

temporal frequency of 8 cycle/sec. In this manner, apparent movement is achieved without there being any temporal modulation of the light flux entering the eye. Such a moving pattern readily evokes potentials that may be recorded both from the occipital area of the scalp and from the eyeball with an electrode in the conjunctival sac.

The resulting responses (Fig. 1) have a simple waveform whose amplitude may be readily measured. The evoked potential from the cortex is the average of 1500 phase shifts, and the electroretinogram is the average of 3000. The screen subtended 4° by 5°, and the spatial frequency of the sinusoidal grating was 10 cycle/deg. Its contrast was 0.5; contrast is defined as the maximum luminance minus the minimum luminance, divided by twice the mean luminance of the grating.

It can be seen that the amplitude and waveform of the results obtained when the grating was oriented vertically and horizontally were very similar. However, when the grating was presented obliquely, the amplitude of the resulting cortical evoked potential decreased.

In order to understand better the relation between the change in psychophysical threshold at different orientations with the change in the amplitude of the evoked potential, we measured the evoked potential with gratings set at a number of contrast levels. The results are shown in Fig. 2, where the amplitude of the evoked potential is plotted as a function of the log contrast level of the stimulus grating. The three orientations are shown. The results for the horizontal and vertical gratings are similar. However, the results obtained with the oblique grating are displaced to the right by 0.3 log unit on the contrast axis. The regression coefficients of the three sets of results are not significantly different. These findings agree well with the change in psychophysical threshold (indicated by the arrows in Fig. 2), for the oblique grating has a threshold about 0.3 log unit higher than the other orientations.

This linear relation between the amplitude of the evoked cortical potential and the log stimulus contrast has been found to hold over a wide range of spatial frequencies. It has also been found that when the regression line is extrapolated to the zero amplitude value it intersects the contrast abscissa at, or very close to, the threshold deter-

mined psychophysically. We elaborate elsewhere how this experimental approach can lead to an objective confirmation of psychophysical data (6). Evoked responses obtained at very high contrast levels sometimes show saturation.

Using the same stimulus and recording technique, we now measure the evoked potential arising from the retina. The responses are shown in Fig. 1 for a vertical, a horizontal, and an oblique grating. It is clear that there is no difference in the amplitude or waveform of the results obtained at these three orientations.

Now it could be argued that, at the contrast level used to obtain the results in Fig. 1, the signals which we record are saturated and therefore any effect due to a small change in contrast sensitivity might be missed. This possibility was excluded by decreasing the contrast of a horizontal grating by 0.15 and 0.3 log unit and using these as the stimuli. The results obtained for the evoked potentials from the cortex and eyeball are shown as control experiments in the lower portion of Fig. 1. Thus, a small decrease in the contrast of the stimulus grating produces a measurable decrease in the amplitude of the recorded signals.

These findings lead us to conclude that there is an electrophysiological correlate of the psychophysical obser-

vation that the visual resolving power in oblique orientations is less than in the vertical and horizontal, and that the mechanism of this phenomenon arises between the site of origin of the electroretinogram and the evoked potential from the visual cortex. These conclusions are in agreement with the finding in the cat that, for simple cells subserving central vision, there is a greater proportion of orientationally selective units in the vertical and horizontal coordinates (5). The histological observations of Colonnier (3) give further anatomical support for the existence of such a mechanism.

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Senescence in Detached Betel Leaves: Role of the Petiole

Abstract. Removal of the petiole from detached betel leaves delays onset of leaf senescence; the delay is nearly proportional to the extent of depetiolation. An agar diffusate from intact midrib or excised petioles induces normal senescence in depetiolated leaves.

The chewing of green betel leaf (*Piper betle*) spiced with arecanut (*Areca catechu*) and lime, and similar flavorings, is a common practice in the Orient. Betel leaf is harvested with the petiole, which is about 3 cm long, smooth, and cylindrical (terete). The removal of petiole during handling of this leaf, though commonly practiced, seems to have neither definite aim nor scientific basis. These aspects are dealt with in this report.

Senescence of betel leaves involves disappearance of chlorophyll and subsequent browning which begins at the petiolar end and progresses distally along the midrib (Fig. 1). Leaves were considered senescent when browning

reached halfway along the midrib (HMS state).

Depetiolation brought about a

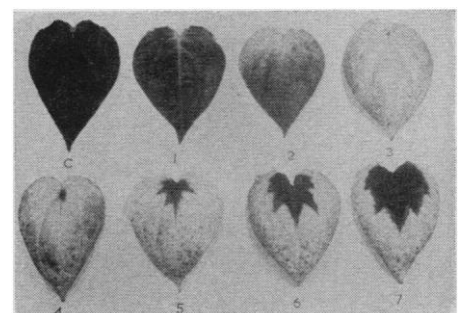


Fig. 1. Freshly harvested green leaf, C; stages of leaf senescence, 1 to 7; and senescent leaf, 7.

Table 1. Days required for indicated percentages of leaves to reach HMS (senescence, as indicated by browning reaching halfway along the midrib). Each value, given with its standard error, represents the mean of four replicates of 25 leaves each.

Senescence of leaf (%)	Time elapsed to HMS in					
	Petioled leaves (days)	Depetiolated leaves with				
		No treatment (days)	Immediate treatment		Treatment after 24 hours	
			Agar (days)	Petiole diffusate (days)	Agar (days)	Petiole diffusate (days)
25	15.9 ± 0.33	20.0 ± 0.91*	15.0 ± 0.23	15.4 ± 0.71	15.7 ± 0.30	16.5 ± 0.42
50	17.5 ± 0.64	26.3 ± 0.24*	16.1 ± 0.91	17.8 ± 0.49	19.7 ± 0.28	19.8 ± 1.01
75	18.7 ± 0.50	31.5 ± 0.29*	17.6 ± 0.23	19.9 ± 0.94	26.8 ± 0.22*	25.7 ± 0.95*
100	23.0 ± 0.71	40.1 ± 0.84*	29.0 ± 0.91*	25.8 ± 0.52	34.4 ± 0.29*	36.0 ± 1.63*

* Values differ significantly from elapsed time in petiolated leaves at $P = .01$.

marked delay in senescence at either 24° or 34°C (Fig. 2). This delay was further enhanced at 24°C, probably because of reduced metabolic activity. Regression coefficient (b) of the extent of depetiolation on time taken for senescence was tested for significance at two experimental temperatures. It was significant at 34°C only. However, at 24°C the depetiolation effect was observed only when the entire petiole was removed.

Osborne and others (1) have reported the presence of a petiolar factor (or factors) that induces abscission and senescence in *Phaseolus vulgaris* and

Coleus blumei. The existence of such a factor or factors in the betel leaf was tested as follows.

Polythene tubings (20 by 2.5 mm) were filled with 2 percent agar which was then allowed to solidify. Excised petioles were inserted in the tubing so that the distal end of the petiole was in contact with agar. After 24 hours, petioles were removed from these tubings. Another batch of leaves was depetiolated, leaving a 5-mm stump of the petiole. Immediately or 24 hours after depetiolation, the leaves were inserted into the tubing containing either petiole diffusate or plain agar. A set of

similarly depetiolated leaves served as control. The leaves treated with petiole diffusate became senescent as did normal leaves, especially when the treatment was given immediately after excision of petiole. A time lapse between depetiolation and application of diffusate delayed senescence but not to the extent observed with complete depetiolation. Leaves treated with agar or with petiole diffusate became senescent at the same time. Laminar senescence could be delayed more than depetiolation alone by removal of the midrib (2). It is thus possible that some senescence-inducing material could have diffused from the midrib into the agar. It is reasonable, in view of the anatomical continuity of the petiole and midrib, that both may be acting as the source of senescence factor or factors.

Another explanation is that the petiole might act as an "attractant" where soluble nitrogen might be emigrating (3). If the petiole were excised, this translocation would be prevented and more soluble nitrogen would be available for protein synthesis, thus enabling the leaf to remain green for a longer period. Similar movements have been demonstrated toward leaf areas treated with kinetin and other hormones (3, 4). The presence of such compounds in the petiole might thus lead to an import of metabolites. However, the situation in betel leaf, where senescence begins at the petiolar end, cannot be explained on this theory of metabolite movement. Therefore, our results indicate that the petiole (and also midrib) controls leaf senescence by acting as a source of senescence factor or factors. The mechanism and site of the synthesis of the factor or factors are not known.

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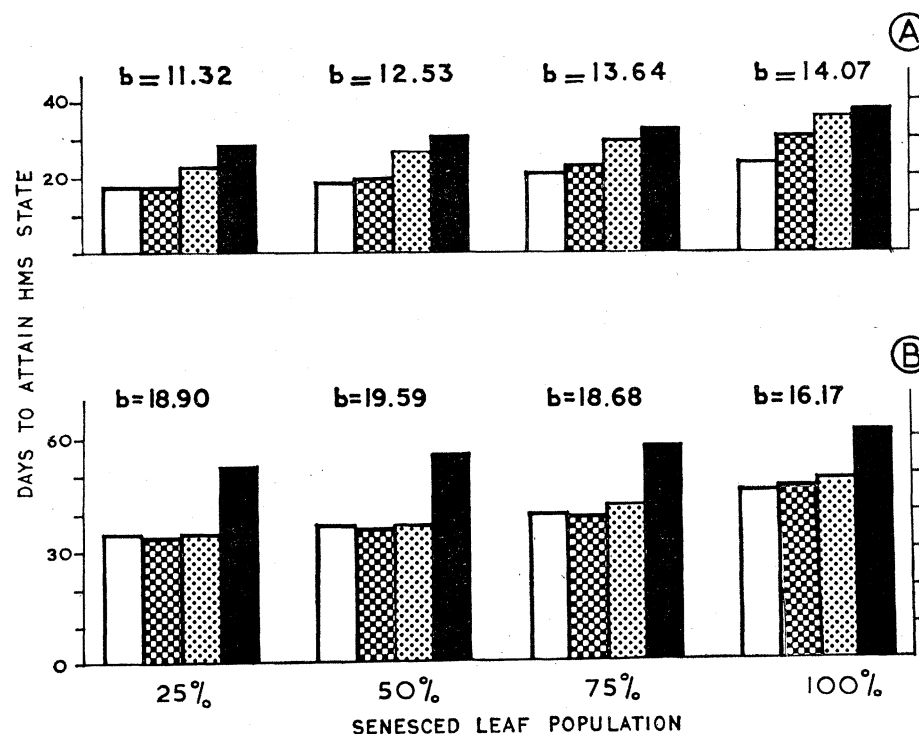


Fig. 2. Relationship between extent of depetiolation and delay in leaf senescence studied at (A) 34°C and (B) 24°C; (open block) no depetiolation; (checkered block) 33 percent depetiolation; (dotted block) 66 percent depetiolation; (solid block) 100 percent depetiolation.