

Spectral Reflectance Changes Associated with Autumn Senescence of *Aesculus hippocastanum* L. and *Acer platanoides* L. Leaves. Spectral Features and Relation to Chlorophyll Estimation

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Received August 9, 1993 · Accepted October 20, 1993

Summary

The reflectance spectra of adaxial surfaces of *Aesculus hippocastanum* L. and *Acer platanoides* L. leaves in the course of autumn pigment transformation were recorded. A dramatic decrease in and almost complete disappearance of chlorophyll (Chl) gave an opportunity for the investigation of relations between the reflectance changes and the pigment concentrations. The signature analysis of reflectance spectra indicated that in the green to yellow leaves of both species the maximal standard deviation of reflectance coincided with the red absorption maximum of Chl a . However, within the leaves with high Chl, minimal sensitivity to pigment variations was observed at 675 nm. The maximal standard deviations were found near 550 to 560 and 700 to 710 nm. The revealed spectral features can serve as sensitive indicators of early stages of leaf senescence. The several functions of reflectance were found to be directly proportional to Chl (a square of correlation coefficient of more than 0.97); that allows an assessment of the pigment concentration ranging from 0.5 to 27.5 nmol/cm² with an estimation error of less than 1.5 nmol/cm². This makes its possible to precisely determine Chl a with a background of variable and high pigment concentration.

Key words: Reflectance, remote sensing, senescence, estimation.

Abbreviations: NDVI = Normalized Difference Vegetation Index; sd = Standard Deviation.

Introduction

A green leaf represents high performance photosynthetic machinery efficiently trapping radiation in the visible part of the spectrum. The specific structure of the leaf surface – epidermal, mesophyll cells, the existence of an air-rich spongy mesophyll layer, as well as highly scattering cell walls and intracellular particles including chloroplasts – creates optical boundaries that control penetration and distribution of light within the leaves. As a result, both the direction and effective pathway of light are considerably altered (Heath, 1969; Vogelmann and Bjorn, 1986; McClendon and Fukshansky,

1990; Donkin and Price, 1991). For these reasons and also because of high chlorophyll (Chl) *a* and *b* and carotenoid concentrations, as well as very effective light absorption by these pigments, both the reflectance and absorption spectra of green leaves are broad and unresolved (Wooley, 1971; Gausman et al., 1976; Thomas and Gausman, 1977; Chappelle et al., 1992).

To date, the techniques for determination of pigment content have usually involved leaf reflectance near the red absorption maximum of Chl at 675 nm, (e.g., Thomas and Gausman, 1977; Chappelle et al., 1992; Szekiela, 1988). This approach can be applied in leaves in which a dramatic

decrease in the concentrations of the pigments has occurred and/or for the samples with a relatively low pigmentation. At present, only limited quantitative information can be obtained directly from reflectance measurements for material with high pigment concentration.

Synchronous autumn leaf senescence in deciduous species, which is accompanied by progressive loss of the bulk photosynthetic pigments (Chichester and Nakayama, 1965; Thomas and Stoddart, 1980; Tevini and Steimüller, 1985; Hendry et al., 1987; Matile et al., 1989; Young et al., 1991), gives a simple and useful model to study the relationships between changes of optical characteristics of, and large-scale pigment variation in, the plant leaves (e.g., Adams et al., 1990; Matile et al., 1992). Moreover, the events occurring in senescing and aging leaves are very close to those taking place in plants under stress conditions: herbicides, pollutants, extreme temperatures, drought, and diseases (Leshem et al., 1986; Elstner, 1982; Hendry et al., 1987; Thompson et al., 1987; Merzlyak, 1991).

The goal of the study was a detailed investigation of the basic spectral properties of the leaves, in order to create optical models of the relationships between their pigment concentration and the parameters of the reflectance spectra. The experiments were carried out on the autumn leaves of two deciduous species to gain insight into the mechanisms of formation of reflectance. The results may serve as a basis for developing indexes sensitive to pigment variation, and acting as indicators of plant senescence or other destructive processes in the leaves of higher plants.

Materials and Methods

The experiments were performed on horse chestnut (*Aesculus hippocastanum* L.) and Norway maple (*Acer platanoides* L.) leaves collected in the Botanical Garden of the Moscow State University in October of 1991 and 1992, respectively. Only leaves having uniform green, green-yellow, yellow-green and yellow color without anthocyanin pigmentation were selected. In addition, the absence of

anthocyanins was checked spectrophotometrically (absorption in the band of 530–620 nm) in ethanol extracts containing 1% HCl.

Chl *a*, *b* and total carotenoid concentrations in the leaves were determined in acetone extracts and were calculated using coefficients for 80% acetone (Lichtenthaler et al., 1982). The average mol wt of 570 for carotenoids was used.

The reflectance spectra were recorded with a Hitachi 150-20 spectrophotometer equipped with an integrating sphere attachment (i.d. 150 mm, part 150-0901) at the rate of 100 nm/min, with response (time constant) set as «slow» and against barium sulfate as a reference standard. The diffuse reflectance of leaves was measured in the region of 400 to 750 nm with a spectral resolution of 1 nm. Black velvet material with reflectance lower than 0.3% was used to absorb the light passing through the leaf. The spectra were determined for the sections of the leaves between main veins (maple) or with the main veins removed (chestnut), with the adaxial surface facing the measuring beam. The spectral data, converted into reflectance (R) values, were stored in a computer.

Results

Changes in pigment concentration in senescing leaves

In the senescing leaves of both species the concentrations of the pigments declined following the preferential loss of Chl *a* (Table 1). During the autumn senescence the absolute concentration of total carotenoids decreased; however, following almost complete loss of both chlorophylls, the concentration of the carotenoids remained at a relatively high level (about 40–50% of their concentration in green leaves). As a result, the ratios of total Chl to carotenoids progressively decreased (app. 10-fold) in the progress of senescence. The data demonstrate the general pattern of the changes in pigment concentration during autumn documented in many other plant species (Chichester and Nakayama, 1965; Tevini and Steimüller, 1985; Matile et al., 1989; Adams et al., 1990; Young et al., 1991).

Reflectance spectral changes in senescing leaves

The reflectance spectral features were found to be the same for both species studied. In the region investigated, the maximal reflectance was found at 750 nm independent of the stage of leaf senescence (Fig. 1 A and B). In this domain, Chl absorption is very small and reflectance is caused only by the scattering properties of the leaves.

The reflectance minima were observed in the bands corresponding to Chl and carotenoid absorption. The green leaves (samples 1 and 2) containing high Chl and carotenoid quantities had low reflectance both in the red (640–690 nm) and blue (400–500 nm) regions of the spectrum. In the progress of senescence, when a considerable fall in Chl took place (samples 3–6), a noticeable increase in reflectance occurred from 510 to 600 nm and at wavelengths longer than 690 nm. In green and green-yellow leaves (samples 1–4), the reflectance changes between 400 and 500 nm, as well as near 670 nm were very small. Only when Chl reached a relatively low level (samples 5–6), a very sharp increase in reflectance was observed between 500 and 750 nm.

Completely yellow leaves (samples 5 and 6) may be recognized by high reflectance, practically constant in the region

Table 1: Pigment concentrations (nmol/cm²) in senescing leaves. Car – total carotenoids.

Pigments	Sample #					
	1	2	3	4	5	6
<i>A. platanoides</i>						
Chl <i>a</i>	27.5	25.4	14.1	7.2	1.1	0.6
Chl <i>b</i>	8.2	7.9	4.8	2.6	0.8	0.7
Chl <i>a</i> + Chl <i>b</i>	35.8	33.3	18.9	9.7	1.9	1.3
Chl <i>a</i> /Chl <i>b</i>	3.3	3.2	3.0	2.8	1.4	0.9
Car	8.7	7.1	4.4	4.4	4.9	2.9
Chl/Car	4.1	4.7	4.3	2.2	0.4	0.4
<i>A. hippocastanum</i>						
Chl <i>a</i>	29.7	27.9	14.0	9.6	0.5	–
Chl <i>b</i>	13.8	11.3	3.9	2.6	0.18	–
Chl <i>a</i> + Chl <i>b</i>	43.5	39.2	17.9	12.2	0.7	–
Chl <i>a</i> /Chl <i>b</i>	2.1	2.5	3.5	3.7	2.8	–
Car	7.8	6.2	3.9	3.4	2.9	–
Chl/Car	5.6	6.3	4.6	3.6	0.2	–

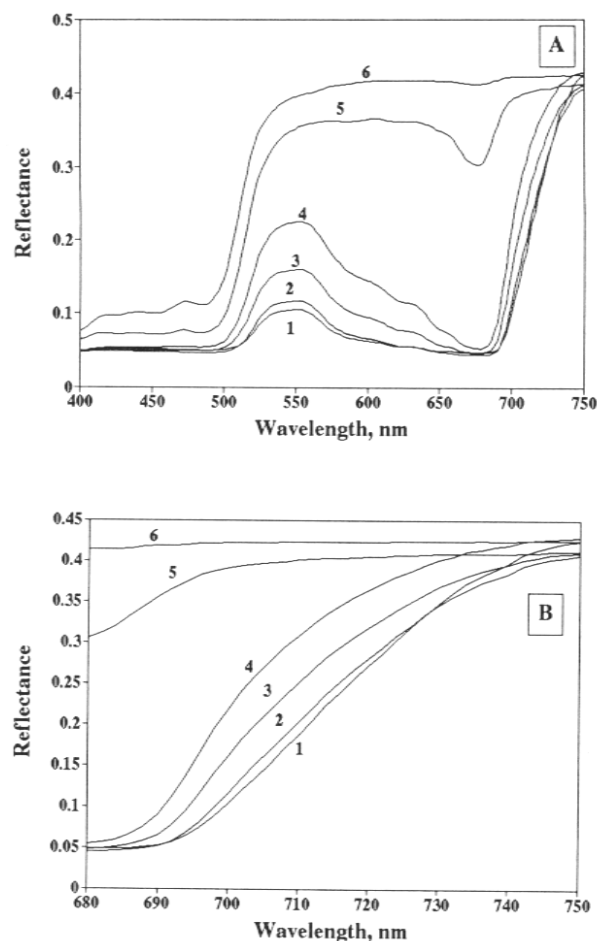


Fig. 1: Reflectance spectra of maple leaves in the progress of senescence. The numbers of the leaf samples (see Table 1) are indicated. The spectra are presented in the PAR region (A) and above the red chlorophyll absorption maxima (B).

between 550 and 750 nm. In these leaves the reflectance below 500 nm (in spite of a considerable decrease in the pigment concentration) remained relatively low. At these stages of senescence the absorption maxima of carotenoids were apparent. Quite similar changes of reflectance have been described in the senescing leaves of a number of plant species (Adams et al., 1990; Matile et al., 1992).

To gain more insight into the nature of the senescing-related reflectance changes, an analysis of the derivatives of reflectance was carried out (Fig. 2). The first order derivative spectra clearly indicated the different behavior of the «yellow» (samples 5 and 6) and the «green» or «yellow-green» (samples 1 to 4) maple leaves. In «yellow» leaves, three distinct minima corresponding to carotenoid absorption maxima near 425, 450 and 480 nm were observed. The slopes of the derivatives near 490 to 510 nm for these samples were two to three times higher than those for «green» ones.

The derivative spectra of «green» leaves were much more complicated. At least two spectral features should be mentioned: the sharp increase in the slopes of the derivatives between 510 and 520 nm in the progress of Chl breakdown,

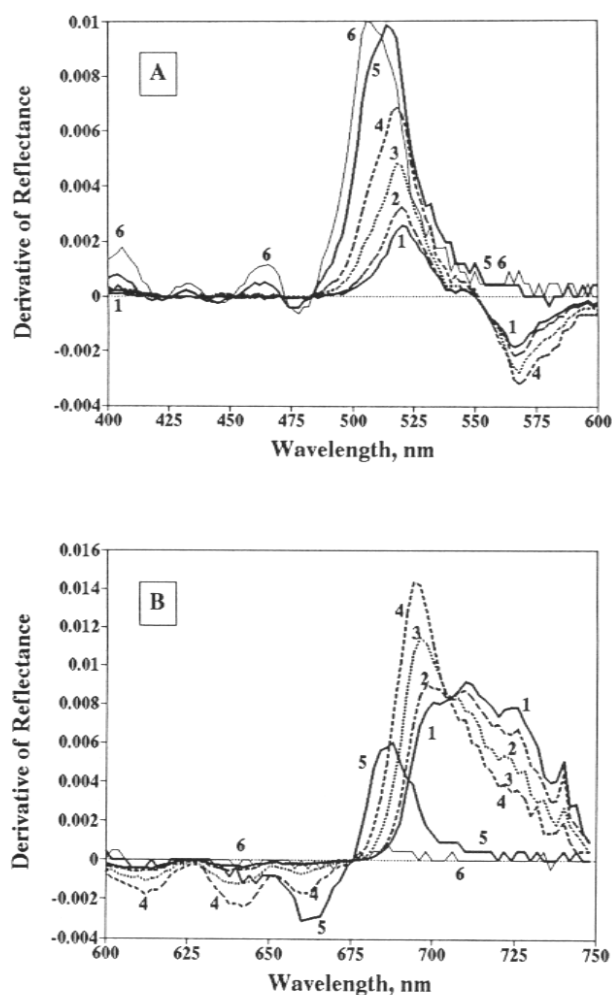


Fig. 2: The first order derivative of reflectance spectra of senescing maple leaves is presented at 400 to 600 nm (A) and 600 to 700 nm (B). The numbers of the leaf samples (see Table 1) are indicated.

and the change of sign of the derivative near 550 nm (Fig. 2 A) and at 675 nm (Fig. 2 B). The increase of the derivative near 500 nm corresponded to both Chl and carotenoid absorptions while that at 675 nm was due only to Chl *a* absorption.

Maxima of the derivatives occurred in the region 500 to 520 nm and their positions shifted to shorter wavelengths in the progress of leaf senescence. A sharp decrease of the derivatives followed the above mentioned maxima, and their magnitudes then became equal at 555 nm. The indicated changes of the derivative sign are characteristic for «green» (but not for «yellow») leaves. Three Chl *a* and *b* absorption bands, weakly resolved in reflectance spectra between 590 and 660 nm (Fig. 1 A), became distinguished in the first order derivative spectra near 590 to 600, 628, and 652 nm (Fig. 2 A and B).

The reflectance minimum at 675 nm was observed for all samples measured. At longer wavelengths, in the leaves with low Chl (samples 4–6), a progressive increase in the derivative occurred. A further increase in Chl (samples 1–3) led

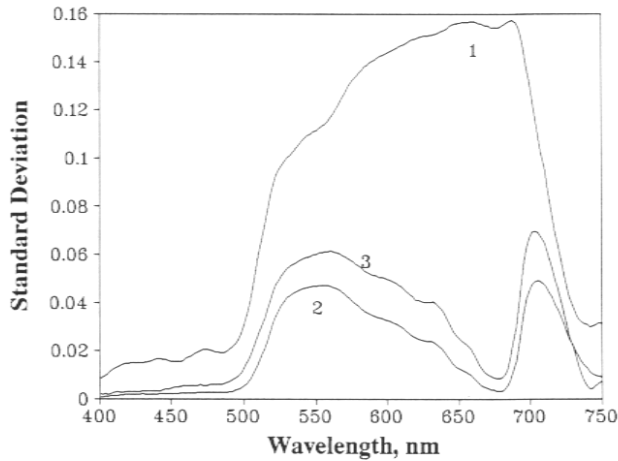


Fig. 3: The spectral dependence of standard deviation of reflectance for senescing leaves. 1 – all leaf samples (1 to 6 for maple and 1 to 5 for chestnut) were analyzed together, 2 – «green» leaves (samples 1 to 4) of maple and 3 – «green» leaves (samples 1 to 4) of chestnut. The numbers of the leaf samples are indicated in Table 1.

to a sharp fall in the derivative magnitude. This process was accompanied by a shift of the position of the derivative maximum towards longer wavelengths (the well known «blue shift» of the red edge). The derivatives became equal for all «green» leaves at 705 nm (samples 1 to 4).

Search of the spectral domains of reflectance sensitive to variation in pigment concentration

To reveal the patterns of the spectral changes sensitive to pigment concentration, analysis of reflectance variation was employed. Figure 3 demonstrates the spectral variation of standard deviation (sd) of the reflectance. Three sets of data were examined. The first included all eleven leaf samples (both maple and chestnut), while the second and the third included just the relatively green leaves (samples 1–4) of maple and chestnut separately. For the first data set, the maximal sd was found near 670 nm, decreasing toward the longer wavelengths (Fig. 3, curve 1). The relatively high sensitivity to the pigment variations was retained between 550 and 690 nm. A very small variation of reflectance was observed in the regions 400–500 and 740–750 nm.

A quite different pattern of the sd spectrum was revealed for the second and the third data sets (Fig. 3, curves 2 and 3). Although the minimal sd was again in the regions from 400 to 500 nm and from 740 to 750 nm, three distinct spectral features were observed. In contrast to the first set, a minimal response to pigment variation was found at 675 nm. Two distinct maxima of the sd were found near 550 to 560 and 700 to 710 nm; at the same wavelengths, equal magnitudes of the reflectance derivatives for green leaves were found (Fig. 2). Taking into account these circumstances, the reflectance spectra (R_i) were normalized to R_{550} and R_{705} (Fig. 4). The main feature of both the data sets was an increase in the reflectance ratios at wavelengths above 705 nm with the increase in Chl. The derivatives of the ratios R_i/R_{555} (Fig. 5)

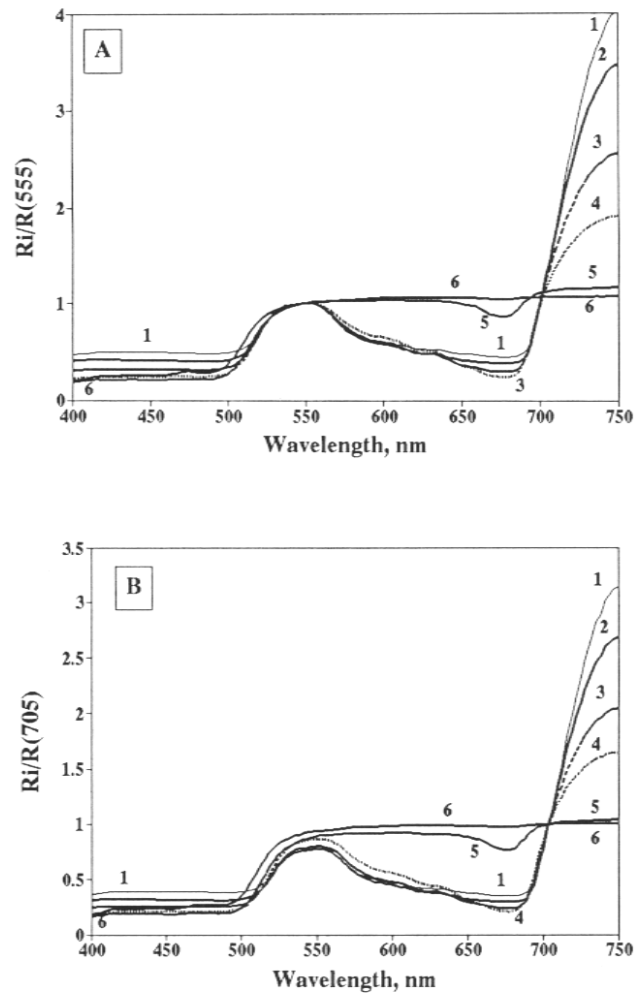


Fig. 4: The spectral dependence of reflectance (R) normalized A: to reflectance at 550 nm (R_{555}) and B: to reflectance at 705 nm (R_{705}) in senescing maple leaves. The numbers of the leaf samples (see Table 1) are indicated.

and R_i/R_{705} were found to be quite similar and sensitive (especially near 700 nm) to pigment variation. In addition, the senescence dependent shift of the maximum position of these functions was observed.

Discussion

To look for a sensitive optical indicator for the physiological state of a plant, one has to develop methods suitable for deriving relatively small variations in pigment concentration in green leaves. This problem was solved by employing specific spectral features of reflectance for leaves with high Chl.

The maximal values of sd for green leaves were found at 555 and 705 nm. Both the reflectance (Fig. 1) and the derivative (Fig. 2) spectra indicated the reasons for this phenomenon. As can be seen from Fig. 1 B, reflectance near 675 nm had approximately the same magnitude for Chl *a* ranging from 7.0 to 27.5 nmol/cm² (samples 4 to 1). This reflects

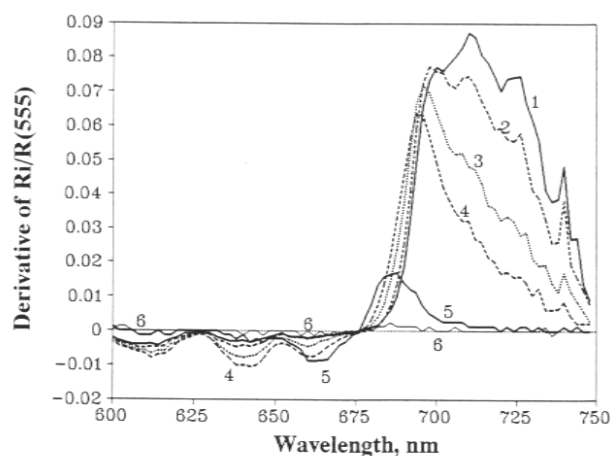


Fig. 5: The spectral dependence of the first order derivative of the reflectance ratio R_i/R_{555} for senescing maple leaves. The numbers of the leaf samples (see Table 1) are indicated.

non-linear dependence of reflectance on Chl content at wavelengths at least up to 700 nm due to very strong absorption by Chl. Wavelength 705 nm seems to be the starting point of a monotonous region of the relationship reflectance vs. Chl; the phenomenon is characterized by maximal and equal values of the derivative.

Quite a strong absorption by Chl *a* and *b* was observed at shorter wavelengths (up to 580 nm). Even at 580 nm, the slope of the relationship reflectance vs. Chl *a* remained very low for the leaves with high Chl (Fig. 1 A). Therefore, this domain cannot be used for precise estimation of high Chl.

The same processes take place in the blue region of the spectrum. Even at 520 nm, the sensitivity of reflectance to pigment concentration is very small. Near 540–560 nm, the long-wavelength wing of «blue» Chl and carotenoid absorption and the short-wavelength wing of «red» Chl absorption overlap, and thus both absorption processes are involved in the formation of a reflectance peak near 550 nm. At 555 nm, the derivative is equal to zero for all green leaves (samples 1–4 – Fig. 2 B); this indicates that at this wavelength the above mentioned absorption processes are in equilibrium.

Minima at 460 and 480 nm in the reflectance spectra of yellow leaves correspond to carotenoid pigments and the dip at 460 nm is due mainly to Chl *b* (Heath, 1969). The decrease in the reflectance above 555 nm is also due to preferential absorption by Chl *b*. For green leaves at 440 nm we could not distinguish any spectral feature. This suggests that Chl *b* absorption almost totally masks that of carotenoids. Hence, at least for our data set, estimation of carotenoid concentrations can be carried out only for leaves with extremely low Chl *b*.

Reflectance Indexes for Deducing of Chl in Leaves

The Normalized Difference Vegetation Index (NDVI), defined as the difference between the reflectances in near infrared and red regions of the spectrum normalized to the sum of these reflectances, is widely used for the evaluation of Chl in leaves and vegetation (e.g., Tucker et al., 1985; Szekiela,

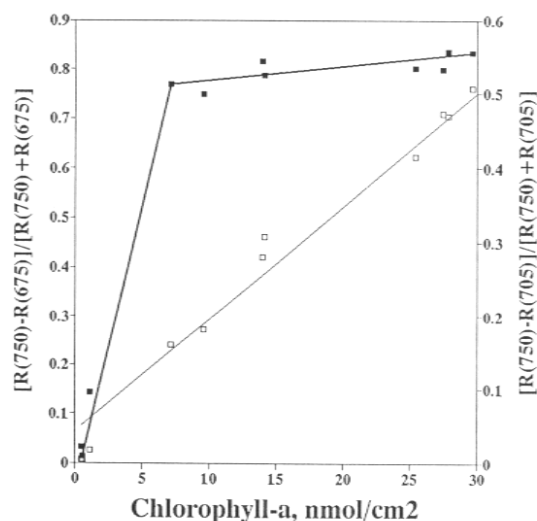


Fig. 6: NDVI (filled symbols, left scale) and the index calculated using reflectances at 705 and 750 nm (open symbols, right scale) plotted versus Chl *a* concentration in senescing maple and chestnut leaves.

1988). However, for our data set, the saturation of the index $(R_{750} - R_{675}) / (R_{675} + R_{750})$ occurs at a Chl as low as 7.0 nmol/cm² and «green» leaves with high Chl could not be distinguished by using this index (Fig. 6).

The spectral features of leaves revealed above can serve as a basis for producing indexes to retrieve pigment concentration for «green» leaves. Reflectances at 555 and 705 nm were found to be maximally sensitive to variation in Chl, while those near 400, as well as at 675 and longer than 730 nm, were minimally sensitive and could be used as references.

The ratios R_{675}/R_{555} and R_{675}/R_{705} vs. Chl *a* are shown in Fig. 7 A. It can be seen that both ratios could be used as indicators for only relatively low Chl. In the study by Chappelle et al. (1992) with soybean leaves, a high correlation between the ratio R_{675}/R_{700} and Chl *a* was found. According to the authors, 700 nm can be considered as «the spectral point at which there is no further contribution from chlorophyll *a* to the reflectance spectra» (therefore, it can be used as a reference) and reflectance at 675 nm is maximally sensitive to Chl. In fact, quite a different situation takes place in green leaves of maple and chestnut: R_{675} and R_{705} have minimal and maximal sensitivity to Chl, respectively. Thus, it seems that the success of the application of the ratio R_{675}/R_{700} for soybeans arose mainly because of maximal sensitivity of the reflectance at near 700 nm to Chl and the use of the R_{675} as a reference.

As a result of our study, it appears that the ratios R_{675}/R_{705} and R_{675}/R_{555} can be used for pigment estimation either for leaves with low or high Chl. However, the relationships between these ratios and Chl *a* are not monotonous and the slopes for «yellow» and «green» leaves have different signs (Fig. 7 A). For the same reason, the application of the NDVI cannot be successful for leaves with high Chl. A more suitable component in NDVI for estimation of high Chl has to involve R_{705} instead of R_{675} . Using the ratio $(R_{750} - R_{705}) /$

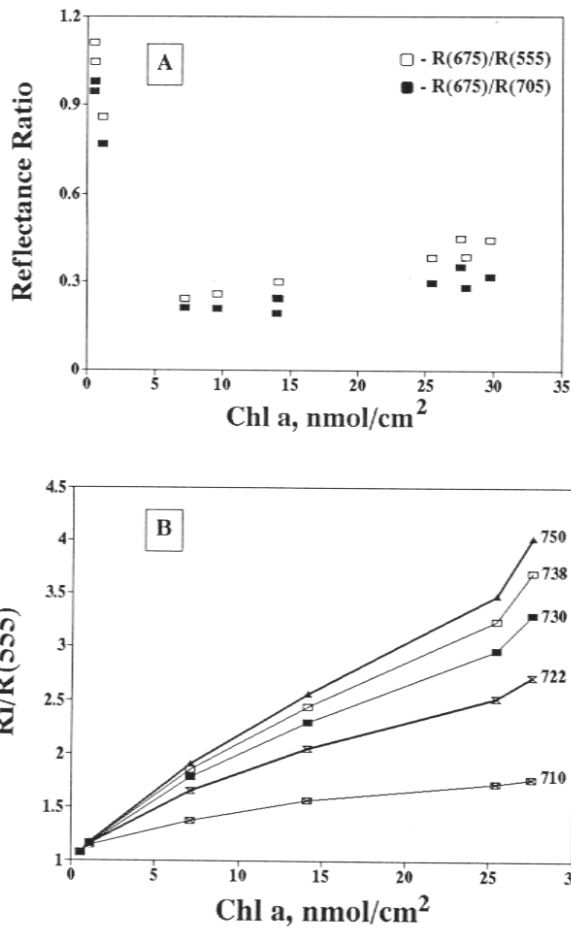


Fig. 7: Reflectance ratios as a function of Chl *a* concentration in senescing maple and chestnut leaves. A: R_{675}/R_{555} and R_{675}/R_{705} . B: Reflectances (R_i) at different wavelengths (indicated in nm) normalized to R_{555} . The ratios were retrieved from a combined data set of maple and chestnut leaves.

Table 2: The algorithms for chlorophyll *a* determination in maple and chestnut leaves, having the form $[Chl\ a] = a + b \cdot X$. X_{max} and X_{min} are maximal and minimal values of the index for Chl *a* ranging from 0.5 to 27.5 nmol/cm². Est. err. is standard error of Chl estimation.

X	a (nmol/cm ²)	b	r ²	Est. err. (nmol/cm ²)	X _{max} /X _{min}
R_{750}/R_{705}	-13.06	15.00	0.980	1.69	13.0
R_{750}/R_{555}	-8.16	8.59	0.974	1.97	4.1
$R_{750} - R_{705}$	-1.05	58.91	0.969	2.16	121.0
$R_{750} + R_{705}$	-1.25	0.57	0.979	1.78	11.5
$\int_{705}^{750} [R(\lambda)/R_{555} - 1] d\lambda$	-0.35	0.88	0.984	1.45	32.7

($R_{750} + R_{705}$), a close correlation between the index and Chl *a* was obtained (Fig. 6, Table 2).

The ratios R_{750}/R_{555} and R_{750}/R_{705} , showing high sensitivity to pigment changes (Figs. 4 and 7 B), were examined for both maple and chestnut leaves. For all the samples studied, linear relationships with Chl *a* were found in a broad range

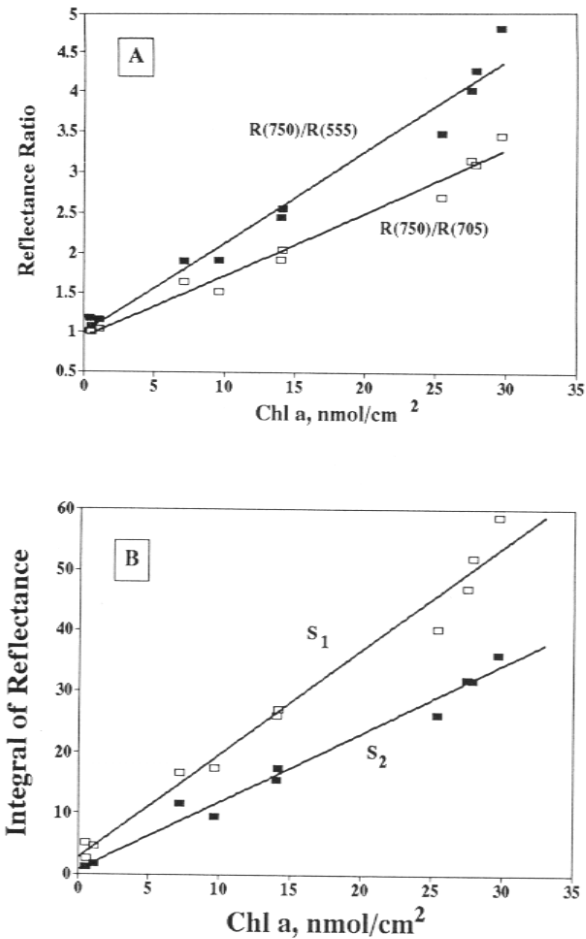


Fig. 8: The developed reflectance indexes as a function of Chl *a* concentration in senescing maple and chestnut leaves. A: R_{750}/R_{555} and R_{750}/R_{705} . B: Reflectance functions calculated as

$$S_1 = \int_{705}^{750} [R(\lambda)/R_{555} - 1] d\lambda \text{ and } S_2 = \int_{705}^{750} [R(\lambda)/R_{705} - 1] d\lambda.$$

of Chl *a* with the correlation coefficients $r^2 > 0.97$ (Fig. 8 A, Table 2).

Both the accuracy and sensitivity of Chl *a* determination in leaves could be further improved by employing the integral of functions $R(\lambda)/R_{555}$ and $R(\lambda)/R_{705}$ in the region 705–750 nm:

$$S_1 = \int_{705}^{750} [R(\lambda)/R_{555} - 1] d\lambda, \quad S_2 = \int_{705}^{750} [R(\lambda)/R_{705} - 1] d\lambda$$

The variations of both functions, with increase in Chl *a*, were found to be very high (Fig. 8 B). For the functions S_1 and S_2 r^2 was > 0.98 . It lowered the estimation error of Chl *a* to 1.78 and 1.54 nmol/cm² for S_1 and S_2 , respectively (Table 2).

Besides the indexes considered (Table 2), the observed reflectance changes provide evidence that many other algorithms could be used to model the characteristics of senescence and other physiological and stress-induced processes.

They might be based on the magnitude and position of spectral features of reflectance (Figs. 2 and 5).

It is interesting to note that the reflectances at 550 and 705 were introduced for remote estimation of phytoplankton Chl in productive inland waters (e.g., Gitelson et al., 1993). This fact emphasizes the fundamental nature of spectral features of chlorophyll-mediated light absorption and scattering processes both in higher plant leaves and in phytoplankton populations. Thus, it appears possible to create remote sensing systems utilizing the same effects and, consequently, the same spectral channels of the scanners, for monitoring these environments.

Conclusions

The signature analysis of the reflectance spectra of maple and chestnut leaves undergoing senescence, accompanied by very high variation in pigment concentration, allows the following conclusions to be drawn:

1. Strong absorption processes, caused by Chl pigments in their main absorption bands (400 to 480 and 630 to 680 nm), lead to the saturation of the relationship between the reflectance in these bands and Chl *a* at a concentration as low as 7.0 nmol/cm².
2. To deduce Chl from reflectance measurements of green leaves, reflectances at wavelengths quite far from pigment absorption maxima have to be selected. On the other hand, to obtain maximal sensitivity of the pigment estimation, wavelengths have to be chosen that are as close as possible to the absorption bands. The reflectances at 705 and 555 nm were found to be most suitable, providing both the sensitivity and linear response.
3. The findings make it possible to create sensitive indexes directly related to Chl for the quantitative estimation of the pigments over a wide range of their variation. An estimation error of less than 1.5 nmol Chl *a*/cm² for maple and chestnut leaves was found for Chl ranging from 0.5 to 27.5 nmol/cm².

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