A general theory of excretion in higher plants

Brian J. Ford

Introduction

Biology teaching is founded on the seven essential characteristics of living organisms: nutrition, respiration, growth, movement, sensitivity (= irritability), reproduction, and excretion. In botanical texts the last of the list is widely ignored, for the term 'excretion' does not appear in the index to the standard volumes on plant physiology. It is usually taught that there are in plants no organs or systems evolved for excretion. There are some phenomena which have been linked with the process, including the deposition of material in bark, the laying down of oxalate crystals in cystoliths (Brocklehurst and Ward, 1977), even the release to the atmosphere of gaseous CO_2 at night.

In primitive plants we can discern the origin of a thickened cell wall in terms of a 'metabolic sink' for the products of photosynthesis (Ford, 1976). Green plants must photosynthesize when exposed to light, and the formation of the polymer cellulose would be a sensible way of routeing excess levels of photosynthetic energy. Clearly, since it is insoluble, laying down deposits beyond the cell's vital constituents (i.e. as cell wall) would make evolutionary sense. The formation of tracheary elements thickened with lignin may be a further extension of this process, allowing the plant cell to site potentially burdensome metabolic products outside the cell body.

Aquatic plants such as the large phaeophyte algae, which can grow to a frond length of 200 metres or more, are able to rid themselves of metabolites through diffusion, in a similar manner to that by which they obtain their nutriment input; for these reasons conducting vascular tissues are not a feature of these types. But a plant that evolves to live on land can utilize the evolution of a thick cell wall as a means of gaining rigidity. The osmotic potential of a plant growing in the soil can be harnessed to provide turgor with which to gain structural resilience, whilst the tracheary components can form the basis of a vascular bundle system.

However, there is in this concept no provision for excretory organs. I now believe that we should examine the cyclical phenomena in plants, for in them we may discern an excretory mechanism that has not been previously recognized.

Conventional models

The suggestion has been made that the reason why plants do not boast an excretory system is that they are 'far less active' than animals of a comparable evolutionary status (Brocklehurst and Ward, 1977). They do not need to rid themselves of a nitrogen burden, true; but though the reduced levels of metabolic activity in a sessile green plant might imply a *reduced* level of excretory load, that should not allow us to deduce that such systems must be entirely non-existent. In principle, the absence of an excretory system is inimical to the process of sustained metabolism.

Objections have been raised to the need for an excretory system in plants because of their autotrophic nature, that is, they produce metabolites through photosynthesis. Though a contrast seems to exist here with animal metabolic behaviour, the dark phase of plant metabolism features a form of metabolism at night which has more in common with that of animals than it has in disparity, and in this catabolic phase we would also expect to find some evidence of an excretory process.

The turnover diagrams of Woolhouse and Jenkins (1983) exemplify the profound deficiencies in contemporary understanding. They show clearly how degradation products of protein cycles give rise to wastes that, in their treatment, are exported to other parts of the plant. Their summary of the hydrolytic breakdown of protein suggests that the eventual fate is through the phloem transport system mediating export from the leaf (Woolhouse and Jenkins (1983), fig. 15.7). Yet we only have such mechanisms of the passing out of excess water in guttation, or into intercellular spaces (as in *Cucurbita*) to offer in response (Strasburger *et al.*, 1912); a single excretory mechanism that would apply to all higher plants remains elusive.

Leaf fall

The loss of leaves from land plants is a widespread phenomenon, and the seasonal fall of leaves in autumnal deciduous species should not direct attention away from the continuous loss of leaves that also takes place in their evergreen counterparts. Though there are well-known advantages in autumnal leaf loss, the existence of similar evergreen species illustrates that overwintering is feasible with leaves, as it is without; thus the process of deciduous leaf loss is not essential.

The widely taught view that the formation of an abscission layer leads to the occlusion of the petiole

Figure 1   Vertical section of *Acer palmatum* during early autumn, showing incipient pigmentation of upper palisade cells. Unstained, decentralized phase, × 100
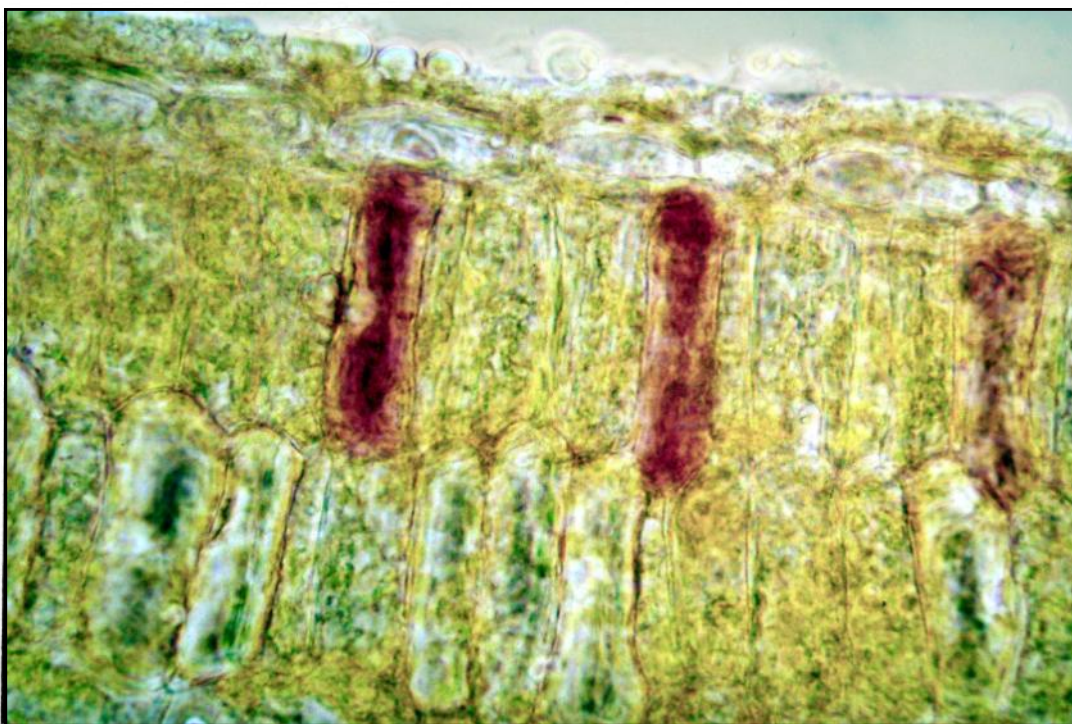

Figure 2   High magnification reveals deposition of pigments in upper palisade cells. The deposits have an amorphous appearance, and increase in extent during the autumnal weeks. unstained, phase contrast, × 260.
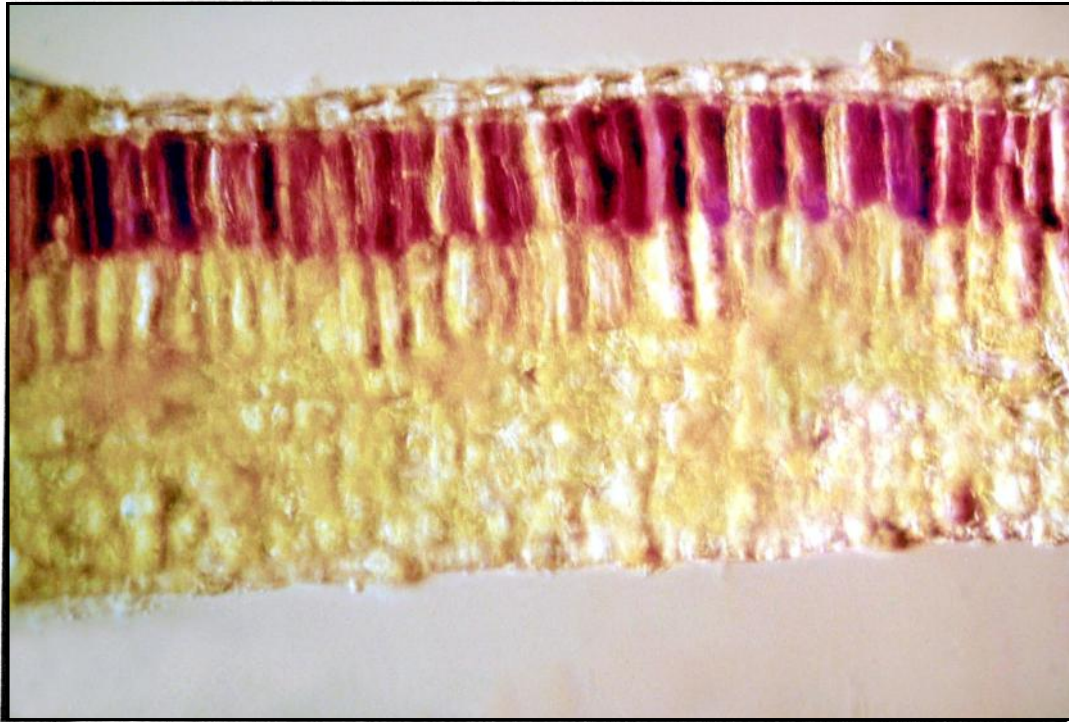
Figure 3   *Acer palmatum* during late autumn shows heavily pigmented upper palisade layer. Pigmentation is restricted to these cells, and increases as abscission approaches. Unstained, phase contrast, × 100.

Figure 4   High magnification shows deep impregnation with pigment. Autumnal colour is here not due to mere translocation of chlorophylls, but to specific deposition of pigments. Phase, × 260.

vascular elements and, thus, the inevitable death of the leaf can be faulted. Leaf fall is observed in plants even when no abscission layer is present. The presence of the layer does not always result in the loss of the leaf. Finally, leaves which ordinarily fall when an abscission layer has developed can be induced to abscind when the layer has yet to form (Meyer and Anderson, 1952).

Why 'senescence'?

Leaf fall is usually seen as the end-point of leaf senescence. However, there are objections to this view. Typical senescence involves a loss of vigour and a lowering of metabolic activity throughout the process. In the leaf changes that precede leaf fall there are several curious phenomena that contradict what we must expect of a senescence process. For instance, respiratory activity remains at a high level during the so-called senescence and in some genera (such as *Tropaeolum*) it may actually increase as the processes progress (James, 1953).

It is too easy to assume that the autumnal coloration is 'revealed' during the translocation of chlorophyll to other areas of the plant body. This is not what happens. Observation of transverse sections of leaf tissue during autumn show that, as the plastids lose their green colour, chromatic bodies develop which are rich in red or yellow pigments and these, I believe, are both the origin of the leaf colour and the mechanisms by which metabolites are laid down for excretion at abscission. Optically active oxalate crystals appear in this phase, too.

It is difficult to designate a leaf as senescent when the plant which bore it has many years to live. We require a term to connote the change of colour which is the hallmark of this process. What the leaf exhibits is *metachromism*, that is a change in colour. The metachromatic leaf is undergoing a precisely coordinated metabolic sequence that removes by translocation substances that are of value to the plant body, whilst consigning specified compounds to be shed. Thus I believe we should view the anthocyanins and tannins, along with the red and yellow leaf pigments so typical of autumn, as excretory products. The oxalates which develop in cystoliths (*supra*) and which increase during the metachromatic phase of maturation in land-borne species, are grouped together under the same category. Little is yet known of the enzyme systems that are involved in translocation, nor of the mechanisms which underlie the autumnal changes in deciduous leaves (Bonner and Varner, 1976), but it is known that protein inhibitors can delay the process (Rhodes, 1980), which is a clear indication that there is an active phenomenon at work, rather than a degenerative 'senescence'.

Thus I propose that we view the leaf not only as the photosynthetic centre in which key biochemical changes take place, but also as the organ into which waste materials are located prior to leaf fall. The shedding of the metachromatic leaf is then seen as the plant's mechanism of excretion. Recycling of the wastes and their processing into a form that can be of value to a future generation of plants and animals is then undertaken by the soil microbiota, many species of which have doubtless specifically evolved to perform this function.

Summary

Of the seven characteristics of living organisms, excretion is usually denied to plants in the orthodox physiological texts. The occasional examples that are cited, including the storage of oxalates in retained tissues, the liberation of CO_2 from growing leaves, and the storage of harmful metabolites in cell walls, do not amount to a universal excretory system for plants. A new concept is postulated, in which the leaf is visualized, not only as the plant's photosynthetic centre, but also as the organ which, at the end of its anabolic programme, is stripped of vital constituents and systematically charged with metabolic wastes. At abscission, these substances (including anthocyanins, tannins, and oxalates) are shed from the plant body.

Leaf fall has long been regarded as an anomalous phenomenon, and the concept that it is a vital part of the plant's metabolic cycle allows us to give it a meaningful place in the teaching of biology. We can, at the same time, complete the list of essential characteristics in the world of higher plants as we have long done for the animal kingdom.

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The author

Brian J. Ford is a Fellow of University College Cardiff and is based at Mill Park House, 57 Westville Road, Cardiff CF2 5DF.