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Fluorescent idioblasts in autumn leaves of *Ginkgo biloba*

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Dedicated to Prof. Dr. Peter Sitte at the occasion of his 65th birthday

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Abstract

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Towards the end of the senescence period, the foliage of *Ginkgo biloba* turns into a brilliant golden colour. This is in part due to an outstandingly high retention of carotenoids during the almost complete breakdown of chlorophyll. Besides, a kind of optical brightener, 6-hydroxykynurenic acid, is accumulated in scattered cells of the mesophyll but also of the vascular parenchyma and even in some epidermal cells. Thus, during senescence a group of cells appears to run through a second differentiation which, in the case of mesophyll cells, is characterized by the development of chloroplasts into gerontoplasts and the simultaneous production of brightly fluorescent 6-hydroxykynurenic acid. These cells may be apostrophized as secondary idioblasts.

Key words: Ginkgo biloba, foliar senescence, fluorescent idioblasts, 6-hydroxykynurenic acid.

Professor Sitte has a special liking and appreciation for beauty as an inherent property of organisms. He is a modern cell biologist but nevertheless keenly interested in phenomena that do not belong to the prevailing concerns of contemporary research. Indeed, he has contributed enlightening reflections about such penomena as symmetries, patterns, shapes and colours as well as about the significance of beauty in general (e.g. Sitte 1984, 1987). It is certainly no coincidence that one of his favourite research topics concerns the chromoplasts, the "colourful objects of modern biology" (Sitte 1977). Hence, an adequate birthday present must deal with a beautiful and colourful phenomenon: the autumn leaves of *Ginkgo biloba*.

Chromoplasts have features in common with the plastids in the mesophyll of senescent leaves which, in the course of chlorophyll breakdown, retain a larger or smaller fraction of the yellow thylakoidal pigments. These carotenoids accumulate, together with other undergraded or undergradable lipids, in numerous and large plastoglobuli so that the structure of senescent chloroplasts resembles quite closely the structure of globular chromoplasts. *Ginkgo biloba* provides a remarkable example as foliar senescence is characterized by the highest retention of carotenoids observed in trees so far (Tôyama and Ueda, 1965; Matile et al. 1992).

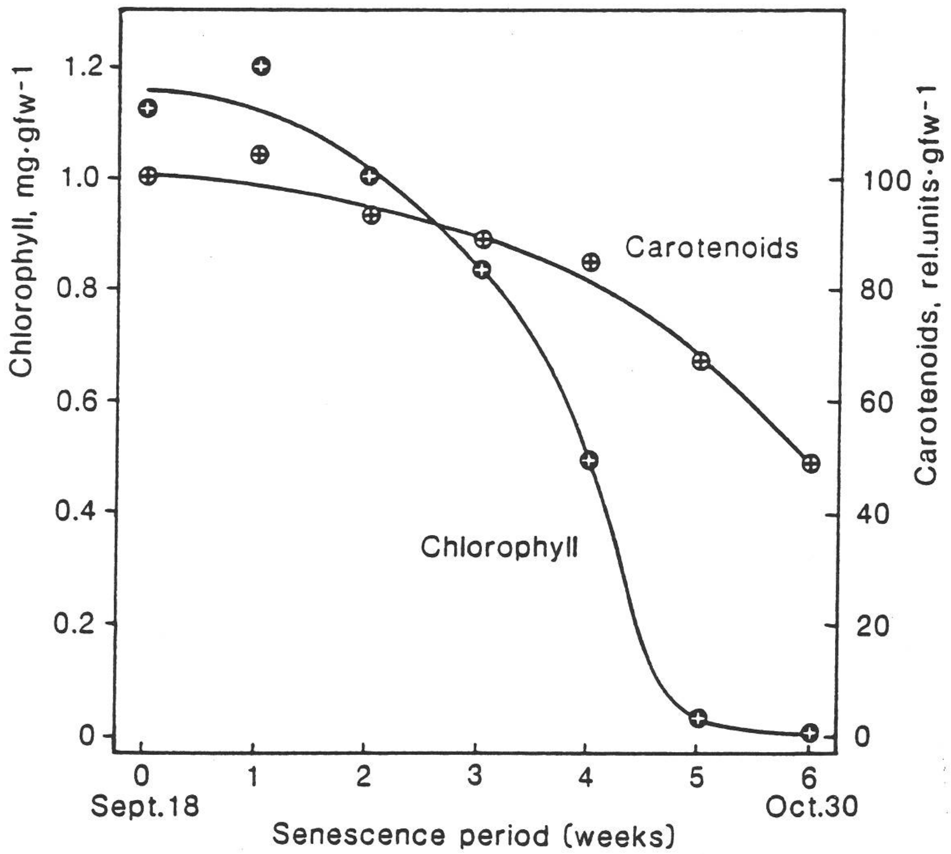


Fig. 1. The yellowing of *Ginkgo* leaves as documented by the changing contents of chlorophylls and carotenoids in the course of a sampling period in 1989. Note the retention by the end of foliar senescence of about half of the total carotenoids present in the presenescent leaves. Adapted from Matile et al. 1992.

Despite these similarities between chromoplasts and senescent chloroplasts, there are marked differences which justify the terminological distinction between chromoplasts and gerontoplasts (senescent chloroplasts) as proposed by Sitte (1977). Thus, chromoplasts retain biosynthetic capacities particularly regarding carotenoids (Sitte et al. 1980) and correspondingly they contain a few copies of the plastome (Haussmann et al. 1985). In contrast, the differentiation of gerontoplasts proceeds under the control of the nuclear genome (Yoshida 1961) and biosynthetic activity fades away as chloroplasts are induced to senesce. Indeed, in rice coleoptiles the nucleoids of chloroplasts have been shown to be lost at incipient senescence (Sodmergen et al. 1989). In any case, the term "gerontoplast" is gradually adopted by the scientific community (e.g. Parthier 1988) and will remain connected with the work of Prof. Sitte.

Ginkgo biloba is a highly valued ornamental tree and this is in part due to the beautiful golden appearance of its autumnal foliage. As shown in Fig. 1 the unusually high retention of carotenoids in the gerontoplasts contributes decisively to the outstanding quality of colour in the senescent leaves. However, there is a second component of colour display: as the leaves begin to senesce they accumulate a fluorescent compound, 6-hydroxykynurenic acid (Schennen and Hölzl 1986) which appears to have the effect of an optical brightener (Matile et al. 1992). The highest contents of this secondary compound are reached towards the end of the senescence period (Fig. 2), shortly before

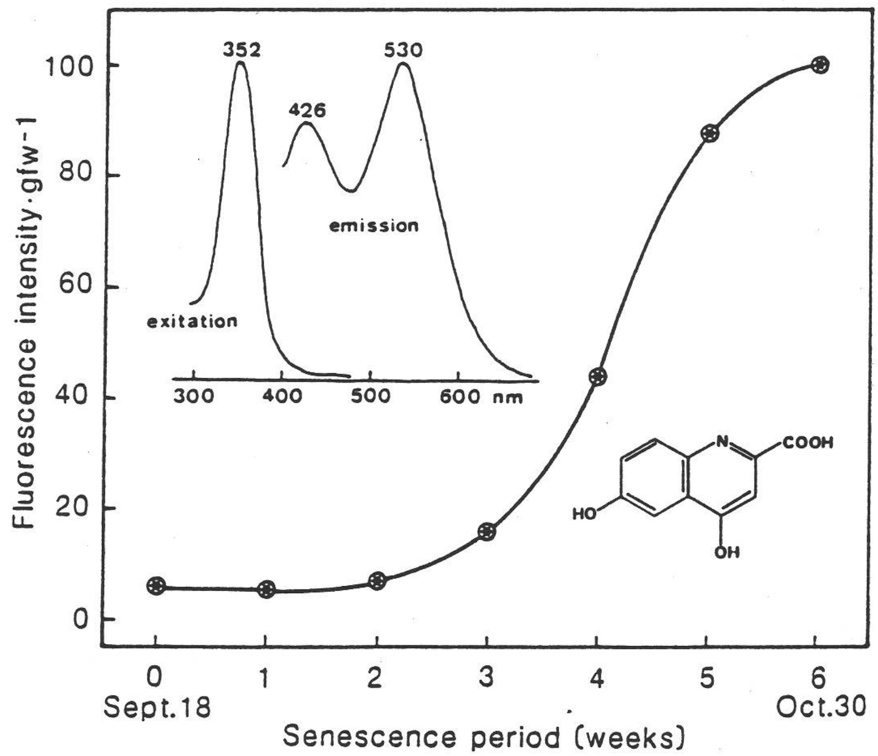


Fig. 2. The accumulation of fluorescent 6-hydroxykynurenic acid during foliar senescence in *Ginkgo biloba*. Insets show the spectra of excitation and emission as well as the chemical structure of the fluorescent compound. Adapted from Matile et al. 1992.

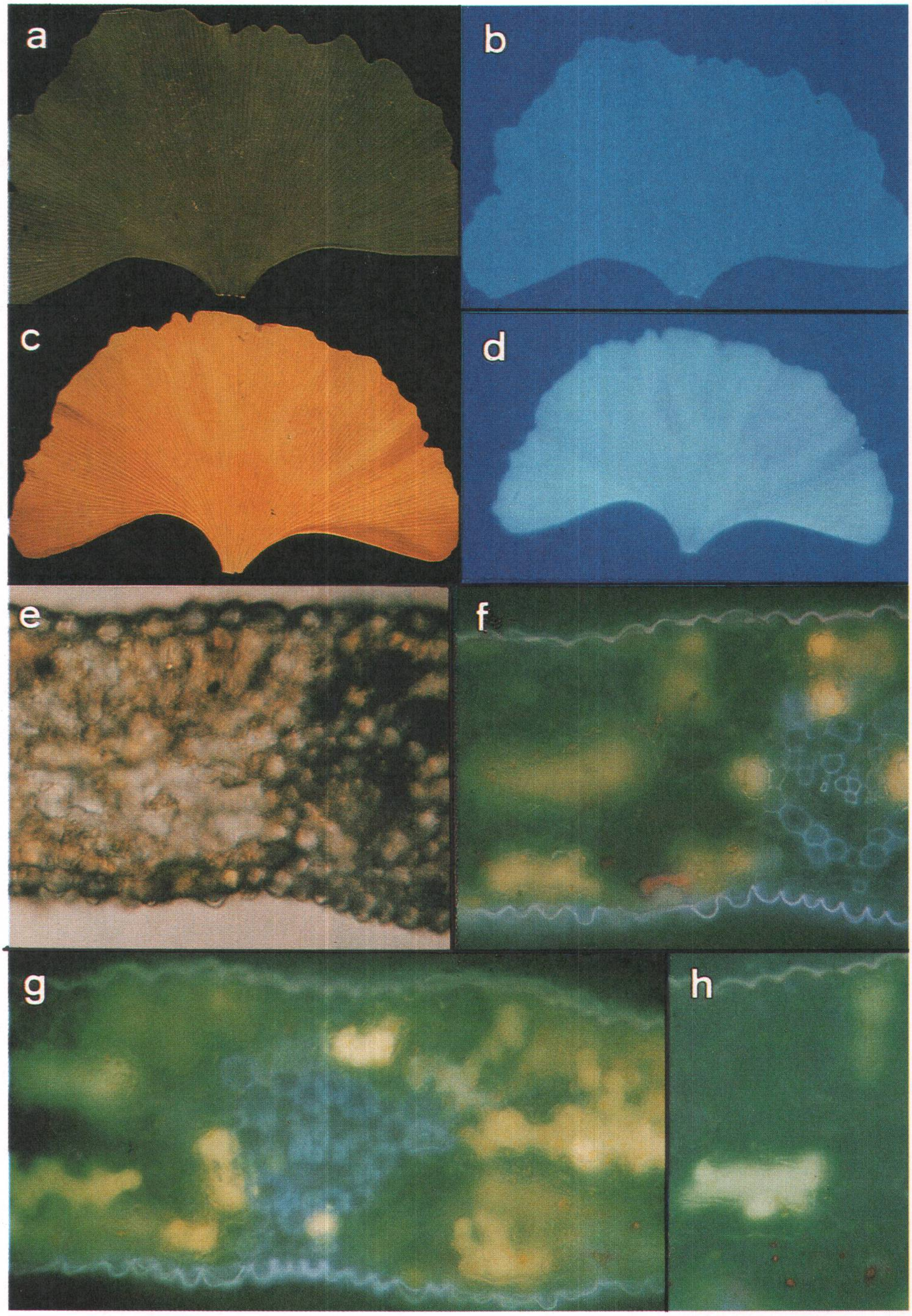
abscission. The fluorescence can easily be seen in the yellowed leaves (Fig. 3d), and the emission spectrum determined by Lang et al. (1991) in intact leaves corresponds very closely with the spectrum of 6-hydroxykynurenic acid (Fig. 2). An examination of senescent leaves of various species which also have a quite brilliant appearance (*Cercidiphyllum japonicum, Liriodendron tulipifera, Cornus Florida, Davidia involucrata*) has yielded negative results regarding the presence of an optical brightener. Thus, *Ginkgo biloba* seems to represent a unique case of colour display enhanced by means of a fluorescent compound synthesized during foliar senescence.

Premortal synthesis of secondary compounds such as anthocyanins occurs in the leaves of many species. In autumn leaves of *Populus tremuloides* for example, the varied colouration from yellow to orange and red in different clones is due to the presence or absence of cyanidin-glycosides (Chang et al. 1989). One of the precursors of anthocyanidins is phenylalanine. In senescent leaves it is probably a product of protein breakdown. The amino group of phenylalanine is eliminated as ammonia in the first step of the phenylpropane pathway leading to anthocyanidins; without doubt ammonia is reassimilated into glutamine and eventually withdrawn from leaves together with other N-containing derivatives of protein breakdown. Indeed, breakdown processes play an important role in the recycling of nutrient elements such as nitrogen, phosphorous and others from senescent leaves into other parts of the plant. Therefore, it is quite remarkable that in *Ginkgo* leaves tryptophan is metabolised to 6-hydroxykynurenic acid which still contains one of the two N-atoms originally present in the precursor amino acid. Even more surprising is the finding that the accumulation of 6-hydroxykynurenic acid does not occur uniformly in all mesophyll cells. Rather is it restricted to scattered cells in the spongy- and palisade mesophyll and in peripheral cells of vascular bundles (Fig. 3, f–h). Occasionally it can also be discerned in epidermal cells. Thus, foliar senescence in *G. biloba* appears to be associated with the differentiation of a kind of idioblasts from cells which in the mature green leaf had been specialized in another function such as photosynthesis. Extensive protein breakdown takes place in the entire mesophyll as indicated by the differentiation of chloroplasts into gerontoplasts. The special feature of differentiation of fluorescent idioblasts must concern the metabolism of tryptophan: its conversion to 6-hydroxykynurenic acid requires at least four specific enzymes, i.e. the senescence-induced expression of the corresponding genes. Since the fluorescent cells represent products of a second differentiation, they may be apostrophized as secondary idioblasts. They may occur in great numbers in one part of a leaf (Fig. 3 g) whilst they may be rare (Fig. 3 f) or even absent in other parts. As a consequence of such an uneven distribution of idioblasts the fluorescence of leaves is often somewhat spotted.

It is difficult to think of a biological function associated with the rather elaborate processes taking place in senescent *Ginkgo* leaves which eventually result in a shortlived premortal display of golden shining foliage. It may be argued that only those parts of metabolism engaged in the vitally important recycling of nutrients have evolved under selection pressure. Other parts of metabolism may not be significant for the vitality of a tree and may have evolved under rules of "harzard" without "necessity". The phenomena observed in *Ginkgo biloba* as well as less spectacular ones in other deciduous trees appear to be based on genetically fixed programmes, yet they are not associated with a biological function except for a high aesthetical merit..

I am indebted to Maya Schellenberg for help with the purification of 6-hydroxykynurenic acid, to Stefan Matile and Wolfgang Woggon for the confirmation of its chemical structure and to Verena Leu for help with the manuscript.

Fig. 3. Presenescent (a, b) and fully senescent (c, d) leaves of *Ginkgo biloba* as viewed under white light (a, c) and uv-B (b, d), respectively. Note the somewhat uneven fluorescence in d. Tissue localizations of 6-hydroxykynurenic acid are shown in handsections f–h. Micrograph e shows the general leaf annatomy and allows the identification of fluorescent cells (f) with individual cells of the spongy mesophyll, of the palisade mesophyll, as well as with cells at the periphery of a vascular bundle. Note the retention of chlorophyll (red fluorescence) in the guard cells of a stoma in the adaxial epidermis. In the section of micrograph g fluorescent idioblasts are abundant whilst in h fluorescence is restricted to only two scattered mesophyll cells.


a
b
c
d
e
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g
h

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