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Machinism of abscission of leaves and reproductive parts of plants — a model

LESZEK S. JANKIEWICZ

Departamento de Fitotecnia, Universidad Autónoma Chapingo, 56230 Chapingo, Méx., Mexico*

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Abstract

Abscission of leaves and reproductive parts of plants is presented in the form of a model which allows the reader to see the process as a whole. The process of abscission was divided into 2 parts: the first of which may be inhibited or reversed by auxin, and the second, which is mostly irreversible. Increased ethylene (ET) production links the earlier phases of senescence with abscission. ET has a double role in the initiation of the abscission process: (1) acting on the leaf blade, it withholds the export of auxin from a leaf, in consequence the abscission zone (AZ) is scarcely supplied with this hormone. When this state lasts sufficiently long, AZ tissues become sensitive to the second action of ET, (2) that is, to its dorect action on the AZ. When this occurs, the further stage of abscission is triggered. The possible roles of abscisic acid, tyloses and the influence of environmental factors are also discussed. During the further, mostly irreversible stage of abscission, marked stimulation of metabolic activity takes place in the AZ and its tissues attract nutrients. Sharp hormonal gradients appear in the AZ, leading probably to the precise localization of the "separation stratum" in the AZ where the detachment finally occurs. Further on, the detachment of the plant part may be accomplished in different ways, however, one "way" does not exclude the simultaneous participation of other(s). Thus, abscission may be accomplished by the enzymatic degradation of the middle lamella and primary cell wall, or by inducing cell divisions in the separation stratum with subsequent breaking of the newly formed cells. It can occur

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* The materials for this publication were partly collected by the author during his work at the Research Institute of Vegetable Crops, Skierniewice, Poland, which is his permanent address.

Abbreviations used: ABA — abscisic acid, AZ — abscission zone, ET — ethylene, ETP — ethephon, GA — gibberellins, CK — cytokinins, SST — separation stratum, (a substitute expression for "separation layer or abscission layer").

as well due to uneven augmentation of the cells belonging to the neighbouring cell layers which results in mechanical strain among them and in tearing apart. Separation may occur also due to a collapse of the cells of the AZ which leads to the formation of empty spaces. The problem of infallibility of physiological processes is briefly discussed.

Key words: abscission model, fruit abscission, leaf abscission

Resumen

Se presenta en forma de un modelo la abscisión de hojas y partes reproductivas de la planta. Esta forma de descripción permite al lector apreciar el proceso completo. El proceso de abscisión se dividió en dos partes: La primera que es reversible por medio de tratamiento con auxina y la segunda que es en su mayoría irreversible. Un aumento en la producción de etileno sirve de enlace entre las fases más tempranas de senescencia y la abscisión. El etileno (ET) muestra un doble efecto en la iniciación. El etileno (ET) muestra un doble efecto en la iniciación de la abscisión: Primero, actuando en la lámina de la hoja, detiene la salida de auxina de la lámina, en consecuencia, la zone de abscisión (ZA) tiene un suministro limitado de esta hormona. Cuando esta condición dura por un período de tiempo suficiente, los tejidos de la ZA se vuelven sensitivos a la segunda acción del ET, en la cual esta hormona actúa directamente en la ZA. Cuando estos dos efectos del ET coinciden, o sea cuando el ET actúa en la ZA ya sensibilizada al mismo, el mecanismo que desencadena las fases posteriores de abscisión se continúa. A partir de este momento el proceso de abscisión no puede ser revertido por la auxina. También se considera los posibles papeles del ácido abscísico, tilosas, y la influencia de los factores ambientales. Después de que el mecanismo que activa los estados posteriores de abscisión continúa, en la ZA se presenta una marcada estimulación de la actividad metabólica así como un aumento en la síntesis de ARN y proteína. La ZA también se vuelve el lugar de atracción de nutrientes, también se presentan marcados gradientes hormonales en la ZA, causando probablemente que el "estrato de separación", en el cual se presenta finalmente la separación esté precisamente localizada en la ZA abarcando frecuentemente no más de 2-3 capas de células. Posteriormente, el proceso de abscisión progresa de diferentes maneras, sin embargo, una manera o forma no excluye participación de las otras en la abscisión de la parte dada de la planta. Las más importantes de estas "maneras" son degradación enzimática de la lámina media y la pared celular primaria de las células, que lleva al desprendimiento ; o inducción de divisiones celulares que cause subsecuentemente el rompimiento de las células recién formadas. Otra "manera" consiste en un aumento desigual de las células que pertenecen a determinadas capas celulares transversales de la ZA. Esto genera una tensión mecánica entre ellos facilitando que se rompa el contacto entre las mismas. En otra "manera" las células de la ZA se colapsan, llevando a la formación de espacios vacíos en los tejidos de esta zona y finalmente a su ruptura. El problema de la infalibilidad de los procesos fisiológicos se discute en forma breve.

Contents

1. INTRODUCTION

Physiological processes such as abscission seem much more complex now than they appeared 10 or 15 years ago. Nevertheless, there is always a need to present them in a simple form. Models are very helpful in this respect.

Several attempts at presenting the process of abscission in the form of a model have already been made (Addicott 1965, Addicott and Wiatr 1977, Osborne 1973, Jankiewicz 1979, 1980), however, all of these models are less complete than the one presented in this paper, or are related only to some specific aspects of abscission.

In the evolution of the plant kingdom, abscission appeared very early, "when two cells separated for the very first time" (Addicott 1982). Precambrian fossils present several examples of separation of bacteria-like cells, blue-green algae cell chains, etc. In the Devonian period, *Rhynia*, a primitive land plant, developed an abscission zone to shed sporangias (Edwards 1980). The *Glossopteridae* from the Carboniferous period shed their short shoots with leaves (Plumstead cit. Addicott and Lyon 1973). Angiosperm trees belonging to the genera existing up to now, as *Crataegus*, *Populus* or *Liriodendron* developed their deciduous habit in the early Cretaceous period (Axelrod 1966), when the climate in the zone, where they were growing, showed marked seasonality. Evolutionary aspects of abscission have been broadly discussed by Addicott (1982). This author also presents multiple examples of abscission in contemporary lower plants such as bacterias, algae, fungi etc.

Abscission, besides being interesting from the theoretical point of view, for instance, as a form of adaptation for survival in adverse conditions (Addicott and Lyon 1973, Addicott 1982), is of great importance in plant production. In fruit orchards different physiologically active substances are used to thin flowers or fruitlets in order to prevent over-bearing of trees. On the other hand, physiologically active substances are used to avoid premature dropping of fruit. Substances facilitating mechanical harvest are of common use in orchards in several countries (Martin 1971, Bukovac 1974, Monselise 1979, Williams 1979, Soczek 1979, Looney 1980, Morris and Cawthon 1981). Fruit detachment force is an important trait in breeding new cultivars, for example of strawberry (Brown and

Moore 1975) or tomato (Rick 1967). Cotton, bean and several other plants are often chemically defoliated or dessicated before harvest (Addicott and Lynch 1957, Rakitin et al. 1961, Gruzinskaya et al. 1978, Borkowski 1976).

Ornamental plant growers and traders are interested in preventing early dropping of petals or flower buds (Nowak and Rudnicki 1979, Halevy and Mayak 1981). In nursery practice the plants are often defoliated before digging and selling (Basak et al. 1973a, b, Larsen 1973, Larsen and Lowell 1977, Marczyński 1977a, b). In sylviculture abscission is important from the point of view of litter formation (Kozlowski 1973). Leaf color change and time of abscission are indicators of species composition in aerial surveying of large areas of forests (Harin 1966). Unfortunately, defoliation of forest trees may be also used as a weapon during war (Galston 1971, Westing 1971).

Premature abscission of leaves and fruits may be a result of disease or insect attack and may influence the survival of a plant (Bystydzieńska and Piotrowski 1973, Jankiewicz 1980, see Addicott 1982) this is true of parasites as well (Feath et al. 1981, Journet 1981). Air pollution may exert great influence on abscission, (Dugger and Ting 1970, Markowski and Grzesiak 1974, Ormond et al. 1976, Cheesman et al. 1980). Several other examples of the economic, ecologic, and taxonomic significance of abscission are known (Kozlowski 1973, Addicott and Lyon 1973, Jankiewicz 1979, Addicott 1982).

2. SOME GENERAL ASPECTS OF ABSCISSION

Abscission in higher plants is generally proceded by senescence of a given plant part, and is frequently considered to be integral part of this process (Webster 1973, Morgan and Durham 1980, see Addicott 1982). Fruit ripening is often considered a special phase of senescence (compare McGlasson 1970). There are only rare cases where shedding of an organ is not preceded by an extended sequence of senesce changes; an example of such an exceptional case are perhaps nursery trees defoliated with ETP in the autumn; they may shed their fully green leaves (Basak and Jankiewicz 1976). On the other hand, there are several species or forms of plants like several tomato cultivars, tobacco, beets or some palms in which leaf senescence does not involve shedding. The leaves remain on them up to disintegration (Webster 1973, Aharoni and Lieberman 1979). Ageing without abscission may result from the attack of some fungi, for instance, apple fruits infected by *Monilinia fruticola* remain on the tree for the whole winter in a mumified form.

One aspect seems important concerning senescence and shedding: both these phenomena may be induced not only in mature organs but also in young ones, for instance in flower buds, young fruitlets, shoot tips etc. (Wertheim 1971, Porlingis 1974, Tamas et al. 1979, Takeda and Crane 1980). In this case the term "premature senescence" or abortion may be preferentially used (compare Addicott 1982).

Shedding of leaves or reproductive organs is preceded by the formation of an abscission zone (AZ). In apple leaf or fruit there is one such zone, in cherry fruit and often in tomato fruits there are two AZ's (Fig. 1). In the *Sambucus nigra* leaf (Osborne and Sargent 1976a, b), in the *Fraxinus* leaf (Facey 1950) or in the avocado pedicel-peduncle there are several AZ's (Fig. 1). In the *Melia azéderach* leaf there are as many as 200-300 AZ's (Morgan and Durham 1980).

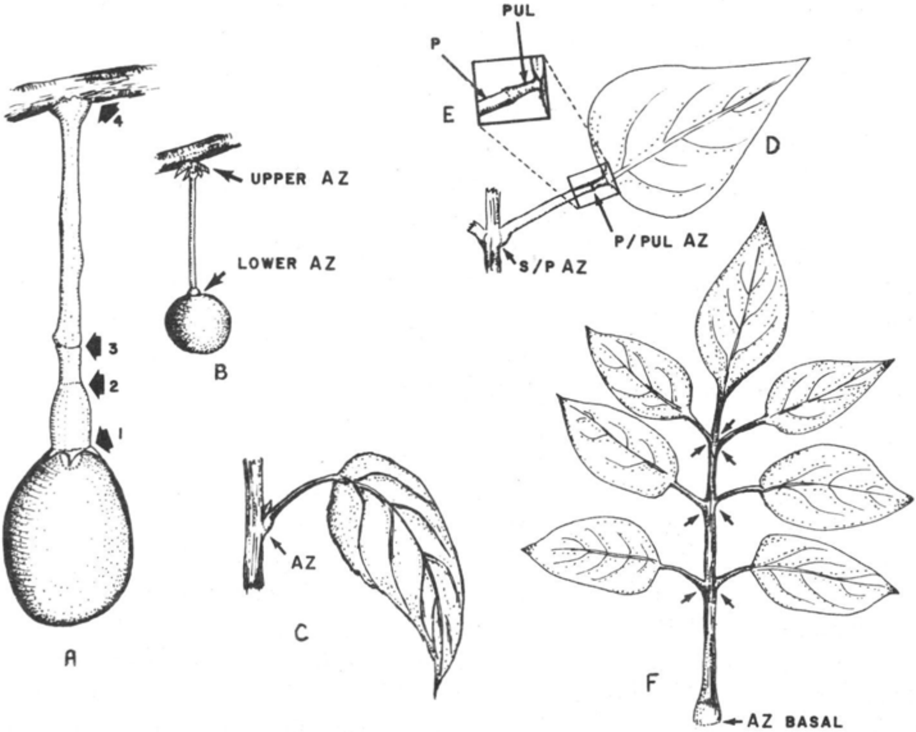

Fig. 1. Abscission zones (indicated by arrows) in different plants: A — avocado fruit (1-4 four abscission zones); B — cherry fruit; C — apple leaf; D — primary bean leaf: S/P and P/PUL AZ — stem/petiole and petiole/pulvinus abscission zones, respectively; E — the part of the petiole and pulvinus used frequently in experiments on abscission; F — ash (*Fraxinus*) leaf

In comparison with adjacent parts of the petiole, pedicel or fruit, the abscission zone shows a specific anatomical structure. The cortical cells are thin-walled, smaller, isodiametrical and are tightly arranged with very little intercellular spaces among them. They also contain smaller vacuoles and are richer in cytoplasm. The xylem and phloem fibers are usually absent from this zone or are small and poorly lignified, (Pfeiffer 1928, Scott et al. 1948, Addicott 1965, Carns 1966, Wittenbach and Bukovac 1972a, Moline and Bostrack 1972, Webster 1973, Esau 1965, 1977, Morrison Baird and Webster 1979, Biaiñ de Elizade 1980, Sexton and Redshaw 1981). There are several other particularities of the AZ structure in some groups of plants which will be partly discussed later in the text (see also Tison 1900, Pfeiffer 1928, Hejnowicz 1980, Addicott 1982). Many, if not all of the mentioned properties of the AZ may facilitate detachment during the abscission process. One aspect of the AZ structure has not been exposed in literature: due to the very tight arrangement of cells, the AZ may be a good barrier for gas exchange between the organ which is abscised and the rest of the plant.

In several species of plants such as in *Fraxinus* (Facey 1950), the AZ forms very early in leaf development, however, it does not undergo futher changes up to the time of onset of senescence. Usually, before abscission approaches, the resistance to breaking of the AZ is not very different from that of the rest of the petiole or pedicel (Rubinstein and Leopold 1963, Dela Fuente and Leopold 1968). In some plants such as *Phaseolus* the AZ is formed shortly before the leaf is abscised (Webster 1968, 1973).

In cherry, blueberry and several other fruits having two AZ's young fruits are abscised at the peduncle/pedicel junction whereas the mature ones at the pedicel/pericarp junction (Wittenbach and Bukovac 1977a, b, Gough and Litke 1980). In cherry fruit the peduncle/pedicel AZ loses its sensitivity to ET during the 3rd stage of fruit development (Wittenbach and Bukovac 1975b).

Usually, at the time close to abscission, a special "separation stratum" (Hejnowicz 1980), differentiates within the AZ, in which abscission subsequently occurs. The term "separation stratum" will be used in the further text in place of "separation layer" used by Esau (1965, 1977) and Addicott (1982) because the "separation layer" is itself composed of layers of cells. Neither will we use the term "separation zone" applied by Osborne and Sargent (1976a, b) because this term is very similar to "abscission zone" and due to this they may be confused.

The separation stratum (SST) has a different role during abscission in particular plant species:

— In most cases the cells of the SST separate due to the activity of enzymes degrading the middle lamella and primary cell wall. This activity increases greatly in the SST at the time preceding abscission. Several data indicate that the enzymes involved are synthesized *de novo* (Morre 1968, Stösser et al. 1969a, b, 1971, Osborne and Sargent 1976a, b, Addicott and Wiatr 1977). Due to their action the SST cells come apart and the given plant part is abscised. Usually this effect is strictly localized and the disintegration of the middle lamella and primary cell walls occurs between 2 neighbouring layers of cells which differentiate across the whole organ (Sexton 1976). Such a strict localization of the detachment process is one of the unsolved facts of abscission. In some cases, like in muskmelon fruit, more cell layers take part in detachment (Webster 1975).

— In some species of plants one or a few layers of cells of the SST undergo divisions (Fig. 2). The newly formed cells may be easily ruptured due to the low mechanical resistance of their walls. On the other hand the the cell walls of the newly formed cells may be easily disintegrated by wall-degrading enzymes since these walls are composed mosty of pectic substances (Webster 1968). Abscission in young apple and cherry fruits seems to occur in this manner (Heinicke 1919, MacDaniels 1936, McCown 1943, Stösser 1967).

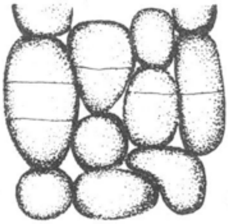

Fig. 2. Abscission by cell divisions: in neighbouring cells of SST the divisions usually occur in similar planes (scheme)

— In some fruits the cells of the SST exhibit plasmolysis and collapse, their contents being subject to autodigestion. This results in the formation of cavities in the AZ whose presence greatly decrease the breaking resistance of AZ tissues (Wittenbach and Bukovac 1972a, Bukovac 1974, Webster 1975). Sometimes the collapse of the cells in the AZ is preceded by their intensive enlargement as in *Ecballium elaterium* (Wong and Osborne 1978). This is an interesting case where the cells already differentiated and quiescent for a long period of time abruptly resume their growth under the action of ET. Osborne (1977) named these cells "target cells" for ET. Cells enlarging in response to ET treatment were also found in some semiaquatic plants (Cooksonn and Osborne 1979, Métraux and Kende 1983, see also Lieberman 1979).

— In several plant species the "differential enlarging" of SST cells plays an important role in abscission (Tison 1900, Wright and Osborne 1974, see Morisson Baird and Webster 1979). The cells situated on the two sides of the future abscission plane behave differently: the proximal ones (sometimes only 1-2 cell layers) enlarge greatly whereas the distal ones enlarge little or not at all (Fig. 3). This obviously causes mechanical strain between these two layers of cells, which consequently leads to the rupture of contacts between them (Wright and Osborne 1974). Other mechanisms which generate mechanical strain between layers of neighbouring cells are mentioned in the model.

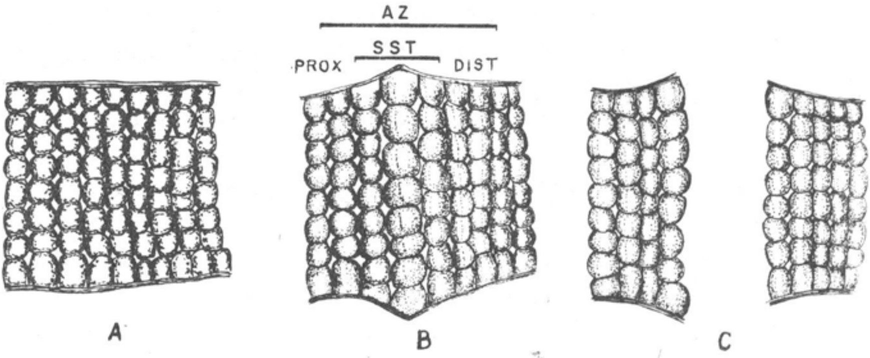

Fig. 3. Abscission due to uneven augmentation of SST cells (scheme): A — the cells of parenchyma and epidermis before the abscission process starts; B — the cells of SST augment unevenly: the proximal ones more; C — rupture occurs between the layers of enevenly enlarged cells, PROX — proximal, DIST — distal part of the peduncle or petiole, SST — separation stratum, AZ — abscission zone

The changes connected with abscission occur across all tissues of the AZ. As mentioned, the tissues of the AZ are mainly parenchymatous; there are uaually no fibers or other sclerenchymatous elements in this zone. Thus the changes connected with abscission spread in the AZ across the cortex parenchyma, xylem parenchyma, phloem, pith, colenchyma and finally epidermis (Sexton 1976, 1979). The tracheary elements are broken mechanically in some plants (Stösser et al. 1969a, b, Webster 1973) or are detached at the middle lamella (Scott et al. 1948, Polito and Lavee 1980). In this last case the neighbouring cells must contribute to the dissolution of the middle lamella joining the tracheary elements. Moline and Bostrack (1972) report partial dissolution of xylem vessel walls as well. It is suggested that such dissolution may be caused by the postulated enzyme lignase attacking a lignified wall (see Addicott 1982). Sieve tube members are usually detached at the junction of their sieve plates. Also in this case the neighbouring companion cells and phloem parenchyma cells probably take part in dissolution of the middle lamella joining two sieve plates, because the sieve tube members do not seem to possess the ability of synthesizing the necessary enzymes *de novo* (Sexton 1976).

In addition to the sequence of phenomena leading to detachment, another chain of events leading to the formation of a protective layer for the future abscission scar also takes place. In some plants these changes precede abscission markedly, in others they take place only afterwards (Lee 1911, Esau 1965, Moline and Bostrack 1972, Hejnowicz 1980). The walls of some layers of cells situated near the future abscission plane become suberized. The suberin layer may be deposited on the external as well as on the internal surface of the walls (Scott et al. 1948, Esau 1965, Webster, 1973). Also tannins may be deposited in phloem cells of the AZ (Webster 1973). These changes make the loss of water from the future scar and infection by microorganisms more difficult. In several species of plants, fellogen is formed below this suberized region. It produces the protective tissues for the abscission scar: phellem and phelloderma (see Esau 1965, Hejnowicz 1980).

The tracheary elements are often occluded by tyloses (Fig. 4) before the organ abscises (Lee 1911, Bornman 1967, Scott et al. 1967). However, cases were found where abscission was not preceded by tylose formation (Polito and Lavee 1980). Occlusion of the vessels by tyloses may be considered part of the formation of a protective zone for the future scar since tyloses diminish water loss from tracheary elements. The physiological regulation of tylose formation has been little investigated, and contradictory data exist concerning the participation of growth regulators in it (Bornman 1967, Scott et al. 1967). An apparently surprising fact is that auxin in concentrations which inhibit abscission seems to stimulate tylose formation whereas ET and ABA, two substances which greatly accelerate abscission, cause scarce tylose formation at the moment of abscission (Bornman 1967, Bornman et al. 1967). We may find, however, a logical explanation for this, phenomenon by considering the situation which exists in the AZ region before detachment: the tyloses "are needed" in the leaf in the proximal side of the AZ to prevent water loss from the future scar. In several plants, for example in *Impatiens sultani* (Sexton and Redshaw 1981), they are indeed formed only on that side. This coincides well with the observation that on this side of the AZ the concentration of auxin during

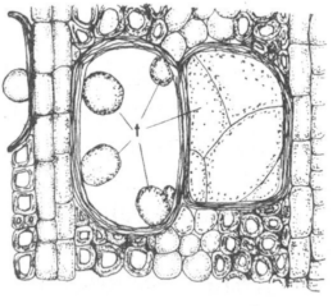

Fig. 4. Tyloses (t) occluding partly or completly the vessels

abscission is often higher (Addicott and Lynch 1955). On the distal side of the AZ, where tyloses usually are absent or scarce, the concentration of ET is probably higher during abscission, as was found is the apple pedicel-peduncle AZ region (Blanpied 1972). We can also expect a higher concentration of ABA on the distal side of AZ (see further text).

In contrast to what occurs in xylem, phloem sieve plates (which are usually partially blocked by callose in mature organs) are deblocked as abscission advances. This process is possibly linked with the intensive withdrawal of nutients from the senescent organ (Scott et al. 1967).

Abscission process may be divided into two stages: introductory in which the normal inhibition of abscission by auxin is gradually lost and the AZ is still insensitive to ET treatment, and the second, in which the AZ tissues can be stimulated by ET to form SST, and auxin is no longer able to inhibit this process (Barlow 1950, Yamaguchi cf. Addicott 1982, Jackson and Osborne 1972, Rubinstein and Leopold 1963). In the description that follows we will consider this division. Sexton and Roberts (1982) distinguish the last part of the second stage as a separate stage taking as the criterion the abrupt decrease of the force necessary to remove the plant organ.

3. THE MODEL

3.1. INTRODUCTORY STAGES OF THE ABSCISSION PROCESS

As was mentioned, abscission may be considered as an integral part of senescence. One of the factors which links the earlier stages of senescence with abscission (Fig. 5) is at least in many plants the increased production of ET by the senescent organ (1), (in the further text the numbers in parentheses refer to the numbers on Figs. 5 and 6). When the level of ET in the given organ surpasses a certain threshold value it causes further autocatalytic stimulation of ET production (2, 3) (Sfakiotakis and Dilley 1973, Kenis and Trippi 1980a). This is a positive feedback reaction, due to which the level of ET in the leaf blade or fruit tissues rapidly increases up to a certain value (after attaining it, ET production may decrease). This climacteric rise in ET production is a well known phonemenon in ripening fruits of many species (Smock and Neubert 1950, Mc Glasson 1970, Rhodes 1970, Walsh 1977), in young abscising fruitlets (Lipe and Morgan 1973) and in senescing leaves (Morgan et al. 1972, see also Thimann 1980). On the other hand, the sensitivity to ET may change as the plant organ gets older, for instance in tissues of a young fruit ET inhibits its own production or is without effect, whereas in tissues of a ripening fruit ET stimulates it (Zerioni and Gill 1976, see also Lieberman 1979). Another example is the cherry fruit approaching maturity: at that time the pedicel/peduncle AZ loses its sensitivity to ET, whereas the pedicel/pericarp AZ gains it (Bukovac 1974, Wittenbach and Bukovac 1974, 1975b).

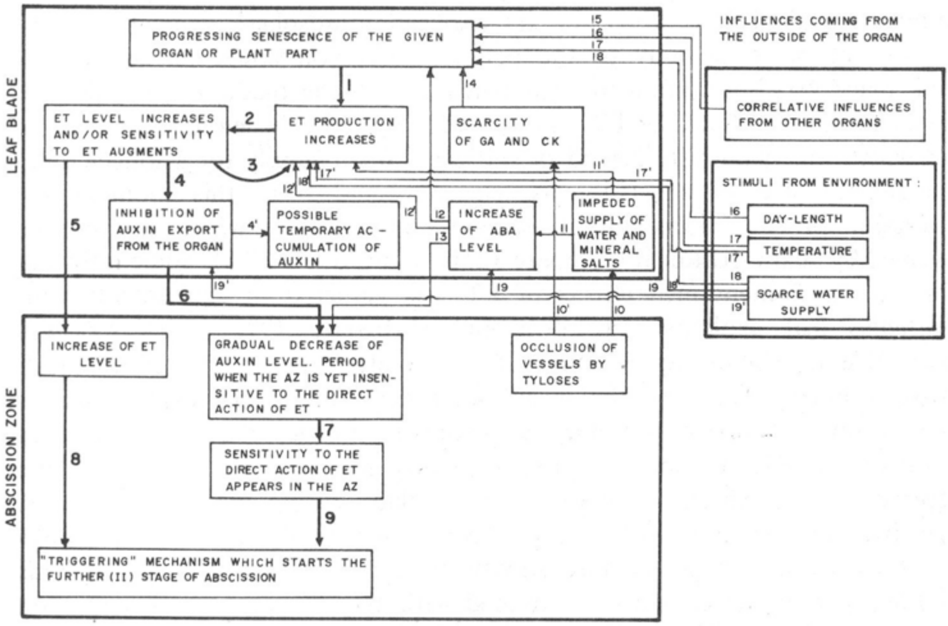

Fig. 5. Model of abscission process (Part I)

Increased ET level in a given part of a plant (2) for instance in the leaf blade, has 2 further consequences:

1. Auxin export form the leaf is withheld (4). In Beyer's (1973) experiment the ability to transport ^{14}C-labelled NAA through the excised leaf petiole decreased markedly during a 3-day exposition to an ET-enriched atmosphere whereas in pure air this decrease was almost insignificant. This inhibition occurs also in the midrib of leaves and auxin conjugation may play a role in it (Riov and Goren 1979, Riov et al. 1982). Blocking of auxin export from the leaf blade may, in some plants cause accumulation of auxin (probably temporary) in the senescent leaf blade (4'), (see Sheldrake 1973). However, in several plants the senescing organs show a decrease or no change in auxin content (Roberts and Osborne 1981). Another consequence of this blockade is an auxin deficit in the AZ (6). This is of great importance for the further course of the abscission process: when the AZ is scarcely supplied with auxin for some period of time its tissues become sensitive to the direct (second) action of ET (7) or also may start its own massive production of ET (Jackson and Osborne 1972).

2. In case of this direct (second) action, ET must act directly on the AZ, coming to it by diffusion through intercellular spaces from more distal parts, or being produced in situ (see also Discussion). That ET exerts these two separate effects was clearly shown by an experiment in which different atmospheres were given separately to the leaf blade and to the petiole (Beyer 1975): when the ET-enriched atmosphere was given only to the leaf blade or only to the petiole, abscission could not occur but took place very soon aften this gas reached both the blade and the petiole. When these two effects of ET finally meet (8,9), (i.e. when ET reaches the AZ which was previously devoid of sufficient auxin supply for a longer time) the further step of abscission is triggered, and from this moment the abscission process enters into its second phase (Fig. 6) which can not be reversed by auxin treatment (compare Jaffe and Goren 1979). Some information on the 2 mentioned effects of ET was gathered in experiments with *Phaseolus* leaf explants (Jackson and Osborne 1972). The AZ was insensitive to ET during the first 24 hours after excission from the leaf. Possibly during this time the initial level of auxin in the explant tissues must drop sufficiently and due to unknown changes the tissue becomes sensitive to ET. If later on the explants are kept in an atmosphere deprived of ET, abscission does not take place during the next 72 hours. Treating the explants with auxin, before this time has elapsed causes a return to the stage of insensitivity to ET. If, however, during this 72 hour period the explants are treated with ET, the process of abscission starts immediately. From this moment (i.e. after initiating the "triggering mechanism") the process of abscission cannot be inhibited or reversed by auxin treatment: the point of no return has been passed,

The mechanism of the two actions of ET in abscission are not well elucidated, and we will probably have to wait for more data on polar auxin transport in order to better understand its inhibition by ET. Riov et al. (1982) reported recently that in the citrus leaf ET causes the conjugation of IAA with high molecular weight compounds. This can lower IAA export from the blade. The second action of ET is probably connected with the phenomena described in the second part of the model (see below). It seems interesting, that the oxidation of ^{14}C-ethylene to CO_2 increases greatly only in the AZ cells after induction of abscission by deblading of the leaf (Beyer 1979). This suggests a special physiological state of AZ cells which permits very active inclusion of ET into metabolism. Auxin suppresses this ET inclusion and ABA slightly stimulates it. Addicott (1982) supposes that ET has a rather secondary role and is the hormone of local coordination. Addicott supposes also that ET production in the AZ is regulated by the signals produced by other hormones, as for example the lowered ratio of IAA to ABA. As ET starts to be produced in larger amounts it causes phenomena of a rather general, non specific

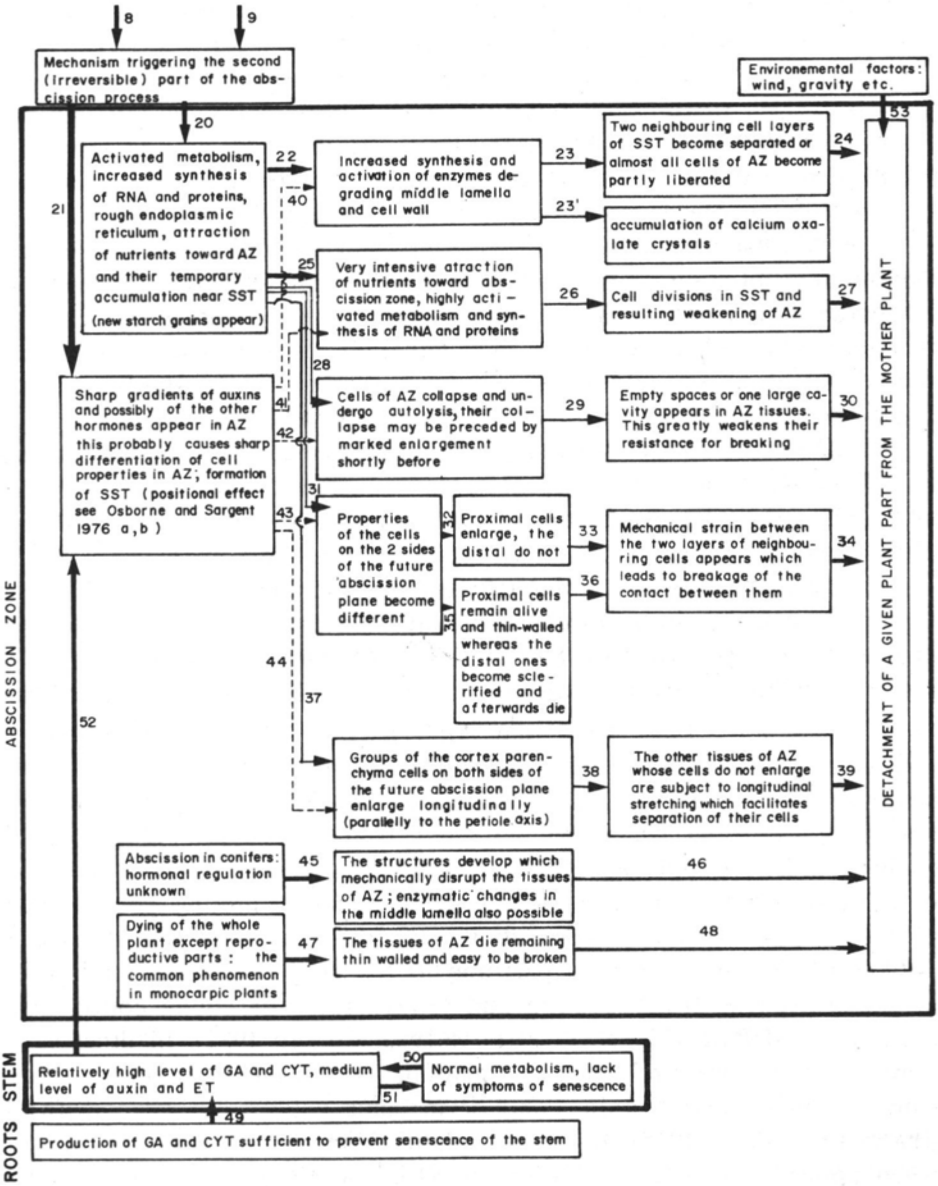

Fig. 6. Model of abscission process (Part II)

nature such as augmentation of membrane permeability (making energy-rich compounds more avalilable for enzyme synthesis). It is also known that ET stimulates respiration, therefore may enhance any enzyme synthesis triggered by other hormones like IAA, CK, GA or ABA. In my opinion however, in the cells, conditions may exist which could channel such unspecific action of ET a very specific one, as for instance increased permeability of only one cellulase isoenzyme, etc. (see further text).

Stimulation of abscission by ABA was demonstrated in many plants (Addicott et al. 1964, Bornman et al. 1967. Tomaszewska 1968, Pieniążek 1971, see also Addicott 1970, 1982, and Milborrough 1974). There were even attempts to defoliate nursery trees with this compound (Larsen 1973). The role of ABA in abscission may be multiple.

— ABA may be considered a component of the hormonal balance determining initiation of senescence. Its increase in relation to some other hormones like auxin, GA and CK seems to promote senescence (12) (Gepstein and Thimann 1981). Accumulation of ABA in senescing organs was observed in several plants (Rudnicki et al. 1968, Rudnicki and Pieniążek 1970, Böttger 1970, see also Addicott 1982).

— ABA may shorten the inital period of insensitivity of the AZ tissues to ET (13). In this case ABA acts antagonistically to auxin (Jackson and Osborne 1972). Antagonism of auxin and ABA takes place in several phenomena (Zajączkowski et al. 1983, see also Addicott 1982).

— Although in young plant parts ABA inhibits ET production (see Lieberman 1979), in senescent tissues it does the reverse: stimulates ET production (Gertman and Fuchs 1972, Mayak and Dilley 1976) — probably indirectly by accelerating senescence (12) (Sagee et al. 1980).

— There was a suggestion that ABA may deblock the mechanism of abscission independently of ET (Cooper and Horanic 1973). This was based on the result that ABA stimulated abscision under conditions of lowered pressure in which ET envolved from the tissues and probably could not act. Also Craker and Abeles (1969) have found stimulation of celulase activity by ABA in the presence of saturating concentration of ET. In some plants a correlation was found between the increase of ABA concentration in a plant part and its tendency to abscise, for instance in young avocado fruits (Adato and Gazit 1977) or young cotton fruits (Vaughan and Bate 1977 cf. Addicott 1982, Guinn 1982). In other cases, however, there was no such correlation, for instance in young peach fruits (Ramina and Masia 1980) or in some cultivars of bean (Subhadrabandhu et al. 1978). In citrus explants ABA did not act on abscission when applied concomittantly with inhibitors of ET synthesis, thus in this case, ABA seemd to influence abscission indirectly, by stimulating ET synthesis (Sàgee et al. 1980). It is probable therefore that the role of ABA in abscission differs markedly in various plant species. Such variability of response to hormones among plant species seems common in the plant kingdom, for instance auxin does not stimulate rooting of some species of plants and sometimes needs cofactors (see Bojarczuk and Jankiewicz 1975), on the other hand ET does not induce leaf abscission in some species (Abeles 1973), etc.

There may exist several other substances influencing the first stages of abscission; for instance, Wright (1956) found a substance in *Ribes* which did not show the properties of auxin but very effectively inhibited abscission. Polyamines inhibit senescence (Apelbaum et al. 1981) and ET biosynthesis (Even-Chen et al. 1982). Methyl jasmonate accelerates the progress of senescence (Ueda and Kato 1980). It would be worthwhile to investigate if these two groups of substances have any direct effect on abscission. Phenolic substances seem to influence abscission *via* its influence on IAA oxidase (Tomaszewska 1968). Malformine was found to influence abscission in connection with the phytochrome system (Curtis 1978). Fusicoccine had no effect on abscission in Jaffe and Goren's (1979) experiments, however was highly active in those of Feldman et al. (1971). Several authors have searched for a "senescence factor" stimulating abscission but with rather inconclusive results (see Osborne 1973, Jacobs 1979). In senescent petioles or pedicels of several plants Dörffling et al. (1978) have found ABA, xanthoxin and an unidentified substance, all of which stimulated abscission; the concentration of ABA did not increase during senescance in their experiments. Several abscission accelarators and retardants (part of them not defined chemically) were also found in young cotton fruits (Lyon, Okhuma and Addicott cf. Addicott 1982).

Abscission also depends on correlative influences coming from other parts of a plant (15), (Dostál 1951, Seth and Wareing 1967). For example an old *Phaseolus* leaf shows an earlier tendency for senescence and abscission when the plant forms new leaves. However, when these new leaves are removed the older leaf lives longer. Its life may be prolonged still when it is excised from the plant and rooted (Chibnall and Wiltshire 1954, Leopold 1961). The petals of some flowers, for example of *Digitalis* are abscised promptly after pollination (Stead and Moore 1979, see also Addicott 1982). In monocarpic plants (which terminate their life with the formation of seeds) the developing seeds induce senescence in the leaves and cause their abscission. The signal for senescence generated by the seeds seems to be transported basipetally and can be transmitted through the xylem (Noodén 1977, 1980, Noodén and Murray 1982). Abscission of young fruits may also be considered to be caused by competition with other fruits or vegetative parts (Schneider 1978, Rodgers 1981b, Tamas et al. 1979). A successful attempt to predict the yield of plants taking into account this competitions was done by Landivar et al. (1983), using the computerized crop simulation model (GOSSYM).

Environmental conditions may influence abscission directly or by affecting senescence (16-19) (see Addicott and Lyon 1973, Addicott 1982). Changes in daylength and temerature may serve as information to the plant about the forthcoming changes in the environment. According to them the plant may initiate the senescence program in the leaves (Tumanov et al. 1964, 1965, Njoku 1964, Vogl 1966, Addicott and Lyon 1973). Kenis and Tripii (1980b) have shown that abscission of *Phaseolus* explants depends on the phytochrome system, far red light stimulating abscission. Similar results have bee obtained by Decoteau and Craker (1983). The observation by Imaseki et al. (1971) that far red light stimulates production of ET in rice plants may be connected with this. As the day length shortens, usually the level of growth promoting hormones such as IAA, GA and CK drops and that of ABA increases or remains unchanged, promoting the advent of senescence (Zeevaart 1976). Sometimes in short day plants, long day treatment promotes leaf abscission (Ojehomon et al. 1968, see also Addicott 1982). Light relations within the plant may also regulate abscission: shading of particular young fruits and flowers in the soybean plant for 24 h or more caused great reduction of the attraction of assimilates by them and subsequent abscission (Heindl and Brun 1983).

Freezing or subfreezing temperatures may accelerate production of ET (17') (Young and Merideth 1971), or change the sensitivity of the tissue to it. This coincides with the observation that apple leaf-fall is accelerated by low positive temperatures 9° and 13°C (Jonkers 1980). Subfreezing temperatures may also increase the level of ABA in sensitive plants (Daie et al. 1981). In experiments on chemical defoliation of ornamental plants, it was shown that a temperature of 13°C promoted abscission of treated plants more than higher or lower temperatures (Marczyński and Jankiewicz 1978).

Water stress lasting for a sufficiently long period of time evokes shedding of older leaves at least. Water-stress favors the induction of earlier senescence (18) by changing the hormone balance toward the prevalence of senescence-inducing hormones (ABA and ET) over those which counteract senescence (CK an GA), (El-Beltagy and Hall 1974, Itai and Vaadia 1971, Ben-Yehoshua and Aloni 1974, Davenport et al. 1977b). However, as is underlined by Wright (1980), the hormone balance changes dynamically during water stress. ABA seems to dominate in these changes since only its content increases rapidly with the onset of stressed conditions (19). Finally, according to Wright (1980), ABA also inhibits ET production in water-stressed plants.

Water stress inhibits basipetal auxin transport throught the petiole (19'), (Morgan et al. 1977, Davenport et al. 1977a, 1980). This may facilitate the direct action of ET on the AZ (compare 18' and 19). Since the older leaves have their auxin export already weakend due to their age it is conceivable that they are shed in the first place during water stress. Inhibition of IAA transport with age may be partly caused by IAA inactivation through the formation of indoleacetylaspartic acid (Veen and Jacobs 1969), however, this is not certain (compare Jaffe and Goren

1979). Other environmental effects on abscission are reviewed by Addicott and Lyon (1973), Jankiewicz (1979), and Addicott (1982).

Occlusion of tracheary elements by tyloses may stimulate further stages of abscission (10, 10'). Tyloses appear in a petiole or pedicel when the organ ages (Bornman 1967, Sexton and Redshaw 1981). They restrict the supply of water and mineral salts to the senescent part (10) and probably also the supply of root-produced hormones: gibberellins and cytokinins (10'). Restricted water supply to the leaf blade by tyloses may in consequence stimulate ABA and ET production. All these facts may speed the process of senescence (10, 10', 11, 12, 14) and promote abscission (11').

3.2. LATER, MOSTLY IRREVERSIBLE STAGES OF ABSCISSION

When the "triggering mechanism" has been set in motion (8, 9) the further stage of abscission, which is usually irreversible by auxin begins (Fig. 6). This stage is usually accompanied or preceded by marked stimulation of metabolic activity in the AZ (20): there is an increase in the amount of rough endoplasmic reticulum (Lieberman et al. 1983) and in the number and size of dictyosomes. The intensity of RNA and protein synthesis is markedly augmented especially in the part of the AZ immediately proximal to the future abscission plane (Abeles and Holm 1966, Holm and Abeles 1967, Morre 1968, Webster 1968, Valdovinos et al. 1972, Sexton and Hall 1974, Webster 1973, 1975, Sexton 1976). The abscission zone shows a marked demand for O_2 (Carns et al. 1951, Wittenbach and Bukovac 1973, see also Addicott 1982), and at the same time the AZ becomes a center of attraction of nutrients (Scott and Leopold 1966). Part of these nutrients is probably temporarily stored in the form of starch grains. The appearance of starch grains in the AZ at the time preceding abscission was reported by many authors (Lee 1911, Wilson and Hendershot 1968, Reed and Hartmann 1976, see also Webster 1973, Morrison Baird and Webster 1979). Activation of amylases observed by Kenis and Trippi (1979, 1980a), proximally to the AZ may be related to intensive carbohydrate transformations. In some plants, part of the accumulated starch disappears as separation approaches, suggesting its utilization in metabolism which is very active at that time (Webster 1970). In other cases, for example in plants treated with ETP, when abscission proceeds very fast, abundant starch reserves persist even after abscission (Polito and Lavee 1980). Cases were also reported when starch accumulation in the AZ are not preceded abscission as in the sour cherry (Stösser et al. 1969a), in this case some of the cells accumulated lipid-like substances.

The other phenomenon connected with abscission is what Osborne and Sargent (1976a, b) have defined as "positional effect" or preferably as "positional differentiation" (21). This phenomenon consists in precise localization in the AZ of a few layers of cells (SST), sometimes only 2-3, between wich detachment will occur. For instance the cells of one layer enlarge markedly under the influence of ET whereas the cells of the adjacent (distal to it) layer do not react in this way. Since an auxin gradient (Addicott and Lynch 1955, Louie and Addicott 1970) is probably superimposed on the contrary ET gradient (Fig. 8), the AZ cells may obtain rather precise hormonal information about how they should be subsequently differentiated (also see Discussion).

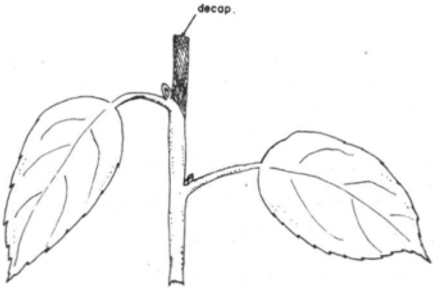

Fig. 7. The decapitated young apple shoot. The shaded part is senescing and will be abscised

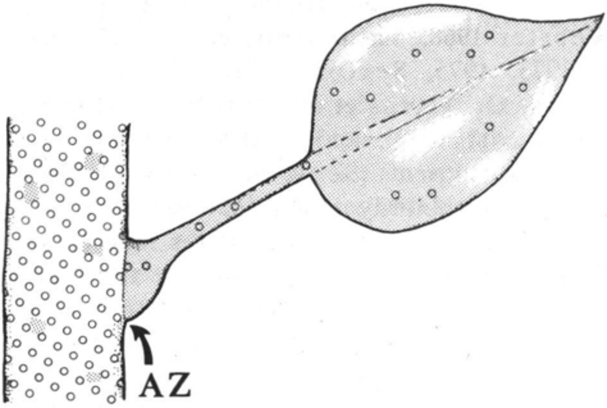

Fig. 8. Sharp hormone gradients take place in the abscising organ: circles — the auxins, dotts or groups of dotts — ethylene, AZ — abscission zone

Further changes leading to abscission may occur differently in various plant species, also depending on the abscised organ and its stage of development (Fig. 6). However, it has to be kept in mind that one "way" or chain of events leading to detachment does not exclude simultaneous participation of others in the abscission process of the given plant part.

— The phenomenon most commonly observed in the SST during abscission is the degradation of the middle lamella and partial degradation of the cell walls (22), this degradation may sometimes occur only between 2 adjacent layers of cells, as in the wild rice, *Zizania aquatica* (Hanten et al. 1980), or may involve as many as 30-40 cell layers as in *Sambucus nigra* (Osborne and Sargent 1976a, b) (23). In this latter case the cells of the AZ become more or less liberated from each other which results in marked weakening of the AZ tissue. Dissolution of the middle lamella and partial disintegration of the cell walls lead to detachment of the senescent plant part (24).

In connection with this phenomenon several authors reported marked stimulation of the activity of enzymes degrading structural polysaccharides of the middle lamella and the cell wall. For example in the AZ of senescent orange or *Phaseolus* leaves, D-galacturonase (polygalacturonase) activity increases markedly (Morre 1968, Riov 1974, Berger and Reid 1979). This enzyme takes part in the degradation of the middle lamella pectins. The degradation of the cell wall also starts from the action of this enzyme. There is a report (see Sexton and Roberts 1982) indicating that D-galacturonase of the AZ is of the exo-type, however, it may be expected that the endo-form of D-galacturonase will also be shown to participate in middle lamella breakdown in the AZ, as was found in ripening fruits (compare Huber 1983). D-galacturonase participates in the breaking of pectic polysaccharides (rhamnogalacturonans) which connect different elements of the cell wall (Albersheim 1976) and constitute the main polysacharides of the middle lamella (Huber 1983). In contrast to D-galacturonase, pectionmethylesterase activity seems to drop during abscission (Osborne 1958, Yager 1960). Its role during abscission as well as during the softening of fruits is not well elucidated (Sexton and Roberts 1982, Addicott 1982, Huber 1983).

Increased activity of one of the cellulase isoenzymes was found in *Phaseolus* leaf and orange fruit AZ after the induction of abscission with ET (Linkins et al. 1973, Reid et al. 1974, Kossuth and Biggs 1977). With immunochemical methods it was shown that this cellulase isozyme (pI = 9.5) is localized in abscising petioles mainly in 3-4 cell layers of the SST (Sexton et al. 1981). Penetration of cellulase from the cytoplasm to the cell wall under the influence of ET was shown by Abeles and Leather (1971). Cellulase may decompose not only celulose but also partly a xyloglucan sheath which surrounds the cellulose fibrils (Labavich 1981). It may be speculated that in this way the fibrils may be libered from the wall structure but may remain otherwise mostly intact. Histochemical investigations sometimes show that the amount of cellulose has changed little or remained unchanged during abscission (Facey 1950, Morre 1968, Polito and Lavee 1980). Electron microscopic observation of the tobacco flower AZ revealed a mass of loose fibrous material in the space between the partly separated cells, which probably derived from the degraded primary cells walls (Valdovinos et al. 1972). In ripening fruits other hydrolases such as B-galactosidase are involved in the breakdown of pectic substances (Huber 1983). As far as I know their participation in the abscission process has not been studied.

The activity of peroxidases and of acid phosphatases in the AZ was found to increase during the period preceding abscission (Henry et al. 1974, Hall and Sexton 1974, Wittenbach and Bukovac 1975a). This is probably connected with the general stimulation of the AZ metabolism during this period (20), however, peroxidases may also take part in IAA destruction (Wittenbach and Bukovac 1975a) and may be involved in progressing senescence of the tissues distal to the AZ (see Thimann 1980).

Complete degradation of the cell wall during abscission was noted by Reed and Hartmann (1976) but it is rather a rare case to be observed.

The observation of the decomposition of the middle lamella and of the cell wall in the electron microscope have shown among other things that the substance of the middle lamella disappears gradually as the abscission process advances. The vesicle-like structures similar to those produced by dictyosomes appear in this region (Valdovinos et al. 1972, Sexton and Hall 1974, Webster 1975). Osborne and Sargent (1976a) suggested that these structures spread from the plasmodesmata to the region of the middle lamella, however, it seems that in several plant systems (see Sexton and Roberts 1982), the plasmodesmata does not play an important role in distribution of pectolytic enzymes. As the empty spaces appeared at the site of the degraded middle lamella the cells gradually separated. In the scanning electron mictoscope the surfaces after detachment usually contained uninjured cells (Sexton 1976). Histochemically and chemically it was shown that pectic materials of the middle lamella and of the cell wall became gel-like, and more soluble pectins were found in the AZ region as the abscission process advanced (Morre 1968).

In some plants the cell wall shows marked swelling before abscission (see Addicott 1982). Huber (1983) mentions that such swelling may result from the removal of methoxy groups from pectic substances by pectinmethylesterase. When this occurs, the galacturonic chains of pectin show a high frequency of negatively charged groups. As it is known, such groups can attract water molecules which results in swelling. A swollen wall may be attacked more easily by enzymes.

Calcium and magnesium ions, which are the normal components of the middle lamella pectates, are liberated during middle lamella degradation being displaced by protons (see Huber 1983). A large part of these liberated ions disappears from the middle lamella region and passes to other parts of the cells or to other cells. This was shown with histochemical methods, among others with microincineration and with microprobe X-ray analysis (Stösser et al. 1969b, Poovaiah and Rasmussen 1973b). At the same time the number of calcium oxalate crystals and their dimensions rapidly increase in the vicinity of AZ (23'). This suggests that Ca^{2+} ions liberated from the middle lamella are incorporated into these crystals (Webster 1973). The important role of calcium in abscission was made evident by treating *Phaseolus* explants immediately after their excission with 0.1 M $CaCl_2$ solution. This treatment prevented abscission completly (Poovaiah and Leopold 1973). Ca^{2+} treatment may also prolong the period in which the explants are insensitive to ET and can lower or prevent their sensitivy to ET (Poovaiah and Rasmussen 1973a). An effect opposite to that of calcium salts is shown by potassium oxalate — it stimulates abscission (Poovaiah and Leopold 1973). In addition to the participation of calcium in pectates of the middle lamella, it has several other functions in the cells which can be related to abscission, for instance in the presence of cytokinins it stimulates the production of ET (Lau and Yang 1974, Lau et al. 1977), it also influences cytokinin uptake which may modify the hormone balance related to senescence (Lieberman 1979). Stimulation of basipetal auxin transport by calcium ions (Dela Fuente and Leopold 1973) liberated from the middle lamellas does not seem to be of importance in the abscission process due to a very local character of Ca^{2+} liberation. There were also attempts to take practical advantage of the differential effect of calcium on citrus leaf abscission and on fruit coloration in the orchard: by addition of calcium acetate (0.05 M) to the ethephon (ETP) spray, coloration was markedly improved and the unwanted leaf drop usually caused by ETP was prevented (Iwahori and Oohata 1980).

In olive trees, application of calcium acetate lowered undesired defoliation which appeared after spraying with an ET-releasing substance Alsol used for faciliting mechanical harvest (El-Tamzini et al. 1982).

— In several plants, marked activation of metabolism in the AZ at the time preceding abscission (25) leads to cell division (26). The newly formed cells having delicate cell walls break easily due to the wind or the organ's own weight, resulting in detachment (27). The delicate walls of the newly formed cells are also very easily degraded by enzymes (see 22-24) (Webster 1968, 1973, Morrison Baird and Webster 1979).

— In several species of plants, and especially in their reproductive parts, abscission is preceded by a process similar to plasmolysis followed by autolysis of the cytoplasm and the collapse of the SST cells (28) (Reed and Hartman 1976). For instance in the unripe *Ecballium elaterium* (L.) fruit the AZ cells are tightly arranged and the AZ is very resistant to breaking. However, during fruit ripening most of these cells begin to enlarge rapidly under the influence of ET. Wong and Osborne (1978) and Osborne (1977) consider these cells the target cells for ET. They may be discerned in *Ecballium* from the other AZ cells by their endoreduplicated DNA. After these cells enlarge, cytolysis starts in them and they collapse and die (28). This causes the formation of empty spaces or of one great cavity in the AZ tissues (29) which markedly weakens the resistance of the AZ to breaking and leads to detachment (30). Sometimes the collapse of SST cells is not preceded by their enlargement, as in cherry fruit (Stösser et al. 1969a, b). An analogical phenomenon of lysis and collapse of cells was observed in roots when aerenchyma was formed under the influence of ET (Kawase 1979, Drew et al. 1981). This phenomenon was accompanied by marked increase in cellulase activity (Kawase 1979, 1981).

— In abscissing plant parts of several species, for instance in *Phaseolus* leaves (Wright and Osborne 1974) one layer of cells in the AZ responds to ET by intensive enlargement (31, 32). At the same time the cells of the adjacent, more distal layer, do not enlarge or do so minimally. Mechanical strain appears therefore between these 2 layers of cells (33) which results in the breaking of the contact between them, and detachment occurs (34).

— In several plants, such as those belonging to the genera *Fagus*, *Castanea* and *Quercus*, abscission occurs between the cells of the fruit which undergo sclerification and die, and those of the involucre which remain alive and thin-walled (35) (Esau 1965). In this case mechanical strain between these two different classes of cells probably appears (36). This phenomenon has been little investigated. In many other plants some mechanical strain across the SST may also be evoked by the differences in the water content of cells: the distal ones usually suffer the lack of water due to the occlusion of vessels by tyloses (see Carns 1966).

— In *Impatiens sultani* leaves (Sexton 1976, Sexton and Redshaw 1981) the groups of cells of the cortex which are situated distally and proximally to the future abscission plane enlarge markedly, mainly parallely to the longitudinal axis of the petiole. This imposes mechanical strain on the other cells of the SST which have not enlarged, causing their separation (37-39). This strain probably greatly facilitates the action of the enzymes dissolving the middle lamella (see 22, 23). A similar process seems to take place in orange leaves (Scott et al. 1948, see also Carns 1966). Sometimes the augmentation of the cells of the SST may be the result of, and not the cause of separation (see Addicott 1982).

— The process of abscission in conifers has been investigated very little, although from the evolutionary point of view it merits attention. According to Facey (1956), abscission in *Picea glauca* and *Abies balsamea* in drying conditions occurs due to mechanical breaking of cell walls above the protective ligno-suberized layer. The authors have not found chemical changes in the cell walls in the region of the future abscission plane

(45, 46). However, Sifton (1965) found that in *Picea*, pectic acids change into soluble pectins at the time when the AZ becomes able to produce abscission in response to dessication treatment.

— In monocarpic plants of several species the desicated seeds ramain attached to the dead plant. In this case the contact between the seed and the mother-plant is broken by rupturing or disintegrating the dead, thin-walled cells of the pedical (47, 48) (Esau 1965). This type of abscission has been investigated very little, although it may be important in seed production of many vegetable crops and medicinal plants.

Probably all parts of the plant may influence, more or less directly, abscission (Fig. 5(15), Fig. 6(52)). The influence of the root system may be revealed by grafting: for example the autumnal defoliation of peach scions occurs earlier when they are grafted on the Siberian C rootstok than when grafted on other types of rootstocks (Layne et al. 1977). Since the roots are an important source of GA and CK, it is possible that their influence on abscission is partly mediated by these hormones (49-52). Senescent or aborting organs, as for instance *Nasturtium* leaves (Chin and Beevers 1970), or cotton fruitlets (Rodgers 1981a), were found to contain a low level of cytokinins, or cytokinins and gibberellins. Also in the unifoliate plant *Streptocarpus* the butanol-soluble cytokinin fraction was low in the parts which had to be shed (Van Staden 1973). The occlusion of vesseles by tyloses may cause a decrease of GA and CK level in the aging organ (10, 14). It is not known if there is a sharp gradient of CK and GA across the AZ tissues but such a gradient seems possible after occlusion of vessels by tyloses (52). Experiments in which CK was applied to the distal ends of *Coleus* explants showed inhibition of abscission by this compound (Gorter 1964), however, blue lupine leaflets treated distally with CK gave very complex results. Abscission was delayed or accelerated by CK depending on the leaflet age or light conditions (Carr and Burrows 1967). Application of CK directly on the AZ delays abscission (Osborne and Moss 1963, Burrows and Carr 1967).

In *Leptospermum* petals CK treatment inhibited natural abscission but not that induced by ET (Zieslin and Gottesman 1983). Cytokinins stimulated ET production in some plants (Burg and Burg 1968) but in others diminish it or have no effect (Zieslin and Gottesman 1983). Cytokinins diminish the sensitivity of organs to ET (Burg and Burg 1968).

Gibberellin applied distally to cotton explants accelerated abscission (Bornman 1967, see also Addicott 1965 and Carns 1966). GA applied proximally, in low concentrations to *Morus alba* petiole explants accelerated abscission early in the growing season but delayed it in the autumn (Trippi and Boninsegna 1966). There is no good explanation of why GA promotes abscission, however, Bornman et al. (1968) report that GA markedly stimulated cell divisions in the AZ — a phenomenon which is rather inhibited by ET. In the experiments of Morgan and Durham (1975) GA promoted abscission at saturation level of ET which indicates that these 2 compounds are able to stimulate abscission in different ways. Rasmussen (1981) suggests, however, that in orange fruits, during the "regreening period" relatively high levels of endogenous GA in the tree cause lowered sensitivity of fruits to ET. Davenport et al. (1979) have investigated the influence of water stress on the transport of GA and CK in petioles: there were no differences found between stressed and control plants.

The growth retardant cycocel which usually acts as a GA-antagonist accelerates abscission in cotton seedlings. Its action in this case could not be reversed by GA although it was reversed by auxin. It is supposed, therefore, that cycocel acts in abscission by lowering the auxin level (Khan and Tolbert 1966).

4. DISCUSSION OF THE MODEL

This model does not include all cases of abscission but the more important ones. Other examples may be found in Pfeiffer's (1928) or Addicott's (1965, 1982) reviews.

The changes taking place in the AZ during abscission show several analogies to those which occur in ripening fruits (Morre 1968, Addicott 1982). For instance, increased activity of enzymes which dissolve the middle lamella occur both during abscission and in ripening fruits (Huber 1983). Abscission and ripening are hastened by ET (Mc Glasson 1970). The prolonged period of deprivation of auxin is necessary for the AZ to start the abscission process and for the fruit cells cultured in suspension to commence their senescence program (Romani et al. 1981). Abscission and ripening are accelerated by H_2O_2 (Kenis and Trippi 1980a, Brennan and Frenkel 1977).

In higher plants, the mechanism of abscission serves principally to reject the senescent parts. It should therefore involve recognition of senescent and non-senescent tissues. This seems to depend, at least partly, on the fact, that the tissues which will persist are supplied with auxin, whereas those to be rejected are not, or much less. For instance in the decapitated young apple plant the remaining stump of the internode usually ages and is abscised up to the line formed by vascular bundles connecting the uppermost bud or leaf (which are auxin producing centers) with the stem vascular system (Fig. 6).

In the scheme (Fig. 7) the tissues of the stem are provided with auxin by non senescent parts situated above them, i.e., by leaves, buds, shoot tip etc. However, the auxin transported in the stem cannot enter into the petiole due to its strictly basipetal movement. On the other hand, the tissues of the petiole basis contain less and less auxin because of the blockade of basipetal transport of this hormone in the petiole as the leaf ages (Beyer 1973, Jacobs 1979). This probably results in the appearance of the sharp auxin concentration gradient at the AZ before abscission, as was shown by Addicott and Lynch (1955). This auxin gradient is considered an important prerequisite of abscission (Addicott 1982).

In the tissues of the petiole deprived of auxin supply, senescence continues and ET production increases (Jackson and Osborne 1972). On the other hand these tissues may receive additional ET from more distal parts, especially when pith tissue is very loose or distorted (although this was not proved up to now experimentally). It may be speculated that in the petiole with compact tissues stepwise stimulation of senescence by ET production may occur: the ET produced by the blade may stimulate ET production autocatalytically in the neighbouring part of the petiole and when this part starts to produce sufficient ET it may stimulate ET generation further down the petiole, and so on up to the AZ. The tissues of AZ seem to respond by especially elevated production of ET to the appropriate stimuli (Marynick 1977).

The AZ tissue, as mentioned, differs from the adjoining tissues by being more compact and having very few intercellular spaces. This may make ET diffusion from the petiolar basis into the stem difficult. However, even if some ET reaches the stem tissue it many not evoke senescence there, because stem tissue, having a relatively high content of auxins, and probably also of cytokinins and gibberellins, is not sensitive or little sensitive to ET action (compare Beyer 1975). Thus, at the AZ, we can expect a sharp gradient in the sensitivity of tissues to ET and possibly also a gradient of ET concentration.

ABA concentration was found to increase in the senescent organs of several plants (Rudnicki et al. 1968, Böttger 1970, see also Addicott 1982) and this hormone is considered an important natural regulator of senescence and abscission (Addicott 1982, Thimann 1980, Tietz et al. 1981, Gepstein and Thimann 1981). We do not know if ABA finds any barrier on its way from the petiole to the stem, but even if such a barrier does not exist, the action of ABA may be different in these two parts of the plant. In the petiole ABA may stimulate senescence because its action is not counteracted by auxin which is scarce there, whereas in the stem, ABA action is probably neutralized both by auxin as well as by CK an GA which seem to be more abundant in stem tissues. According to Zajączkowski et al. (1983) auxin can bring information not only in the form of its concentration level but also in the form of wave-like oscillations of transported amounts of this hormone. From the point of view of this hypothesis it is interesting that ABA greatly diminishes oscillations in auxin transport whereas CK abolishes the effect of ABA.

Possibly there must also be a kind of mutual influence between the neighbouring senescent and non-senescent cells at the SST which causes that the preparations for detachment take place on both sides of the future abscission plane, but we know very little about these interrelations. Probably they may cause that the layer of "target cells" for ET is formed at the boundary between senescent and non-senescent tissues (compare Osborne 1977, Beyer 1979). Experiments in which AZ is formed in sites where it normally does not occur may help to elucidate this problem (Webster and Leopold 1972, Pierik 1980).

Findings concerning the mechanism of abscission are promptly utilized in reseach connected with practice. For example the recently discovered inhibitor of ET synthesis, aminoethoxyvinylglycine hydrochloride (AVG), markedly reduced the preharvest drop of apples (Bangerth 1978). An inhibitor of ET action, silver thiosulfite, was used to prevent petal fall from ornamental plants (Cameron and Reid 1981, see also Halevy and Mayak 1981). In *Leptospermum*, however, this compound did not inhibit the abscission of petals (Zieslin and Gottesman 1983). On the other hand, the newly found intermediate of ET synthesis, 1-aminocyclopropane-1-carboxylic acid (ACC), (Yu and Yang 1979, 1980) caused a great, short-lasting surge of ET production in plants (Cameron et al. 1979), however, it did not cause the shedding of olive leaves (Lavee and Martin 1981), on the contrary, ETP which caused long-lasting ET production, did caused shedding.

New substances releasing ET as well as substances which evoke abscission by stimulation of endogenous ET production are intensively tested in orchards (Humanes et al. 1978, Reed and Hartman 1976, Wheaton et al. 1977, Olien and Bukovac 1982, Evensen et al. 1982, Kadman and Ben-Tal 1983), and their effects on fruit physiology are investigated. An interesting affect of ET-releasing compounds found recently is the great reduction of photoassimilate transport from leaves to the fruit (Krewer et al. 1983 and literature cited there).

Working with abscission we also encounter the problem of infallibility of physiological processes. The leaves of a deciduous tree have to be shed before the cold or dry season because this is advantageous for the survival of the plant. Therefore the plants have developed several alternative mechanisms to achieve this "goal". Having several mechanisms is safer than having one, because when one fails the other may partly or fully replace it (Jankiewicz and Stecki 1976). Having more than one mechanism to achieve the same „goal" allows the plant to respond more flexibly to external conditions, because different mechanisms may be differently sensitive to changes in temperature, light etc.

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Mechanizm zrzucania liści i reproduktywnych części roślin przedstawiony w postaci modelu

Streszczenie

Przedstawiono proces zrzucania liści i reproduktywnych części roślin w formie modelu, który pozwala czytelnikowi zorientować się w całości tego procesu. W zjawisku zrzucania części roślin można wyróżnić dwa okresy. W pierwszym z nich zjawisko to może być zahamowane lub odwrócone pod działaniem auksyn, natomiast w drugim już jest nieodwracalne. Zwiększona produkcja etylenu (ET) łączy wcześniejsze fazy zjawiska starzenia się danego organu z jego zrzuceniem. Etylen ma podwójną rolę w inicjacji zrzucania: 1) Działając na blaszkę liściową zatrzymuje eksport auksyn z niej i w konsekwencji strefa odcinania (SO) u podstawy organu jest skąpo zaopatrywana w ten hormon. Gdy ten stan trwa dostatecznie długo, SO staje się wrażliwa na bezpośrednie działanie ET. Gdy to nastąpi, zostają zainicjowane dalsze stadia procesu zrzucania. Rozpatrzono także rolę kwasu abscysynowego i tyloz w zrzucaniu, oraz wpływ czynników środowiska i wpływy korelacyjne ze strony innych organów. 2) W czasie następnego okresu występują już nieodwracalne zmiany w SO. Następuje znaczna stymulacja aktywności metabolicznej w SO i jej tkanki stają się miejscem przyciągania składników odżywczych. Pojawiają się w SO ostre gradienty hormonalne umożliwiając prawdopodobnie dokładną lokalizację specyficznej warstwy (lub warstw) odcinania w ramach SO, w których ostatecznie zachodzi odcięcie. Następnie, odłączenie części rośliny może dokonać się w rozmaity sposób, przy czym jeden z opisanych sposobów nie wyklucza innych. Tak więc zrzucenie może dokonać się za pomocą enzymatycznej degradacji blaszki środkowej i ściany pierwotnej komórek w warstwie odcinania lub przez zaindukowanie w niej podziałów komórkowych, z następującym w konsekwencji rozerwaniem delikatnych ścian komórkowych nowo utworzonych komórek. Może również zajść dzięki niejednakowemu powiększaniu się komórek w sąsiadujących z sobą warstwach SO, co prowadzi do powstania napięć mechanicznych między nimi i do zerwania się między nimi kontaktu. Odcięcie może także nastąpić wskutek zamierania komórek co prowadzi do powstania pustych przestrzeni w tkankach SO. Problem niezawodności procesów fizjologicznych jest krótko przedyskutowany.