo an intolerable inflation if there were no elimination. Considering these facts, it is astonishing that, in contrast to the activities of animal nephridia or kidneys, plants are believed to lack elimination processes. Before this axioma is disproved, the following must be considered.

Substances may be eliminated directly after resorption, after assimilation or finally after dissimilation:



According to this scheme three types of elimination processes must be distinguished: recretion eliminating unnecessary resorbates, secretion secreting assimilates and excretion eliminating dissimilates.

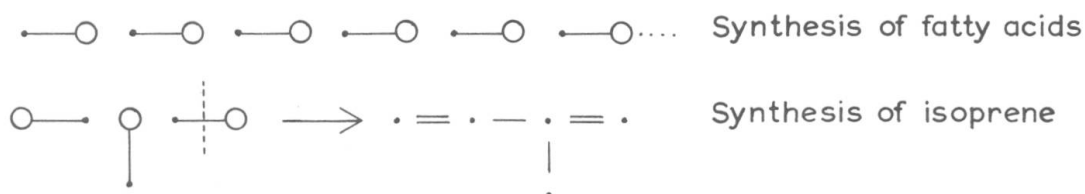
These definitions are not in accordance with those used in animal and human physiology, sciences which define excretions as products containing eliminated katabolites (dissimilates) such as urine or sweat, and secretions as fluids which serve a certain physiological purpose such as gastric sap, bile, tears etc. This classification is illogical insofar as excretion is defined as a metabolic step, whilst secretion is characterized by teleological considerations. In plant physiology this view is unacceptable because it is impossible to assign general physiological "purposes" to such eliminates as latex, resins, phlobaphenes, waxes etc. Of course there are many teleological hypotheses which, however, are unsatisfactory. Therefore, I proposed the more biochemical classification described based on metabolism. Another reason for its introduction was the fact that the mineralization of wood, ageing leaves and straw is not necessary for the strength of the reinforcing tissue in plants, in contrast to the function of bones in animals. For example, the haulms of non silicified cereals have the same strength as when mineralized with this ash component. As a consequence the concept of recretion was created (Frey-Wyssling 1935a).

In the system proposed elimination products are defined as compounds which are not stored for remobilization and redistribution of their enzymatic degradation products, such as starch, glycogen, inulin, reserve proteins, phytin etc., but as metabolites which are withdrawn from active translocation. Whether such metabolites are excretions or secretions depends on their status as dissimilates or assimilates. In the following discussion it will be shown why most of the secondary plant compounds (Paech 1950) must be considered as dissimilates.

Excretions (eliminated dissimilates)

Terpenoids

In the synthesis of terpenoids the same catalyst, co-enzyme A, is involved as in the synthesis of fatty acids (Bonner & al. 1954). In both cases groups of acetate (CH_3COOH or —O) are linked together:



However, there is a difference in that fatty acids are generated by a head tail arrangement of the acetate groups, whilst for the biosynthesis of terpenes three such groups are arranged in an unorthodox way leading to mevalonic acid which, after decarboxylation is transformed into isopentenyl-pyrophosphoric acid and finally into isoprene, i.e. the monomeric configuration of the terpenes (rule of Ruzicka 1938). In this way the terpenes are dissimilated from the very beginning of their biosynthesis, because their molecular structure does not resemble that of the assimilates fat and phosphatides with their extended fatty acid chains. As a consequence the terpenes (rubber, resins, betulin, etheric oils etc.) do not play any physiological role.

Alkaloids

Many alkaloids are formed by cyclization of amino acids (Mothes 1969). In this process amino groups —NH_2 become members of heterocyclic rings by transformation into imino bridges —NH— . In this state, nitrogen is no longer available for transamination so that the important function of the amino group as N-donor in the transformation of α -keto-acids into amino acids is lost. From this point of view such alkaloids are dissimilated because they are removed from the chain leading to the amino acids necessary for the synthesis of specific proteins.

In the purine alkaloids (theobromine, coffeine etc.) another phenomenon of dissimilation occurs. These compounds correspond to the purine bases of nucleotides. However, instead of being used for incorporation into nucleic acids, they are methylated (theobromine = 3,7-dimethyl-xanthine, coffeine = 1,3,7-trimethyl-xanthine), whereby their polarity is increased so that they become soluble in water, whereupon they are excreted into the sap of the cell vacuole.

Glucosides

The aglucones of plant glucosides are not easily dissolved or even insoluble in water (Frey-Wyssling 1942). This is especially true for polyphenols and anthocyanidins. Glucosidation facilitates the solution of these compounds in water, so that they can be excreted into the central vacuole of the plant cell.

Glucosides are not definite elimination products because they may be metabolized. This has been shown for anthocyanins (Frey-Wyssling & Blank 1943, Zenk 1967) and tannins (Taylor & Zucker 1966). However, the view that glucosides represent reserves of sugars must be abandoned because their amount fixed by glucosidation is negligible as compared to the sugar content in starch, glycogen or in the sell sap. For instance, a seedling of red cabbage 30 mm long) contains 800 μg reducing sugars but only 4 μg glucosidic sugar (Frey-Wyssling 1949: 265).

The instability of the glucosides in the vacuoles is natural because these organelles represent lysosomes with a set of hydrolases, but the fact that they are constantly produced and appear rhythmically in the vacuole (Zenk 1967) is an indication that the aglucones represent a product of elimination. However, they are not definite but intermediate products of the katabolism.

Secretions (eliminated assimilates)

In plant physiology it is rare that a function can be attributed to the elimination products. Therefore, as indicated in the introduction, I have proposed calling all eliminated assimilates secretions, irrespective of whether they fulfill an obvious function or not. In opposition to storage compounds (starch, oil, aleuron), the assimilates secreted are reconveyed to metabolism, if at all, only in minor quantities.

The bulk of secretions is represented by the plant cell wall (Frey-Wyssling 1935b). Its compounds are eliminated through the plasmalemma by the activity of special organelles. The hemicelluloses, pectic material and mucilages are secreted in an oligomeric state by means of Golgi vesicles, whilst in the case of cellulose, which arises extracellularly, monomeric molecules leave the cell and form cellulosic elementary fibrils by concomittant polymerization and crystallization. It is of special interest that, although the cells of higher plants contain cellulase, cell walls already formed are not, as a rule, attacked by this enzyme. Only exceptionally when cell fusions of xylem elements or latex vessel members occur, an obvious turnover of cell wall compounds is observed. In contrast to the internal skeleton of animals with its pronounced turnover, the bulk of the wall material in the external skeleton has been eliminated definitively by the plant cell.

Further secretions are the sugars of nectar. Since nectaries are met with in the flowerless pteridophytes (e.g. *Pteridium aquilinum*), the wide-spread extrafloral nectaries of the phanerogams must be phylogenetically older than the

floral nectaries and, therefore, the nectarial sugars acquired their biological significance for entomophily only in more recent times.

Nectar contains, besides its sugars, small amounts of many other compounds (Lüttge 1961) such as malic acid which may be the product of anabolic as well as of katabolic metabolism (Ziegler 1965). However, the lower carbonic acids are not final but typically intermediate metabolic products, small quantities of which are of general distribution in the plant. In a similar way the excretion of urea and uric acid by the kidney is accompanied by the elimination of minor quantities of oxalic acid, hormones and other compounds. In such mixtures only the main component should be used as a criterion in deciding whether the eliminated fluid is an excretion or a secretion.

Recretions (eliminated resorbates)

All living cells constantly resorb salts in order to maintain the intracellular ionic equilibrium necessary for metabolic processes. The uninterrupted influx of salts must be compensated by their continuous elimination. In plants this activity is enormous. In special cases the ash content of leaves or bark can reach over 90% of their dry weight, whereas the protoplasts need only 1-2% of their dry weight in salts for the performance of their metabolism.

The spectacular accumulation of mineral compounds is due to the lack of elimination organs. Only a few halophytes have developed glands for salt elimination. Therefore, the salts are accumulated in the cell walls, where the water of transpiration which was their vehicle is evaporated. As a consequence the leaves become more and more mineralized. Since the univalent ions K^+ and Na^+ are elutriated by rain (cuticular recretion), the mineralization is mainly represented by lime and silica incrustations.

The recretion of these two ash substances can also be performed by special cells (idioblasts) which produce cell wall invaginations that become incrustated with carbonate of calcium (cystoliths) or silica (silica cells).

An important feature is the elimination of calcium ions in crystals of oxalate. Calcium oxalate is one of the most insoluble salts, and it is interesting that often specially preformed cells are the only place where the two ions Ca^{++} and $C_2O_4^{--}$ are allowed to meet and crystallize. This physiological control of the crystallization is the reason for the astonishing morphological variety of the recreted calcium oxalate (crystal sand, solitary crystals, druses, styloids, raphides).

Since oxalic acid can be metabolized in different ways, the view that the formation of its calcium salt is a means of eliminating the "poisonous" oxalate ion cannot be valid. Also another theory according to which the oxalate crystals are considered as a reserve substance for calcium (because in plants brought into a culture medium without calcium the crystals may display signs of corrosion) must be refuted because plants which eliminate calcium oxalate grow naturally on soils which contain sufficient calcium.

Translocation of elimination products

For long distance transport assimilates, and therefore also secretions, are translocated in the phloem. In contrast to this kind of displacement, excretions behave in quite another way. Two examples may be mentioned.

Wanner & al. have shown by means of the isotope method that coffeeine eliminated into the cell vacuole is no longer displaceable, in opposition to trigonelline (1961) or allantoin (1966). It is true that coffeeine, as all contents of the vacuole, can be katabolized into allantoin or even CO_2 , but the possibility of its transfer is lost. This is unexpected because coffeeine is water soluble which is the prerequisite for the elimination of its labelled molecules into the vacuole. Whereas C_{12} (saccharose), C_{18} (raffinose) and C_{24} (stachyose) compounds are readily dislocated in the tissues, the molecule of coffeeine with its 12 members (C_8N_4) cannot be translocated unless it is transformed by the turnover.

Most interesting is the long distance translocation of nicotine which is synthesized in the root of the tobacco plant. The translocation does not occur in the phloem, but unexpectedly with the water for transpiration in the xylem. This can be shown with bromocyanic acid which is a fluorochrome for nicotine (Schmid 1948). As a consequence of this transport the older (lower) leaves of the tobacco plant which transpire for a longer period than the younger (upper) leaves, contain more nicotine per weight and per surface unit.

The passive long distance transport of nicotine in the xylem is equally valid for all the alkaloids which are produced in the roots of other *Solanaceae*.

Eliminating organs

For the physiologist the question which compounds of the cell contents have to be considered as elimination products has become obsolete because the turnover can attack almost all cellular compounds (Zenk 1967). On the other hand the histologist has to deal with a variety of characteristic elimination tissues in higher plants. Haberlandt (1884/1918) distinguished with good reasons storage tissues with reserve compounds which may be quantitatively brought back into metabolism and tissues of elimination (organs for secretion and excretion) which eliminate substances definitively or deposit them in specialized cells (idioblasts for tannins, resin ducts, laticifers etc.). Therefore, one must not belittle the problem of elimination in plants. Phylogeny shows that special localities for the deposition of certain compounds, the reason of which is not yet known, have evolved.

A short characterization of such elimination and deposit systems follows.

Emissaries

The glands (Ziegler 1965) for the elimination of sugars (nectaries), water (active hydathodes) and salts have a similar histological structure allowing the elimination of liquids across the cuticular barrier. Sometimes it is difficult to distinguish between hydathodes and nectaries or hydathodes and glands for salt elimination, because exuded water may contain small amounts of salts or sugars. For these reasons, Pfeffer (1897) proposed subsuming the three types of glands mentioned under the common term "emissaries". In this way a decision whether the exuded substances are excretions, secretions or recretions may be avoided.

However, histological specialities of the emissaries give some indications concerning the physiological status of the different products of emission. Many emissaries show direct relations with vascular bundles, nectaries being connected with the phloem (Frey-Wyssling 1955) whilst hydathodes and salt glands communicate with the xylem. This means that the nectaries are provided with assimilates (secretions) and the hydathodes with inorganic recretions.

Hydathodes often contain a special tissue called "epithem", which serves for the resorption of valuable ions contained in the water of the transpiration stream, so that the guttation fluid exuded is very poor in minerals or enriched in recretional calcium and silicic acid.

Another function is found in the elimination tissue of the nectaries where phloem sap is transformed by inversion of its saccharose and a change of its other substances, so that finally the composition of the nectar differs considerably from that of the original sap in the sieve tubes (Lüttge 1961). In both nectaries and hydathodes the elimination tissues contain striking amounts of acid phosphatase as shown by the Gomori test (Häusermann & Frey-Wyssling 1963). As this enzyme could not yet be revealed in the salt glands of *Statice*, maybe there is no resorption activity involved.

Glandular hairs

Glandular hairs are capable of exuding elimination substances through the cuticular barrier in a similar manner as emissaries. Most diversified compounds are eliminated by such glands: in the first place volatile terpenes (etheric oils), but also guttation water, mucilages and, in insectivorous plants hydrolyzing enzymes for extracellular digestion.

Whereas no conclusion has been reached concerning the cell organelle (plastids? endoplasmic reticulum? groundplasm?) producing terpenes in the glandular cells of the hairs (Schnepf 1969), the secretion of mucilages is known to be performed by the Golgi apparatus through exocytosis (Schnepf 1968, 1969).

The elimination activity of glandular hairs can thus apply to dissimilates as well as to assimilates.

Intracellular and intercellular accumulation

Kisser (1926, 1958) has shown that, after the loss of the glandular hairs, the labiate *Plectranthus* accumulates its terpenes in peridermal cells. These "oil

cells" are characterized by an intracellular sac into which the elimination products are excreted. As a rule the cell wall of such idioblasts is subsequently suberized, so that the nature of their contents is clearly that of dissimilates which are definitively eliminated; i.e. although accumulated in a living tissue they are no longer accessible to metabolism.

However, the capacity of such oil cells is limited. As a consequence a more considerable production of eliminates is deposited in extracellular oil ducts, schizogenous or lysogenous cavities, resin canals, slime ducts etc. In this way extracellular spaces are produced for the storage of both excretions (terpenes) and superfluous assimilates (mucilages, slimes), which cannot be eliminated through the hydrophobic protective "skin" of the transpiring plant.

Of course, such internally accumulated products are subject to biochemical changes by dehydration, oxidation or enzymatic decay, similarly to eliminates which have left the organism (e.g. urine, excrements). Therefore, the opinion that only metabolic products which remain quantitatively and qualitatively unaltered after elimination can be called excretions must be abandoned.

Latex tubes

The same is true for the contents of laticifers and latex tubes. Spence & McCallum (1935) established that the rubber content in the terpene holding parenchyma of the Mexican rubber plant guayule (*Parthenium argentatum*) changes periodically with the seasons. For instance, they found in May 55g, in October 65g and in February 60g rubber per plant. From this they concluded that rubber was a reserve substance like starch. However, these changes are small as compared to those of starch which, in a budding shoot, may disappear completely from the xylem parenchyma. Moreover acetone was used for the separation of rubber from other hydrophobic contents in the guayule shrub, so that oxidized rubber which is soluble in this solvent was lost. Since oxidation phenomena cannot be excluded in the parenchyma cells into which rubber is excreted, the changes observed may reflect seasonal transformations of formed rubber into oxirubber.

This example shows that not only an intracellular turnover caused by the lysosomal hydrolases takes place, but that also biochemical reactions occur which do not lead to units for a renewed anabolism. As a consequence there is no substance inside the cells which is proof against chemical transformation, and thus there are no unchangeable metabolic "endproducts", unless they leave the organism. Only at that moment definite elimination products can be collected before their post-metabolic transformation (by dehydration, oxidation, microbial hydrolysis etc.) occurs extracellularly.

Vacuoles

Here we meet the most difficult problem concerning elimination in plant cells, i.e. the question whether certain substances in the central vacuole may or must be considered as elimination products. As long as only vacuoles containing tannins, the variable contents of which never become completely free of phenols, and aleuron vacuoles, whose proteins are quantitatively resorbed

in germinating seeds, were known, the functions of the central vacuole seemed to comprise, besides osmoregulation and cell elongation, the accumulation of reserve products (sugars, proteins) and dissimilates (excretions).

However, the discovery of lysosomes in plant cells by Matile (1968) has completely changed the situation. It can be shown (Matile 1969) that provacuoles given off from strands of the endoplasmic reticulum and their derivatives, including central vacuoles as in yeast, contain numerous hydrolytic enzymes. With this discovery the clue was found for an understanding of the cellular turnover.

This turnover poses the following important problem. As the organism and each cell continuously resorbs ions and molecules as long as it lives for its anabolism, the turnover would be indefinitely inflated, if there were no eliminatory processes. Therefore, that part of the assimilates which is not invested in growth or accumulated in storage tissues is balanced by adequate elimination, and since not all metabolites are katabolically reduced to water and carbonic acid, all kinds of excretions may result.

Phylogeny of elimination processes in plants

The development of biochemistry preceded biological morphogenesis by a kind of phylogeny called chemical evolution. No chemical compound could assume a physiological function before it had been produced by "mutational steps". Whether such chemical mutations were random or directed is irrelevant, because in any case synthesis had to precede function.

The algal phyla could only evolve after photosynthesis had been established and higher plants could only leave the sea and settle on land after, among all the many types of carbohydrate oligo- and polymers (Frei & Preston 1964, 1968) found in algal cell walls, cellulose had proved to be most suitable for the cellular exoskeleton of terrestrial organisms. And only after the incrusting substance lignin had been "created", the tensile strength of the cell walls became sufficiently resistant to compressive stress for the development of an efficient water conducting xylem enabling the enormous size of mammoth trees.

Similarly the different terpenes and alkaloids arose in the plant kingdom by mutational variations in existing trends of synthetical possibilities. However, many of the substances produced have not gained the same metabolic importance as nucleic acids, proteins and carbohydrates.

Since phylogeny is essentially conservative, syntheses of organic compounds realized are often firmly adhered to and, in general, progress consists in varying these in all possible directions, where upon the value of the new substances produced is "tested" by trial and error. In this way, besides useless substances, the valuable metabolites have evolved. From this point of view it is not astonishing that among the terpenes and alkaloids serving no useful purpose, some physiologically important compounds, such as certain carotenoids and terpenoid sterenes have arisen. However, these indispensable physiological agents play a negligible role quantitatively, as compared to the amounts of resins produced by certain conifers or to the rubber in a *Hevea* tree. Therefore, most terpenes must be

considered as eliminates with the restriction that also in biology there is no rule without exceptions.

In any case, the problem of elimination must be considered in the first place from a chemical and not from a functional point of view, because in phylogeny any compound must have come into existence before it could take charge of a function. The task of primary assimilates (building material, reserve substances, enzymes, vitamins, hormones etc.) is evident, but for secondary compounds the attributing of doubtful functions bases on unscientific teleology.

Summary

During growth and later in connection with the equilibrium metabolism, the cell continuously resorbs substances, the major part of which are assimilated and subsequently enter the turnover. Since this cellular turnover cannot be arbitrarily inflated, a certain amount of these substances must also be permanently eliminated. Insofar as these metabolites are not the respiration products water and carbonic acid, similar problems arise as for resorbed substances, i.e. active translocation with energy consumption, selectivity etc. Since in higher plants only about a third of the assimilated carbon is respired, a considerable amount of organic matter must continuously leave the symplast.

Recretion

The resorption of salts include complex anions (NO_3^- , HPO_4^{--} , So_4^{--}) which are assimilated and cations (K^+ , Mg^{++} , Ca^{++}) which establish the physico-chemically balanced environment necessary for the metabolic performances in the cell. The intake of these ions is governed by the two principles of ion competition and ion selectivity. However, the ion selection is not fully efficient. As a consequence, the continuous intake of necessary and superfluous ions must be balanced by a constant elimination of salts in an analogous way to the continuous elimination of sodium chloride from the blood by the kidneys. This elimination which regulates physiologically the optimum table of ions and salts in the cell is *Recretion*.

Secretion

Not all organic matter assimilated by the plant passes through the turnover. There is a considerable excess which is temporarily deposited in storage tissues or definitively invested in cell walls. For removal processes, the cell has special organelles at its disposal: plastids for the storage of starch, lysosomal vacuoles for the production of aleuron grains, spherosomes derived from the endoplasmic reticulum for the accumulation of lipids and the Golgi apparatus for the transfer of carbohydrates into the pericellular wall. Whereas stored reserve material may be quantitatively brought back into metabolic circulation, cell wall material is,

as a rule, not remobilized although the plant possesses the necessary enzymes for the degradation of hemicelluloses and cellulose. The bulk of the substances invested in secondary cell walls is, therefore, definitively eliminated by a process of *Secretion*.

Excretion

Higher plants are protected against excessive loss of water due to transpiration by elaborate hydrophobic surface layers (cuticle, cutinized epiderm, periderm). Because organs for substance elimination are a source of water loss, as shown by the emissaries, no general elimination system has been developed in plants comparable to the nephridia or the kidneys in the animal kingdom. As a consequence the so-called secondary compounds produced by plant metabolism must be deposited intracellularly (latex tubes, vacuoles) or intercellularly. Since these substances do not leave the organism, their chemical composition may change due to enzymatic oxidation or degradation. In this respect their destiny is similar to that of eliminates which have left the organism and are attacked by atmospheric influences, bacteria and fungi. Since such substances do not represent plastic material used in growth processes but aplastic accumulations which may rise to substantial amounts (e.g. nicotine more than 10% of the dry matter in leaves of *Nicotiana rustica* or rubber more than 60% in fresh latex of untapped *Hevea* trees), they must be regarded as *Excretions*.

Intermediate metabolic products

A special group of metabolites are the lower carboxylic acids, as for instance the representatives of the citric acid cycle which occur as assimilates in the anabolic (e.g. pyruvic acid in the synthesis of alanine) as well as katabolic dissimilates (e.g. pyruvic acid in anaerobic fermentation). However, such compounds are typical building stones for the synthesis of plastic material which is not the case for the alkaloids, terpenes and phenols, even if they may partly be used as substrates for respiration.

For all these reasons, the classification of the elimination processes in the plant kingdom into recretion, secretion and excretion seems to be helpful, as long as no better, more lucid or logical terminology is found. It permits the placing of the elimination of mineral matter, terpenes and alkaloids which, in general, are treated only superficially, if at all, in introductory courses in plant physiology into the framework of *General Physiology*.

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