COLOUR VISION OF THE CITRUS PSYLLA *TRIOZA ERYTREAE* (DEL GUERCIO) (HOMOPTERA: PSYLLIDAE) IN RELATION TO ALIGHTMENT COLOUR PREFERENCES

BY

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ABSTRACT

The colour vision of adult citrus psylla, Trioza erytreae, was investigated in the laboratory using the behavioural parameters: alightment and walking.

Light green flushing leaves (under which the nymphs develop) were significantly preferred, visually, to dark green mature leaves for alightment. Diffuse reflectance spectroscopy showed (when expressed in the parameters of human colour vision) that flush has a very slightly longer dominant wavelength, and roughly double the reflectance and purity. Alightment frequency correlated almost equally well with "purity" (as noted by Moericke, 1952 et seq., in "yellow-sensitive" aphids) as with the aphidological colour parameter "long/short ratio" developed by Kennedy et al. (1961).

Elucidation of the mechanism underlying the citrus psylla's alightment colour preference was initially attempted with a printed spectrum and several paint series of measured spectral characteristics. It was clear that T.erytreae belongs to the "yellow-sensitive" group of Homoptera, but it was impossible to distinguish which parameter(s) of colour the psyllids were responding to.

Phototactic (walking) response to the individual parameters of colour was therefore measured using a monochromator. The phototactic action spectrum (against wavelength) was tri-modal, with peaks in the yellow-green (YG), blue (B), and ultra= violet (UV). Rate of phototaxis was not influenced by bandwidth (roughly equivalent to purity), but was proportional to intensity (roughly equivalent to reflectance).

To investigate the influence of the above three wavelength regions on alightment, use was made of a very simple flight chamber incorporating a target of coloured light. Yellow-green and UV light both independently stimulated alightment. Their effect was additive. Different thresholds indicated distinct YG and UV receptor systems. Blue light alone did not stimulate alightment, and was strongly alightment-inhibitory in combination both with YG and with UV light.

On the basis of the above physiological/behavioural findings, a new alightment formula was drawn up for describing the homopteran's apparent manner of alightment-determining integration of surface reflectance. The flush preference and alight= ment distributions on the series of artificial surfaces were found to correlate slightly more accurately, on average, as well as more consistently, with the new formula than with previously-available colour parameters.

These findings are placed in perspective to the literature, and their possible economic relevance is discussed.

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INTRODUCTION

Citrus psylla, Trioza erytreae (Del Guercio), is a pest of economic importance in the Ethiopian region (Commonwealth Institute of Entomology, 1967) where it has been incriminated as the only known vector of the "greening" disease pathogen. An overwhelming indictment has been built on the evidence of field distribution correlations (Oberholzer, von Staden & Basson, 1965), transmission experiments and symptomatology (McClean & Oberholzer, 1965), and electron microscopy both of greening-diseased leaves (Lafleche & Bove, 1970) and of T.erytreae haemolymph and salivary glands (Moll & Martin, 1973). In heavily-greened areas of South Africa, severe crop losses (30-100 %) are common (Schwarz, 1967). Vector status assumes importance in view of the opinion that greening-related diseases are the biggest problem facing global citriculture (McClean, Schwarz & Oberholzer, 1969).

Greening can be ameliorated by trunk injection of tetracycline antibiotics (Schwarz & van Vuuren, 1972), but "prevention is better than cure" and tree infection can be prevented or greatly reduced by controlling citrus psylla infestations (McClean et al., 1969). New groves should be sited in hot, desiccating areas, which are lethal to psylla eggs and nymphs (Moran & Blowers, 1967). Effective chemicals have been recommended for psylla control in outbreak areas (Bot & Hollings, 1971), but insecticide usage does have definite drawbacks associated with resistance, disruption of natural control, and pollution (Smith, 1970). Alternatives to the use of insecticides therefore seem a worthwhile goal. Biological control is not a promising alternative because an efficient hyperparasitoid complex inhibits natural control of T.erytreae (McDaniel & Moran, 1972). Other alternative methods of control can only be rationally formulated with basic knowledge of the physiological response of the pest species to various physical and chemical stimuli (Wigglesworth, 1971), which, in the case of the citrus psylla, include those of its host plants.

Rutaceous flush (i.e. the material of new shoots of plants in the family Rutaceae) is a prerequisite for population explosions of citrus psylla (van der Merwe, 1941; Catling, 1969). T.erytreae is a typical member of the Psyllidae, in that the majority of species are mono- or oligo-phagous and breed on the flush of perennial dicotyledonous plants (Gegechkori, 1968; Catling, 1969; Eastop, 1973; references cited by Hodkinson, 1974). Information on the mechanism of flush location in T.erytreae therefore has potentially wide relevance to other psyllid species and perhaps to other Homoptera.

It was decided firstly to investigate the possible role of vision in flush location by T.erytreae; secondly, to attempt to elucidate the physiological/behavioural mechanism underlying alightment colour preferences; and lastly to consider the alternative methods of pest control suggested by this fundamental knowledge.

Table 1. Plant species, and uses to which they were put, besides leaf reflectance measurement. Ru. = Rutaceae; Ster. = Sterculiaceae; culture = *Trioza erytreae* culture.

Common name	Species -(and family)	Used for
rough lemon	*Citrus jambhiri* Lush. -(Rutaceae)	culture & visual choice
white ironwood	*Vepris undulata* (Th.) Verdoorn & Sm. -(Ru.)	" " " "
Australian flame	*Brachychiton acerifolium* F.Muell -(Ster.)	visual choice tests
mulberry	*Morus alba* L. -(Moraceae)	" " "
eureka lemon	*Citrus limon* (L.) Burm. -(Rutaceae)	" " "
sweet orange	*Citrus sinensis* (L.) Osbeck -(Rutaceae) cultivar Moss seedless mid-season	

Table 2. Plateau (and range of) conditions of controlled environment rooms.

Controlled Environment Room	Phase	Temperature (^{o}C)	Relative Humidity (%)	Room vol. (m^3)	Fresh air exchange rate (room volumes. h^{-1})
lab 1	photo-	ca. 22	ca. 55	13	ca. 2
	scoto-	ca. 17	ca. 65	-	-
lab 2	photo-	25(24,5-25,5)	65(62-68)	13	4
	scoto-	15(14,5-15,5)	75(72-78)	-	-

Table 3. Basic lighting details of controlled environment rooms. See also Figs 1-4.

Controlled Environment Room	Photophase Start	Duration(h)	Lights Number x Type	Illuminance, bench height (1x)
lab 1	08h30	14	22 x 60 W "cool white" fluorescent tube Philips S.96 T12/33 Siliconed, R.S.A.	ca. 5 000
lab 2	05h00	14	12 x 200 W "cool white" fluor. Powertube Sylvania F72T 12-CW-VHO, Canada.	ca. 3 200
			16 x 60 W incandescent bulbs, Atlas,RSA. (behind vinyl-glass ceiling in lab 2)	ca. 600

MATERIALS AND METHODS (GENERAL)

Organisms Used and Environmental Conditions.

Insects. This study was confined to one species of insect: Trioza erytreae (Del Guercio). Morphology of nymphs and leaf galls tallied with the description of Del Guercio (1918), and that of adults with Boselli (1930). A sample of adults (in 70 % ethanol) taken from the laboratory culture has been deposited for possible future reference in the National Collection of Insects, Plant Protection Research Institute, Pretoria. This species is restricted to sub-Saharan Africa and the surrounding islands (Commonwealth Bureau of Entomology, 1967). The laboratory culture used was originally started by Moran (1967) with psyllids from citrus at Forest Hill, near Letaba in the north-eastern Transvaal, where T.erytreae reaches pest proportions (Catling, 1970), and was occasionally supplemented with citrus psylla collected in Graham's Town, in the eastern Cape Province, where the species is of no importance (Moran, 1967) and with psyllids from Rhodesia. Mature insects, initially of 0,5-3 week post-emergence age, were normally used in a sex ratio of 1:1, and the participants were destroyed after each experiment so that no psyllid made more than one choice. In an effort to reduce variability, in later experiments (with colour filters) age was controlled to 9,5 $\pm$ 1,2 d post emergence, although the range was still 4-15 d.

Plants. The plant types listed in Table 1, which were used for culturing psyllids or testing their visual responses, were also all used in spectral reflectance measurements. The state of Citrus taxonomy (Reece, 1969) is such that the nomenclature can only be quoted tentatively; the names used here are after Singh & Nath (1969) and Scora, England & Chang (1969). Potted seedlings were used for culturing T.erytreae, after the method of Annecke & Cilliers (1963). The plants were fertilized at approximately fortnightly intervals, and allowed to recover outside for some months after producing a batch of psyllids. Unwanted insect species were initially removed manually before bringing seedlings into the culture room, but later the plants were given four days treatment in a fumigation room containing 3 Vapona strips (Shell Chemicals).

Temperature, Humidity and Air Exchange. Two controlled environment rooms (hereinafter referred to as lab 1 and lab 2) were employed, with plateau conditions as recorded opposite (Tables 2 & 3). The pattern of daily temperature and humidity change has been described by Moran & Blowers (1967): approximately 20 % of the time was spent changing from one plateau condition to the other in lab 1, and less than 10 % of the time in lab 2, i.e. the stable conditions were achieved for 80-90 % of the time. Cultures were maintained in both rooms. Most of the alightment experiments using leaves and painted surfaces were carried out in lab 1, and all those using colour filters in lab 2. As the colour responses of a citrus insect

have been shown to be affected by the presence of citrus vapour in the air (Vaidya, 1969), and antennal host plant chemoreception has been demonstrated in T.erytreae (Moran & Brown, 1973), it should be noted that the rate of air exchange with that outside (measured by Lambrecht thermal anemometer) was such that essential oil vapour, though presumably present in the air, was below the human olfactory threshold concentration.

Light. The term "light" is used here to refer to electromagnetic radiation, not only in the human-visible, but also in the near-ultraviolet (UV) and infrared (IR) regions of the spectrum. Basic lighting details are recorded in Table 3. The illuminance was measured using a Gossen lux meter. Absolute intensity and spectral distribution of environmental lighting were of fundamental importance in this study, and they form the subjects of the following section and of Chap. 1 of the Results.

Light Intensity Measurement.

The quantum flux from coloured light targets and the environment room lighting reaching the test population of T.erytreae was measured using an Hilger Schwarz vacuum thermopile with a Philips DC microvoltmeter, and the following equation and description of units from Seliger & McElroy (1965, p.361).

$$I = \frac{R}{K} \cdot \frac{\lambda}{1987} \cdot 10^{12}$$

where I is the number of "photons/sec-cm^2" incident on the thermopile face;

R is the net reading in microvolts when the thermopile is placed in the light beam to be quantified;

λ is the wavelength of incident light in Angstrom units;

K is the calibration constant of the thermopile with the units "$\mu V/\mu W/cm^2$".

"R" was found as follows. The microvoltmeter reading on the scale appropriate to the meter sensitivity being used, was read before, during and after exposure of the thermopile element to the light stimulus, so as to obtain the "zero light" reading (mean of "before" and "after") during meter drift. The voltage due to the infra-red (IR) component of the radiation was determined by measuring the colour filter stimulus with and without an IR filter (Kodak Wratten Gelatin filter No. 89B, which transmits nil below 670 nm and ca.90 % above 800 nm (Weast, 1968)). The voltage due to the IR component was subtracted from that due to the total radiant flux to give the voltage due to the light flux within the psyllid's visible spectrum. In the case of a monochromator stimulus, no correction (other than the "zero light" reading) was applied: it was assumed that the IR component would be negligible at the narrow bandwidths used in the human-visible and the near-ultraviolet, and the stray radiation over the entire range of the instrument was less than 0,2 % according

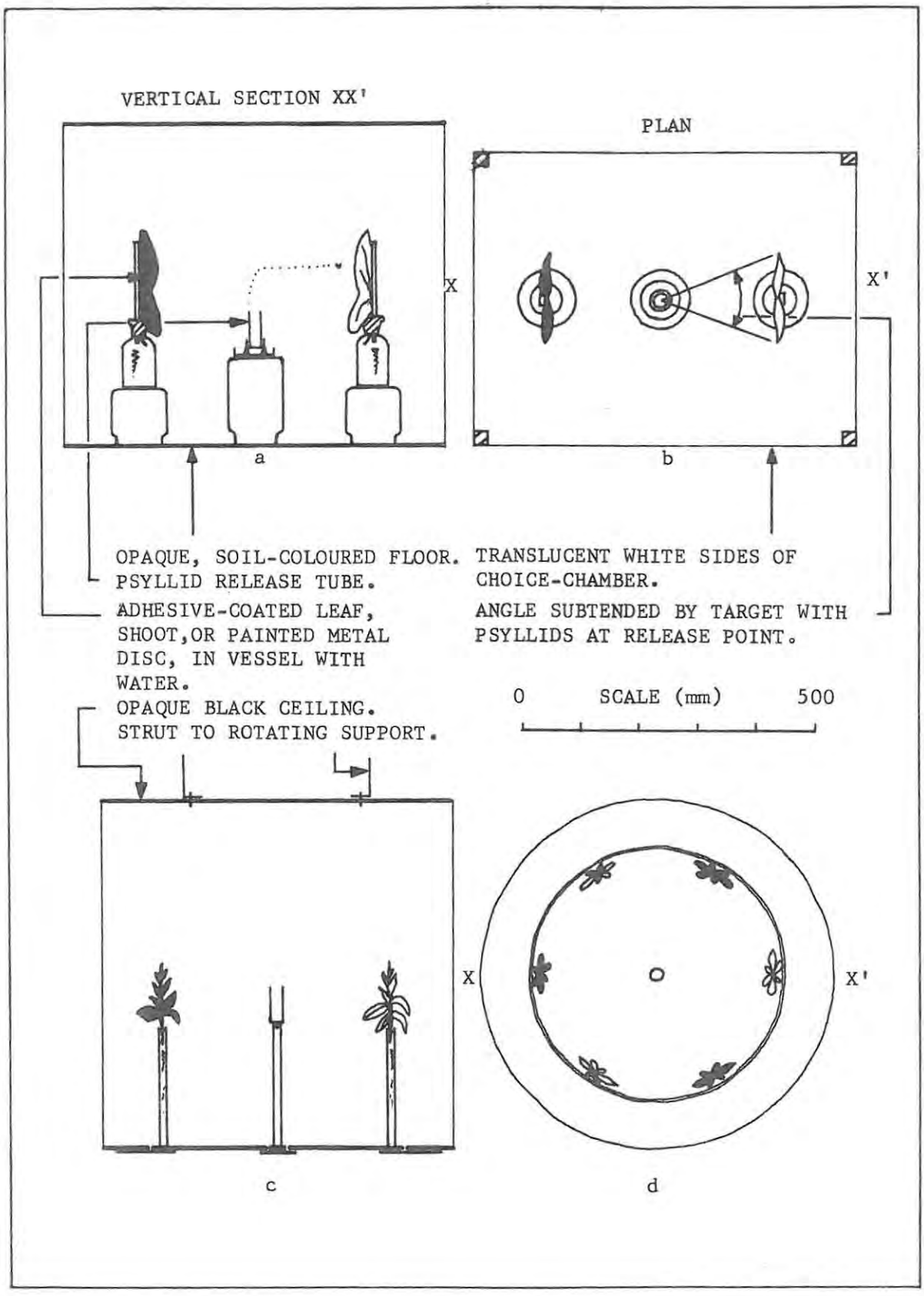

Fig. 1. The choice-chamber set-up for measurement of alightment preferences of T.erytreae. Chamber 1 (a,b) was stationary and was used in lab 1. Chamber 2 (c,d) slowly rotated (1,2 r/min) and was used in lab 2.

to the manufacturer (Beckman Instruments Inc., 1963). In the case of environment room lighting, the IR fraction specified by the fluorescent tube manufacturer was accepted.

"λ" was taken as the centre of the monochromator bandpass. In the case of colour filter and environment room lights, which have complex spectral distributions, λ was calculated by proportional weighting of the relative spectral distribution of quanta of each stimulus, as shown in the example in Table 4. The nominal wavelength figures are recorded in the text in nm (in Section 1.2 and in Chap. 5, Table 5) and these were multiplied by 10 to bring them to Angstrom units for substitution in the above equation.

"K" was calculated as follows. The manufacturer's calibration of the thermopile (Hilger, 1950) was 28 $\mu V/\mu W$ and the exposed or "hot" thermopile element surface was 9,0 x 0,5 mm = 4,5 mm^2. The units of K ("$\mu V/\mu W/cm^2$" according to Seliger & McElroy, 1965) were interpreted as "$\mu V.\mu W^{-1}.cm^2$". The value of K was therefore taken to be 28 x 0,045 = 1,26 $\mu V.\mu W^{-1}.cm^2$.

The values of "I" calculated by the above equation in its original form were converted to an acceptable SI form (SABS, 1973) $quanta.s^{-1}.mm^{-2}$.

Alightment Preference Measurement.

Test surfaces were coated with a thin, transparent layer of a sticky, tree-banding compound, either Ostico or Formex. Alightment preferences were determined by exposing these surfaces to batches of (usually 100) psyllids in a choice-chamber and recording the number of psyllids trapped on the sticky test surfaces after a certain time. The choice-chambers used had an opaque floor and ceiling, and translucent white organdie sides (organdie plus paper in the case of the choice-chamber in lab 1) to admit diffuse illumination. The psyllids were collected from the laboratory culture in an aspirator or "pooter" of the type figured by Southwood (Southwood & Leston, 1959, cited by Southwood, 1968) and "released" (i.e. allowed to take off) in their own time from the glass pooter vial. The release tube was placed either in the centre of the chamber, midway between the test leaves, shoots or coloured discs set vertically 0,20 m away, or in the centre of the ceiling when a test series of artificial surfaces was presented on the floor. The choice-chamber set-up is illustrated in Fig. 1.

Tests were started 4,5 h after "light on" and it was found necessary to run the tests for nine-hour periods to allow the batch of psyllids time to leave the release tube. Chamber 1 (Fig. 1a,b) (380 lx at release point in lab 1) was stationary, so that, to control for possible unevennesses of illumination, the test surfaces had to be alternated in position (east-west) for the second "run" of each "replicate"

(completed with another batch of psyllids on the following day). Chamber 2 (Fig. 1c,d) (1275 1x at release point in lab 2) slowly rotated (1,2 r/min) so that unevennesses of illumination were balanced out and each day's "run" therefore constituted a complete "replicate".

Colour Measurement.

Photoelectric (Kalitin, 1940) and photographic techniques (Kevan et al., 1973, modelled on Daumer, 1958) have been developed for measuring the reflectance of vegetation in the field, using a series of colour filters, but these yield data at only a few points on the spectrum. Complete spectra of diffuse reflectance are preferable because "...spectrophotometric measurements furnish a basis for color specification which is unique and fundamental..." (Grum, 1972) and these were determined in the laboratory by the technique described below.

In their book on reflectance spectroscopy, Wendlandt & Hecht (1966) explain that "diffuse reflectance" comprises regular (mirror-like) reflection, and diffuse reflection due to partial absorption and multiple scattering of the light by the particles in the interior of the sample. Diffuse reflectance spectra of leaves and artificial surfaces (not coated with adhesive) were recorded using a Pye-Unicam SP800 UV-visible spectrophotometer over the wavelength range 300-700 nm (i.e. the near-UV (below 400 nm) as well as the human-visible) along with that of a freshly-prepared magnesium oxide standard. Particulars of the technique and apparatus are given by Wendlandt & Hecht (1966). Preparation of the standard by hydraulic compaction of the MgO powder, as suggested by Grum (1972), was found to be quicker than the fuming technique and to give a more robust standard of identical reflectance. The absorption of the adhesives, at the thickness used, was found to be too small to warrant inclusion as a correction. The curves were corrected for the diffuse reflectance of the standard at 10-nm intervals, converted from logarithmic to linear scale and plotted.

As an initial computation to enable colour comparison on a numerical basis, each diffuse reflectance spectrum was converted into values of the 3 human-physiological (hereinafter referred to as "human") parameters of colour (which are well-established and were used in Moericke's (1952 et seq.) work on aphids): "dominant wavelength", "reflectance" and "purity". At 10-nm intervals from 400 to 700 nm, the value of the diffuse reflectance curve was multiplied by the value of the spectral energy distribution of C.I.E. (Commission Internationale de l'Eclairage) standard illuminant "C" (average daylight) and, separately, by the values of the 3 spectral colour-matching functions of the "standard observer" for a 2 ^{o} field of subtense, as described more fully by Wright (1969). Ratios of areas under the 3 product curves gave the chromaticity co-ordinates, which were plotted on the standard chromaticity diagram, as illustrated in Fig. 7d, from which the human colour parameter values

were obtained. The technique was tested on published spectra (Sears & Zemansky, 1960) and found to agree closely with their evaluations.

The aphidological (hereinafter referred to as "aphid") colour parameters formulated by Kennedy et al. (1961), "long/short ratio" and "total energy", were calculated for each surface with respect to the spectral distribution and intensity of ambient illumination inside the choice-chamber (Fig. 5).

Initially in the present work, no colour computation more relevant to psyllids was possible, as no colorimetric work had been done on Homoptera that was comparable with that of Daumer (1956) on the honey-bee. After gathering fundamental information on T.erytreae's visual physiology, however, (Chaps 4 & 5), the alightment formula apparently most relevant to the citrus psylla was drawn up. These "relative alight= ment stimulus", usually called "RAS equation", values of the targets were then also computed with reference to the ambient (choice-chamber) illumination, and plotted in part "c" of the figures (Figs 8 & 10-16) for comparison with psyllid alightment frequency distributions. The "RAS equation" colour parameter will only be properly understood later, however, once its derivation has been dealt with (Section 6.1). For this reason, correlations of psyllid alightment frequency with "RAS equation" values were deferred until Section 6.2.

Transmittance and specular reflectance measurements of leaf and artificial surfaces were also carried out using the spectrophotometer mentioned above.

Statistical Analysis.

Units were expressed in SI (Le Systeme International d'Unites) form, as detailed in a guide to the International Metric System (:SABS, 1973).

Chi-square tests (2-way choices and 2 x 2 contingency tables) were applied (i) only to the absolute numbers of psyllids participating; (ii) only if the expected number was five or more; and (iii) routinely with Yates' correction (Bailey, 1969). The non-randomness of distribution was considered not significant for $p \geqslant 0,05$, significant for $0,01 \leqslant p < 0,05$, strongly significant for $0,001 \leqslant p < 0,01$, and highly significant for $p < 0,001$.

Student's 't' test of the significance of difference between means was applied after testing whether or not its assumptions of normality of data and homogeneity of sample variances were fulfilled, using commercial programmes for skewness and kurtosis, and Bartlett's test (Hewlett-Packard, undated). If the assumptions were not tested, this was noted in the text.

Both regression and correlation were used to assess the possibility that relations might be ones of cause and effect. Sokal & Rohlf (1969) state that:

"Science aims at mathematical descriptions of relations between variables in nature, and... regression analysis permits us to estimate functional relationships between variables...". Besides providing a least-squares equation of best fit to the data points, regression analysis yields an informative quantity, the regression coefficient. A negative regression coefficient (i.e. slope, in the case of a linear regression) of psyllid alightment frequency against the values of any colour parameter of a series of surfaces presented, immediately rules out the possibility that the colour parameter under consideration is the excitatory stimulus eliciting alightment. To determine, for purposes of comparison, the "goodness of fit" of the linear regression of any potentially-causative colour parameter with observed alightment frequency, the tool employed was the coefficient of determination, r^2 . According to Sokal & Rohlf (1969) "...an important measure of the proportion of the variation of one variable determined by the variation of the other... [is] the square of the correlation coefficient, r_{12}^2 ,[which] is called the coefficient of determination." The notation "r_{12}" is a symbol for the product-moment correlation coefficient of two different variables, Y_1 and Y_2 ,whose correlation (i.e. degree of association) is to be estimated. In the present study, Y_1 and Y_2 were usually the relative psyllid alightment frequency on a series of surfaces and any one colour parameter of that same series of surfaces. The value of r^2 ranges from 0 (indicating no association between the variables under consideration) to 1 (indicating perfect "goodness of fit").

Another statistic employed was the coefficient of variation, which is the standard deviation expressed as a percentage of the mean (Sokal & Rohlf, 1969). This enabled a comparison of the overall variability of the r^2 values when different colour parameters were considered.

RESULTS (INCLUDING SECTIONAL METHODS AND DISCUSSIONS)

The results comprise six chapters. In Chapter 1 the spectral distribution of light in the choice-chamber environments was measured in absolute terms because this information was essential for quantifying the stimuli of the coloured targets presented in alightment preference tests. Alightment preferences of T.erytreae were determined when populations of psyllids were presented with choices between leaves of different colours (Chap. 2) and series of coloured artificial surfaces (Chap. 3). In each case the alightment distributions were examined in relation to established colour parameters of the targets presented, in an initial attempt to discover the alightment stimulus. It was found necessary to measure the relative strength of phototactic response of T.erytreae to different wavelengths, intensities and bandwidths of target lights (Chap. 4). The manner in which light stimuli in the main sections of T.erytreae's visible spectrum influence its alightment response when presented alone or in various combinations was then determined (Chap. 5). In Chapter 6 of the results, the basic physiological/behavioural information gathered in the two previous chapters was used to draw up a new colour parameter called the "relative alightment stimulus-" or "RAS equation". The "goodness of fit" of the previously-observed alightment distributions of T.erytreae with the old and new colour parameter values of the various series of coloured targets presented was then calculated for purposes of comparison of the parameters' alightment-explanatory or -predictive value.

1. SPECTRAL DISTRIBUTION OF LIGHT IN PSYLLID CULTURE AND CHOICE-CHAMBER

Spectrally-quantitative information on the illumination within the choice-chambers was essential for an accurate assessment of psyllid responses to coloured targets presented therein, because "the stimulus of the color... may be completely specified... when the spectral [reflectance] data are mathematically treated with physical specifications of the energy distribution from the illuminant" (Grum, 1972). Concerning the most appropriate method of recording the physical specifications of the energy distribution from the illuminant, Seliger & McElroy (1965) state that: "all... photochemistry is based on the absorption of quanta and what we are really interested in is the number of quanta per second per square centimeter incident within the absorption bands of the... [insect's visual] pigments...". Accordingly: "... the proper description of a light beam must include the spectral distribution as well as the number of quanta per second per square centimeter."

A second, though very minor consideration, was the following. Various insects, including honey-bees (von Frisch, 1914, 1914-15, cited by von Frisch, 1967), wasps (Mazokhin-Porshnyakov, 1960) and butterflies (Swihart, 1970, 1972a) can be trained to forrage on particular colours. Light irradiating psyllids during their development on flushing citrus seedlings could perhaps also condition them to associate a certain colour with food availability. Consequently, information on the spectral distribution of light in the psyllid culture could provide one hypothetical explanation for different behavioural responsiveness of the psyllids when their receptors of different spectral sensitivity are independently and equally stimulated.

Materials and Methods (light spectrum).

The relative energy emission spectra of the environment room lights were obtained from published data. Emission spectra of the "cool white" fluorescent tubes used in lab 1 and lab 2 (Philips, 1955; Sylvania, 1970) were very similar over the human-visible wavelength range, 400-700 nm; the spectrum published by Sylvania (recorded as EF in Fig. 2) was used for all calculations because their data extend to 300 nm in the UV. The emission spectrum of the incandescent lamp (QI) is from Seliger & McElroy (1965, p.19) and refers to an 100 W tungsten lamp at a colour temperature of 2800 K.

To enable description of the spectral distribution of light falling directly upon adult psyllids within the culture cages, the transmittance of the 6,5 mm thick vinyl-glass ceiling (Shatterprufe Fadeban UV393) below the environment room lights in the case of lab 2, and the transmittance of the 5 mm thick perspex roofs and front walls of the citrus and psyllid culture cages was measured against air in a spectrophotometer. The basis of a possible conditioned response of phototaxis to the colour of leaves for feeding was investigated by measuring, firstly, the diffuse

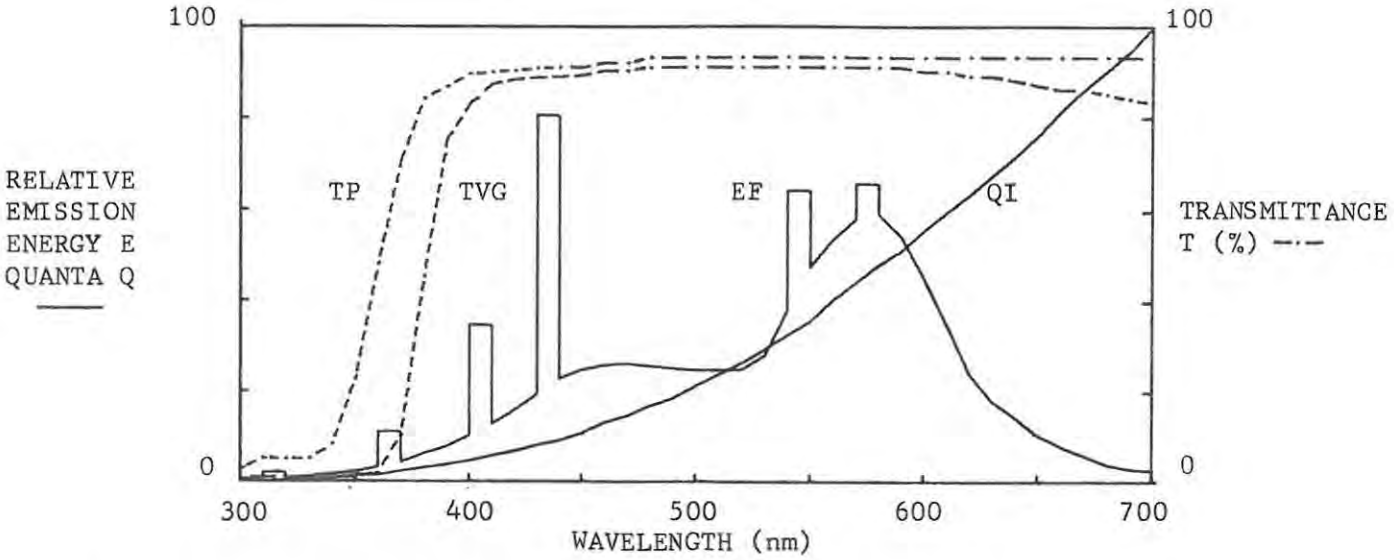

Fig. 2. Relative spectral emission of energy (EF) by the "cool-white" fluorescent tubes, and of quanta (QI) by the incandescent bulbs used in the controlled environment rooms. Transmittance of the vinyl-glass ceiling of lab 1 (TVG) and of the perspex culture cage roofs (TP) are as given. For convenience, the emission lines of the mercury are shown as 10 nm wide bands (superimposed on the continuous emission of the phosphor).

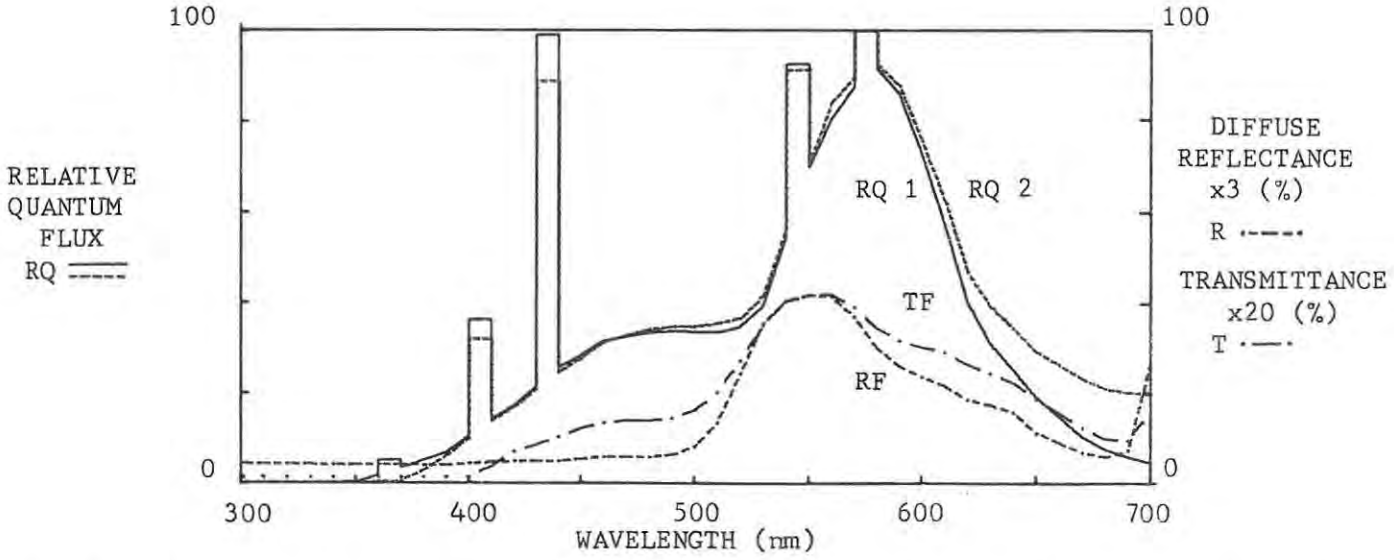

Fig. 3. Relative spectral distribution of quanta irradiating Citrus jambhiri and Trioza erytreae cultures in lab 1 (RQ1) and lab 2 (RQ2). Typical spectra of flush leaf diffuse reflectance x3 (RF) and transmittance x20 (TF) are also given. For convenience, the emission lines of the mercury are shown as 10 nm wide bands (superimposed on the continuous emission of the phosphor).

reflectance spectrum of flush leaves, in the manner described on p.8, and secondly, the spectral transmittance of typical Class B flush of citrus (under which the psyllid nymphs develop) using the technique of Shibata (1958) with ground glass in place of opal glass.

To calculate the relative spectral distribution of light which penetrated the choice-chambers laterally from the environment room walls, it was also necessary to measure the diffuse reflectance spectrum of the white environment room wall paint and the transmittance spectrum of the organdie or organdie-plus-paper wall of the choice-chamber using the spectrophotometric techniques referred to above.

The total absolute light intensity in the centre of the choice-chamber was measured using the thermopile technique (see p.7) and was calculated from the mean of the microvoltmeter readings obtained when the thermopile faced horizontally in the 8 main compass directions. This information was used to convert the relative spectral data to absolute terms. The absolute spectral distribution of quanta was expressed in the form of a step-function having the units quanta.s^{-1}.mm^{-2}.$10nm^{-1}$ (where the "10nm" refers to a wavelength interval) in order to follow Seliger & McElroy (1965) (as quoted in the introduction to this chapter) as closely as possible, and yet to conform with the SI metric system of units (as described by SABS, 1973).

1.1 Relative Spectral Distribution of Quanta.

In Fig. 2 are recorded some of the data which served as the basis for calculating the spectral distribution of light reaching the psyllid cultures and the targets in the choice-chambers. The emission of the fluorescent tubes, which provided the major component of the environment room illumination (Table 3), was mainly in the yellow (around 580 nm) and the blue (around 470 nm), with very little UV (wavelengths less than 400 nm) (Fig. 2). The addition of incandescent light (Fig. 2) boosted the proportion of red light in lab 2, whilst the absorbance of the vinyl-glass ceiling in lab 2 and of the perspex roofs and front walls of the culture cages (Fig. 2) reduced the proportion of UV light reaching the citrus and psyllid cultures.

Figure 3 shows the relative spectral distribution of quanta irradiating the citrus and psyllid cultures directly from the lights of lab 1 (RQ1) and lab 2 (RQ2). These curves were calculated from the data of Fig. 2 at 10-nm intervals over the wavelength range 300-700 nm. Conversion of fluorescent tube emission from relative energy to relative quanta was by multiplication by the ratio of the particular wavelength to a fixed wavelength of high relative energy (Seliger & McElroy, 1965). The relative spectral composition of the lab 2 light source was taken to be the sum of the relative spectral distribution of quanta of the fluorescent and incandescent constituents, when the total fluxes of those constituents were in the ratio of

Table 4. Example of calculation of absolute spectral distribution of quanta from a light (within T.erytreae's visible spectrum). In this example, the light is the ambient illumination within the choice-chamber in lab 1 (i.e. step-function AQ1 of Fig. 5). Column 1: For purposes of calculation, the spectrum was divided into 10-nm waveband segments; 2: EF of Fig. 2 (from Sylvania, 1970); 3: Obtained by multiplication by the ratio of the particular wavelength to a fixed wavelength of high relative energy (Seliger & McElroy, 1965); 4 & 5: RW & TC of Fig. 4 (measured by spectrophotometer); 6=3.4.5.0,01; 7: Proportional weighting (7=1.6) for calculation of effective wavelength (λ) for substitution in formula (given on p.7) for determination of total absolute quantum flux, using the thermopile technique; Here $\lambda = \Sigma 7 / \Sigma 6 =$ 136228 nm/241 = 565 nm; 8: Relative data (6) converted to absolute by multiplication by ratio of total absolute quantum flux (within T.erytreae's visible spectrum) obtained from above formula (p.7) to the total relative quantum flux ($\Sigma 6$) (i.e. 1072/241 = 4,448).

Wavelength, centre of 10-nm band (nm)	Emission of environment room light		Reflectance (%) of TiO_2-white wall	Transmittance (%) of choice chamber wall	Quantum flux inside choice chamber		
	Relative Energy	Relative Quanta			Relative	Proportionally weighted (nm)	Absolute ($.10^9$ quanta $.s^{-1}.mm^{-2}.10nm^{-1}$)
1	2	3	4	5	6	7	8
305	0,005	0,00	2,4	21,4	0,000	0	0,000
315	0,020	0,01	2,4	22,9	0,006	2	0,027
325	0,005	0,00	2,4	23,4	0,000	0	0,000
335	0,010	0,01	2,2	22,9	0,005	2	0,022
345	0,015	0,01	2,1	21,4	0,005	2	0,022
355	0,020	0,01	2,3	20,9	0,005	2	0,022
365	0,110	0,07	3,0	20,4	0,042	15	0,187
375	0,040	0,03	4,6	20,4	0,028	11	0,125
385	0,060	0,04	7,2	20,4	0,058	22	0,258
395	0,075	0,05	14,1	20,0	0,141	56	0,627
405	0,345	0,26	32,4	19,5	1,643	665	7,308
415	0,125	0,10	61,5	18,2	1,119	464	4,977
425	0,155	0,12	70,0	14,1	1,184	503	5,267
435	0,805	0,70	75,0	14,5	7,613	3312	33,864
445	0,225	0,18	77,0	17,0	2,356	1048	10,480
455	0,245	0,20	78,5	20,0	3,140	1429	13,967
465	0,255	0,22	79,5	21,9	3,830	1781	17,036
475	0,260	0,23	80,4	24,0	4,438	2108	19,741
485	0,255	0,23	81,0	26,3	4,900	2377	21,796
495	0,250	0,23	81,3	28,2	5,273	2610	23,455
505	0,245	0,23	81,8	29,5	5,550	2803	24,687
515	0,245	0,23	82,3	31,6	5,982	3081	26,609
525	0,255	0,25	82,4	33,1	6,819	3580	30,332
535	0,275	0,27	82,3	34,7	7,711	4125	34,300
545	0,640	0,64	82,3	36,3	19,120	10420	85,048
555	0,470	0,48	82,3	37,2	14,695	8156	65,365
565	0,530	0,55	82,3	38,9	17,608	9949	78,323
575	0,655	0,69	82,3	38,9	22,090	12702	98,259
585	0,590	0,63	82,1	38,9	20,120	11770	89,496
595	0,560	0,61	81,3	38,9	19,738	11744	87,797
605	0,450	0,50	80,7	41,7	16,826	10180	74,844
615	0,350	0,39	79,4	41,7	12,913	7941	57,439
625	0,240	0,27	78,9	42,7	9,096	5685	40,460
635	0,180	0,21	78,5	43,7	7,204	4575	32,044
645	0,145	0,17	78,5	44,7	5,965	3847	26,533
655	0,105	0,13	78,5	44,7	4,562	2988	20,292
665	0,080	0,10	78,1	45,7	3,569	2373	15,875
675	0,060	0,07	77,6	45,7	2,482	1675	11,040
685	0,040	0,05	77,6	45,7	1,773	1215	7,887
695	0,030	0,04	77,6	46,8	1,453	1010	6,463
Σ300-700 nm					241	136228	1072

their illuminances as given in Table 3. Class B flush leaf transmittance and diffuse reflectance spectra over the UV-visible wavelength range had a single peak in the yellow-green (at ca. 550 nm) (Fig. 3).

1.2 Absolute Spectral Distribution of Quanta.

Table 4 is an example of the calculation of the absolute spectral distribution of quanta from a light (within T.erytreae's visible spectrum). In this example, the light is the ambient illumination within the choice-chamber in lab 1. Multiplication, at 10-nm wavelength intervals across the spectrum, of the values of the appropriate emission spectrum of Fig. 2 (converted from relative energy to relative quanta) by the values of the pertinent diffuse reflectance and transmittance spectra shown in Fig. 4 gave the relative spectral distribution of light quanta reflected from the environment room walls and transmitted into the choice-chamber (i.e. column 6 in the example, Table 4).

Conversion of the relative data to absolute figures required the thermopile voltage due to the total absolute UV+visible radiant energy flux in the centre of the choice-chamber, as well as the effective wavelength, λ , of the ambient light, for substitution in the equation on p.7. Approximately 39 % of the total radiant energy of fluorescent tubes is in the UV and visible range (Sylvania, 1970), and a figure of 35 % was used here to make some allowance for the greater proportion of infrared in the incandescent component of lab 2 light. In the case of the ambient illumination within a choice-chamber, the effective wavelength was calculated by proportional weighting as shown in the example (Table 4) to be 565 nm in lab 1 and 547 nm in lab 2. Calculations using these figures gave a value for the total absolute quantum flux (within the insect-visible spectrum, i.e. ca. 300-700 nm) of $3{,}6 \times 10^{12}$ quanta.s^{-1}.mm^{-2} in the centre of the choice-chamber in lab 2. This intensity can be written as $10^{12{,}56}$ quanta.s^{-1}.mm^{-2} and is recorded on the abscissa of figures as L = 12,56 where L is the logarithm of light intensity measured in quanta.s^{-1}.mm^{-2} .

Total intensity in the centre of the choice-chamber in lab 1 was assumed to be an amount less than that in the choice-chamber in lab 2, in direct proportion to the reduction in illuminance (i.e. from 1275 to 380 lx) because the relative spectral distribution of radiation in the two environment rooms (Fig. 3) was similar. Total intensity in the choice-chamber in lab 1 was, therefore: (380/1275) $3{,}6 \times 10^{12} = 1{,}08 \times 10^{12}$ quanta.s^{-1}.mm^{-2}, i.e. L = 12,03 . The calculated absolute spectral distribution of light quanta in the centre of the choice-chamber in lab 1 (AQ1) is listed in column 8 of the example (Table 4), and these data, as well as similar data for the choice-chamber in lab 2 (AQ2), are recorded in Fig. 5. The data were presented as step-functions (of wavelength) to facilitate subsequent calculation of areas under functions in different spectral regions.

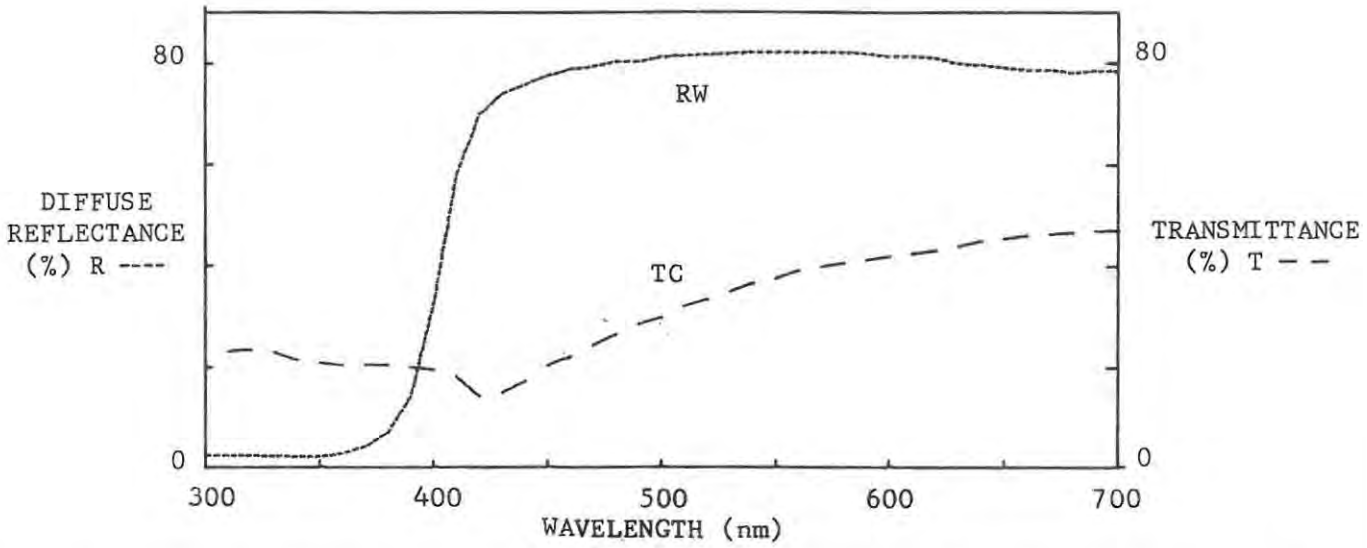

Fig.4. Diffuse reflectance (RW) of TiO_2-white wall paint of controlled environment rooms (measured with respect to MgO), and transmittance (TC) of white organdie-and-paper wall of lab 1 choice-chamber (measured with respect to air).

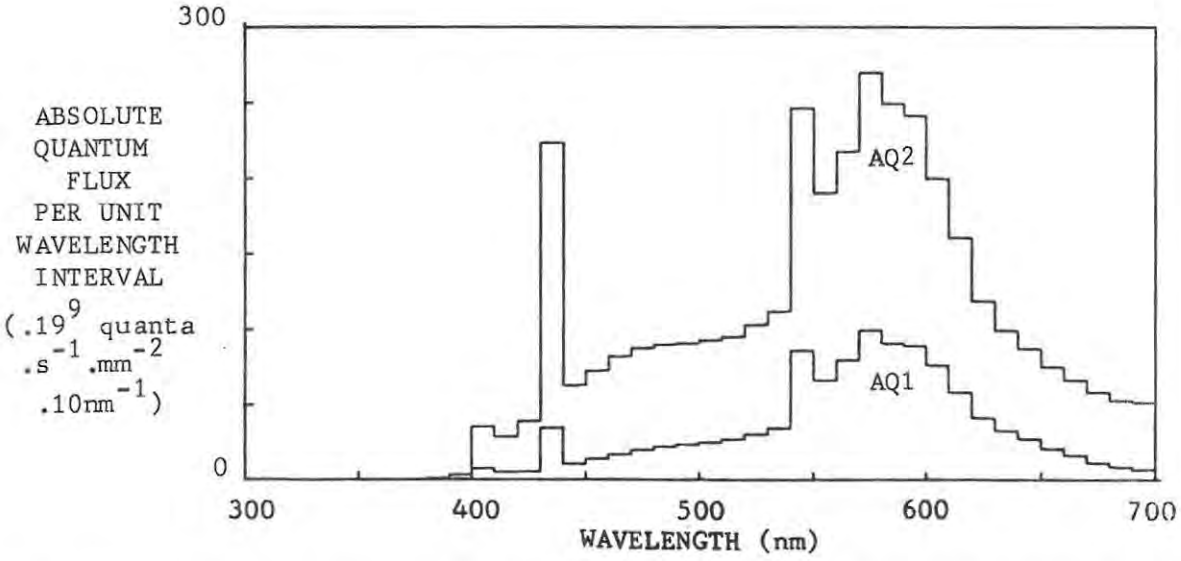

Fig.5. Absolute spectral distribution of (light) quanta at centre of choice-chamber in lab 1 (AQ1) and lab 2 (AQ2). The data are presented as step-functions (of wave= length) to facilitate subsequent calculation of areas under the functions in differ= ent spectral regions.

Discussion (light spectrum).

Incident light irradiating the citrus and psyllid culture (Fig. 3) had energy peaks in the yellow-green (500-600 nm) and the blue region of the spectrum (400-500 nm). This light was deficient in UV (300-400 nm) compared with sunlight (values given by Kennedy et al., 1961, from Moon, 1940) or blue skylight (values given by Autrum & von Zwehl, 1962, from Viaud, 1948). The individual forms and the similarity of shapes of transmittance and diffuse reflectance spectra of leaves have been shown previously (Pokrowski, 1925, cited by Shull, 1929; Shibata, 1958; Woolley, 1971). From Fig. 3 it is evident that the transmitted or reflected light reaching (and possibly conditioning) citrus psyllids feeding on or under flush leaves would be composed predominantly of the wavelengths we see as yellow-green (YG) (around wavelength 550 nm), with very little blue (B) (around 450 nm) and virtually no UV (below 400 nm). The fact that the incident, reflected and transmitted light in the environment of T.erytreae all possessed a decreasing intensity trend from YG to B to UV is taken up again in the discussion to Chap. 4.

The absolute data on the spectral distribution of light quanta within the choice-chambers (Fig. 5) were used in the assessments, in Chapters 2, 3 and 6, of the colours of surfaces presented in the choice-chambers for alightment preference tests using T.erytreae.

2. ALIGHTMENT ON LEAVES IN RELATION TO THEIR COLOURS

Moericke studied visually-stimulated alightment preferences of aphids in the field by exposing dishes of water with painted or leaf-covered bases. He demonstrated the possible use of vision in both host plant location (though certainly not to the extent of species recognition) and flush location. The mealy plum aphid, Hyalopterus pruni, alighted twice as frequently on the grey-green leaves of its host plant, reed, as on the purer green leaves of a non-host, beet (Moericke, 1969). Aphids in general alighted 2 - 11 times as frequently on light, yellow-green, flush-like leaves as on dark green, mature leaves (Moericke, 1953), and Moericke noted that the landing colour preference (for yellower leaves) seemed to be widespread among phytophagous insects, including many Homoptera, such as psyllids.

An outstanding feature of T.erytreae's biology is the dual restriction of its oviposition to young, rutaceous flush (references cited on p.5). Moran and his students have sought the possible causes. They have shown that Rutaceae-recognition could involve antennal chemoreception (Moran & Brown, 1973) and that oviposition could be confined to young flush due to the physical impenetrability of mature leaves to the psyllid's ovipositor (Moran & Buchan, 1975). The initial aim of the present study was to determine whether or not host plant and flush location by T.erytreae could be based on vision. The subsequent aim was to discover the physiological/behavioural basis of T.erytreae's alightment colour preferences.

Both Moericke and Kennedy have attempted to discover the alightment stimulus responsible for the observed colour preferences of homopterans. Moericke (1952 et seq.) evaluated the test surfaces in terms of the established parameters of human colour vision, and found a close correlation between aphid alightment frequency and target "Sattigung" i.e. "purity". Obviously, a colour evaluation more relevant to insects was desired, but could only be based on a knowledge of aphid visual physiology, to which Moericke (1950 et seq.) made valuable contributions which will be discussed in the following chapter (dealing with artificial surfaces). In 1961, Kennedy et al. considered that Moericke had provided enough fundamental information for them to be able to formulate an aphid colour parameter, the "long/short ratio", which will also be discussed in the following chapter. They found that the relative frequencies of aphid alightment on leaves in the field (either naked leaves or ones covered with petri dishes of water) also correlated well with this alightment formula. The colours of the leaves and artificial surfaces presented to T.erytreae in choice tests, were, therefore, assessed in terms of the 3 human colour parameters (used by Moericke), as well as the 2 aphid colour parameters (formulated by Kennedy et al.), and a single "RAS equation" colour parameter (derived in a later stage of the present study, viz. Section 6.1).

Fig.6. Development of spring flush of sweet orange, Citrus sinensis. (a): Class A flush, ideal for oviposition by T.erytreae, sprouting from mature leaves of the previous season. (b): The same shoot completely developed into Class B flush four weeks later.

Materials and Methods (leaves).

To determine T.erytreae's visual preferences for alightment on leaves, and whether or not these were adequately explained by colour parameters previously used in work on Homoptera, techniques based on the work of Moericke and Kennedy were employed. In addition to the general methods already given (p.8), the following details applied in the case of leaves.

Pairs of leaves or flush shoots of different colour were carefully chosen so as to match in other visible characteristics (size, shape and freedom from blemishes). Silhouette areas were determined by tracing the outlines of the leaves on paper and weighing the paper cut-outs. Adhesive-coated leaves were supported vertically against a narrow strip of rigid, clear plastic ("perspex") with their petioles immersed in water in clear glass bottles, and did not appear to change colour during a two-day replicate. At the end of each run, the distribution of psyllids which alighted and were trapped on the adhesive-coated leaves was noted for each sex on each leaf (numbers on adaxial surface, edge, and abaxial surface).

Diffuse reflectance spectra and the colour parameter values of the surfaces presented in each alightment choice test series were recorded in graphical form alongside the graph of relative alightment frequency. Comparison of alightment frequencies with the colour parameter values of the surfaces presented, was performed visually in this chapter. Rigorous mathematical correlations of linear regressions were postponed till later (mainly Section 6.2) so that a comparison could be made of human, aphid, and "RAS equation" colour parameters for describing the alightment frequency of T.erytreae on all leaf and artificial surfaces presented.

2.1 Colour Change during Flush Growth and Maturation.

Although the large, light green leaves (called "Class B" flush and described more fully by Catling, 1969) are the most conspicuous feature of the flush shoot (Fig. 6b), oviposition by T.erytreae is confined to the smaller, more tender leaves ("Class A" flush) at and near the apex (Fig. 6a). Whilst it is desirable to know whether or not the psyllids could use vision to locate the Class A flush, its size makes this difficult to test. The problem was approached in two ways: firstly, the colour of Class A flush of sweet orange was measured and compared with that of Class B flush and mature leaves on the same branches (results presented in this section), and secondly, the effect of size on a colour preference was studied using an artificial system (Section 3.3).

As individual Class A flush leaves were too small for measurement of diffuse reflectance in the spectrophotometer used, composite samples of 4 - 6 leaves were prepared by attaching these to clear adhesive tape covering the sample-holder.

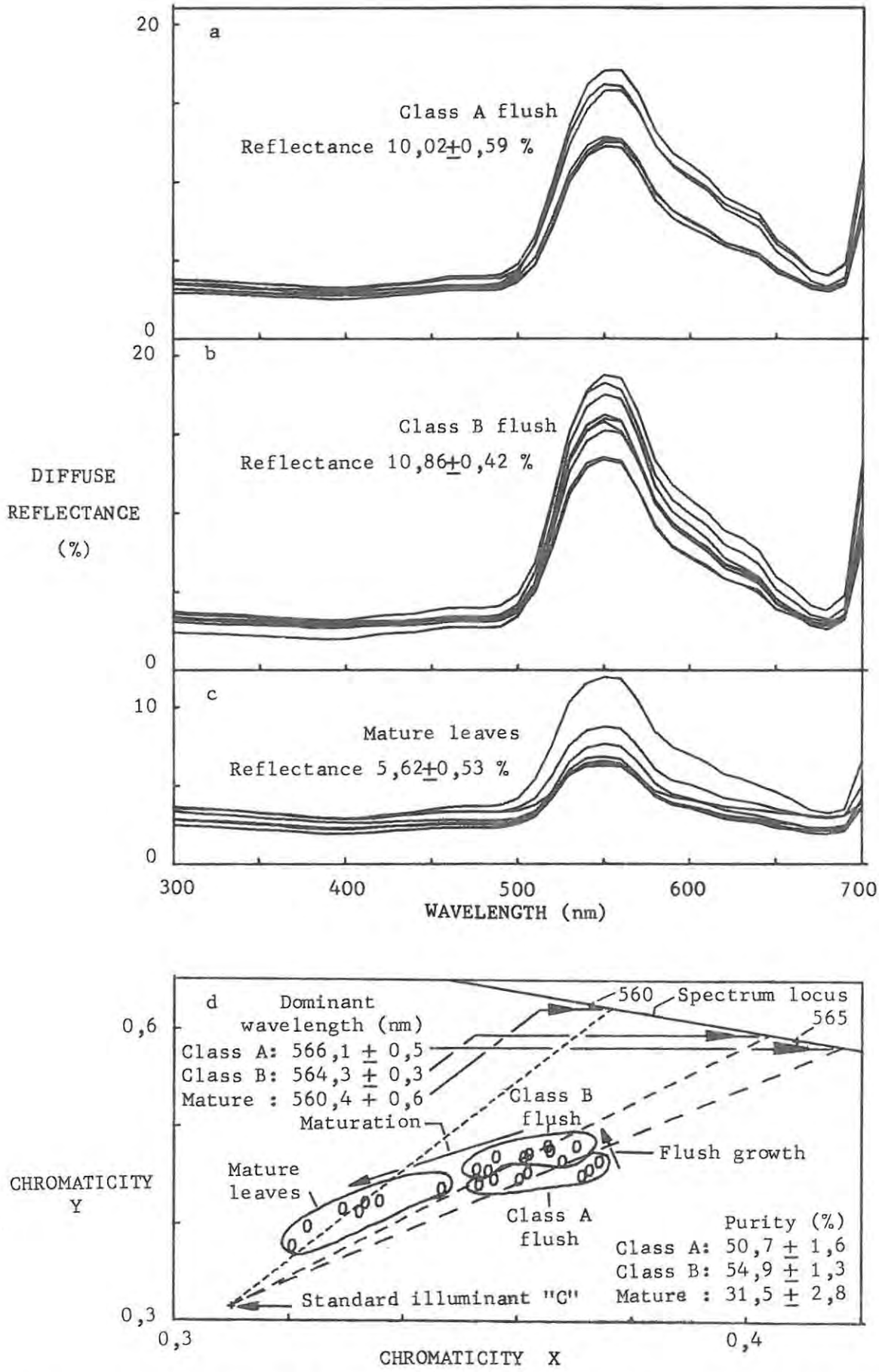

Fig. 7. Colour change of sweet orange flush, Citrus sinensis, during growth and maturation. Diffuse reflectance spectra of (a) Class A flush (n = 7 composite samples), (b) Class B flush (n = 9 leaves), and (c) mature leaves (n = 7), sampled from the same trees at the same time and measured with respect to an MgO standard. (d): Their colour point positions on the standard chromaticity diagram (inset) are given to demonstrate the change in dominant wavelength (intercept on the spectrum locus) and purity (ratio of distance from point "C") that takes place as the leaf expands and matures. (For further details, see text).

The curves from 7 such composite samples are recorded in Fig. 7a.

Diffuse reflectance spectra of all the leaves of sweet orange (Figs 7a-c) exhibited a single prominent peak in the visible spectrum at a wavelength of about 555 nm (which we see as yellow-green); the large variability within the samples of all leaf classes was apparently confined to the overall strength of diffuse reflectance. During flush growth and leaf maturation (Figs 7a-c) the diffuse reflectance did not change much in the near-UV and blue regions (i.e. over the wavelength range 300 to ca. 480 nm), but decreased markedly in the yellow-green region (ca. 480-670 nm). (This corroborated the findings of Shull (1929), and of Tageeva, Brandt & Derevyanko (1960) who, in addition, correlated increasing leaf absorbance with increasing concentration of chlorophyll.)

These diffuse reflectance spectra were converted into the numerical values of dominant wavelength, reflectance and purity to facilitate colour comparison between the different leaf classes. Dominant wavelength was obtained from the standard chromaticity diagram (Fig. 7d), where the line from the standard illuminant through the colour point under consideration intersected the spectrum locus. The dominant wavelength values for each leaf class are recorded on Fig. 7d. Class A flush had a very slightly (ca. 2 nm) but significantly ($0,001 < p < 0,005$ by the 't' test, applied without confirming that its assumptions were fulfilled) longer dominant wavelength than Class B flush, as did the latter compared with mature leaves ($p < 0,001$ by the 't' test, as above). With increasing age of orange tree leaves, therefore, the dominant wavelength decreased and moved away from the wavelength region we see as yellow.

Reflectance was calculated mathematically (as outlined briefly on p.9), but could also be estimated from the relative heights of the diffuse-reflectance peaks in the yellow-green region of the spectrum (see Figs 7a-c, on which the calculated reflectance values of each leaf class are also recorded). Clearly, the reflectance of the two classes of flush was very similar (although that of Class A was slightly lower than that of Class B on average) and approximately double that of mature leaves. Purity was also obtained from the standard chromaticity diagram (Fig. 7d), as the ratio of the distance from the standard illuminant "C" to the colour point of the surface under consideration, to the length of that whole line extrapolated to the spectrum locus. The degree of overlap of the samples of Class A and Class B flush, and their more distal position from the illuminant point on Fig. 7d, demonstrated that they were of similar purity (though that of Class A was again slightly lower than that of Class B on average, as seen from the purity values recorded on Fig. 7d) and that their purity was almost double that of mature leaves. The significance of difference between percentage reflectance, and percentage purity, of the different leaf classes was not tested (although statistical tests are available

for this purpose (Sokal & Rohlf, 1969)) because both reflectance and purity of Class A and B flush leaves (given on Figs 7a, b & d) were clearly significantly different from that of mature leaves (given on Figs 7c & d).

All 3 parameters of Class A flush, therefore, had values closer to those of Class B flush than to those of mature leaves. Class A flush evidently differed visually from Class B flush only very slightly in colour, though considerably in size.

2.2 Visual Preference for Light Green Leaves.

Concerning the visual choice between light- and dark-green leaves, the alight= ment measurements, including edge and decoy effects, summarized below, are from an earlier study (Urban, 1971). The arrestment measurements, diffuse reflectance measurements, colour parameter computations, and correlation tests (presented below and in Chap. 6), were all subsequent extensions of the earlier study.

Trioza erytreae showed an approximately three-fold alightment preference (2,96 $\pm$ 0,56) for light green rather than dark green leaves in the choice-chamber (14 replicates, with 678 participants) (Fig. 8c). This preference was rather variable, and ranged up to 9,68 though was never below 1,00. (The net ratio of participants was somewhat less than the mean: 472/206 = 2,29). Alightment distri= bution was significantly to highly significantly biased in 9 out of 14 replicates (chi-square test), and there was 75-90 %probability of significant bias in 3 repli= cates. The cumulative chi-square probability was highly significant ($p < 0,0005$) . The preference existed regardless of the sex or adult maturity of psyllids, or the species of host plant on which they were reared (Citrus or Vepris), or the species or shape or size (above 1×10^{-2} m^2 at 0,20 m distance) of non-host leaves (Morus or Brachychiton) offered as a choice.

In darkness, the light-green over dark-green leaf alightment distribution was 1,03 $\pm$ 0,21 (Fig. 8c) (8 replicates, with 214 participants) with a range of preference from 0 to 2 times. By raising the temperature 11 ^{o}C in 3 replicates, the activity was increased and sufficient numbers alighted to allow chi-square analysis. The distribution was always random, with a cumulative probability of $0,25 < p < 0,50$.

Non-visual cues were not involved in these experiments (: the adhesive coating on the leaves prevented choices based on gustation and mechanoreception, and the randomness of distribution in darkness indicated the absence of olfactory compli= cations). The significant preference for light green flush demonstrated here by T.erytreae was, therefore, purely visual.

The attractiveness of the light green leaves in these experiments was not influenced by the presence of the psyllids already on those leaves. This was

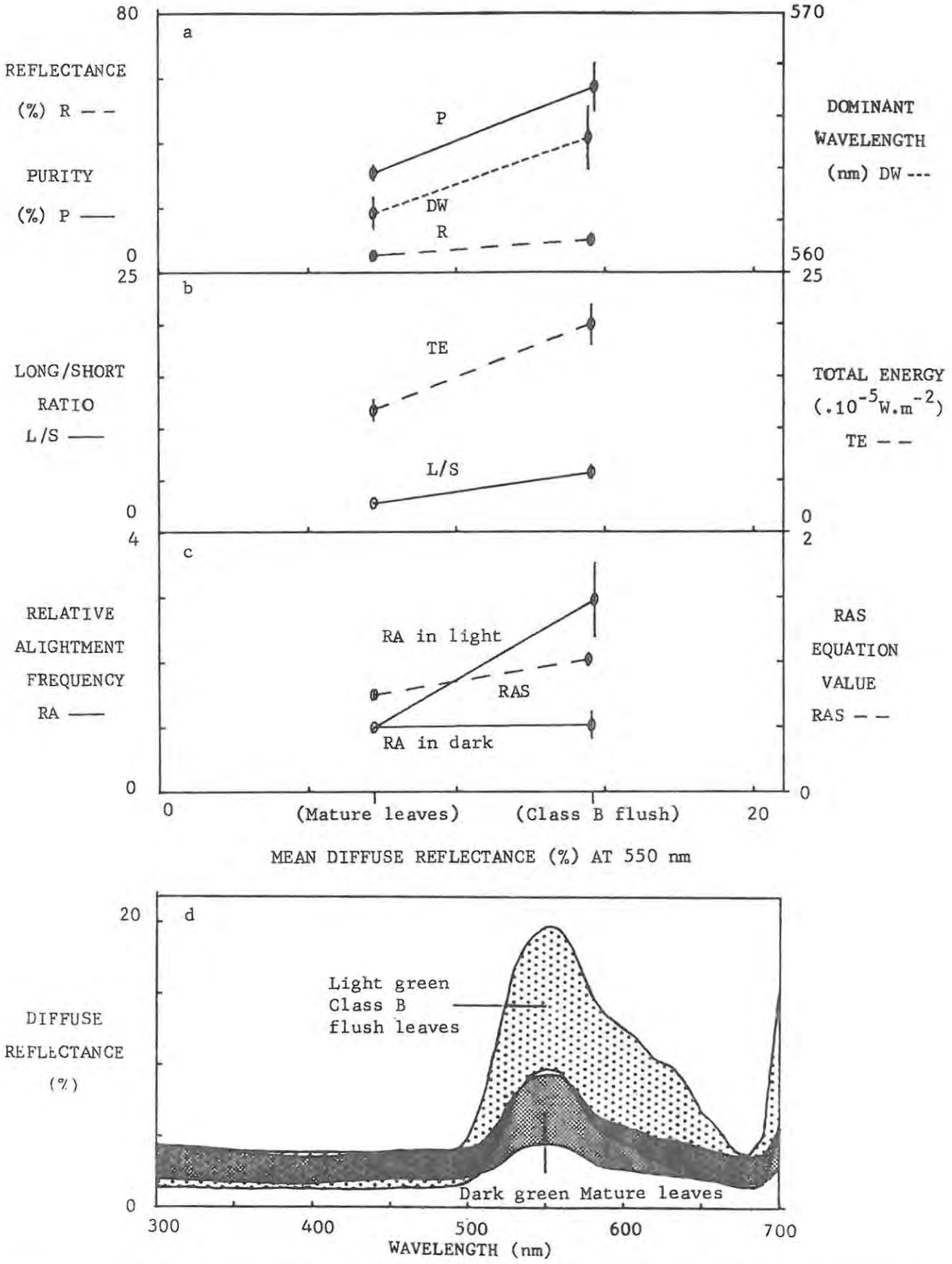

Fig. 8. (c): Relative alightment frequency (RA) of T.erytreae (mean ± 1 standard error of 14 replicates in light or 8 in darkness in lab 1 : data ex Tables I and II of Urban, 1971) on choices of light green flush and dark green mature leaves of the non-hosts Morus alba and Brachychiton acerifolium in relation to the range of their diffuse reflectance spectra (n = 7 for each group) (d), and their colour parameter values: (a) human dominant wavelength (DW), reflectance (R), and purity (P); (b) aphid long/short ratio (L/S), and total energy (TE); and (c) the "RAS equation" (RAS) derived in Section 6.1. (For further details, see text).

established by determining the alightment distribution between a pair of light green leaves, then placing up to 70 adult T.erytreae decoys/10^{-2} m^2 on one leaf of the pair and re-determining the alightment distribution. Two-by-two contingency tests showed that the alightment distribution was not significantly affected by psyllid decoys in any of the 7 replicates ($p > 0,90$ in 5 replicates).

Distributions of trapped psyllids showed a strong bais towards alightment on the edge of leaves. The number of Trioza that alighted within a narrow zone approximately 3,5 mm wide along the perimeter of the leaf was routinely recorded. the number expected was calculated as the product of edge area expressed as a fraction of leaf area, and the total number of psyllids which alighted on that leaf. Observed over expected edge ratios were highly significant ($p < 0,0005$) in 9 out of the 14 "daylight" replicates of Fig. 8, indicating the existence, in T.erytreae, of a strong response to leaf edges.

Locomotor arrestment in response to leaf colour stimuli was also investigated. Batches of 100 adult Trioza were enclosed in a flat gauze cage over a glass plate, behind which were 1 to 3 pairs of light- and dark-green leaves. The mean number of psyllids arrested (in characteristic probing attitude, or just standing directly over a leaf) was noted after 4,5 h . Flush over mature arrestment ratios varied between 1,48 and 3,10 (mean 1,99). Chi-square tests were significant in 7 out of the 10 replicates and the cumulative probability of non-random distribution was highly significant ($p \ll 0,001$).

Spectral reflectance curves of samples of 7 light green flush and dark green mature leaves of the non-host species used in the visual preference tests were measured (Fig. 8d). Within each leaf class there was as much variation in diffuse reflectance at any wavelength as found in the host plants (Fig. 7b,c). Host plant leaves generally reflected slightly more than non-hosts over the human-visible wavelength range (400-700 nm), but this was possibly an artifact due to slight wilting, as these leaf samples were taken from shoots brought in (in water) from a citrus grove 20 km from the laboratory, and an increase in diffuse reflectance with loss of turgor has been recorded before (Pearman, 1966; Woolley, 1971). The significance of the difference between the mean reflectance of host plants and non-hosts could not validly be put to the 't' test as the percentage values were too low (according to Sokal & Rohlf, 1969). The host plant leaves did not appear to exhibit any special feature in their diffuse reflectance spectra which could permit visual discrimination of hosts from non-hosts (Figs 7b & c compared with Fig. 8d).

Light green flush leaves, however, had roughly twice the diffuse reflectance of mature leaves in the 500-700 nm wavelength range (Fig. 8d), and did not differ from mature leaves in the blue (400-500 nm) or near-UV (300-400 nm). Compared with dark green mature leaves, the dominant wavelength of light green leaves was shifted

Fig. 9. Red Class A flush of Eureka lemon, Citrus limon, showing the rapid colour change during development into typical light green Class B flush.

slightly (ca. 4 nm ,i.e. ca.1 % of the average human and insect visual range) towards the more longwave (i.e. yellow) region of the spectrum (Fig. 8a). In light green flush, both reflectance and purity were approximately double that of dark green mature leaves (Fig. 8a) (which presumably corresponded to the fact that the spectral reflectance peaks of flush were about twice the amplitude, and had about twice the height to base-width ratio (Fig. 8d)).

Trends increasing from mature to flush leaves in a manner basically similar to the frequency of alightment response to these leaves (shown in Fig. 8c) were seen not only in all 3 human colour parameters of the leaves (Fig. 8, c compared with a) but also in both the aphid colour parameters (Fig. 8, c compared with b) (the derivation of which is discussed in the introduction to the following chapter : 3) and in the "RAS equation" colour parameter (Fig. 8c) (the derivation of which is dealt with in Section 6.1). There were thus theoretical grounds for the observed visual flush preference by T.erytreae in all 6 parameters of colour studied (i.e. dominant wavelength, reflectance, purity, long/short ratio, total energy, and RAS equation). There was, therefore, no evidence at this stage, as to which parameter or combination of parameters was the stimulus responsible for T.erytreae's alightment colour preferences.

2.3 Visual Non-preference for Red Flush.

In common with numerous species of plants (Onslow, 1925; Lawrence et al., 1939), the Class A flush of some varieties of citrus is distinctly reddish. That of Eureka lemon is plum-coloured or brownish-red (Fig. 9), quite different in colour to the Class A flush of sweet orange (Fig. 6a) dealt with in the previous section. Representative diffuse reflectance spectra which illustrate the progressive colour change from plum-coloured Class A flush to light, yellow-green Class B flush, are given in Fig. 10d. In red leaves there is always a low and broad reflectance peak in the red at 640 nm . The human colour parameter values of the lowest curve in Fig. 10d (which is a composite sample of 8 very dark, purplish-red leaves) were: dominant wavelength, the complement of 496 nm ,i.e. bluish-red; reflectance 3,3 % ; purity 3,7 % . Figure 10d shows that as the reddish flush grows, the height of the yellow-green (555 nm) peak increases relative to that of the red peak, until the leaf assumes the colour of normal light green flush, the yellow-green peak having the typical red shoulder.

Choice-tests were performed to determine the relative visual attractiveness of reddish Eureka lemon flush compared with yellow-green Class A flush of rough lemon (of which a reflectance curve is given in Fig. 10d: dashed line). Three whole shoots of each colour were used at a time, each comprising 8-17 leaves. The shoots were presented in alternating array, each at one corner of a hexagon, 0,20 m from the Trioza release point in the rotating cylindrical choice-chamber (see Fig. 1c,d) in lab 2.

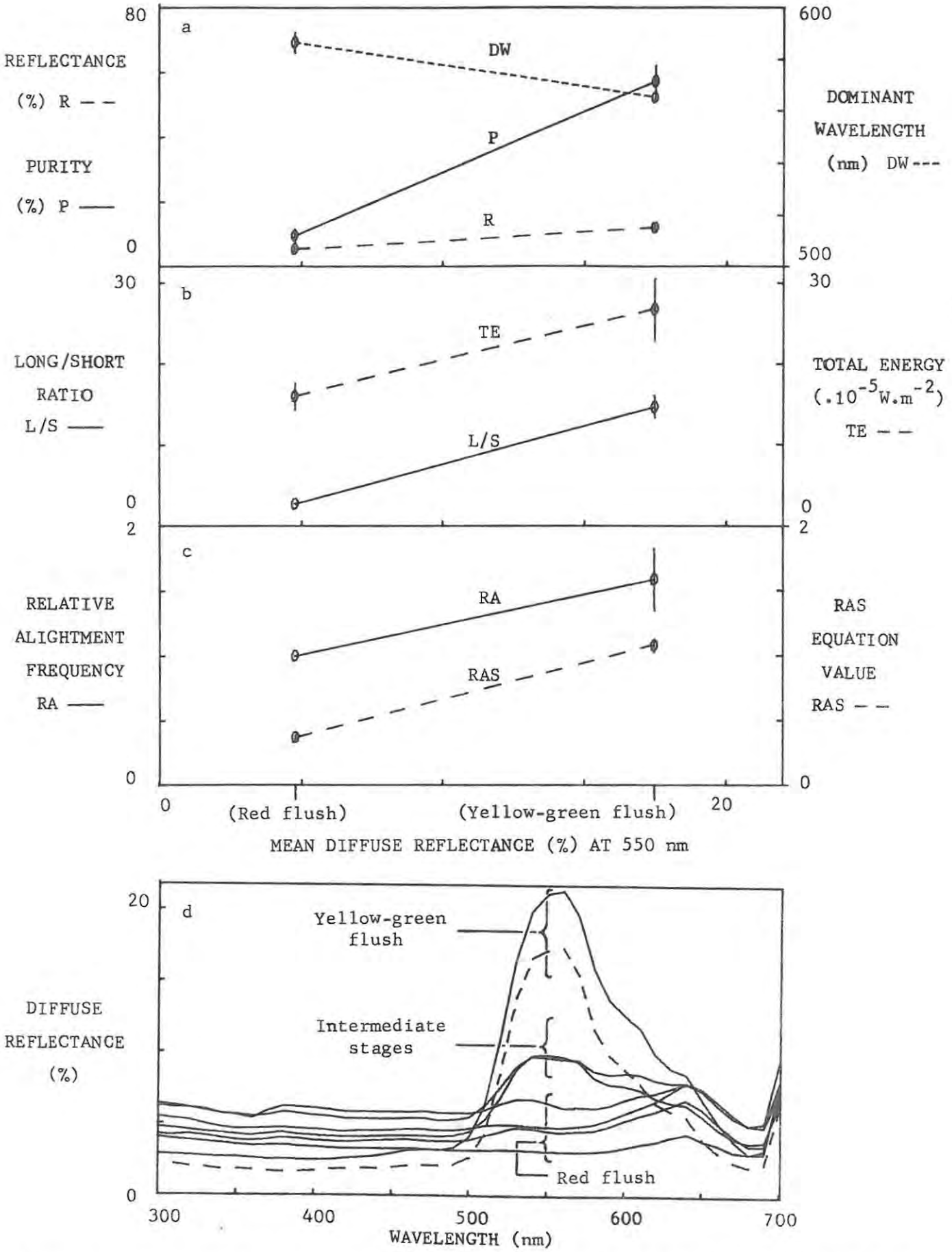

Fig. 10. (c): Relative alightment frequency (RA) of T.erytreae (mean ± 1 standard error of 9 replicates in lab 2) on choices of 3 shoots each of yellow-green Citrus jambhiri flush (dashed line in (d)) and reddish C.limon flush, in relation to their diffuse reflectance spectra (d) (showing progressive leaf colour change during development from red Class A to yellow-green Class B flush), and their colour parameter values: (a) human dominant wavelength (DW), reflectance (R), and purity (P); (b) aphid long/short ratio (L/S), and total energy (TE); and (c) the "RAS equation" (RAS) derived in Section 6.1. (For further details, see text).

Alightment favoured yellow-green rather than red flush in 7 out of 9 replicates (YG/R alightment ratio 1,59 $\pm$ 0,24 ; range 0,90 - 3,13 ; net ratio of numbers alighted 409/260 = 1,57). The distribution was highly significantly biased ($p < 0,001$) in 2 replicates, and showed a 75 - 90 % probability of significant bias in 3 replicates. Of the 4 replicates with approximately random distributions, the lack of a significant colour preference might have been due to the following factors. One replicate employed rather large shoots, as a result of which the "red" shoots had leaves of a colour between red and yellow-green, and thus did not contrast much with the yellow-green shoots. In the remaining 3 replicates, the degree of psyllid participation was very low, undoubtedly partly because the flush shoots were rather small, averaging $0,17 \times 10^{-2}$ m^2 in total leaf area, and decreasing colour preference in a choice test was later shown to be associated with decreasing target size (Fig. 18) and psyllid participation (Fig. 21). (Arrestment experiments (with psyllids caged over glass, behind which were the flush shoots) showed a stronger arrestment by yellow-green than by red flush in all 4 replicates (range of YG/R ratio: 1,75 to 2,17). There was, however, only 75 - 90 % confidence that the arrestment distribution was significantly biased).

Comparison of the signs of the slopes of the graphs showed that alightment frequency and dominant wavelength of the leaf choices presented were negatively correlated (Fig. 10a, c), which established that T.erytreae's alightment was not in response to dominant wavelength alone. Positive correlations with alightment frequency indicated that the other 5 of the 6 colour parameters tested (Fig. 10a-c) could, theoretically, have been responsible for the recorded alightment preference.

Discussion (leaves).

Glossiness is an optical property of leaves, other than pigment colour, which is more intense in flush than in mature leaves. The possibility of the visual flush preference shown by T.erytreae being based on glossiness was investigated briefly, because the light reflected from shiny surfaces is polarized - there is, indeed, a measurable degree of polarization in the visible light reflected from leaves (Woolley, 1971) - and insects have been recorded (though there are conflicting findings) not only as adopting orientations at specific angles to the plane of polarization but also as being more strongly phototactically responsive to polarized than to non-polarized light (Kovrov & Monchadkii, 1963, cited by Mazokhin-Porshnyakov, 1969). Specular (i.e. mirror-like) reflectance (with which degree of polarization of reflected light could be expected to correlate) of Class B flush and mature leaves of Citrus limon was measured over the wavelength range 300 - 700 nm. The specular reflectance spectra were tri-modal, with broad peaks (in decreasing order of reflectance) in the UV (ca. 310 nm), blue (ca. 430 nm) and yellow-green (ca. 560 nm). At all wavelengths, however, specular reflectance was less than 0,04 % . As the diffuse

reflectance of similar leaves commonly peaked at ca. 17% and was never, at any wavelength, less than 2%, the intensity of specularly-reflected light was generally at least 2 orders of magnitude less than that of diffusely-reflected light, i.e. it was comparatively minor. The topic of glossiness (and specular reflectance) was, therefore, not dealt with further.

Host plant location. The bands covered by the diffuse reflectance spectra of the samples of host plant and non-host leaves in either class (light green Class B flush in Figs 7b and 8d, or dark green mature leaves in Figs 7c and 8d) were broadly overlapping. This has two important consequences. Firstly, T.erytreae's visual flush preference, demonstrated with these non-hosts, most also exist equally strongly among the host plants. Secondly, host plant location, i.e. Rutaceae recognition, by colour discrimination, is impossible. Host plant location by visual discrimination of form is also impossible for T.erytreae (in spite of the possibility that the capacity for form-learning and -recognition might conceivably exist in the citrus psylla, this capacity having been demonstrated in at least one species of insect (von Frisch, 1914-15, and other workers, cited by von Frisch, 1967)) because leaf shape within the Rutaceae is very varied (Urban, 1883) and is often very similar to that of many non-hosts of T.erytreae. Visual host plant discrimination is, therefore, out of the question. This is in agreement with the general conclusions of Moericke (1950, 1952) and Kennedy (Kennedy & Booth, 1951; Kennedy et al., 1961) from their work on aphids.

Moericke's (1969) record of slightly "host-plant-specific colour behaviour" (see the introduction to this chapter) involved the species Hyalopterus pruni, which belongs to a group of grass and sedge aphids which are relatively "non-yellow-sensitive" (Taylor & Palmer, 1972). If one is to accept, that the preference of this group of aphids for leaf-hue surfaces that are unsaturated in colour (Moericke, 1955a,c), is an adaptation to the relatively unsaturated colour of their host plant groups (i.e. Gramineae and Cyperaceae), then the converse must, logically, also be accepted. The converse is that the preference of the group of "yellow-sensitive" aphids (and psyllids and aleyrodids) for leaf-hue surfaces that are saturated in colour (references cited in the following chapter) is an adaptation to the relatively saturated colour of their host plant groups (i.e. non grass/sedge families). Although a few diffuse reflectance spectra of grasses have been recorded in the literature (e.g. by Moericke, 1955a; Woolley, 1971), a thorough comparison of grass/sedge and non- grass/sedge vegetation colours has yet to be made to test the validity of the above concept of adaptation to the colour of host plant groups.

Alightment on leaves in proportion to their yellowness is a response considered likely to have survival value for T.erytreae engaged in the process of host plant location. Assume that T.erytreae disperse in a series of repeated flights, alightments and taste probes, as in the classical figure of Moericke (1955c) for aphids,

and feed readily on non-hosts like other psyllids (Pletsch, 1947; Hokdinson, 1974). (The term "oligophagous" mentioned in the Introduction (p.5) as being typical of the Psyllidae, is slightly misleading as it refers to the number of kinds of plant, not for feeding, but for oviposition and nymphal development.) It is hypothesized that the strong response to yellow (evident in the results presented in the following chapter, Sections 3.1 and 3.2) will cause dispersing citrus psyllids (as has been suggested for aleyrodids (Lloyd, 1921) and aphids (Moericke, 1952)) to alight preferentially on senescing and yellows-diseased leaves and on light yellow-green flush, the diffuse reflectance spectra of which are more similar than those of mature leaves, to that of yellow (Shull, 1929; Kennedy, 1961; present study, Figs 7, 8 & 12). The relative growth rate of homopterans, which is correlated with the concentration of soluble nitrogen in the food (van Emden et al., 1969; Webb, 1974), was found to be better on yellows-diseased leaves than on healthy leaves (various authors cited by Kennedy, 1951) and on senescing and young leaves than on mature leaves (van Emden & Bashford, 1971). The yellowness of leaves, therefore, is a good indicator of their nutritiousness to Homoptera. The alightment response to yellow shown by T.erytreae consequently corroborates the "nutrient discrimination" part of Kennedy's "dual discrimination theory" (Kennedy & Booth, 1951), namely that one set of responses is to stimuli betokening leaf nutritiousness. It is therefore suggested that:

> the response to yellow will lead dispersing T.erytreae, at each successive alightment, to a nutritionally-rich source of phloem sap from which to replenish the metabolic fuel required for the remaining flights of the host-finding journey.

Flush location. Although host plants cannot be discriminated on the basis of vision, flush leaves certainly can. The choice-chamber experiments established a statistically highly significant visual preference in the citrus psylla for light, yellow-green flush rather than dark green mature leaves both in alightment and in arrestment responses. This corroborates Moericke's (1953) statement that the visual preference for yellowish foliage seems to be a property of phytophagous insects in general. It must be stressed, however, that the strength of this preference is not strikingly great in T.erytreae, being only 2- or 3-fold in the laboratory.

In the field, background colour and light intensity will affect the alightment response to a different extent to that in the laboratory situation. When light green flush leaves are seen against the background of dark green mature leaves, the contrast itself will stimulate alightment because T.erytreae displays a strong edge response (Section 2.2) or "optomotor reaction", which, as Kennedy et al. (1961) have shown, is a component of the alightment stimulus and depends upon contrast. The greater light intensity in the field (ca. 10^5 1x (Seliger & McElroy, 1965)) than in the choice-chamber in lab 1 ($3{,}8 \times 10^2$ 1x (Results, Chap. 1)) will enhance the

response to flush because the strength of T.erytreae's colour preference increases with ambient light intensity (Section 3.3, Fig. 17).

Of interest here is the note on psyllid trapping in the field by Wilde (1962) that twice as many pear psylla, Psylla pyricola, were caught in Anjou pear trees with light yellowish-green foliage, as in Bartlett trees with darker green leaves. Whilst nothing is known of the various other possible causative factors, it is known that the pear psylla's phototactic responses are similar to the citrus psylla's in at least some respects (being strong towards yellow and ultraviolet (Kaloostian & Wolf, 1968)), so it is possible that the biased varietal distribution is due to a visual response to leaf colour. This possibility is supported by the finding that the alightment frequency of aphids on the leaves of several varieties of peas in the field was proportional to leaf yellowness (Cartier, 1963).

The laboratory results presented in this section, when extrapolated to the field situation, suggest the following hypotheses. Catling (1967) found that the most common flight activity of T.erytreae in the field is a trivial, circling flight of one or two seconds duration close to the citrus tree canopy. The psyllids probably remain within the effective range of Class B flush shoot colour stimuli during these flights, as leafhoppers were attracted to plants by visual stimuli from a distance of 3,6 m (Saxena & Saxena, 1975). Alightment of the citrus psylla after these trivial flights will be significantly biased towards flush shoots, when they support sufficient light green leaves to present conspicuous targets (i.e. subtend 15° or more with flying psyllids (see Section 3.3)). Visual locomotory arrestment will keep the psyllids that have alighted slightly longer on average on the light green leaves before the next take-off. Repetition of this sequence will result in aggregation of psyllids on the flush shoots. Trioza erytreae's common habit of walking along the mid-rib to the leaf axil and up the stem could take it to the Class A flush. (Class A flush itself is recognized by mechanoreception of low leaf hardness (Moran & Buchan, 1975), and possibly also by gustation of a preferred concentration of phloem nutrients, of which aphids are capable (e.g. Mittler & Dadd, 1964), or of a preferred combination of various constituents of the essential oil, which differ in concentration with citrus leaf age (Scora & Torrisi, 1966)). The probable role of vision in flush location is summarized in the following hypothesis:

> Groups of light green flush leaves are used by T.erytreae as "visual flares" which assist flush location en route to the oviposition site.

Ecological significance of leaf redness. Relatively few groups of insects are adapted to feeding and living on spermatophytes, and one of the main evolutionary hurdles to doing so is probably nutritional (Southwood, 1973). Compared with other plant tissues, however, flushing and senescing leaves are both rich in liquid

nutrients (references cited on p.25) and are the preferred sites of parasitism by homopterans (Kennedy, Ibbotson & Booth, 1950). In terms of the evolution of plant defences against insects, it may have been crucial to protect this stock of nutrients from removal by excessive insect attack. It is hypothesized here that:

reddening of flush and autumn leaves is a "non-preference" resistance mechanism against alightment and probing by Homoptera.

Painter (1951) stated that the "non-preference" type of resistance could be based on colour. Other hypotheses for transient leaf redness which have been reviewed in the literature (Onslow, 1925; Lawrence et al., 1939; Harborne, 1965) are all physiological and/or environmental (usually high carbohydrate or stress conditions) rather than ecological. The red pigment is undoubtedly an anthocyanin (Shull, 1929; Lawrence et al., 1939; Harborne, 1965). A typical conclusion of these botanists or phytochemists is that "... there is little or no reason for supposing that they [i.e. anthocyanins] are of any importance as such in young and autumn leaves" (Lawrence et al., 1939). Whilst in no way denying the association of anthocyanin production with various physiological factors, it does seem possible that the pigment has ecological importance. Homoptera are generally insensitive and unresponsive to red as regards alightment, walking towards, and probing (work cited by Gross, 1913; Moericke, 1950, 1952, 1953; Mound, 1962; Žďárek & Pospíšil, 1966a; Macdowall, 1972; Vaishampayan et al., 1975a; the present study, Figs 11 & 23). Reddening of flush and autumn leaves, therefore, would have the selective advantage to the plant of retarding the frequency of alightment on, and probing of, these organs by homopterans. A markedly-reduced alightment frequency has been demonstrated in aphids, towards red-leafed varieties of cabbage (Moericke, 1955c; Daiber, 1971) and lettuce (Müller, 1964) compared with green and yellow-green varieties, and in a species of aleyrodid, towards red bracts compared with green leaves of poinsettia (Vaishampayan et al., 1975b). Similarly, small red flush shoots of citrus are significantly less attractive to the citrus psylla for alight= ment than similar-sized green flush (Section 2.3).

The red pigment becomes masked by a yellow-green pigment (undoubtedly chloro= phylls (Rabideau, French & Holt, 1946; Tageeva, Brandt & Derevyanko, 1960)) as the leaf grows. Red Class A flush develops into normal light green Class B flush which would act as a typical visual "flare": this is borne out by the fact that the citrus psylla did not show significant non-preference in tests with large shoots, which had already developed to this stage (Section 2.3). This visual non-preference resistance mechanism (if indeed it be such) therefore breaks down during development and only provides protection for the youngest (and otherwise most vulnerable) flush.

On the topic of non-preference resistance of citrus to homopterans, based on leaf colour, considering the striking lack of alightment and probing response of

aphids in general (Moericke, 1950, 1952, 1953), aleyrodids (Mound, 1962; Vaisham= payan et al., 1975a), and the citrus psylla (Fig. 11) to blue and violet targets, and the conclusion that blue-violet light actually inhibits the alightment response to yellow (Vaishampayan et al., 1975a; the present study, Sections 5.2 & 5.3), it would be of interest to know whether or not the statement that "... even the young lemon leaves are blue and violet ..." (Sternlicht, 1974) could be supported by measurements of diffuse reflectance spectra.

Basis of alightment colour preferences. The visually-cued alightment prefer= ence of T.erytreae for light green flush rather than red flush or dark green mature leaves suggested a possible maximal response to "dominant wavelength" between 560 and 580 nm (Figs 8 & 10). In addition, alightment was positively correlated (Figs 8 & 10) with both of the other human colour parameters, "purity" and "reflectance" as well as both of the aphid colour parameters, "long/short ratio" and "total energy", and the values of the "RAS equation" (which is derived in Section 6.1). Causation, as opposed to correlation, however, remained unknown. Further attempts at discovering the stimulus responsible for the citrus psylla's alightment colour preferences, by comparing alightment frequency distributions with target colour parameters, this time using artificial surfaces, form the subject matter of the following chapter.

3. ALIGHTMENT ON ARTIFICIAL SURFACES IN RELATION TO THEIR COLOURS

It was noted quite early that a species of aphid (Das, 1918 p.190) and a species of aleyrodid (Lloyd, 1921) alighted more frequently on yellow than on white or blue surfaces, but it was some time before an attempt was made to explain these colour preferences.

Moericke (1952; 1955a,b; 1957) found that the "langwelligen" i.e. longwave region of the spectrum (wavelengths 500-600 nm) (including especially the yellow) was alightment-stimulatory for aphids, psyllids and aleyrodids. He also found that the "kurzwelligen" i.e. shortwave region (400-500 nm) (namely the blue) did not stimulate alightment, and was a complementary colour to yellow for the aphid, Myzus persicae (Moericke, 1950). Using filters over yellow-white colour papers, he established that blue reflected light, in combination with yellow, markedly reduced the alightment frequency of a "yellow-sensitive" aleyrodid (Moericke, 1955a). Moericke (1952, 1955a,c) linked the reduced alightment frequency on white compared with that on yellow surfaces to the decreased "Sattigung" i.e. purity of the stimulus, with which there was certainly a positive correlation.

White borders around yellow traps and suction traps markedly reduced the alightment of aphids, psyllids and aleyrodids (Moericke, 1955a,b). Moericke observed that these insects turned aside or upwards away from the white, and he concluded that they were negatively phototactic to white light at this stage. As the long-wave (yellow) component of white was known to be attractive, it was reasonable for him to hypothesize that the complementary, shortwave component of white light (which he took to be blue and/or UV) must be repellent (Moericke, 1955b). At the same time, however, Moericke (1955a) noted that UV light (300-380 nm) stimulated rather than inhibited alightment of an aleyrodid, as well as of the "non-yellow-sensitive" aphid, Hyalopterus pruni, and, to a much lesser extent, of "yellow-sensitive" aphid species. There was at this stage, therefore, no formal proof of repulsion by blue light, and the effect of UV on the alightment of "yellow-sensitive" aphids was not clearly established.

Kennedy et al. (1961), "... following Moericke for the time being, ..." assumed that longwave light (500-640 nm) elicited alightment of aphids, and that shortwave light, which they took to be 300-500 nm (i.e. UV as well as blue), "... tends rather to turn them away." Proceeding logically, they took a significant step forward in formulating, as the apparent alightment stimulus, the ratio of attractive longwave to "repellent" "shortwave" light energy reflected from any surface. Testing this aphid colour parameter, Kennedy et al. (1961) found good correlation of aphid alightment frequency with the "long/short ratio" of the surfaces presented.

The alightment frequency of T.erytreae on test surfaces was compared with the values of the human colour parameters of the surfaces presented (as done by Moericke, 1952 et seq.) and also with the values of the aphid colour parameters (formulated by Kennedy et al., 1961) and the "RAS equation" colour parameter (devel= oped in the present study, Section 6.1) of the same surfaces. The idea was to isolate the alightment-stimulatory colour parameter(s) by a process of elimination of those parameters which showed, under certain conditions, a negative correlation with psyllid alightment. Initial attempts, using leaves (previous chapter), were extended using several series of artificial surfaces (this chapter) so as to present a wider range of test colours. Miscellaneous factors affecting T.erytreae's colour preference were also studied here, mainly in the hope of discovering some of the causes of the large behavioural variation observed in citrus psylla populations.

Materials and Methods (artificial surfaces).

Basically, the methods are those recorded in the previous chapter, with the following details relevant to the artificial surfaces used. To determine the alightment distribution of T.erytreae, a 0,562 x 0,128 m print of the Kodak Visible Spectrum (claimed by the manufacturer to be "the most faithful reproduction of the visible spectrum that can presently be attained by the printing process") was covered with adhesive-coated window glass and exposed on the floor of the choice-chamber to psyllids "released" from the centre of the choice-chamber ceiling.

Glue-coated, painted metal rectangles (0,080 x 0,128 m) were exposed on the floor either in a row of 7 surfaces, or as an open square of 4 surfaces to equalize angle of subtense with psyllids at the release point. Matched pairs of green and yellow discs (of varying size) were exposed vertically, 0,40 m apart, with psyllids released midway inbetween, as with leaf choices described in Chap. 2. Paint series were made up with volumetric mixtures of Pinnacle Canary Yellow 001 , Windsor Green 010 and Black 103 (manufactured by Bellgrove & Snell, East London, South Africa), and Greyhound Flake White 24 , a basic lead carbonate paint (formerly made by Reeves & Sons, Enfield, England). One series of painted surfaces (designated "leaf hue") was dusted with magnesium oxide (MgO) or carbon black (C) powder to decrease the purity of the colour (at the same time increasing or decreasing the reflectance, respectively) and was then covered with adhesive-coated clear cellophane.

Diffuse reflectance spectra were measured using print and paint surfaces which were dry, except in the case of the dusted "leaf-hue" surfaces covered with glue-coated cellophane. Correction for the double-passage absorption of the adhesive-coated glass (used over the printed spectrum) was determined as the difference between the diffuse reflectance spectrum of an UV-reflecting white surface when exposed and when covered by the glass.

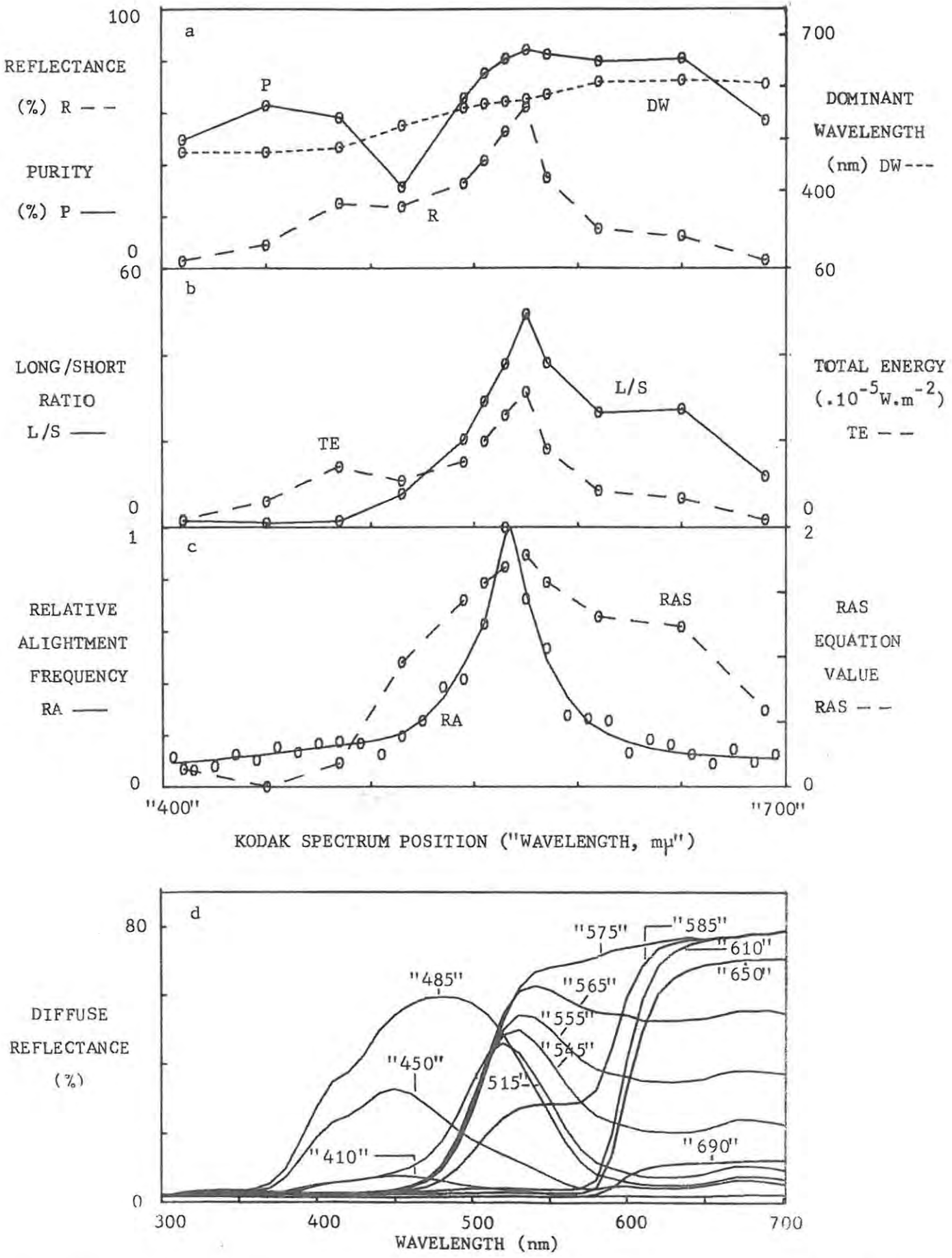

Fig. 11. (c): Relative alightment frequency (RA) of T.erytreae on a print of the Kodak visible spectrum (combined result of 8 replicates, in which 231 psyllids alighted on the most attractive of the thirty 10-nm wavebands i.e. RA=1 at "560"-"570 mμ"), in relation to the diffuse reflectance spectra (d) of 12 points on the print, and their colour parameter values: (a) human dominant wavelength (DW), reflectance (R), and purity (P); (b) aphid long/short ratio (L/S), and total energy (E); and (c) the "RAS equation" (RAS) derived in Section 6.1. (For further details, see text).

Most of the alightment measurements on the printed spectrum and those on the green to yellow paint series summarized below are from an earlier study (:Urban, 1971). The arrestment measurements (on the printed spectrum), alightment measurements on other paint series, and all diffuse reflectance measurements, colour parameter computations, and correlation tests, were subsequent extensions of the earlier study.

3.1 Printed Spectrum.

The positions on the Kodak spectrum are referred to in inverted commas because the Kodak axis markings ("wavelength, mμ") were found to indicate dominant wavelength more-or-less accurately in the region 485-610 nm, but to be increasingly inaccurate outside this region (Fig. 11a).

Alightment distribution of T.erytreae on the printed spectrum (number of psyllids per 10- "mμ" segment) was unimodal (Fig. 11c) with the peak in the greenish-yellow colour at the Kodak axis position "565", which had a dominant wavelength of 571 nm (Fig. 11a). Peak alightment was at this position when the psyllids were released from the ceiling, and from the floor (when the spectrum was placed on the ceiling), and when the spectrum was cut into 2 parts and re-presented to the psyllids with the yellow-green region displaced far to one end of the target and of the choice-chamber. Arrestment distribution of walking psyllids over the spectrum (which was not then covered with adhesive-coated glass) in a flat gauze cage was very similar to the alightment distribution, with the peak on the yellow at Kodak position (and dominant wavelength) 575 nm . Random alightment distribution on a black and white photograph of the Kodak visible spectrum indicated that the colour spectrum distribution was a response to colour and not simply to intensity.

Diffuse reflectance spectra measured at 12 points on the printed spectrum are given in Fig. 11d. Spectra of the most stimulating colours shared the characteristics of high reflectance at wavelengths greater than ca. 500 nm and, at the same time, very low reflectance at wavelengths less than 500 nm . Peak alightment and arrestment on the printed spectrum (Fig. 11c) coincided with peaks of both the human colour parameters, "reflectance" and "purity" (Fig. 11a), as well as with peaks of both the aphid colour parameters "long/short ratio" and "total energy" (Fig. 11b) and with the "RAS equation" colour parameter (Fig. 11c) (the derivation of which is dealt with later (Section 6.1)). Correlation, or "goodness of fit" of linear regressions of colour parameters against relative alightment frequency, was tested using the coefficient of determination, r^2 . The linear regressions were all of positive slope here. Alightment frequency correlated well with reflectance and total energy (r^2 = 0,837 and 0,815 respectively), less well with long/short ratio (0,618) and poorly with purity (0,323). The printed spectrum study, therefore, suggested that intensity was important in the psyllid alightment stimulus. None of

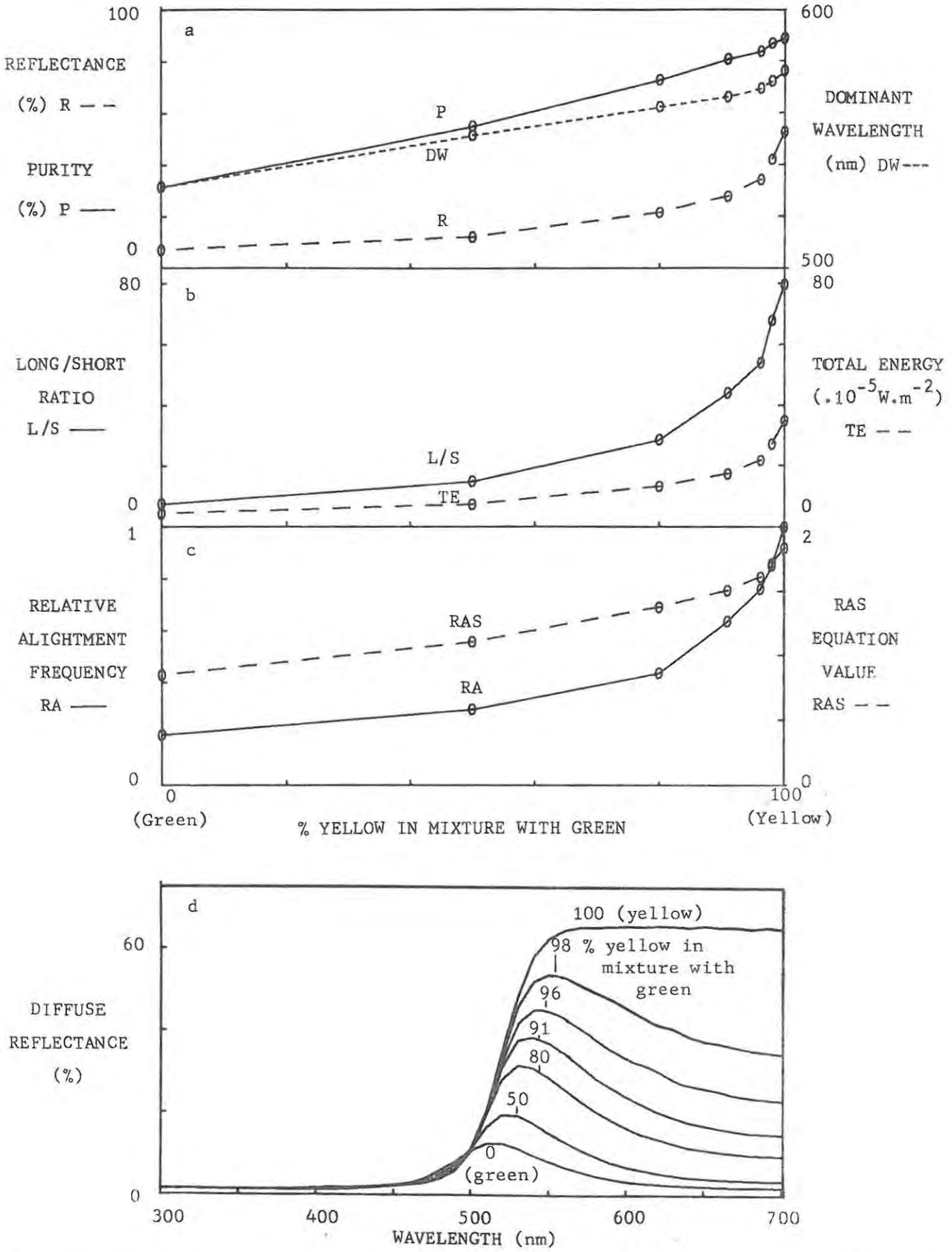

Fig. 12. (c): Relative alightment frequency (RA) of T.erytreae on a green to yellow series of painted metal rectangles (mean of 4 replicates, in which 144 psyllids alighted on the most attractive of the 7 targets i.e. RA=1 on yellow), in relation to their diffuse reflectance spectra (d) and their colour parameter values: (a) human dominant wavelength (DW), reflectance (R), and purity (P); (b) aphid long/short ratio (L/S), and total energy (TE); and (c) the "RAS equation" (RAS) derived in Section 6.1. (For further details, see text).

the human nor aphid nor "RAS equation" colour parameters was ruled out as a possible alightment stimulus.

3.2 Paint Series.

On a green (G) to yellow (Y) paint series, the alightment frequency of T.erytreae increased in proportion to target yellowness (Fig. 12c). Alightment was positively correlated with the amount of diffuse reflectance at wavelengths above 500 nm (i.e. "longwave" energy of Moericke, 1950, and Kennedy et al., 1961) (Fig. 12d), indicating that this could be an alightment-stimulatory parameter. Alightment correlated well with all human (Fig. 12a), aphid (Fig. 12b) and "RAS equation" (Fig. 12c) colour parameters in this series, (r^2 was always between 0,825 and 0,995), so it was not possible to say, after this series of experiments, to which colour parameter(s) the psyllids were responding.

On a green to lead-white (PbW) series, there was no marked colour preference (Fig. 13c). Going from green to lead-white, diffuse reflectance in the apparently alightment-stimulatory longwave region (Fig. 13d) increased as much as in the previous (G to Y) series (Fig. 12d), but, in contrast, increased as well at wavelengths below 500 nm (i.e. in the "shortwave" region of Kennedy et al., 1961). The lack of increasing attraction when proceeding from green to white (compared with that in the former series, going from green to yellow) suggested that shortwave energy might be either repellent in its own right, or alightment-inhibitory in combination with longwave energy. Psyllid alightment frequency on this series was positively correlated with purity (Fig. 13a) (r^2 = 0,581) and long/short ratio (Fig. 13b) (r^2 = 0,539) and "RAS equation" values (Fig. 13c), but was negatively correlated (i.e. had regressions of negative slope) with reflectance and total energy (Fig. 13a,b) (with r^2 values of 0,655 and 0,654).

On a black (Blk) to yellow to lead-white series, there was a high plateau of psyllid alightment frequency from pure yellow to 67% lead-white in yellow (Fig. 14c). Lowering the longwave energy by the addition of black (Fig. 14d) therefore masked the alightment stimulus more effectively than raising the amount of possibly repellent or alightment-inhibitory shortwave energy by the addition of white. As in the above (G to PbW) series (Fig. 13), alightment here was better correlated with purity or long/short ratio (r^2 = 0,545 and 0,574) than with reflectance or total energy (Fig. 14a,b) (r^2 = 0,169 and 0,126).

The above findings were essentially confirmed when only the yellow to lead-white series was presented (Fig. 15a-d), but alightment this time was maximal on pure yellow, best correlated with purity (r^2 = 0,956), and again strongly negatively correlated both with reflectance and with total energy (r^2 = 0,95 and 0,98).

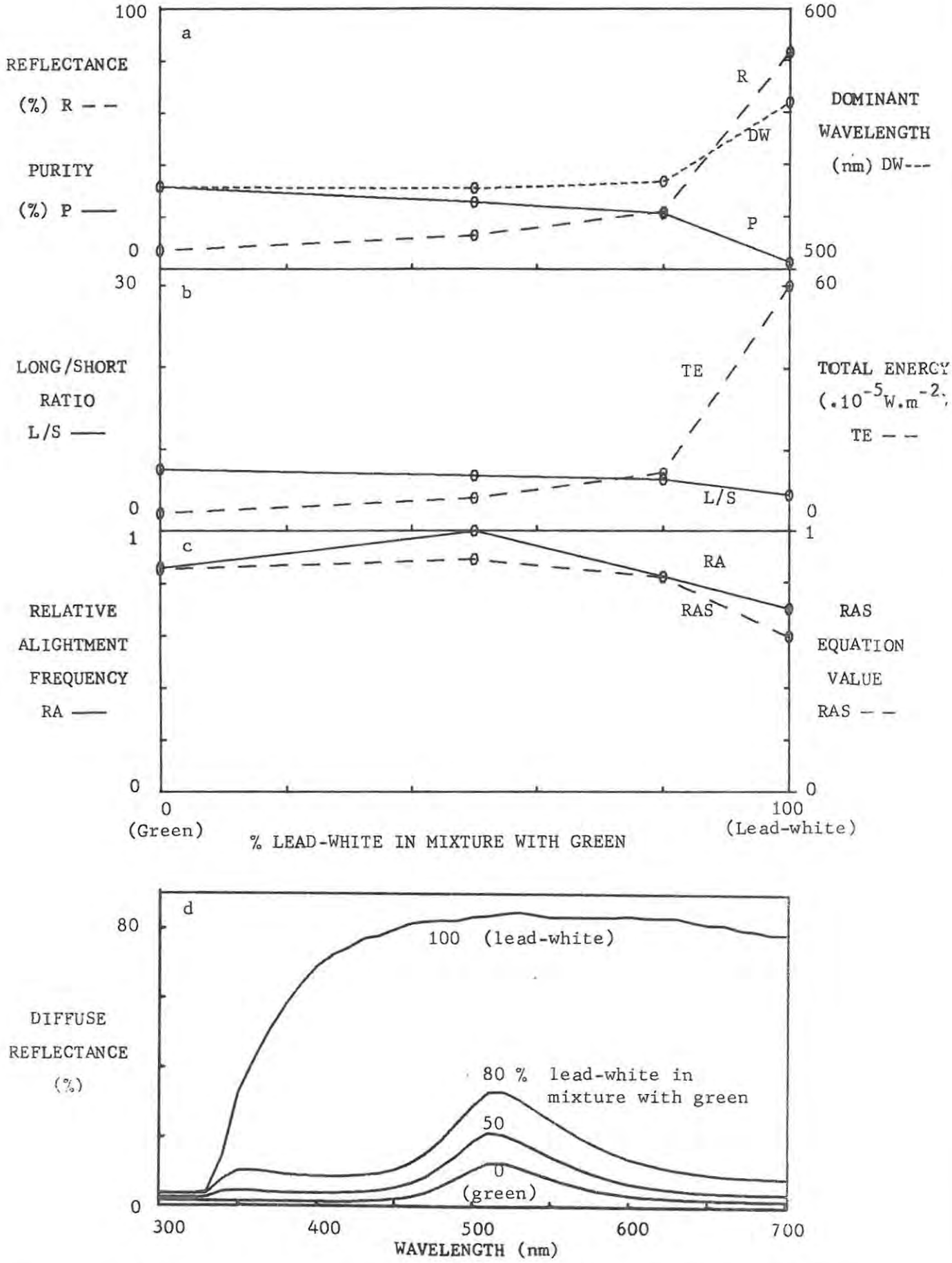

Fig. 13. (c): Relative alightment frequency (RA) of T.erytreae on a green to lead-white series of painted metal rectangles (mean of 2 replicates, in which 57 psyllids alighted on the most attractive of the 4 targets i.e. RA=1 on the surface containing 50 % lead-white in mixture with green), in relation to their diffuse reflectance spectra (d) and their colour parameter values: (a) human dominant wavelength (DW), reflectance (R), and purity (P); (b) aphid long/short ratio (L/S), and total energy (TE); and (c) the "RAS equation" (RAS) derived in Section 6.1. (For further details, see text).

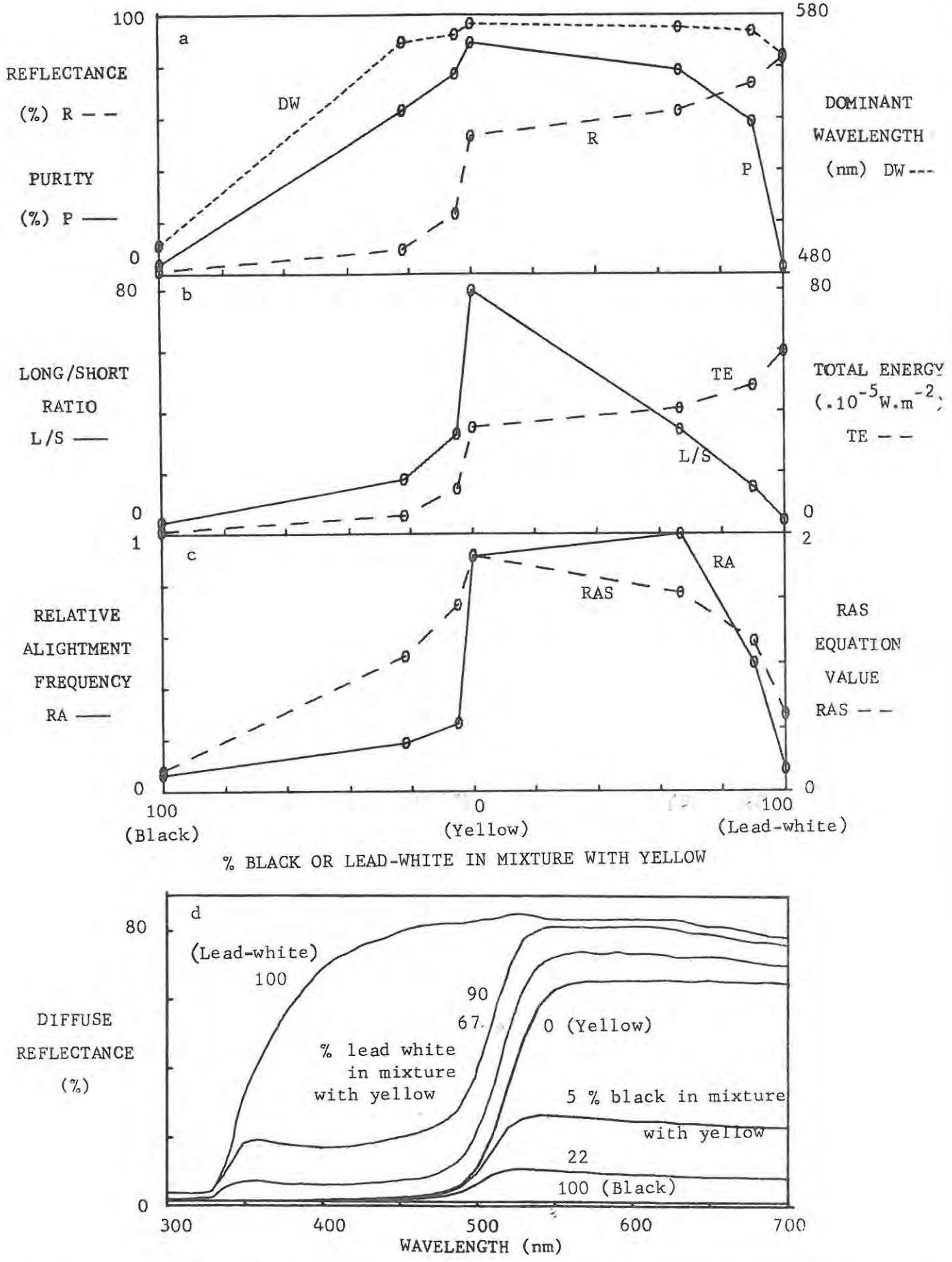

Fig. 14. (c): Relative alightment frequency (RA) of T.erytreae on a black to yellow to lead-white series of painted metal rectangles (mean of 4 replicates, in which 19/ psyllids alighted on the most attractive of the 7 targets i.e. RA=1 on the surface containing 67 % lead-white in mixture with yellow) in relation to their diffuse reflectance spectra (d) and their colour parameter values: (a) human dominant wave= length (DW), reflectance (R), and purity (P); (b) aphid long/short ratio (L/S), and total energy (TE); and (c) the "RAS equation" (RAS) derived in Section 6.1. (For further details, see text).

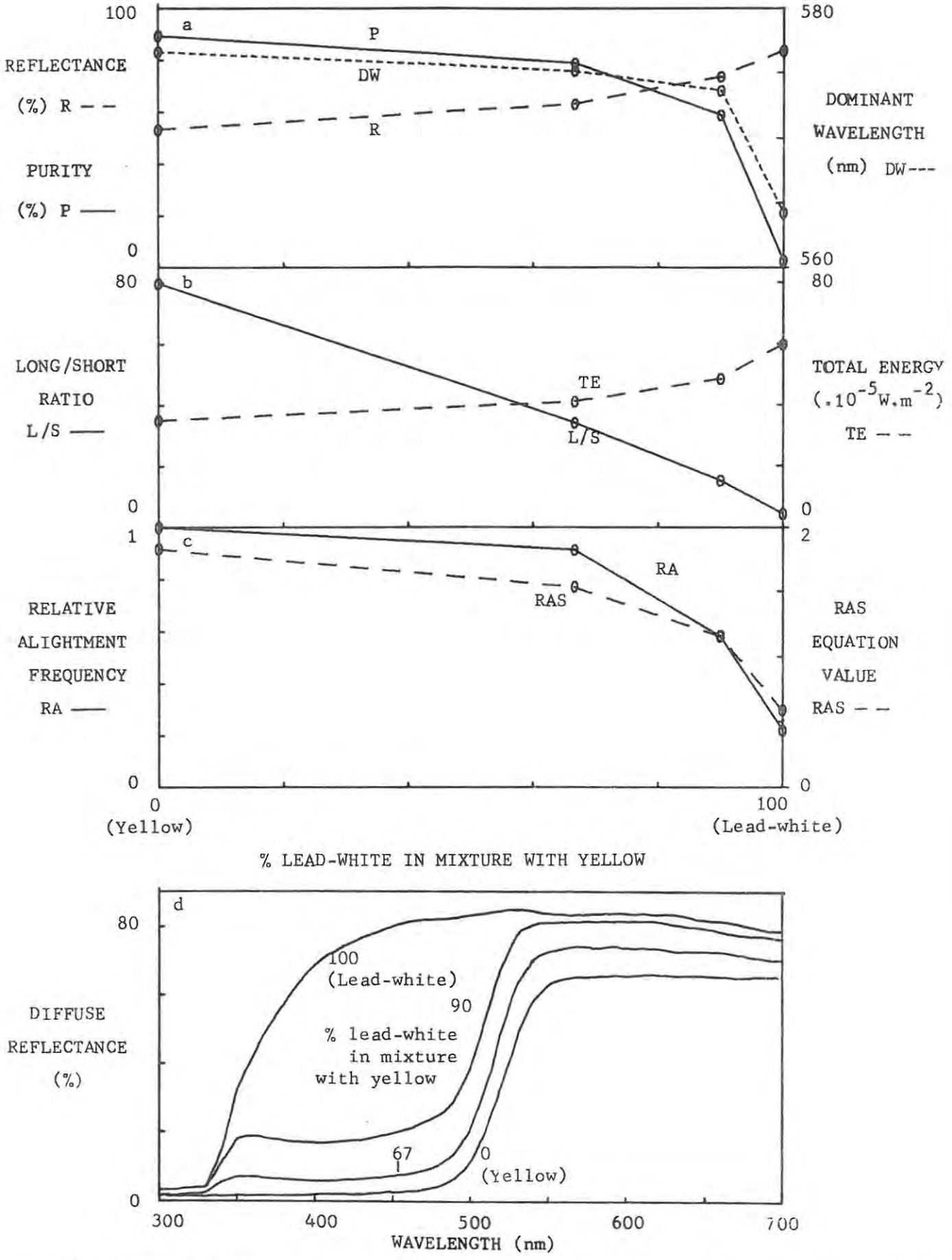

Fig. 15. (c): Relative alightment frequency (RA) of T.erytreae on a yellow to lead-white series of painted metal rectangles (mean of 2 replicates, in which 114 psyllids alighted on the most attractive of the 4 targets i.e. RA=1 on yellow), in relation to their diffuse reflectance spectra (d) and their colour parameter values: (a) human dominant wavelength (DW), reflectance (R), and purity (P); (b) aphid long/short ratio (L/S), and total energy (TE); and (c) the "RAS equation" (RAS) derived in Section 6.1. (For further details, see text).

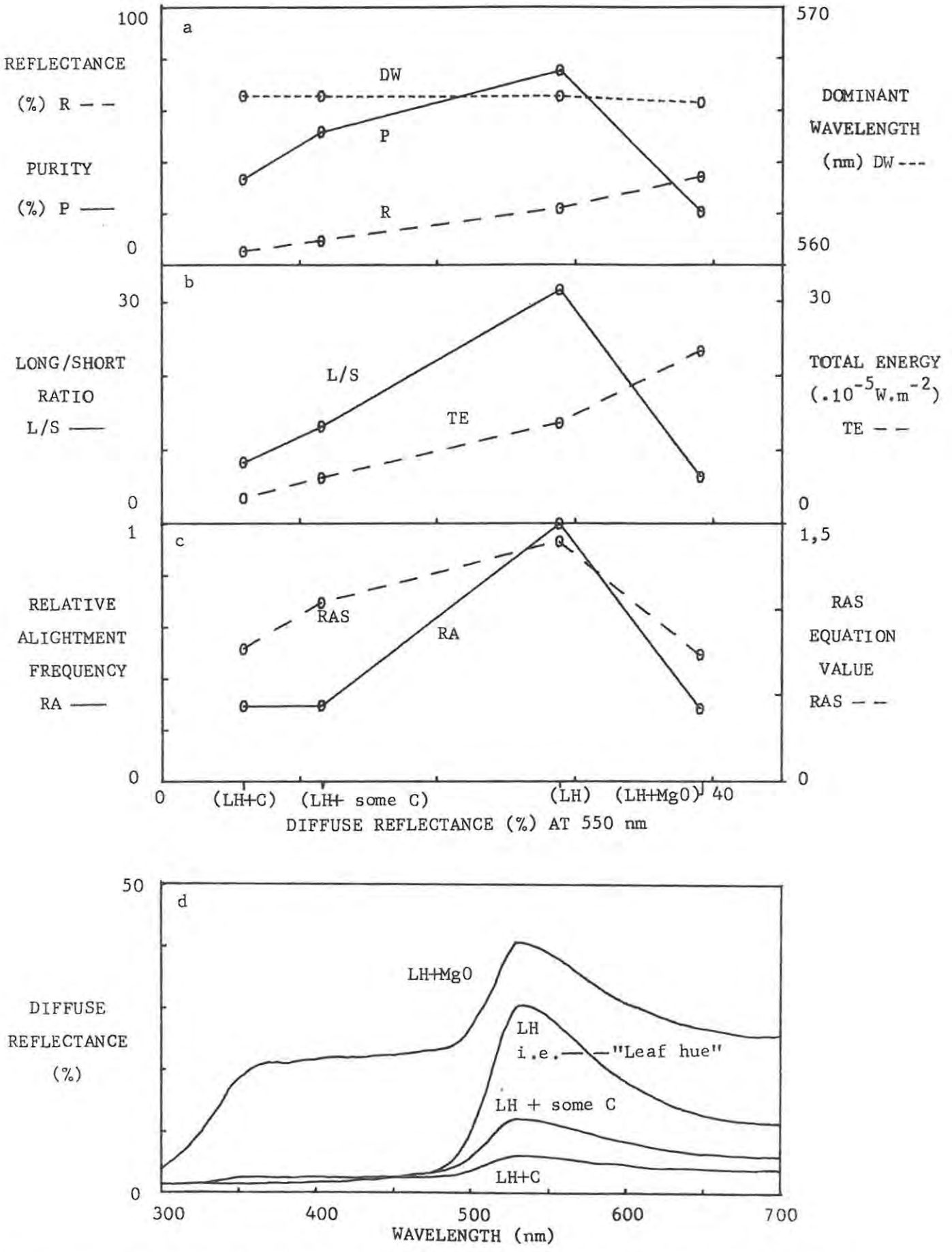

Fig. 16. (c): Relative alightment frequency (RA) of T.erytreae on a series of metal rectangles painted "leaf hue" (LH) (i.e. paint mixture 3 yellow: 1 green) and dusted with carbon black (C) or white megnesium oxide (MgO) (mean of 8 replicates, in which 565 psyllids alighted on the most attractive of the 4 targets i.e. RA=1 on the LH surface), in relation to their diffuse reflectance spectra (d) and their colour parameter values: (a) human dominant wavelength (DW), reflectance (R), and purity (P); (b) aphid long/short ratio (L/S), and total energy (TE); and (c) the "RAS equation" (RAS) derived in Section 6.1. (For further details, see text).

On a series of metal rectangles painted "leaf hue" (LH) (i.e. 3Y:1G) and then dusted either with increasing amounts of carbon black (C) or with white magnesium oxide (MgO), psyllid alightment frequency peaked on the pure leaf-hue surface (Fig. 16c). The increasing attraction when going from leaf-hue plus carbon to pure leaf-hue could (from the above results) be tentatively ascribed to the increasing amount of longwave energy (Fig. 16d), whilst the decreasing attraction when going from leaf-hue to leaf-hue plus magnesium oxide occurred, in spite of a further increase in alightment-stimulatory longwave energy, due probably to an increase in the amount of either repellent or alightment-inhibitory shortwave energy reflected. The alightment distribution was described fairly well by purity (Fig. 16a) (r^2 = 0,723), but best in this series by the long/short ratio (Fig. 16b) (r^2 = 0,944).

Correlations of psyllid alightment frequency with the values of the various colour parameters of the surfaces presented, are discussed at the end of this chapter, and are dealt with further in Section 6.2.

3.3 Effects of Ambient Light Intensity, Angle Subtended by Target, and Psyllid Sex, Age and Degree of Participation.

Effect of Ambient Light Intensity. Batches of 100 mature, adult T.erytreae of average age (see Materials and Methods (General) p.6) and sex ratio 1:1 were released midway between the choice of adhesive-coated yellow and green discs of 15° subtense (each 0,219 x 10^{-2} m^2 in area, presented at a distance of 0,20 m) in nine-hour test runs. Two replicates (of 2 runs each) were performed at each of 5 ambient light intensities. At the normal light intensities in the choice-chambers in environment rooms 1 and 2 (1,07 x 10^{12} and 3,61 x 10^{12} quanta.s^{-1}.mm^{-2} , i.e. L = 12,03 and 12,56 on the abscissa of Fig. 17) the yellow/green (Y/G) alightment ratio was about 3,3 (Fig. 17). Strength of colour preference depended significantly upon ambient light intensity (F test: $0,01 < p < 0,05$): with decreasing intensity (fewer fluorescent tubes) the colour preference dropped rapidly to the base line (Y/G = 1) at L = ca. 10,0 on Fig. 17, namely at an ambient light intensity of approximately $10^{10,0}$ quanta.s^{-1}.mm^{-2} .

Effect of Angle Subtended by Targets. The method was basically that of the previous sub-section (of 3.3) though psyllids were usually used here in batches of 200 (sometimes 100) per replicate. Four replicates were performed with each of 10 disc sizes, subtending angles ranging from 2,5° (0,006 x 10^{-2} m^2 discs) to 60° (4,184 x 10^{-2} m^2 discs, at a distance of 0,20 m on either side of the T.erytreae release point). Colour preference was constant for targets subtending 30° or more (Fig. 18) (upper and lower 95 % confidence limits for slope of linear regression: +0,14 and -0,20 i.e. slope did not differ significantly from zero). Colour preference decreased in proportion to decreasing angle subtended below 30° (F test on linear regression: $p < 0,001$). The colour preference was consistently statistically

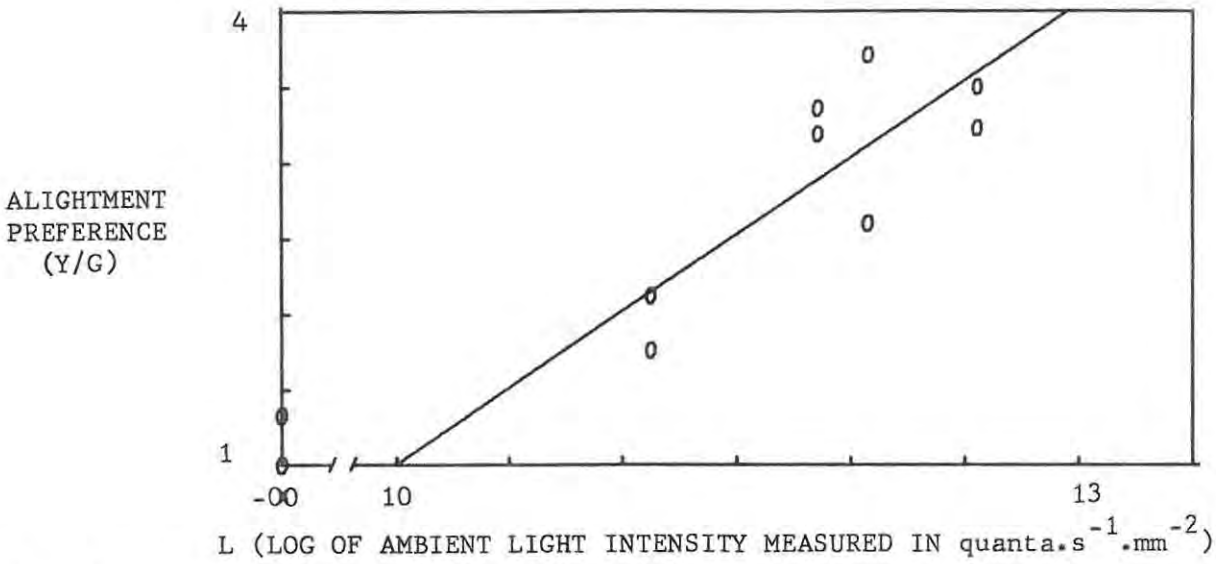

Fig. 17. Strength of T.erytreae's colour preference as a function of ambient light intensity. Yellow (Y) and green (G) discs each subtended an angle of 15 ^{o} with the psyllid release point. The 2 replicates in darkness could not be included in the linear regression. Each of the points included represents the net preference of an average of 92,6 psyllids that participated in a choice test by alighting on a coloured disc.

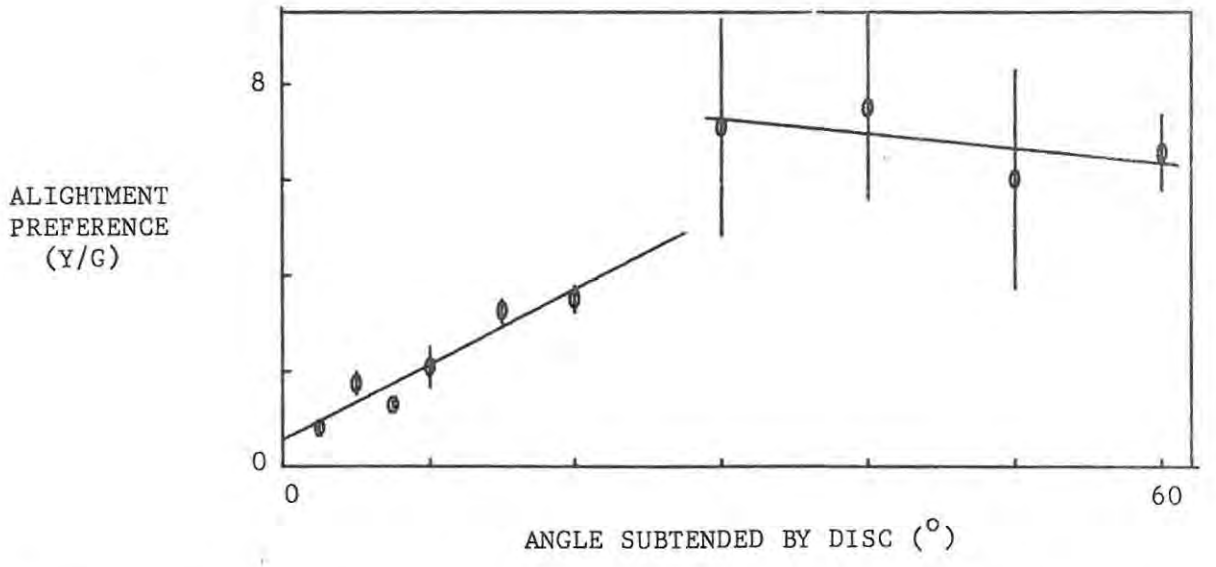

Fig. 18. Strength of T.erytreae's colour preference as a function of angle subtended by target. Yellow (Y) and green (G) discs of varying diameter were presented at 20 cm on either side of the psyllid release tube. Each point represents the mean, and the vertical bars ± 1 standard error, of 4 replicates. In the upper regression (targets subtending 30-60^{o}) the average number of psyllid participants per replicate was 107,7 ; in the lower regression this number decreased markedly with decreasing angle subtended below 15 ^{o}, from 99,0 at 15 ^{o} (57,4 % participation) to 8,5 at 2,5 ^{o} (4,3 % participation).

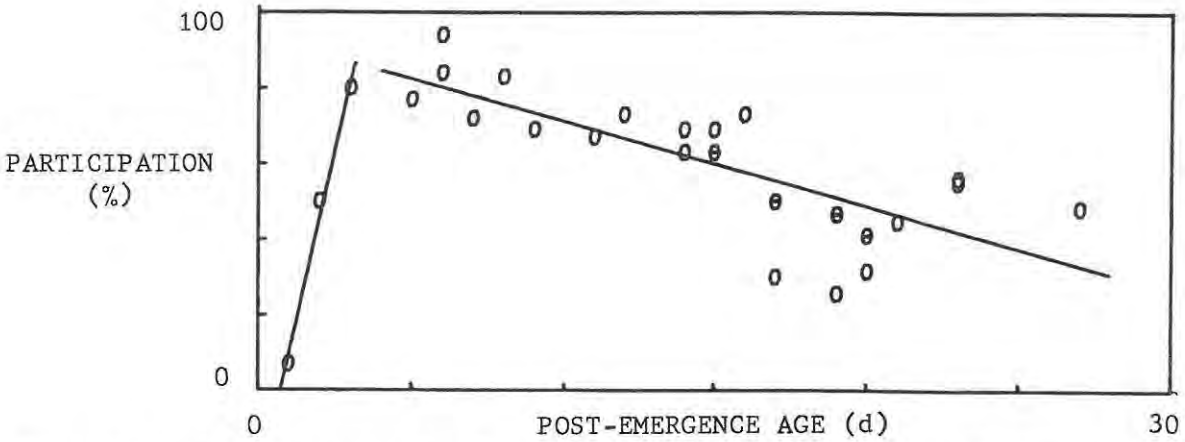

Fig. 19. Participation by T.erytreae (both sexes combined) in a colour choice experiment, as a function of post-emergence age. (Pairs of yellow and green discs, all of 30 ° or more subtense except the 4 marked differently (θ), were presented for 9 h in the choice-chamber at the normal lab 2 light intensity of $10^{12,56}$ quanta $.s^{-1}.mm^{-2}$, to batches of 100 or 200 psyllids of sex ratio 1:1). The regression lines are discussed in the text.

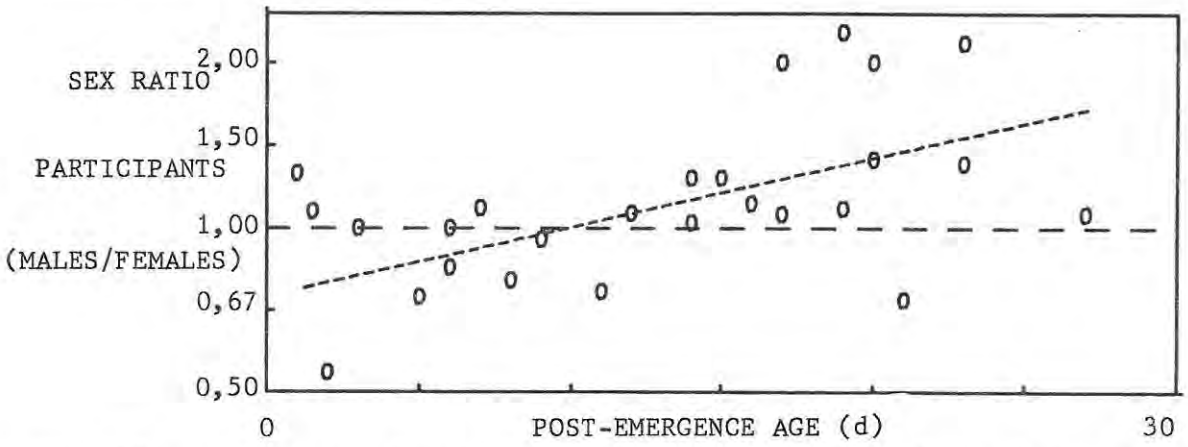

Fig. 20. Sex ratio of T.erytreae participants in a colour choice experiment, as a function of post-emergence age. (These data were obtained from the same experimental series as those of Fig. 19. For details of method, see legend of Fig. 19). The curve of Fig. 20 was fitted by eye because of the unequal scaling of the ordinate.

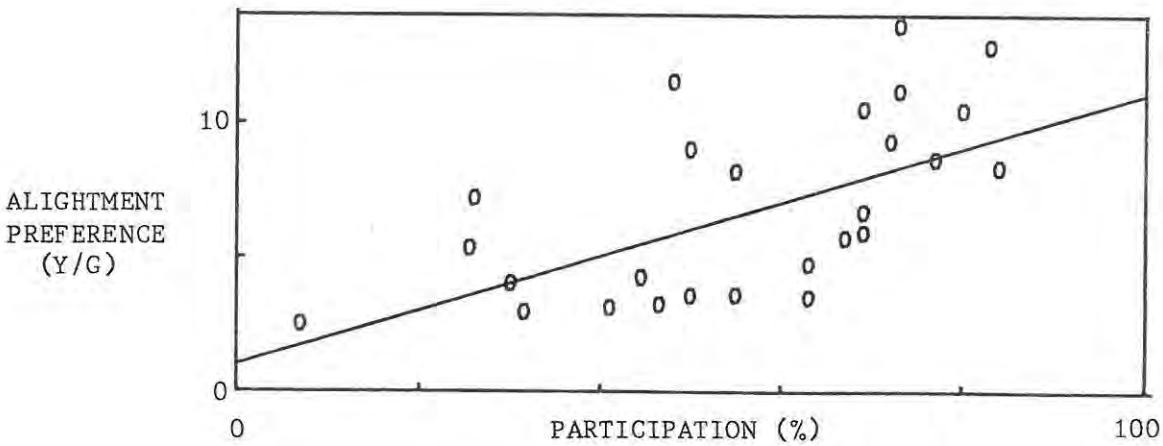

Fig. 21. Strength of T.erytreae's colour preference for a yellow (Y) rather than a green (G) disc, as a function of degree of participation in the experiment. (The data were obtained from the same experimental series as those of Figs 19 and 20. For details of method, see legend of Fig. 19). The regression is discussed in the text .

significant (by chi-square test) only when the angle subtended by the targets was 15 ^{o} or more. When the data were confined to the numbers of T.erytreae trapped on the edge and front side of the disc only, i.e. facing the psyllid release point, a similar result was obtained.

Effect of Psyllid Sex, Age and Degree of Participation. Sticky yellow and green discs of maximally attractive size (all 30 ^{o} or more subtense, except the 4 marked differently in Fig. 19) were presented at the normal light intensity in the choice-chamber in lab 2 to 26 batches of T.erytreae of varying known mean age. This provided the data for the following analysis, and for Figs 19 - 21.

Participation (i.e. flight from the release tube and alightment on a coloured target) rose very rapidly from a minimal level at 1 d to a maximal level at 3 d post-emergence age, then declined gradually over the next 24 d (Fig. 19, both sexes combined). The linear regression of the line of rising response with psyllid age in Fig. 19 described 90,5 to 98,6 % of the variation in participation by females and by males respectively ($r = 0,9513$ and $0,9931$), but the equation was not significant (F test: $p > 0,05$) because it was based on so few points. The linear regression of the line of declining response with psyllid age was highly significant for both sexes ($P \ll 0,01$), and 44 to 61 % of the variation in participation of males and females, respectively, could be ascribed to variation in psyllid age ($r = -0,6631$ and $-0,7807$). The implications of this finding are dealt with in the discussion.

Sex ratio of participating psyllids varied with age (Fig. 20), the linear regression being strongly significant (F test: $0,001 < p < 0,01$) although only 26 % of the variation in sex ratio could be ascribed to variation in age ($r = 0,5136$). (The line drawn on Fig. 20 was fitted by eye: a regression could not be plotted owing to the unequal scaling of the ordinate to give a more equal distribution to the scatter of ratios greater than and less than 1). Over the first 11 d, the females predominated among participants; after that, the males. This change-over was due to the fact that, compared with the males, the participation of the females rose at the same rate (same slope) but slightly sooner (higher intercept on the ordinate), reached a higher plateau level, and declined later and at a greater rate (greater negative slope). (The relevant regression data are not presented because this point is of peripheral interest).

Colour preference was not significantly related to psyllid age greater than 0,5 week (i.e. the "average" age of Materials and Methods (General) p.6) (the linear regression of the data of Figs 19-21 yielded $F = 2,1736$; $DF = 1$ & 21; $p > 0,10$; also upper and lower 95 % confidence limits of slope were $+0,0684$ and $-0,4014$ i.e. slope was not significantly different from zero) and only about 10 % ($r^2 = 0,0938$) of the variation in colour preference could be attributed to the variation in age of psyllids used.

Colour preference was proportional to degree of participation (Fig. 21), the linear regression being highly significant ($p<0,001$), and 38 % of the variation in colour preference could be ascribed to variation in participation ($r = 0,6155$). The implications of this finding are dealt with in the discussion.

Discussion (artificial surfaces).

Response variability: underlying factors, and their relevance. One theoretically possible cause of the observed colour preference variation, was the effect of angle subtended by the target. Colour preference was not related to size of targets of 30 ^{o} or more subtense (i.e. of greater than $0,90 \times 10^{-2}$ m^2 single side lamina area presented at 0,20 m from the psyllid release point) (Fig. 18). Because all the light green flush and dark green mature leaves presented at the same distance (0,20 m) in leaf choice tests (Chap. 2) fell within the size range $1,01 \times 10^{-2}$ to $2,72 \times 10^{-2}$ m^2, none of the observed leaf preference variation could be ascribed to variation in leaf size.

Below 30 ^{o} subtense, however, colour preference diminished with reduction in target size (Fig. 18) and became non-significant below 15 ^{o} subtense. Class A flush (required by T.erytreae for oviposition) is similar in colour to the visually-attractive Class B flush (Figs 6 and 7), but would (from Fig. 18) undoubtedly be comparatively difficult for psyllids to locate visually in the field (whilst in trivial flight near to the citrus tree canopy) owing to its small size. It seems likely, therefore, that in the case of flush shoots containing both A and B leaves, the large, light green Class B flush would be used as a visual "flare" in the process of locating the (Class A) oviposition site (as suggested above: p.26).

The skew distribution of participation (i.e. flight and alightment) against post-emergence age (Fig. 19) peaked (in both sexes) at 3 to 8 d . A basically parallel graph was obtained by Catling (1970) for the mean egg production of 5 T.erytreae, with a peak somewhat later, at 8 to 10 d . The sequence of flight and oviposition peaks in T.erytreae fitted Johnson's (1969) "oogenesis-flight syndrome" in which flight is considered to be mainly a pre-oviposition phenomenon in forms that migrate strongly.

Yellow trap catches of mature males but teneral females of the psyllid, Pauropsylla tricheata, lead Eastop (1961) to suggest that post-teneral females either rapidly autolyze their wing muscles or lose their response to yellow. From the results given in Section 3.3, it seems possible that Eastop's results may simply have been due to proximity of the traps to a source of newly-emerging adult psyllids, because females are more active than males as regards flight and alightment in the first few days after emergence (Fig. 20).

The significant decrease in colour preference with decrease in degree of participation (Fig. 21) provides a good explanation for the results of those red versus green flush choice replicates in which participation (and colour preference) was abnormally low (see Section 2.3).

Strength of colour preference depends about 40 % on degree of participation (Fig. 21), which, in turn, depends about 60 % on age (Fig. 19). This could be interpreted as meaning that about a quarter (because 40 % of 60 % = 24 %) of the large variation in strength of colour preference observed in experiments using adults of "average" age (noted e.g. in Section 2.2) could be attributed to variation in age of the test population. The direct regression (results given in Section 3.3) indicated that a slightly different amount, namely only about 10 % of the variation in colour preference could be ascribed to the variation in psyllid age. Consequently, even if age had been standardized as closely as possible, there would presumably still have been about 75 to 90 % as much variability in colour preference.

Major causes of the variability exhibited by T.erytreae in colour preference tests, therefore, remain to be established. Uncontrolled flight history is a possible cause of colour response variability. In flight chamber experiments with Aphis fabae, Kennedy & Ludlow (1974) demonstrated that duration of prior flight affected subsequent alightment responsiveness to a yellow target. Shortly after the start of migratory flight, exposure of a yellow target was commonly not attractive and sometimes even increased the rate of climb of A.fabae, whereas, with increasing duration of flight, the same yellow target elicited alightment increasingly strongly. Trioza erytreae were collected from plants housed in roughly cuboid cages of side length ca. 0,6 m, which permitted repeated short flights during the days of adult life prior to their use in colour choice experiments. Variation in average plant condition and in psyllid population density may have resulted in very varied frequency of flight in the cages prior to the collection of psyllids for experiments, and hence the variability in strength of their subsequent alightment colour preference.

"Yellow sensitivity". Alightment distributions on the printed spectrum and paint series with maxima on or very close to yellow (Figs 11, 12 & 15) indicated clearly that T.erytreae belongs to the "yellow sensitive" group of Homoptera, known to include numerous species of aphids (Das, 1918 p.190; Broadbent, 1948; Moericke, 1952), some aleyrodids (Lloyd, 1921; Mound, 1962) and some psyllids (Kaloostian & Yeomans, 1944, cited by Kaloostian & Wolf, 1968; Moericke, 1955b, 1957). Trioza erytreae's behaviour corroborates Moericke's (1955b, 1957) finding that psyllids generally are very highly responsive to yellow. The biological value to T.erytreae, of the alightment response to yellow, has already been discussed because it relates to leaves (Chap. 2). (It was considered both to enhance the chances of psyllid survival during the process of host plant location, and to directly enable flush location en route to the oviposition site).

Arrestment of walking T.erytreae over the yellow region of the printed spectrum (Section 3.1) is of considerable interest. Inhibition of locomotion as a result of stimulation of the ventral part of the eye by yellow light was also found by Moericke et al., (1966) in flying Trialeurodes vaporariorum. Depending upon the region of the eye (anterior or ventral) illuminated, therefore, a yellow light will either stimulate alightment and walking towards the stimulus, or will inhibit flight and walking once over the stimulus (respectively). This combination of responses will tend to bring homopterans to, and keep them on, yellow objects.

Basis of alightment colour preferences. As far as discovering which parameter of the light preflected from surfaces is responsible for the alightment colour preferences of T.erytreae, a little progress was made here. Negative regression coefficients of alightment frequency against a colour parameter appeared twice in each of the same two parameters (reflectance and total energy) on two paint series (Figs 13 & 15). The printed spectrum study (Section 3.1) had suggested that reflectance and/or total energy were important in the alightment stimulus for T.erytreae; the negative correlations did not entirely contradict this suggestion, but did demonstrate that neither reflectance alone nor total energy alone was the alightment stimulus.

Purity and long/short ratio were never negatively correlated with alightment, but the correlations (considered as the "goodness of fit" statistic, r^2) ranged very widely, from 0,323 to 0,956 (in the case of purity) and 0,539 to 0,995 (in the case of long/short ratio) on different colour choice series (Figs 11-16). One would expect a more consistent correlation from a causative parameter. Correlations of alightment frequency with any colour parameter might range as low as perhaps 60 % (i.e. $r^2 = 0,60$) on some test series, due to colour preference variation caused by uncontrolled and/or uncontrollable factors. The correlation of alightment frequency of T.erytreae both with purity and with long/short ratio fell below 60 % in 2 or 3 of 6 series of artificial surfaces presented (Figs 11, 13 & 14) which cast doubt on their possible causative character.

Of the colour parameters previously used in describing the alightment preferences of Homoptera, therefore, dominant wavelength alone had been ruled out in the study with red flush (Section 2.3), reflectance alone and total energy alone were ruled out here, and purity and long/short ratio both seemed rather unlikely to be the alightment stimulus of T.erytreae. The indications were that the homopteran alightment colour stimulus was imperfectly understood.

One consistent trend did emerge, however, from the examination of alightment distributions in relation to the diffuse reflectance spectra of series of surfaces presented. Increasing alightment response of T.erytreae was associated with increasing reflectance of apparently alightment-stimulatory longwave light (ca. 500 -

700 nm), and simultaneously with decreasing reflectance of apparently repellent or alightment-inhibitory shortwave light (ca. 400-500 nm) (Section 3.2) as in "yellow-sensitive" aphids (Moericke, 1952 *et seq.*). This suggested that alightment might be a response to long/short ratio (as proposed by Kennedy *et al.*, 1961), or, equally well, to long - short difference. The alightment response to reflected ultraviolet light (ca. 300-400 nm), however, remained unknown, because the choice-chamber environment contained virtually no UV light (Fig. 5). An indication was also obtained that the positive alightment response to longwave light in the choice-chamber in lab 1, only occurred above a threshold light intensity of approximately $10^{10,0}$ quanta.s^{-1}.mm^{-2} (Fig. 17).

The above preliminary indications were confirmed and extended in later studies using colour filters (Chap. 5). At this stage, however, it was evident that it was impossible to explain *T.erytreae*'s colour preferences properly, without fundamental information about the phototactic responses of this species to the individual physical (as opposed to physiological) parameters of coloured light. This information was gathered as described in the following two chapters.

4. PHOTOTACTIC (WALKING) RESPONSE TO MONOCHROMATIC LIGHT

Fundamental information was required firstly on the range of T.erytreae's visible spectrum, and the relative phototactic responsiveness of this species to different wavelengths at uniform intensity within this range. Such information is called a "spectral efficiency" curve or "action spectrum" (Burkhardt, 1964) (not to be confused with curves of "spectral sensitivity"). The relevant wavelength range included not only the human visible (which we see as different "hues" from blue at ca. 400 nm to red at ca. 700 nm) but also the near-ultraviolet (300-400 nm) to which all insects are also sensitive (Burkhardt, loc. cit.). The second important aspect was to determine how rate of phototaxis varies with physical intensity (physiological "brightness") of light at a fixed wavelength. The third topic investigated was whether or not there was any response to stimulus bandwidth, which is related to the human colour parameter, "purity".

Could the action spectrum of T.erytreae have been adequately inferred from previous work on related insects? The phototactic responses of homopterans to light of different colours had already been investigated by several workers, using gradually improving techniques and more thorough standardization.

The first technique was the use of coloured lamps. In two early studies (Kelsheimer, 1932, cited by Weiss, 1943; Gui, Porter & Prideaux, 1942) a comparison was made of the response of leafhoppers to coloured light bulbs which used electric energy at an equal rate (i.e. wattage). Attraction was greatest to ivory, followed by green, in the first study, and to white, followed by amber-orange, in the second, but nothing was known of the wavelength distributions or physical intensities of the stimuli presented. In three later studies, the relative strength of phototactic (flight plus alightment) response of 4 species of grain aphid (Coon, 1968), the pear psylla, Psylla pyricola (Kaloostian & Wolf, 1968), and the black bean aphid, Aphis fabae (Kring, 1969), was measured to choices of coloured fluorescent tubes of which the relative intensity was also measured (and the spectral emission recorded in the last case). Attraction was strongest to "blacklight" lamps (emission mainly 320-390 nm) and in proportion to their intensity and purity of UV emission, and was relatively weak to yellow in these studies with fluorescent lamps in contrast to the earlier studies (above) with incandescent lamps.

In the second technique, colour filters were used over light sources. Blue light was found to stimulate orientation activity in aphids more strongly than red light in one of the earliest studies (Loeb, 1890, 1893, 1905, cited by Gross, 1913) but the spectral characteristics and intensities of the lights used were unknown. A high degree of standardization was involved when the phototactic preferences of numerous insects, including 3 species of cicadellid, were investigated using a multi-choice apparatus containing a series of broad-band colour filters of known

wavelength transmission characteristics at uniform physical intensity (Weiss et al., 1941a,b). The most stimulating wavebands were always UV (around a peak at 365 nm) and blue-green (around 492 nm), but, unfortunately, no yellow-green or yellow filters (peak wavelength between 515 and 606 nm) were used in these earlier experiments. The yellow region was included in later choice experiments on the green peach aphid, Myzus persicae, and the bean aphid, Aphis fabae, using broad-band (Pospíšil, 1962, 1963) or narrow-band colour filters (Ždárek & Pospíšil, 1966a) over a fluorescent light, and on the pea aphid, Acyrthosiphon pisum, using coloured rubber membranes over feeding cells illuminated from behind (Cartier & Auclair, 1964). In these experiments, the spectral distribution and intensity of the colour stimuli were determined only approximately, but it was consistently found that the most attractive colour was that omitted in the experiments of Weiss et al. (loc. cit.) namely yellow or orange (of wavelength 500-600 nm according to Pospíšil, or of maximal spectral transmittance 595 or 615 nm according to Cartier & Auclair or 558 nm according to Ždárek & Pospíšil).

In the third technique, a greater degree of monochromacy of the stimulus was achieved. Moericke (1950) measured frequency of probing in a population of M.persicae as a function of wavelength, by dispersing sunlight into its component colours using a prism, and presenting each stimulus independently. Probing in Myzus was elicited by all wavelengths in the zone 490-660 nm, with a peak at about 550 nm in the yellow-green, and Moericke discovered that blue light (any wavelength in the zone 410-470 nm) was a complementary colour to yellow-green to the aphids (as evident from a "successive colour contrast" reaction, namely their probing on normally-unstimulating grey after exposure to blue light). Wavelengths in the UV were not included in Moericke's 1950 work. In more recent work (Macdowall, 1972) a monochromator was employed to determine an alightment action spectrum for the greenhouse whitefly, Trialeurodes vaporariorum. This instrument employed essentially the same principle as that used by Moericke (1950) and gave a similar peak of response to yellow-green; responses to wavelengths in the blue and UV were not reported, however, except that the response to UV (measured at only one wavelength: 350 nm) was found to be similar to the response to yellow-green light at 550 nm.

From the above survey of previous work on the action spectra of Homoptera, it was apparent that, whilst there were some mutually-confirmatory results (viz. strong positive response to UV and to yellow-green found by different workers), there were always gaps in the spectral range that should have been tested, as well as some mutually-contradictory results, namely reports of very strong and very weak responses to blue-green and to yellow light. It was clear that the phototactic action spectrum of T.erytreae could not have been adequately inferred from previous work, and therefore had to be determined here.

Materials and Methods (monochromator).

Phototactic responses of T.erytreae to the individual physical parameters of coloured light were determined using a Beckman DU monochromator. This instrument dispersed the light from a 12 V DC quartz-halogen source by means of a quartz prism, and threw the coloured beam out into clear space at one end of the machine which was convenient for irradiating the test insects and observing their response.

Before the instrument was used, a variety of calibrations was either checked or made. The calibration accuracy of two of the instrument's dials was checked as follows. One of 4 narrow-band interference filters was placed over the monochromator outlet aperture, and the wavelength-selection dial was adjusted to give maximum relative intensity sensed by a thermopile monitored by a galvanometer. Wavelength dial readings were all within 1 nm of the wavelength of peak transmission of the filter as measured using a spectrophotometer. Spectral bandwidths were measured at selected monochromator slitwidths using a Beck wavelength reversion spectroscope. The half-bandwidth per mm slitwidth measured at 4 points on the visible spectrum was within 2,5 nm of the manufacturer's specification (Beckman, 1963, e.g. 25,0 nm/mm at 550 nm) and the latter was, therefore accepted without modification.

Calibration of the instrument to deliver a fixed quantum flux at different wavelengths was done as follows. At each wavelength, the slitwidth was first adjusted to pass a standard spectral bandwidth of 15 nm : slitwidth varied from 1,852 mm at the UV end wavelength used, 310 nm , to 0,178 mm at the red end wavelength used, 675 nm . The monochromator was then moved forwards or backwards (along a specially-made set of rails) so as to irradiate a target of fixed size, 10 mm wide at the entrance to the phototaxis tube : distance from monochromator outlet flange to target varied from 199 mm at 310 nm to 268 mm at 675 nm . An RCA IP22 photomultiplier operated at 1,2 kV , was placed in the light beam, and the relative magnitude of the current caused by the light was monitored using a galvanometer. Figure 22a is a general view of the calibration set-up. The expected galvanometer deflection due to a fixed quantum flux at each wavelength employed, was calculated using the fact that the galvanometer deflection is a linear function of photomultiplier current (Sears & Zemansky, 1960) which itself is a linear function of radiation intensity (Seliger & McElroy, 1965) after taking into account the photomultiplier's almost parabolic (S8-type) spectral sensitivity curve (RCA, 1962). To obtain the calculated galvanometer deflection at each wavelength, the source intensity was adjusted, using a rheostat, to a suitable voltage: voltage varied from 13,00 V at 310 nm to 2,80 V at 675 nm . Changing from one wavelength to another during experiments at fixed quantum flux was then simply a matter of selecting the wavelength and adjusting the slitwidth, distance and voltage to the calibrated values.

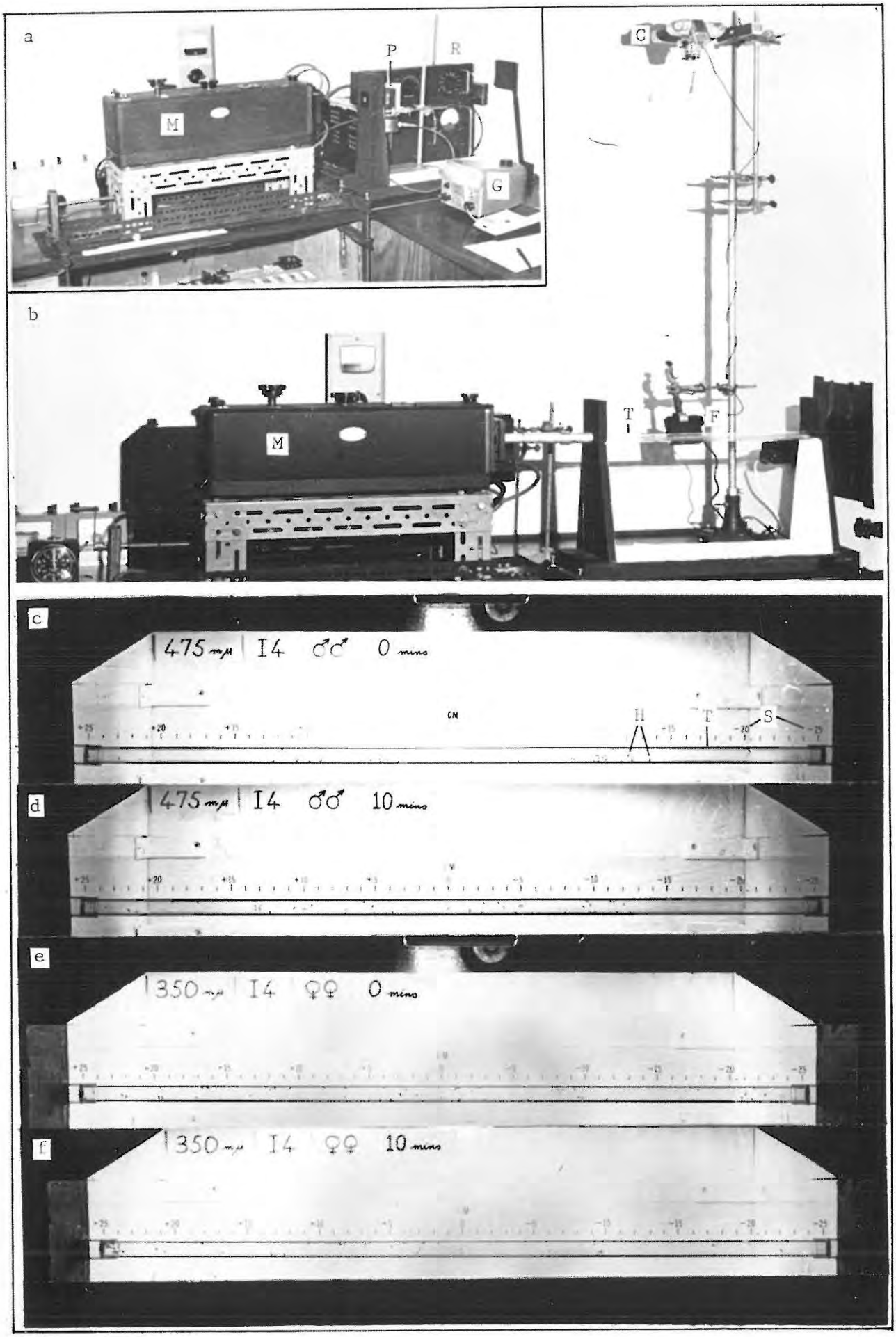

Fig. 22. Monochromator (M) set-up, (a): during calibration with photomultiplier (P), showing rectifier and transformer (R), and galvanometer (G); (b): during phototaxis measurement, showing phototaxis tube (T), camera (C), and flash unit (F). Examples of phototaxis records showing T.erytreae (H) as dots in phototaxis tube (T) resting on a glass plate calibrated in centimetres (S):- (c) and (d): little net movement, during 10 min exposure, towards light of wavelength 475 nm entering tube at the + i.e. left-hand end; (e) and (f): positive phototactic response to UV light (350 nm).

Intensities were determined in absolute terms using the thermopile plus microvoltmeter technique (described in Materials and Methods (General) p.7). The light intensity used for the action spectrum was effectively sub-threshold for the thermopile (owing to the high "zero" reading due to the intensity of the infrared background) which necessitated measuring the quantum flux at a higher light intensity, and relating that to the action spectrum light intensity using the photomultiplier.

For experiments, the source was enclosed in a light-tight box through which compressed air was passed for cooling purposes. All experiments were conducted in the dark in a temperature-controlled photographic darkroom at 25 °C (range 24-26 °C). Fifty psyllids of 1 sex were collected from the culture in a 500 mm long, 10 mm diameter glass tube with gauze ends. They were dark-adapted (and starved) for 1 h prior to a test. The tube was then positioned on a calibrated glass plate along the axis of the monochromator light beam, and flash-photographed at the start and end of the 10- min replicate. Figure 22b is a general view of the experimental set-up. The photographs (examples shown in Fig. 22c-f) were examined under a binocular microscope, and the position of each psyllid was read off the scale alongside the phototaxis tube and recorded. The response to each stimulus was tested in 4 replicates: 1 replicate using 50 psyllids of each sex was performed in the morning and in the afternoon. Population phototaxis to each stimulus was calculated as the mean response of 200 different psyllids, i.e. their mean position at time 10 min minus their mean position at time 0 min .

Response to wavelength was measured at 310 nm and in 25-nm steps from 325 nm to 675 nm (i.e. at a total of 16 wavelengths). Spectral bandwidth was kept constant at 15 nm , and intensity at $10^{9,54}$ quanta.s^{-1}.mm^{-2} . Response to intensity was measured at 10 intensities at fixed wavelength of 550 nm , and fixed bandwidth of 15 nm except in high-intensity experiments in which the monochromator was replaced by a 500 W slide projector and a narrow-band interference filter (which had maximum transmittance at 550 nm) of half-height bandwidth 23 nm . Response to bandwidth was measured at 5 bandwidths at a fixed central wavelength of 512,5 nm and fixed intensity of $10^{10,09}$ quanta.s^{-1}.mm^{-2} .

Using the above techniques it was possible to accurately control wavelength, intensity and bandwidth of the standard-size coloured target presented to T.erytreae in the phototaxis tube, and therefore to determine their response to each of the individual physical parameters, wavelength, intensity and bandwidth.

4.1 Wavelength.

Mean population phototaxis of T.erytreae (in mm) at each wavelength is recorded in Fig. 23a. (The whole of Fig. 23 will be discussed once the derivation of Fig.23b has been dealt with).

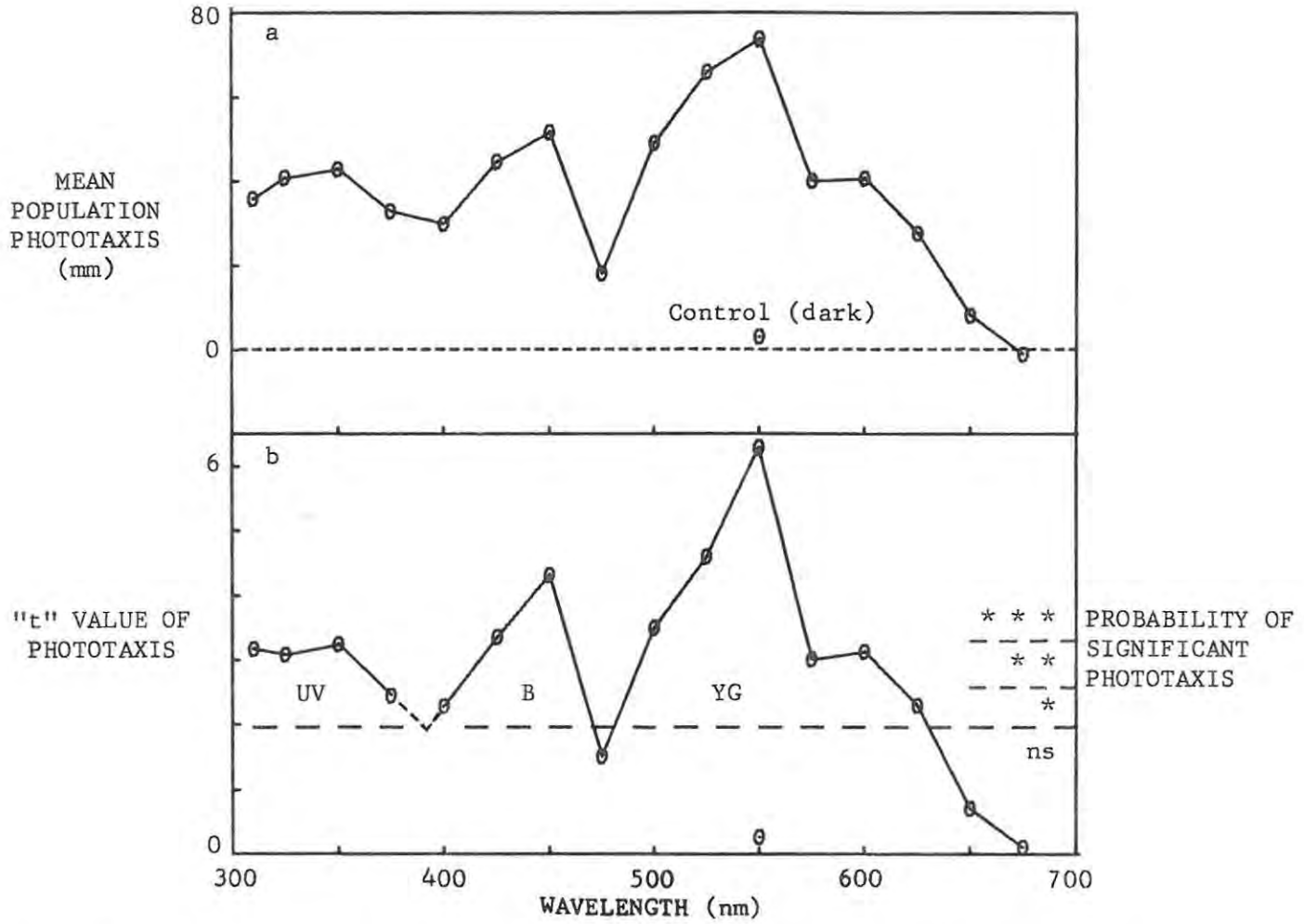

Fig. 23. Phototactic action spectrum of T.erytreae to different wavelengths at constant intensity ($10^{9,54}$ quanta.s^{-1}.mm^{-2}) and constant purity (spectral bandwidth 15 nm). (a): Mean population phototaxis in 10 min . 200 different psyllids were tested at each wavelength, 50 in each of 4 replicates. (b): Student's "t" test value of the statistical significance of the difference between the mean position of the psyllids at time 10 min and that at time 0 min . Not significant ($p \geqslant 0,05$) ns; significant ($0,01 < p < 0,05$) *; strongly significant ($0,001 < p < 0,01$)**; highly significant ($p < 0,001$) ***. Phototaxis was strongly significant in 3 regions of the spectrum: yellow-green (YG), blue (B) and ultraviolet (UV).

Statistical analysis was considered necessary because phototaxis was extremely variable in different replicates at any given wavelength. The reality of phototaxis at each wavelength was evaluated by a 't'- test of the significance of the difference between the mean psyllid position at time 0 and that at time 10 min . Before the 't' test was applied, its assumptions of normality of distribution and homogeneity of variance were investigated using the results at 500 nm as a test case. Distribution was not significantly skewed at time 0 min ($p > 0,5$), but was very slightly skewed to the left at time 10 min ($0,025 < p < 0,05$). At both times, the distribution was leptokurtic (i.e. peaked) ($p \ll 0,001$). The data were not transformed, however, on the grounds of Sokal & Rohlf's (1969 p.377) statement that: "The consequences of nonnormality of error are not too serious. Only very skewed distribution would have a marked affect on the significance level of the F test ...", which applies to the present situation because the "t test is ... merely ... a special case of the analysis of variance." The 0- and 10- min variances were apparently homogeneous by the F-ratio test ($0,10 < p < 0,05$) (Rohlf & Sokal, 1969), but heterogeneous by the chi-square evaluation of Bartlett's test. Evidently, the samples were on the borderline between homo- and hetero-scedasticity. Sokal & Rohlf (1969) provide an "approximate t-test" for treating 2 samples of unequal variance. Because of the large number of individuals (200) in each of the present samples, however, both the relevant expression and the degrees of freedom were unchanged from those of the usual t-test. Application of the t-test to the data of the phototaxis experiments was, therefore, valid.

The 't' values (Fig. 23b) supported and refined the general picture of the relative strengths of phototactic response of T.erytreae to different wavelengths (Fig. 23a). Additional 't' tests of lumped results indicated that the observed variability was not contributed to markedly by the different overall responsiveness ($0,025 < p < 0,05$) of the segregated sexes (mean phototaxis 32,5 and 43,3 mm), but undoubtedly was by the greater responsiveness of psyllids ($p \ll 0,001$) in the afternoon replicates than in the morning (58,1 compared with 18,8 mm mean movement).

The phototactic action spectrum (Fig. 23) yielded the following information. Trioza erytreae's visible spectrum was found to extend from probably slightly below 300 nm in the UV to about 670 nm in the red. Phototaxis was always positive, i.e. no wavelength was repellent; phototaxis at 675 nm appeared at first glance to be negative but the amount of movement was completely non-significant ($p \gg 0,5$). Within its visible spectrum, T.erytreae displayed 3 peaks of phototactic response of which the probability of significance was above the 99 % level (**): the main peak in the yellow-green at ca. 550 nm (range 480-630 nm), and secondary peaks in the blue at ca. 450 nm (range ca. 395-470 nm) and the UV at ca. 350 nm (range ca. 300-395 nm). The main peak had a shoulder in the red at 600 nm. Phototaxis was not significant ($p > 0,05$) on the far-red side of the yellow-green response peak (i.e. at wavelengths

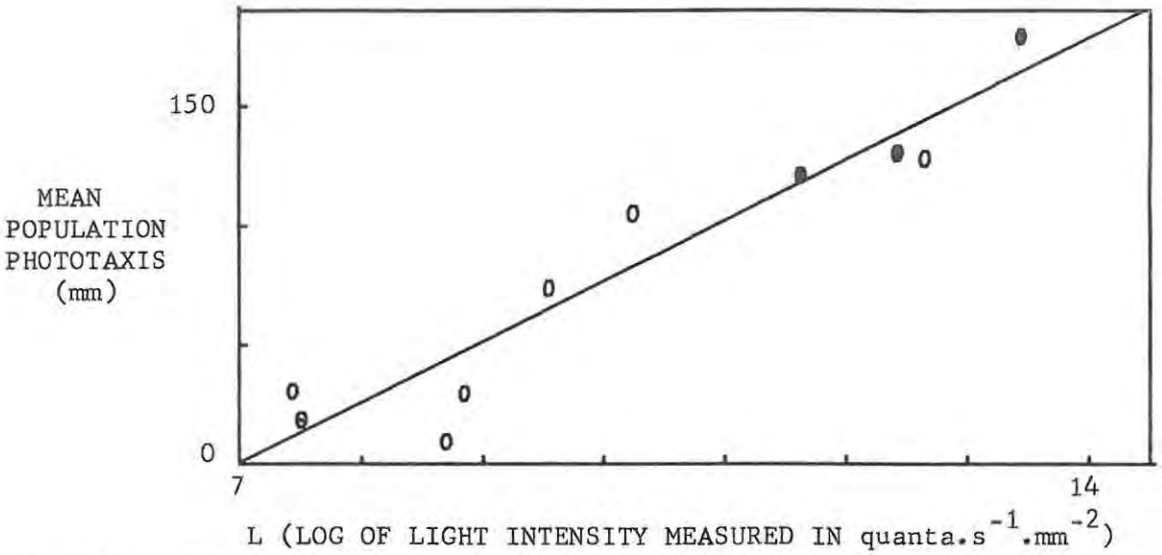

Fig. 24. Strength of phototactic response of T.erytreae as a function of stimulus intensity at constant wavelength (550 nm) and nearly constant bandwidth (15 nm in the case of the monochromator; 46 nm when using a narrow-band interference filter at the 4 highest intensities). Each point is the mean phototaxis in 10 min of a population of usually 200 different psyllids (except points at which 400 (⊕) or 100 (⊖) psyllids were used), tested in groups of 50 per replicate. Coefficient of determination of linear regression: r^2=0,903 .

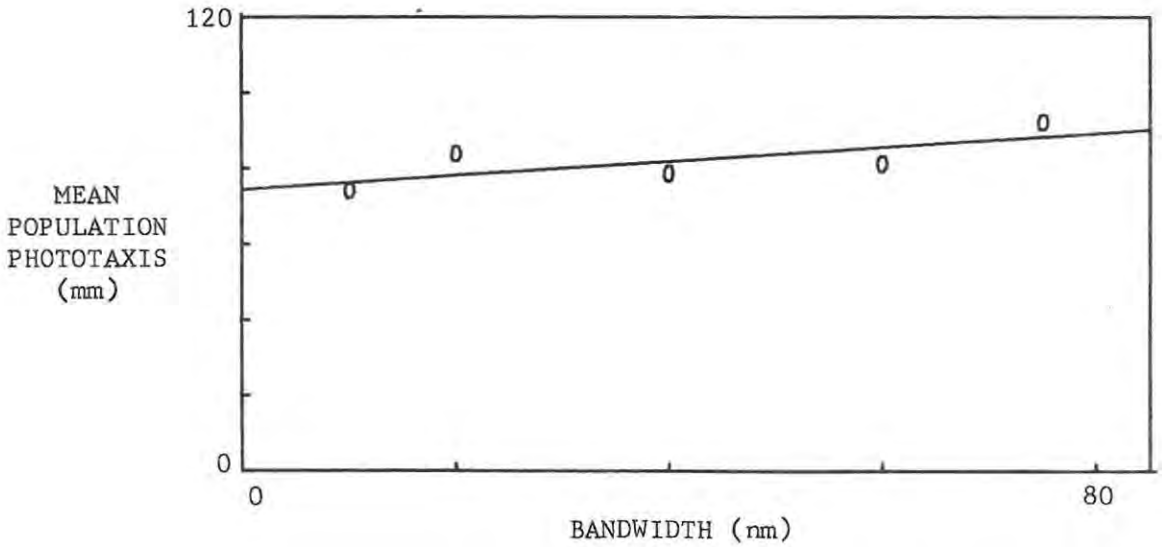

Fig. 25. Strength of phototactic response of T.erytreae as a function of spectral bandwidth of stimulus, at constant wavelength (512,5 nm) and constant intensity ($10^{10,09}$ quanta.s^{-1}.mm^{-2}). Each point is the mean phototaxis in 10 min of a population of 200 different psyllids, tested in groups of 50 per replicate. Slope of linear regression was not significantly different from zero (0,25>p>0,10).

above 630 nm), between the yellow-green and the blue response peaks (470-480 nm), and possibly also between the blue and the UV response peaks (at ca. 395 nm).

Teneral adults of 2 d post-emergence age were tested at wavelengths 350 , 450 and 550 nm . Mean population phototaxis was not significant ($p > 0,10$) to UV or to blue; the response to yellow-green was significant ($0,001 < p < 0,005$) although only about half as strong as that of mature adults of average age.

4.2 Intensity.

At constant wavelength (550 nm) and nearly-constant bandwidth (15 nm with the monochromator and ca. 46 nm with the narrow-band interference filter), the rate of phototaxis of T.erytreae was proportional to the logarithm of the light intensity (Fig. 24). Ninety percent of the variation in phototaxis was accounted for by the linear regression of phototaxis against log of quantum flux ($r^2 = 0,903$). This relationship held good over 6 orders of magnitude. The phototaxis threshold of flash-photographed dark-adapted psyllids to yellow-green light was ca. $10^{7,0}$ quanta.s^{-1}.mm^{-2} under the experimental conditions.

4.3 Bandwidth.

Spectral bands centred at 512,5 nm were used because the action spectrum was approximately linear in this region (Fig. 23). At constant intensity of $10^{10,09}$ quanta.s^{-1}.mm^{-2} , there was no correlation between phototaxis and bandwidth over the range of bandwidths tested: 10-75 nm (Fig. 25). The slope of the linear regression was not significantly different from zero (95 %upper and lower confidence limits about the slope were +0,049 and -0,012). The use of 2 different bandwidths within this range, therefore, could not have influenced the result of the intensity experiment (Fig. 24).

Discussion (monochromator).

The peak in the yellow-green of the phototactic action spectrum of T.erytreae as measured by walking (Fig. 23) was very similar to that of the green peach aphid, Myzus persicae, as measured by probing or alightment (Moericke, 1950, 1952) and to that of the greenhouse whitefly, Trialeurodes vaporariorum, as measured by alightment. Peak responsiveness of T.erytreae to light of wavelength 550 nm coincided with peak reflectance of leaves in the insect-visible range, namely 555 nm (Figs 7 & 8): positive phototaxis, alightment and probing in response to leaf colour are excellent adaptations for a phytophagous life, as has been noted for other Homoptera by Lloyd (1921), Weber (1930), Butler (1938), Moericke (1952), Pospíšil (1963), Macdowall (1972), and Vaishampayan et al. (1975a).

The shoulder in the red at 600 nm on the phototactic action spectrum of Trioza

erytreae (Fig. 23), was remarkably similar to that of Trialeurodes vaporariorum (measured by Macdowall, 1972). A colorimetric investigation performed by Macdowall demonstrated that this shoulder belonged to the same receptor as the response peak in the yellow-green. Increased response at and above 600 nm in both these cases was presumably a "pseudopeak" due to increased transmission of red light by a red screening pigment, as Goldsmith (1965) demonstrated to be the case in flies. This hypothesis is supported by Moericke's (1950) results which show a consistent "Purkinje shift" (in the peak response of Myzus persicae) towards longer wavelengths at higher light intensities.

In the infrared (IR) region (above 700 nm), the reflectance of citrus leaves is vastly more than in the visible region (Hart & Myers, 1968) (as is the case with leaves in general (Woolley, 1971)), and the IR reflectance changes with new flushes of citrus growth (Hart et al., 1973). In spite of the claim that some insects can optically perceive IR, and perhaps use this ability in host plant location (Callahan, 1965), it seems unlikely that the citrus psylla could respond to the IR reflectance of citrus leaves, and so locate the flush, because of the complete cut-off of the phototactic response of T.erytreae below 700 nm (Fig. 23). This is supported by the finding that no phototactic response could be elicited in Aphis fabae by IR light (wavelength 800 nm) (Ždárek & Pospíšil, 1966a).

The response peak of T.erytreae in the blue (Fig. 23) (shown by walking) was in that portion of the spectrum which is complementary to yellow for probing in M.persicae (Moericke, 1950) and which is also more effective than yellow in stimulating take-off in that species (Darst, 1972). The peak of phototaxis in T.erytreae to light of wavelength 450 nm coincided with peak radiation intensity of the blue sky, namely ca. 455 nm ,(Viaud, 1948, cited by Autrum & von Zwehl, 1962; Grum, 1972): take-off and flight in response to sky colour (though this has not been demonstrated in T.erytreae) would be interpreted by Johnson (1969) as evidence of excellent "adaptive behaviour at exodus" for aerial dispersal.

The phototaxis peak of T.erytreae in the UV (Fig. 23) corroborates the finding of Weiss et al. (1941b), Kaloostian & Wolf (1968), Macdowall (1972), and Vaishampayan et al. (1975a) that Homoptera (cicadellids, a psyllid and an aleyrodid) are strongly phototactically responsive to UV, in common with all insects studied (various authors cited by Goldsmith, 1961, and Mazokhin-Porshnyakov, 1969). Ultraviolet sensitivity enhances visual contrasts for bumble-bees (Kugler, 1947) and was found to enhance the alightment response of the citrus psylla to the yellow-green colour of leaves (demonstrated in the following chapter, Section 5.3).

Goldsmith (1961) expressed the opinion that "... it is also important to ask why, in terms of animal behavior and evolutionary history, particular sensory systems exist." It must be mentioned at this point that the 3 response peaks in the photo-

tactic action spectrum of T.erytreae (Fig. 23) are due to 3 independent receptor systems, though the experimental evidence is only dealt with in the following chapter (5). Unlike the leaf-green and sky-blue receptor systems of T.erytreae, which are remarkably closely attuned to the wavelengths of prominent photic stimuli in the environment that elicit alightment for feeding and presumably flight for dispersal, respectively, it was not at all obvious what (if any) feature of the photic environment could have merited the selection of a receptor system sensitive to UV in the citrus psylla and other insects.

The raison d'être (i.e. the original cause of the existence) of insect sensitivity to UV is a philosophical enigma that has intrigued insect visual physiologists. Mazokhin-Porshnyakov (1969) considered that the sensitivity and responsiveness of insects to UV has apparently evolved because "UV radiation delivers the most typical indication of open space", but the relative emission of UV (300-400 nm) is only one-third that of blue (400-500 nm) in blue sky, as measured from the figure of Viaud reproduced by Autrum & von Zwehl (1962) who concluded that the blue receptor system of the honey-bee is far better adapted than the UV receptor system to the colour of the sky. Chernyshev (1959) suggested that insect vision in the UV is "connected with their organization", presumably meaning that it is a faculty of compound rather than vertebrate-type eyes, but Goldsmith (1961, citing Wald, 1949, 1952) pointed out that the only reason why vertebrates do not see UV light is the UV-absorption of the vertebrate lens which "was probably introduced ... to relieve chromatic aberration, a problem which is not met in compound eyes." Whilst this may be true, it does not answer the question of why insects should have acquired pigments sensitive to UV in the first place.

> For the reasons discussed below, the following hypothesis seems plausible:
> Visual sensitivity to UV light is a physiological endowment that was selected for as a contrast-enhancing mechanism in ancestral marine arthropods.

The importance of visual contrast-enhancement to arthropods is evident from the fact that it has merited the selection of the following 3 independent mechanisms to that end: (i) lateral inhibition, which accentuates contrast at borders between light and dark areas in the visual field (Hartline, Ratliff & Miller, 1961); (ii) polarization sensitivity, which enhances contrast between solid natural objects (from which the reflected light is almost, though not completely, non-polarized (Woolley, 1971; Clay, 1973)) and the environmental light (which is markedly polarized both in the case of skylight (Stockhammer, 1959, cited by von Frisch, 1967) and underwater spacelight (Lythgoe, 1972)); (iii) colour vision, which produces visual contrast between objects of different spectral absorbance.

In addition to all insects studied (as noted above), UV-sensitivity has been demonstrated in the xiphosuran (horse-shoe "crab"), Limulus, (Chapman & Lall, 1967), true arachnids including scorpions, mites (Goldsmith, 1972) and spiders (e.g. De Voe, 1975), and some crustaceans including a marine and a fresh-water species of prawn (Goldsmith & Fernandez, 1968a) and many cladocerans (various workers cited by Waterman, 1961). Most of these arthropods have also been shown to sense the direction of plane polarized light (numerous authors cited by von Frisch, 1967) and to have the capacity for colour vision (authors cited above). Because of the widespread nature of its occurrence in extant arthropods, it is reasonable to postulate that UV-sensitivity arose in their ancestral stock.

Of relevance here is the conclusion that "the transformation of the primitive creeping polychaetes to the first arthropods occurred in ancient Pre-Cambrian seas" (Sharov, 1966). Extant animals possess visual pigments that are closely adapted to the major wavelengths of their photic environment (as concluded in reviews by Denton, 1960; Goldsmith, 1972; Lythgoe, 1972). Downwelling irradiance in marine water peaks at a wavelength of about 475 nm in the blue, and becomes increasingly monochromatic with increasing depth; as a result, deep-sea fish and crustacea have little alternative but to have visual pigments which peak in sensitivity at about 475 nm , and this has been confirmed experimentally (various workers cited by Lythgoe, 1972). The ancestral arthropods had well-developed compound and/or simple eyes, as is evident in fossil Proboscifera, Trilobitomorpha, Chelicerata and Crustacea from the Cambrian, and Eurypterida from the Ordovician (Sharov, 1966), and it is reasonable to suppose that their visual pigments were adapted to utilizing available light in that part of the Cambrian or Ordovician ocean in which they dwelt.

The low degree of absorption of the lethal (200-300 nm) part of solar near-UV radiation by atmospheric ozone in Pre-cambrian times would have forced animals to live at depths below about 10 m in the ocean (Berkner & Marshall, 1965, cited by Smart & Hughes, 1973). The amount of less-harmful (300-400 nm) near-UV radiation at a depth of 50 m in the open sea is physiologically useful now and was even more so in ancestral times: its intensity at a wavelength of 350 nm is about one-tenth that of the blue (Lythgoe, 1972). The light is still polarized at a depth of at least 200 m in the sea, and suspended particles disturb polarization less in the UV than at longer wavelengths (various authors cited by von Frisch, 1967). The UV receptors are essential for polarization sensitivity in the desert ant (Duelli & Wehner, 1973) and are the sole polarization detectors in the honey-bee (von Helversen & Edrich, 1974). In the development of contrast-enhancing mechanisms based on colour and/or polarization sensitivity, the ancestral arthropods would have made use of randomly-evolving visual pigments centred on the predominant blue waveband of their photic environment, namely pigments absorbing in the blue itself, and others absorbing on the longwave side of blue, namely in the green, and on the shortwave

side of blue, namely in the near-UV. This is put forward as an hypothesis for the original selection of arthropod sensitivity to UV light.

Spectral positions of the 3 phototactic response maxima of T.erytreae (namely in the UV, blue or blue-violet, and yellow-green (Fig. 23)) were the same as those of the 3 populations of retinal units suggested by phototactic intensity discrimination experiments in one species of crustacea, the clodoceran, Daphnia, (Heberdey, 1949, cited by Waterman, 1961). Similarities between the division of the spectrum in Homoptera and in Daphnia have been noted previously (Koehler, 1924, cited by Moericke, 1950; Smith & Baylor, 1953, cited by Kennedy et al., 1961). The actual wavelengths of the 3 spectral response maxima of T.erytreae (viz. ca. 350, 450 and 550 nm , Fig. 23) were remarkably close to the wavelengths of sensitivity maxima of all 3 retinula cell types in two species of insect, namely the drone of the honeybee, Apis mellifera (and possibly also in the worker, if the 430 and 460 nm receptors are considered as effectively one type) (Autrum & Thomas, 1973), and in a heteropteran, the backswimmer, Notonecta glauca (Bruckmoser, 1968). The possibility that T.erytreae might also have a trichromatic visual system was investigated further as described in the following chapter (5).

Relative heights of the action spectrum peaks (Fig. 23) were very approximately proportional to the relative intensities of those wavelength regions in the psyllid culture light (Fig. 3). The dominance of the yellow-green peak in particular, therefore, could conceivably be the result of adaptation to the lab light, just as well as to a conditioned association of the colour yellow-green (reflected from or transmitted through leaves) with food availability, or to a preponderance of yellow-green receptors (as in Apis (Autrum & von Zwehl, 1964) and in Notonecta (Bruckmoser, 1968)), or to weighting in neural integration.

Response to intensity. Phototaxis of T.erytreae increased as a linear function of the logarithm of the stimulus intensity (Fig. 24). A relationship of this kind is typical of the amplitude of the electroretinogram of single visual cells as seen in species of Hymenoptera, Orthoptera and Hemiptera (Autrum & von Zwehl, 1964; Bennett, Tunstall & Horridge, 1967; Bruckmoser, 1968). A linear versus logarithmic relationship is also seen in the alightment frequency of the greenhouse whitefly when Macdowall's (1972) "hyperbolic" data are re-plotted on a log intensity scale (r^2 = 0,886). This corroborates Burkhardt's (1964) statement that the subjective "brightness" of light of any given wavelength, as measured behaviourally by an animal's reaction, normally increases with physical intensity of the stimulus and the relationship is logarithmic. It furthermore suggests that the whole organism, or population, behaves in this way due ultimately to the nature of the receptors' response.

Extrapolation of the linear regression in Fig. 24, indicated a threshold intensity of about $10^{7,0}$ quanta.s^{-1}.mm^{-2} for T.erytreae under the experimental conditions.

Thresholds are markedly affected by the state of light- or dark-adaptation, and the conditions used here were 1 h dark-adaptation followed by a flash photograph at the start of a phototaxis test. Goldsmith (1964) states that the rate of dark-adaptation depends on the duration of the previous light-adaptation. In view of the speed of dark-adaptation, e.g. the electroretinogram threshold of Periplaneta ocellus dropped 4 or more orders of magnitude after only 1 min in the dark following 2 min of bright light-adaptation (Ruck, 1958), and the fact that the electronic flash, though of high intensity, was only of about 0,001 s duration (Karsten, 1968), it seems reasonable to assume that the response threshold determined in T.erytreae refers to the dark-adapted state. This is supported by the fact that the threshold of phototactic response to yellow-green stimuli was 3 orders of magnitude lower here than in the choice experiments in lab 1 (i.e. ca. $10^{7,0}$ in Fig. 24, as against ca. $10^{10,0}$ quanta.s^{-1}.mm^{-2} in Fig. 17). The importance of the colour response theshold under choice test conditions was not appreciated at this stage. As a consequence, it was difficult to see how flush leaves could elicit about twice as great an alight= ment frequency as mature leaves, when the strength of phototactic response was pro= portional to log of light intensity (Fig. 24) and the reflectance was only 2-fold, i.e. 0,3 of a log unit, greater from flush than from mature leaves (Fig. 8). This apparent anomaly was finally explained in the following chapter.

Response to bandwidth. Strength of phototactic response in T.erytreae did not change with changing spectral bandwidth from 10 to 75 nm (Fig. 25). Bandwidth is a measure of the "purity" of a colour: as bandwidth increases, purity decreases. Moericke (1952 et seq.) noted that the alightment frequency of "yellow-sensitive" aphids was correlated with the purity of the stimulus. The citrus psylla was found to belong to the "yellow-sensitive" group of Homoptera (Chap. 3), but the bandwidth experiment indicated that T.erytreae does not respond to stimulus purity per sé. The correlation of aphid alightment with surface purity that was noted by Moericke, appeared, therefore, to be caused, not by purity, but by some (as yet unknown) purity-correlated colour parameter.

Basis of alightment colour preferences. Fundamental information has thus been obtained on the wavelength sensitivity of T.erytreae, and the nature of its response to intensity. It was necessary at this stage to determine the manner in which these factors influenced alightment, and the experiments performed to this end are descri= bed in the following chapter.

Table 5. Details of colour filters and filter combinations used in alightment experiments with T.erytreae, giving the nominal wavelength used for absolute intensity calculation, and the colours of the major mercury source emission lines transmitted. YG = yellow-green; B = blue; UV = ultraviolet; Δ = a small amount of; + = superimposed filters; & = optically-mixed colour beams from separate colour filters.

Apparatus	Filter numbers and combinations	Filter thickness (mm)	Nominal wavelength (nm)	Colours transmitted
"Basic"	GG495 + BG18	2 + 1	556	YG_1
(filters used	GG400 + BG25	2 + 1	447	B_1
singly or in	WG305 + UG11	2 + 1	355	UV_1
superimposed	GG495	2	561	YG_2
pairs)	GG400	2	531	$(B + YG)_1$
See Fig. 26a	GG400 + BG18	2 + 1	527	$(B + YG)_2$
	BG25	1	429	UV + B
	GG19	1	532	ΔUV + B + YG
	WG305	2	509	$(UV + B + YG)_1$
"Colour-	GG495	2	559	YG_3
mixing"	GG495 low intensity	2	559	YG_4
(Filters used	UG11	1	357	UV_2
separately,	UG11 low intensity	1	357	UV_3
coloured	(GG495) & (UG11)	2 & 1	536	$(UV + YG)_1$
beams mixed	(GG495 low) & (UG11 low)	2 & 1	536	$(UV + YG)_2$
optically)	(GG400 + BG25)	2 + 1	445	B_2
See Fig. 26b	(GG400+BG25) & (GG495)	2 + 1 & 2	500	$(B + YG)_3$
	WG305	2	519	$(UV+B+YG)_2$
	WG305 low intensity	2	519	$(UV+B+YG)_3$

5. ALIGHTMENT ON MONO-, DI- OR TRI-CHROMATIC COLOUR FILTER TARGETS

It is readily accepted that "... the capacity for color vision requires at least two photoreceptors with different spectral sensitivities" (Goldsmith, 1964), but it is less obvious that the existence of an action spectrum with 2 or more peaks tells one nothing about the existence (or otherwise) of colour vision in that species (Goldsmith, 1964; Burkhardt, 1964). Remarkable coincidence was found between the 3 wavelengths of peak response in the action spectrum of T.erytreae and the peak sensitivities of the 3 colour receptors of Apis drones and Notonecta (as noted in Chap. 4), which suggested (and no more) that T.erytreae might also possess tri= chromatic vision. Behaviourally-different responses to the 3 wavelengths would indicate the existence of 3 different colour receptor systems, and hence the possi= bility of colour vision.

More importantly, to be able to interpret the alightment colour preferences of T.erytreae it was essential to know how each of the 3 wavelength regions of peak phototactic response, as shown by walking (Fig. 23), affected the particular behav= ioural response to be explained, namely alightment. From the work on other Homoptera dealt with in the introduction to Chaps 3 and 4, it was anticipated that the photo= tactic response peaks of T.erytreae in the yellow-green (YG) and the UV (Fig. 23) might be associated with alightment stimulation, and that the response peak in the blue (B) might be associated with alightment inhibition, but it was appreciated that this fundamental information would have to be obtained for T.erytreae before the alightment colour preferences of this species could be explained.

Materials and Methods (colour filters).

The opinion has been expressed that "The day has all but passed when anything significant will be learned with broad-band color filters, ...such experiments ... do not help us much in understanding the senses of insects" (Goldsmith, 1964). Broad-band colour filters were used here, but only in combination with a line source, thus producing effectively narrow-band stimuli. A mercury vapour lamp was used: Philips Reproduction Lamp HPR 125 W . In addition to a very low-intensity contin= uous spectrum, this lamp emits 5 high-intensity lines of relevance here: 2 in the YG and Y (at 546 and 578 nm), one B (436 nm), one UV (366 nm), and one intermediate between B and UV (405 nm) (Philips, 1955). Colour filters were chosen from a cata= logue (Schott, 1970) so as to select, from the line source, radiations close to the peak wavelengths of the phototactic action spectrum of T.erytreae, either individually or in different combinations. Table 5 contains details of the colour filters or filter combinations used (manufacturer's number, thickness, nominal wavelength over the mercury source (used for calculation of absolute intensity)) and the colours of the major mercury emission lines transmitted. Graphs of the spectral distributions of the quanta of the targets are given in Figs 28b and 29b.

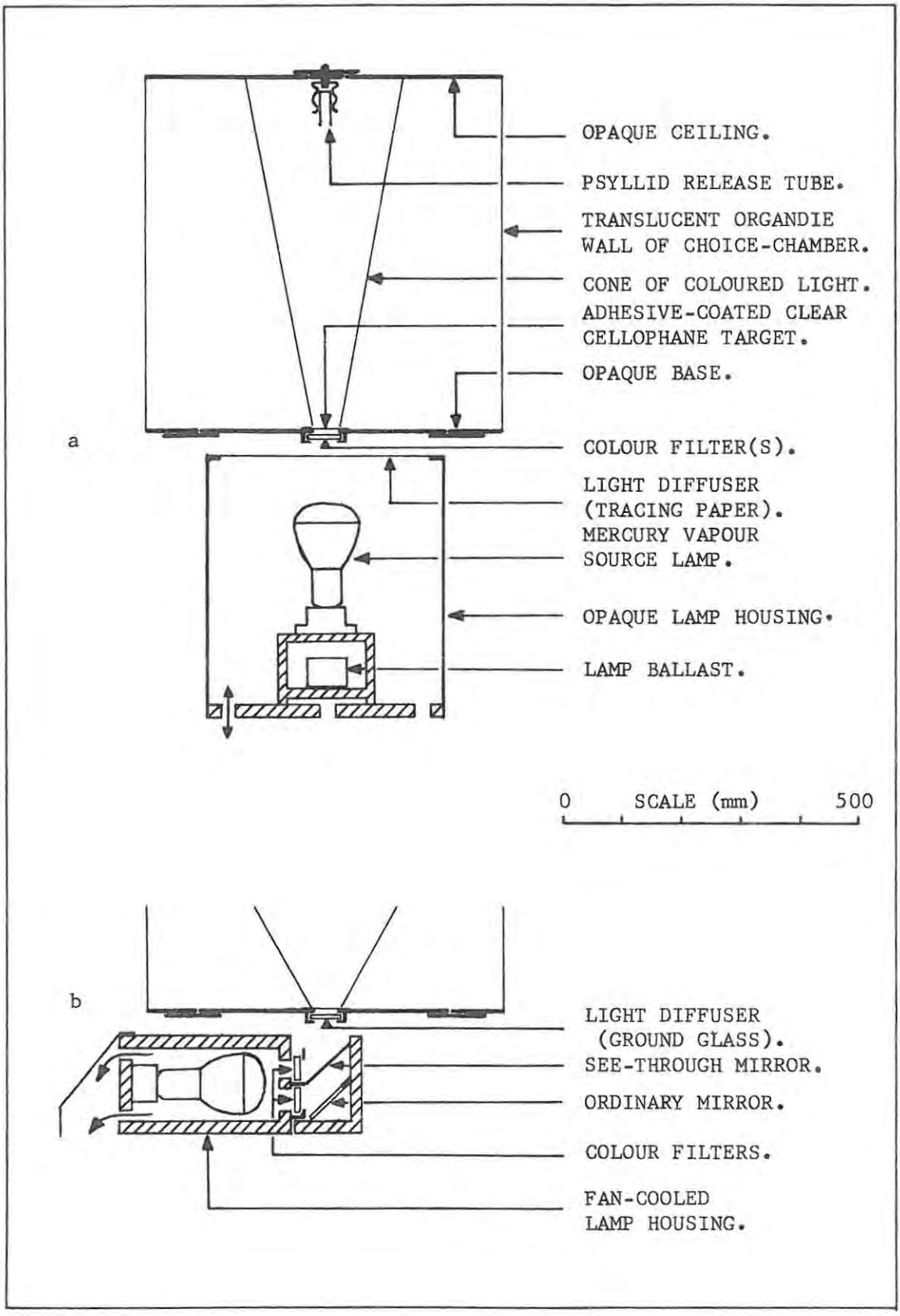

Fig. 26. Section through experimental set-up used for determination of alightment response of T.erytreae to colour filter targets. (a): "Basic" apparatus, in which the target consisted of light from the mercury source passed directly through a colour filter or superimposed pair of filters. (b): "Colour-mixing" apparatus, in which the target consisted of the optically-recombined beams from separate colour filters or filter combinations.

In all colour filter alightment experiments, the psyllids were "released" from a clear glass tube in the centre of the ceiling of the slowly-rotating cylindrical choice-chamber (Fig. 26). A single 43 mm diameter colour filter target in the centre of the choice-chamber base was illuminated from below and covered above by adhesive-coated cellophane to trap the alighting psyllids. The experiments were choice tests only inasmuch as they were conducted with the full complement of environment room lights (lab 2) switched on. In the "basic" apparatus, the mercury source light was diffused by a layer of tracing paper before reaching the filter or superimposed pair of filters in the target bracket in the choice-chamber base (Fig. 26a). In the "colour-mixing" apparatus, filters were placed in two separate brackets on the front of the fan-cooled source housing. The two coloured beams were then combined by means of one ordinary and one see-through mirror (the latter a thin glass photo-graphic plate, finely coated with vapourized aluminium), and the mixed beam was shone onto a ground-glass diffuser in the target bracket on the choice-chamber base (Fig. 26b).

Relative spectral distribution of light in each coloured target was calculated by multiplying (in 10-nm steps from 300 to 700 nm) the values of the emission spectrum of the source (Philips, 1955) by the transmission or specular reflectance spectra of the filters, mirrors and diffusers in the relevant optical pathways, in a manner similar to that indicated in the example of Table 4 (facing p.15). Absolute inten-sities of the coloured targets were measured with the laboratory lights switched off, by the thermopile technique, using the nominal wavelengths listed in Table 5 (each of which was calculated as in the example in Table 4) for substitution in the formula given on p.7. The relative spectra were then converted to absolute numbers, and are recorded in Figs 28b and 29b.

The environmental conditions under which the colour filter experiments were con-ducted, were chosen on the following grounds. During the population explosion of Trioza erytreae in the field in spring, the mean monthly temperature maxima are about 23,5 to 25,5 °C (Catling, 1970). Flight activity of Trioza nigricornis in the field was found to be limited by light deficiency, to be directly proportional to temperature, and to peak at relative humidities between 60 and 70 % (Müller & Unger, 1952). To simulate field conditions, and to stimulate flight, therefore, the photo-phase conditions of lab 2 were set at maximum illuminance (3800 lx), 25 °C and 65 % relative humidity.

Trioza erytreae were used in batches of 100 mature adults of 9,7 ± 1,2 d post-emergence age and sex ratio 1:1 , reared on Citrus jambhiri entirely in the laboratory (lab 2). Psyllids trapped on the sticky cellophane over the coloured target were counted, sexed and destroyed at the end of a 2,25 h replicate; those still in the release tube, on the soil-coloured floor, and on the white organdie walls were counted separately and destroyed. These counts were used for calculating "take-off" and

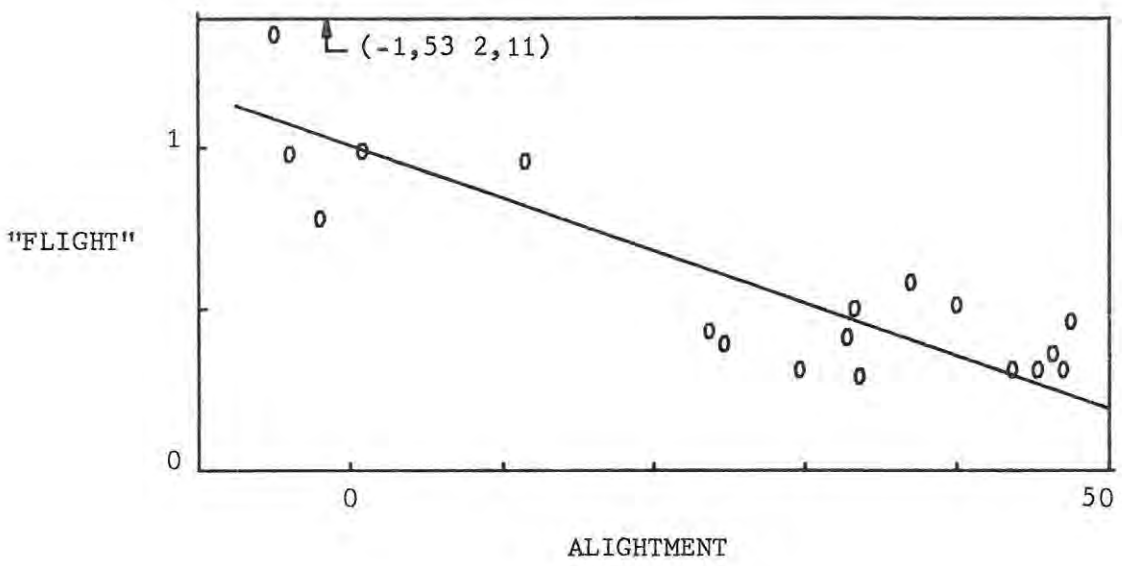

Fig. 27. Relationship between "flight" and alightment of T.erytreae in the choice-chamber. Alightment refers to the mean number of psyllids (of 100 released in each of 6 replicates) that alighted on the coloured target, minus the mean number that alighted on the black target control during the same time of day. "Flight" refers to the following parameter of psyllid distribution:

$(W/F)_{\text{coloured target, median}} / (W/F)_{\text{black target control, median}}$

where W = number of psyllids on translucent organdie wall of choice-chamber

F = number of psyllids on opaque wooden floor of choice-chamber at the end of the 2,25 h replicate.

The slope of the linear regression is statistically significant. (Details are given in the text).

"flight" as follows. "Take-off" was calculated as the total number of psyllids recovered minus those left inside and outside the release tube, expressed as a percentage of the total number recovered. "Flight" was calculated using the median wall/floor distribution ratio of psyllids in the choice-chamber at the end of a coloured target treatment, expressed as a ratio to a similar median wall/floor ratio at the end of the black target control. Six replicates of each filter treatment were performed: 2 each in the morning (10h00) (a.m.), mid-day (13h00), and afternoon (16h00) (p.m.), (i.e. beginning 5 8 and 11 h after "light on"). The control (12 replicates) was run with the mercury light source switched on, and black paper in the target bracket.

5.1 "Take-off" and "Flight".

General activity of T.erytreae tested in the choice-chamber increased during the daily experimental period. The a.m., mid-day and p.m. colour filter experiments averaged a "take-off" of 77,1 90,5 and 93,7 % of the test population, respectively, and a mean alightment on the coloured targets of 30,1 42,2 and 54,9 % of the test population (or 39,0 46,6 and 58,6 % of the flying population). In the case of the black target control, the mean a.m., mid-day and p.m. "take-off" was 73,5 88,1 and 88,6 % , and alightment was 12,8 16,0 and 29,3 % of the test population. Flight activity of Trioza urticae in the field peaked just after mid-day (Lewis & Taylor, 1965), as did that of T.nigricornis, apparently in response to environmental temperature (Müller & Unger, 1952). The increasing activity of T.erytreae in the laboratory during the daily series of experiments, therefore, might have been due to a gradual rise in temperature of the floor and ceiling of the choice-chamber, which was above the warm mercury source and its ballast (see Fig. 26). The reason for the increasing activity is not required here; the important point to note is simply that, to make allowance for the increasing general activity throughout the day, the behaviour of the test population was always evaluated with respect to the control for that time of day.

In 15 out of the 19 (six-replicate) treatments, "take-off" in the presence of a coloured target was not significantly different from "take-off" in the presence of the black target control: using the paired 't' test, the probability was always $p > 0,1$. For the remaining 4 of the 19 colour filter target treatments, the comparisons of treatment and control which had been found to be significant by the paired 't' test of batches of 6 pairs, were found never to be significant by the chi-square test of pairs individually ($p > 0,05$) or accumulated ($p > 0,1$). It is reasonable to conclude that "take-off", when calculated (as described above) from the psyllid distribution only at the end of a 2,25 h experiment, was not affected by the colour of the target.

"Flight" and alightment were negatively correlated (Fig. 27). The slope of the linear regression was significant (upper and lower 95 % confidence limits: -0,0112

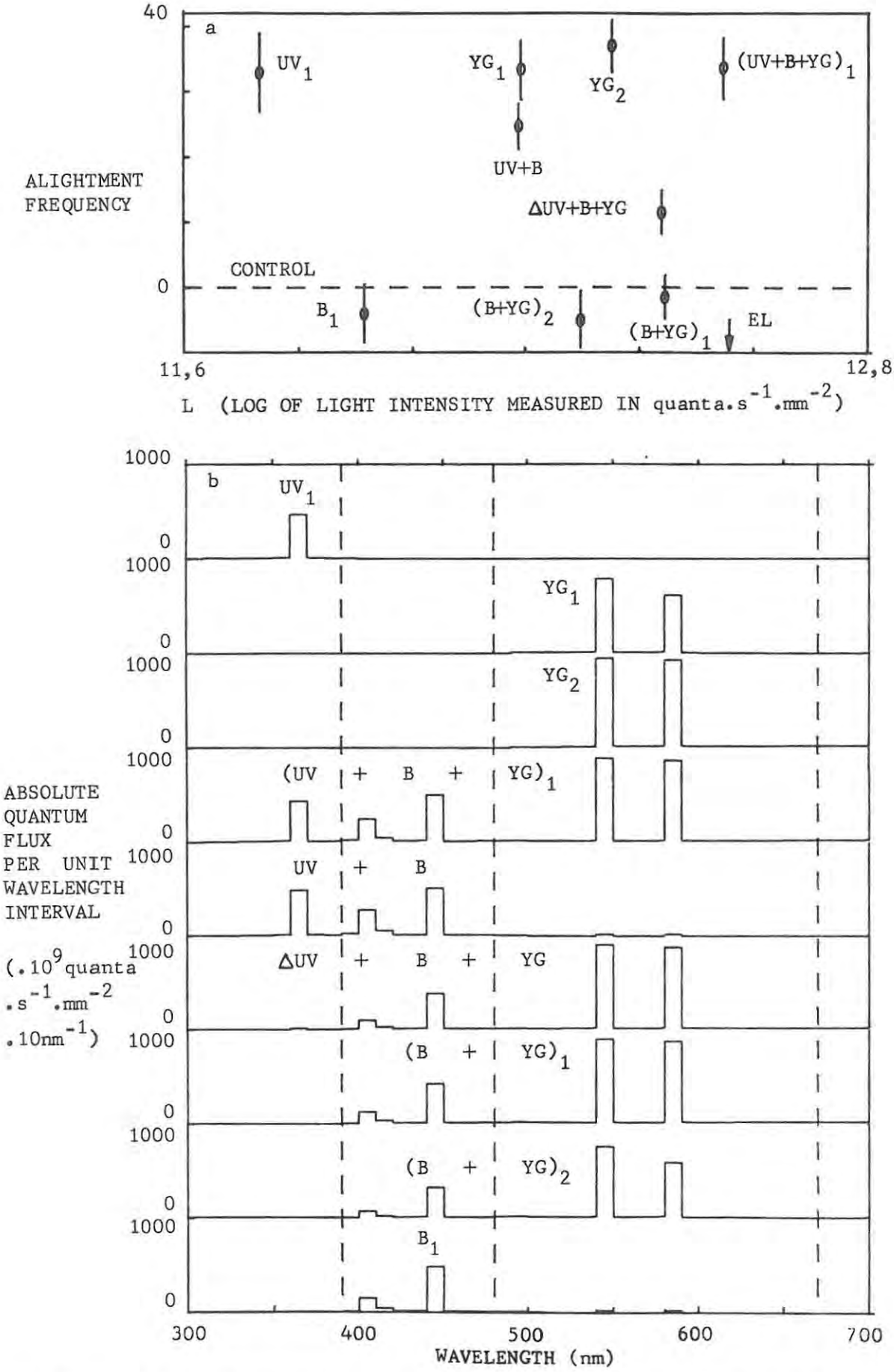

Fig.28. (a): Alightment frequency of T.erytreae (mean±1 standard error of 6 replicates, in each of which 100 psyllids were released in the choice-chamber opposite a single coloured target, and alightment was evaluated with respect to the black target control for that time of day) plotted against intensity of coloured target in "basic" apparatus (shown in Fig. 26a). EL=environmental light intensity (within T.erytreae's visible spectrum). (b): Spectral distribution of quantum flux from each coloured target presented. Lettering refers to composition (UV= ultraviolet, B=blue, YG=yellow-green) of light transmitted through Schott colour filters (detailed in Table 5) used in conjunction with mercury source.

and -0,0265) and this equation accounted for 61 % of the observed variation (r^2 = 0,613). (Parabolic and exponential regressions accounted for only slightly more of the variation: r^2 = 0,665 and 0,720 respectively).

5.2 Alightment in "Basic" Apparatus.

Frequency of alightment of T.erytreae in the "basic" apparatus (Fig. 26a; Table 5) was completely unrelated to the intensity of the colour filter targets ($F = 0,0063$ $p > 0,75$).

From the clustering of the mean alightment frequency (Fig. 28a) it was clear that the colour filter targets fell into 3 groups: either (i) strongly alightment-stimulatory, eliciting a mean alightment of 30-40 psyllids more than the control on the target, or (ii) non alightment-stimulatory, eliciting a mean alightment of 0-10 psyllids less than the control on the target, or (iii) intermediate, eliciting an alightment frequency between those of the first 2 groups.

Alightment was stimulated strongly by yellow-green light alone (YG_1 , YG_2), and by ultraviolet light alone (UV_1). At this stage it was impossible to say whether alightment was elicited by excitation of 2 independent receptor systems, or simply 1 receptor system sensitive to both UV and YG light.

Alightment was not stimulated at all by blue light alone (B_1). Furthermore, alightment was inhibited completely by blue light in combination with yellow-green light ($(B+YG)_1$, $(B+YG)_2$), and partially by blue light in combination with ultraviolet (UV+B). The existence of a behaviourally-different response to blue light, compared with that to yellow-green or to UV light, indicated the presence of a distinct blue-sensitive receptor system in T.erytreae. In addition, it was inferred that the neuronal integration of the B receptor system must differ from that of the YG and UV receptor system(s) (in some unknown way), such that they ultimately have opposite effects on alightment.

Compared with the non-stimulating targets below the zero alightment control line, the "intermediate" targets UV+B and ΔUV+B+YG elicited greater response (Fig. 28a), approximately in proportion to their greater UV content (Fig. 28b). This confirmed that ultraviolet light is alightment-stimulatory for T.erytreae, and suggested that alightment is a response to the combined stimulation of UV and yellow-green light.

5.3 Alightment in "Colour-mixing" Apparatus.

In the "colour-mixing" apparatus (Fig. 26b; Table 5) there was a similar clustering of mean alightment frequency of the test population into 3 groups, indicating that the colour filter targets were either strongly alightment-stimulatory, or non alightment-stimulatory, or intermediate (Fig. 29a). "Strong" alightment frequency was

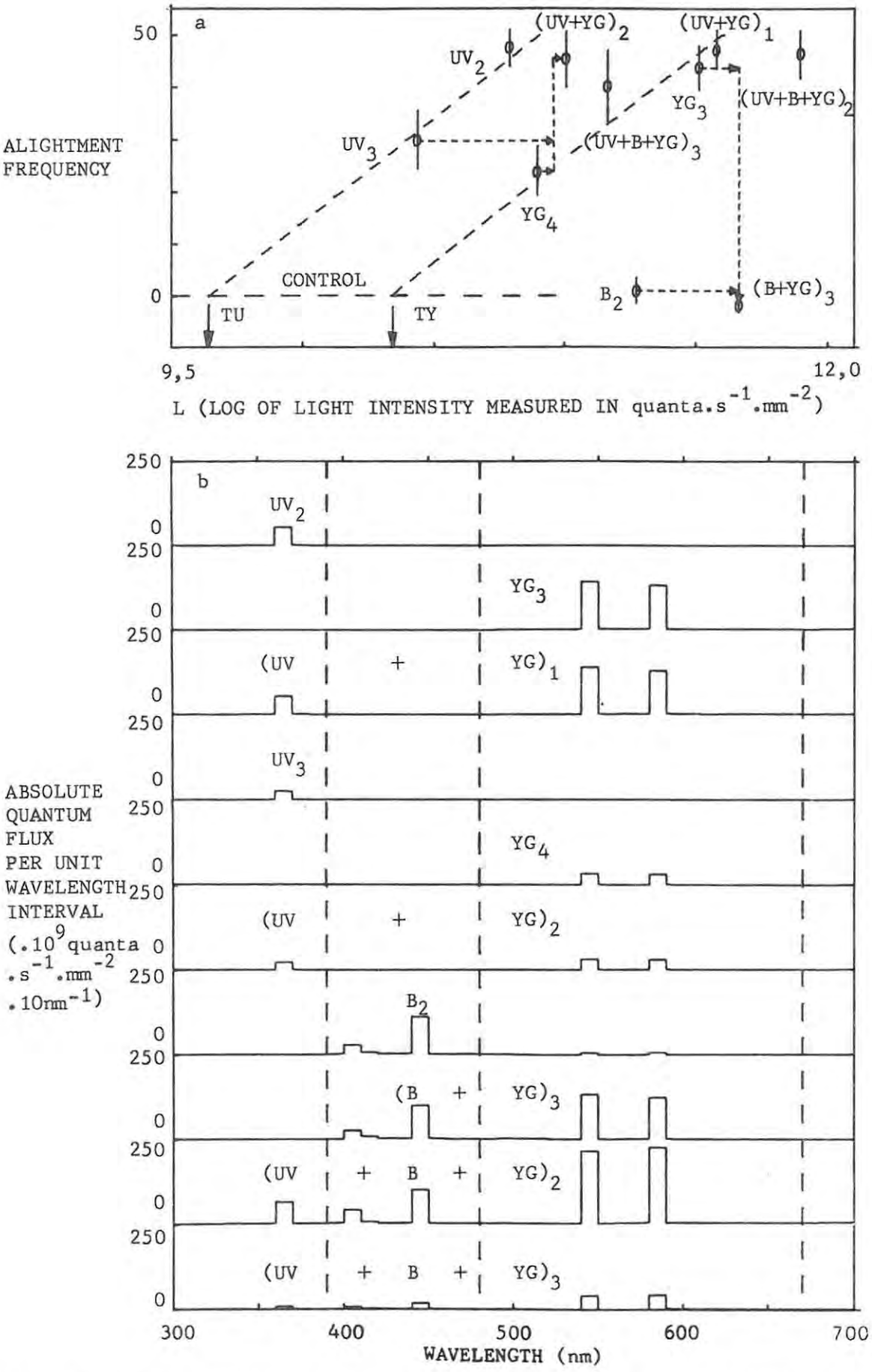

Fig. 29. (a): Alightment frequency of T.erytreae plotted against intensity of coloured targets (of which the spectral distributions of quantum flux are recorded in (b)) that were presented in the "colour-mixing" apparatus (shown in Fig. 26b). TU and TY are tentative threshold intensities of alightment in response to UV and yellow-green (YG) stimuli, at an environmental light intensity (within T.erytreae's visible spectrum) of $10^{12,56}$ quanta.s^{-1}.mm^{-2} . The dotted lines indicate the effect on alightment obtained by mixing 2 colours, each of which had been presented previously alone. B=blue. Other details as in legend to Fig. 28.

slightly greater in the "colour-mixing" apparatus, 40-50 psyllids more than the control on the target (compared with 30-40 psyllids in the "basic" apparatus), possibly due to greater light scattering as a result of the light diffuser being right at the target in this case (see Fig. 26, b compared with a).

Alightment was again stimulated strongly by YG alone (YG_3), and by UV alone (UV_2), and not at all by B alone (B_2). Addition of B to YG ($(B+YG)_3$), in this case achieved by optical mixing of 2 coloured beams, again completely inhibited alightment; but the B component of $(UV+B+YG)_2$ and of $(UV+B+YG)_3$ was not sufficient to inhibit the combined effect of the stimulatory YG and UV components. Intermediate alightment response was elicited both by UV at lower intensity (UV_3) and by YG at lower intensity (YG_4).

The "colour-mixing" apparatus was designed to determine the effect of mixing YG and UV, without B, which could not be achieved using any one colour filter offered by the manufacturer. The mixture of UV and YG ($(UV+YG)_1$ or $(UV+YG)_2$), obtained by combining either higher- or lower-intensity components, was also strongly alightment-stimulatory. When the 2 lower-intensity components were mixed, the effect of the combination on alightment was approximately additive (Fig. 29a). A linear relationship of phototaxis to log of stimulus intensity was demonstrated for walking T.erytreae (Fig. 24), and for alightment in a related homopteran, Trialeurodes vaporariorum, (as determined by re-working the data of Macdowall, 1972; see discussion of Chap. 4), so it seemed reasonable to assume that this would also apply to alightment in T.erytreae. When the assumed linear relationship was applied to the UV and the YG results of Fig. 29a (although the resultant graphs must obviously be regarded as preliminary in the absence of further replicates at a variety of intensities), and extrapolated back (broken lines) to the zero alightment response line, tentative UV and YG alightment thresholds (TU, TY) were obtained for T.erytreae under the experimental conditions. When light intensity was expressed in logs of quanta. $s^{-1}.mm^{-2}$, at the environmental intensity (within T.erytreae's visible spectrum) of 12,56 , the UV and the YG alightment response thresholds were approximately: TU = 9,64 ; TY = 10,34 (Fig. 29a). The existence of different response thresholds to UV and to YG light, indicated the existence of distinct UV and YG receptor systems in T.erytreae.

Discussion (colour filters).

Colour vision. Trioza erytreae has colour vision. It is the first species of the Psyllidae and the third species of the Homoptera in which this ability has been rigorously demonstrated (the others being Myzus persicae of the Aphididae (Moericke, 1950), and Trialeurodes vaporariorum of the Aleyrodidae (Vaishampayan et al., 1975a)). Moericke, in 1950, proved very elegantly that M.persicae has true

colour vision (as explained in the introduction to Chap. 4), and this was accepted in the 1953 edition of a general text on insect physiology (as is evident from the referenct list in a more recent edition: Wigglesworth, 1965). In several reviews of insect colour vision, however, Moericke's (1950) work was not mentioned (namely von Frisch, 1960; Goldsmith, 1961; Dethier, 1963; Burkhardt, 1964; Goldsmith, 1964), then accepted with scepticism (by Mazokhin-Porshnyakov, 1969) and finally accepted unreservedly (by Autrum & Thomas) only in 1973. Macdowall (1972) also doubted the existence of colour vision in the whitefly (but the reason for his conclusion was surely that his colorimetric study was restricted to a single (the yellow-green) receptor system). The nature of colour vision in the aleyrodid (Vaishampayan et al., 1975a) and in the psyllid studied (the present work) is very similar to that found in the aphid, M.persicae, and, therefore, strongly supports Moericke's (1950) findings. There are no reasonable grounds for scepticism about the existence of colour vision in Homoptera.

Colour vision can be di-, tri-, or perhaps tetra-chromatic (when based on either 2, 3 or perhaps 4 colour receptor systems in the same part of the eye). Mazokhin-Porshnyakov (1969) concluded from the evidence of various authors that dichromatic colour vision exists in species of Odonata, Dictyoptera, Orthoptera, Coleoptera and Diptera, and trichromatic vision only in Hymenoptera, though there is now evidence that the latter also exists in Heteroptera (Bruckmoser, 1968) and Lepidoptera (Swihart, 1970, 1972a,b), and that tetrachromatic vision might exist in Hymenoptera (Autrum & von Zwehl, 1964; Autrum & Thomas, 1973). Trioza erytreae's vision is trichromatic, with individual receptor systems sensitive either to the UV or the B or the YG regions of the spectrum, as had been suggested by the phototactic action spectrum (Fig. 23). The evidence for trichromatic vision in T.erytreae is that UV and YG lights elicit the same behavioural response above different thresholds (Fig. 29a), and B light elicits a behaviourally-different response (Figs 28 & 29).

The term "receptor system" used here is tentative. It could refer to portions of receptors containing 2 photo-transduction pigments, as are common in Calliphora (Burkhardt, 1964; Horridge & Mimura, 1975), because UV and YG elicit the same type of behavioural response in T.erytreae, and have the same slope of response against intensity, though above different thresholds (Fig. 29a). It seems more likely, however, that there is a distinct mono-pigment UV receptor in homopterans, because this type of receptor has also been found in Calliphora (Smola & Meffert, 1975) and in a species of insect more closely related to the Homoptera, namely the heteropteran, Notonecta (Bruckmoser, 1968).

Basis of alightment colour preferences. Alightment of T.erytreae is stimulated through the UV and YG receptor systems, and inhibited through the B receptor system (Figs 28 & 29). The positive alightment response of T.erytreae to YG (or Y) and to

UV light, corroborates similar findings reported in studies of the colour responses of other homopterans: aphids and psyllids in general (Moericke, 1952 et seq., especially 1955c; Kaloostian & Wolf, 1968; Halgren, 1970a), as well as aleyrodids (Macdowall, 1972; Vaishampayan et al., 1975a) and male monophlebid coccoideans (Doane, 1966). Surfaces simultaneously reflecting or transmitting B in addition to UV or Y light, stimulated alightment less than did pure UV or Y surfaces, in members of the first 3 of the above homopteran families (as is evident from the data of Butler, 1938; Moericke, 1955c; Mound, 1962; Coon, 1968; Vaishampayan et al., 1975a; the present study, Figs 28 & 29). From the areas of correspondence pointed out above, and in the discussions to the previous chapters, it is reasonable to hypothesize that:

> the "yellow-sensitive" (and perhaps the "non-yellow-sensitive") Homoptera are qualitatively homogeneous as regards their colour responses.

Qualitative experimental findings on any one species in this group, have a high probability of valid applicability to other species in the group. Acceptance of this hypothesis effectively enlarges the pool of basic knowledge that can be drawn from in an attempt to explain the colour responses of any homopteran.

Moericke (1955a) inferred that the reduction in alightment frequency of aphids (on addition of B) was due to the decrease in purity (of a formerly pure Y stimulus), but the monochromator experiments demonstrated that T.erytreae does not respond to purity per sé (Fig. 25). Mound (1962) suggested that white surfaces were equal to or less attractive than Y, in spite of their greater reflectance of UV light, because the whiteflies could not respond to UV at the same time as to Y; but the colour-mixing experiments on T.erytreae (Fig. 28a and especially 29a) indicated that the alightment stimulation of UV and YG are additive. The colour filter experiments proved that blue light is alightment-inhibitory for the citrus psylla (Figs 28 & 29) and Vaishampayan et al. (1975a) independently reached the same conclusion, dealing with the greenhouse whitefly. The correlation between decreasing alightment frequency and decreasing purity (going from Y to Y+B or from UV to UV+B) in the experiments on a variety of homopterans cited in the paragraph before this one, therefore, can be considered to have had as its causation, not the decrease in purity per sé, nor the possibility that B light might be repellent, but the fact that the added B light was alightment-inhibitory. Furthermore, the partial recovery in attractiveness going from zinc-white (reflecting Y+B light) to lead-white targets (reflecting Y+B+UV light) (Moericke, 1955c; Mound, 1962) was evidently due to the partial overcoming of the effect of alightment-inhibitory B by the addition of alightment-stimulatory UV light, as in the above experiments with T.erytreae (Figs 28 & 29).

From their work on the response of Trialeurodes vaporariorum to colour filters, Vaishampayan et al. (1975a) suggested that red light (wavelengths 610-700 nm) "may moderately inhibit attraction". All the evidence collected by other workers on the

same or related species, however, contradicts this suggestion. Moericke (1950) found that far red light (from a filter with a transmittance $< 0,1$ % at wavelengths below 690 nm) stimulated probing of Myzus persicae at very high light intensity, in the same way as YG light: the fact that the latter (YG) is alightment-stimulatory (as noted above) suggests that the former (red) also stimulates rather than inhibits alightment. Particularly strong evidence against the suggestion of Vaishampayan et al. (op. cit.) is Macdowall's (1972) finding (cited in the discussion to Chap. 4) by colorimetry on the same species (Trialeurodes vaporariorum) that there is only a single type of colour receptor in the (green to red wavelength) range 502-623 nm . In addition, receptor spectral sensitivity determinations on the worker and the drone honey-bee (Autrum & Thomas, 1973) and on the heteropteran, Notonecta, (Bruckmoser,1968) in no way support the implication (necessitated by the suggestion of Vaishampayan et al. (above)) that either there is a receptor system for red light distinct from that for (alightment-stimulatory) yellow-green light, or the receptor system for (alightment-inhibitory) blue light is more sensitive at wavelengths above 610 nm than that for yellow-green light. The suggestion of Vaishampayan et al. (op. cit.) that red light is alightment-inhibitory, is, therefore, not accepted.

The influence of colour vision on flight and alightment. In the experiments with T.erytreae, the single colour filter target was relatively small, just under 0,1 % of the surface area of the choice-chamber, and relatively dimly illuminated, ranging from just under 1 % to just under 100 % of the intensity of the environment room lighting (within T.erytreae's visible spectrum) (see the intensities of the colour filter stimuli in Figs 28a and 29a presented at an environmental intensity of $10^{12,56}$ quanta.s^{-1}.mm^{-2}). The colour filter targets in the laboratory thus more-or-less simulated typical reflecting surfaces in the field. Accordingly, and bearing in mind the apparent qualitative homogeneity of homopteran colour response, it is not unreasonable to use these basic laboratory results in an attempt to explain, in very broad terms, the behaviour of related homopterans in the field.

One of the most interesting aspects of the colour-related behaviour of homopterans in the field, is their changing phototactic response during the dispersal flight. Dispersal is similar in psyllids and in aphids. Like aphids, (various authors cited by Dixon, 1971, and by Kring, 1972), psyllids emigrate actively at the end of the teneral period (White, 1970; also a suggestion in this study: Fig. 19) mainly under conditions of high temperature and high light intensity (Müller & Unger, 1952; Lewis & Taylor, 1972; Watmough, 1968) and disperse with the wind (Hodkinson, 1974), then descend, and (once in their boundary layer) alight on surfaces in a frequency proportional to their yellowness (Moericke, 1955b, 1957). Dispersing homopterans initially fly upwards, towards the bright, polarized, blue (i.e. relatively shortwave-transmitting) sky, and after a period of flight they do not

simply drop (though this might occur immediately over the landing target (Moericke, Schneiders & Vogt, 1966)) but fly actively downwards (Kennedy & Fosbrooke, 1973) towards the relatively dim, non-polarized, green and brown (i.e. relatively longwave-reflecting) earth. The problem is to discover to which of these 4 possible stimuli (gravity, light intensity, polarization, colour) there is a change in response during the dispersal flight.

A change in sign between positive and negative geotaxis and phototaxis, associated with various physiological and environmental conditions, has often been reported in the literature (reviewed by Jander, 1973). The combination of positive phototaxis and negative geotaxis (and the converse combination) is more frequent in insects generally than other behavioural associations (Jander, loc.cit.), and this was borne in mind when homopteran behaviour was studied. Partial coating of the eyes of a positively phototactic cicada usually much exaggerated its negative geotaxis in flight (Chen & Young, 1943). Aphids taking off for the first time were found to be strongly attracted by a light source, not only upwards but also sideways or obliquely downwards (Moericke, 1955c; Kennedy & Booth, 1963a), which demonstrated that a positive phototactic component overwhelms any possible negative geotactic component in their behaviour at this stage. It is reasonable to assume, therefore, that the subsequent change from "distance flight" to "alighting flight" is not simply due to a weakening of or a reversal from negative geotaxis, but involves mainly a change in phototaxis.

No one has studied the possibility of a weakening of or reversal from positive "polarotaxis", where the term "polarotaxis" is used here to mean movement towards an area of polarized light (rather than orientation at one or more specific angles to the plane of polarization, as used by Waterman, 1966). Enhanced movement of insects towards a light due to its polarization has been claimed, but reports are conflicting (as noted in the first paragraph of the discussion to Chap. 2). A change in "polarotaxis" could conceivably bring about the change from distance to alighting flight, and precede preference behaviour exhibited during the alighting flight, between non-polarized surfaces of different colour and intensity.

Various hypotheses involving colour and intensity that have been put forward to explain the change in phototactic response of homopterans during dispersal are (in chronological order) that: (i) the response to white or to shortwave (blue and/or UV) light changes from positive to negative during flight (Moericke, 1955b); (ii) the response to longwave light increases during flight relative to the response to shortwave light (Kennedy et al., 1961); (iii) ultraviolet light induces migratory behaviour and yellow light vegetative behaviour, and the balance between the two is altered by the strengthening of the response to yellow after a period of flying (Mound, 1962); (iv) the preferred intensity for phototactic response decreases

during flight, and the phototaxis eventually becomes negative (Kennedy & Booth, 1963a); (v) flight up towards the sky is the result of positive phototaxis to light of about 550 nm (i.e. yellow-green) and negative geotaxis, and the subsequent plant colour preference is caused by the change in physiological condition due to tiring by flight (Žďárek & Pospíšil, 1966a).

After emergence and six hours stay in the dark, alate Aphis fabae that were tested in a two-way choice-chamber showed a phototactic preference for yellow-green (558 nm) or green (518 nm) rather than blue light (459 nm) which increased steadily (and approximately doubled) from the 7th to the 10th hour of their post-emergence age (Žďárek & Pospíšil, 1966a). This was not interpreted as a changing phototactic response: it was suggested that aphid orientation is always determined by yellow-green light, and that the results are due to increasing development of phototactic responsiveness. Subsequent flight chamber studies on the same species (A.fabae), however, demonstrated a shift in colour preference during flight, from a shortwave overhead light to a longwave one (Kennedy & Fosbrooke, 1973), which strongly supports the 1961 hypothesis of Kennedy et al. (alternative (ii) above) concerning the basis of the changing phototactic response during dispersal.

The present work, however, demands a modification of the Moericke-Kennedy conceptual dichotomy of spectral stimuli into "shortwave" and "longwave". A trichotomy is required, because alightment in T.erytreae is stimulated both by yellow-green (longwave) and by UV (lower shortwave) light, whereas it is inhibited only by blue (upper shortwave) light (Figs 28 & 29). Vaishampayan et al. (1975a) independently found the same basic situation, in their study of the colour responses of an aleyrodid. Their apparatus was inverted in comparison to the one used here (Fig. 26), and this ruled out the possibility that blue light simply elicits negative geotaxis: blue light evidently influences phototaxis itself.

Phototactic stimuli influencing aerially-dispersing homopterans are of 2 distinct types: those that elicit "flight" (i.e. take-off and substrate-avoiding flight) and those that elicit alightment (i.e. substrate-approaching flight and landing). This fundamental difference in flight behaviour, namely avoidance of objects and approach towards objects, was used by Kennedy (1961) to characterize, respectively, migratory and non-migratory behaviour. The response here termed "flight" is probably equivalent to "Distanzflug" i.e. distance flight of Moericke (1955c), or "migratory behaviour" of Mound (1962), or "cruising flight" or "migratory flight" of Kennedy et al. (vide infra), or "phase 1 flight" of van Emden et al. (1969), or "object-avoiding flight" of Kring (1972). Similarly, the response here termed "alightment" is probably equivalent to "Befallsflug" i.e. attacking or alighting flight of Moericke, or "hovering" and "attacking flight" of Johnson (1958), or "vegetative behaviour" of Mound, or "phase 2 flight" of van Emden et al., or the

"approach" and "landing" parts of the "settling" response complex, or "directed flight", or "targeted flight" of Kennedy *et al*. (references cited below).

There is some preliminary evidence that "flight" and "alightment" are mutually antagonistic in *T.erytreae* (Fig. 27), as suggested (Johnson, 1958; Mound, 1962) and rigorously proved (Kennedy & Ludlow, 1974) in other homopterans. Kennedy *et al*. have demonstrated very thoroughly that the responses, flight and "settling", are mutually antagonistic in *Aphis fabae* (Kennedy & Booth, 1963b, 1964; Kennedy, 1965, 1966a, b, 1967; Kennedy & Fosbrooke, 1973). Kring (1972) pointed out that "Some of the factors that result in an aphid alighting are also in part those that ... result in settling", and this is supported by the fact that the same colour stimulus (yellow) is most effective in eliciting both alightment in homopterans generally (references cited above) and inhibition of flight in *Trialeurodes vaporariorum* (Moericke *et al*., 1966) and arrestment of walking in *Trioza erytreae* (Chap. 3). The relevance of this to the present work is that Kennedy's conclusions concerning "settling" are doubtless applicable to "alightment", as is borne out by the similarity of the results of his more recent study on "targeted flight" (Kennedy & Ludlow, 1974) to those of his earlier studies, on "settling" (cited above).

Concerning the organization of the mutually-antagonistic behaviour patterns of flight and settling, Kennedy (1966b) pointed out that "... one clearly cannot learn much about it from experiments on one kind of reaction at a time." The present study was concerned with the effects of colour vision on alightment only; flight was not specifically investigated here (though see Section 5.1). Take-off and flight have, however, already been thought to be stimulated by shortwave light (Moericke, 1962), and subsequently been shown to be more strongly stimulated in aphids by the light from blue fluorescent tubes than by that from yellow (Kring, 1969) and by shortwave light (below 500 nm) from broad-band colour filters than by longwave light (above 500 nm) (Darst, 1972). In view of these results, and of the complementary finding that blue light inhibits alightment (references cited above) which is antagonistic to flight (references also cited above), it is reasonable to assume that the major excitatory chromatic stimulus to the homopteran flight motor is through the blue receptor system.

(This in no way implies the absence of endogenous stimuli, nor of achromatic exogenous stimuli to the flight motor. Homopteran flight is, indeed, known to be stimulated by the (non-host) chemical nature of the substrate (Kennedy & Booth, 1963b, 1964; Kennedy, 1965) and by increasing temperature and light intensity (Halgren, 1970a,b). Moericke's (1955b, 1962) suspicion that UV light is flight-stimulatory, and Halgren's (1970a, b) subsequent finding that aphid take-off and flight are significantly stimulated by increasing the proportion of UV in a stimulus light of constant total physical intensity, might in fact be an achromatic, light-intensity response due to the greater physiological brightness of UV-rich light to

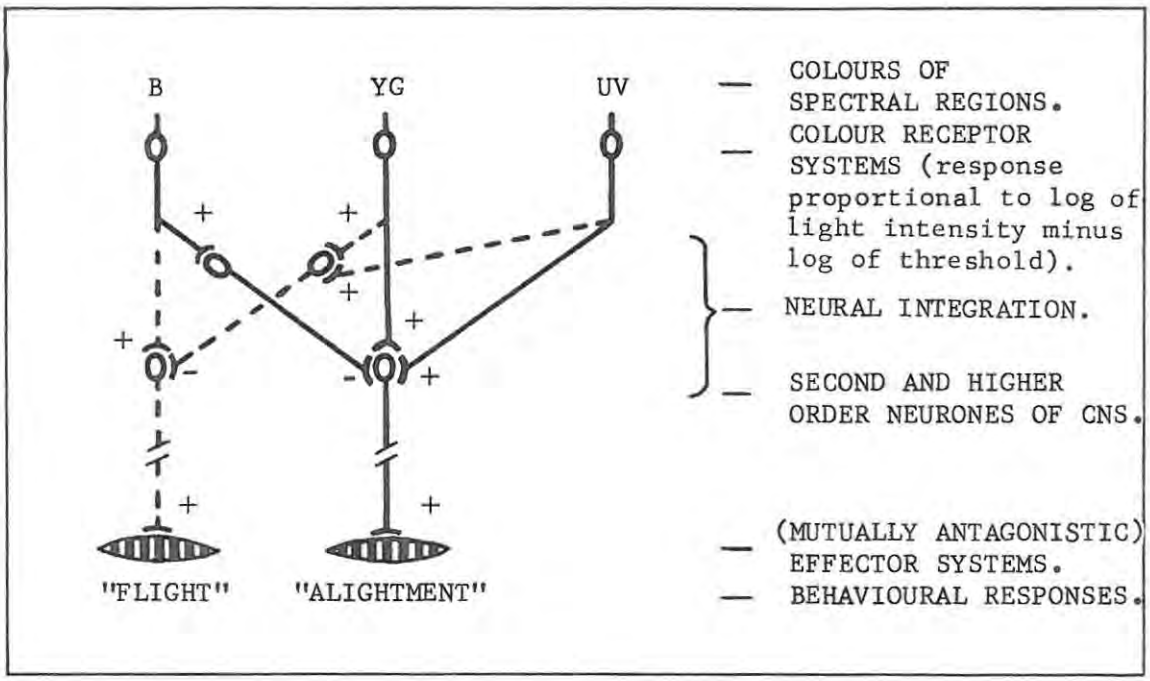

Fig. 30. Hypothetical neuronal "wiring" diagram of apparent homopteran system of selective chromatic stimulation and lateral inhibition of "flight" (i.e. take-off and substrate-avoiding flight) and "alightment" (i.e. substrate-approaching flight and landing). B=blue, YG=yellow-green, UV=ultraviolet light; CNS=central nervous system; +⊥=excitatory, -⊥ = inhibitory ending of axon at synapse. (In this synthesis of work on T.erytreae and other Homoptera (discussed in the preceding text), no attempt has been made to include achromatic exogenous stimuli, nor endogenous stimuli, which doubtless affect the behavioural output).

homopterans resulting from a lower threshold to UV than to other colours (as in T.erytreae, Fig. 29a).)

Kennedy (1967) came to the conclusion from his behavioural studies on Aphis fabae (vide supra) that "Eliciting either of the antagonistic activities, flight or settling, not only inhibits the other entirely for the time being, but also has an after-effect on it ... [which] is due to the temporary central inhibition imposed on the antagonistic activity by the stimulus that elicits the protagonist." Electrophysiological studies have proved the existence of reciprocal "lateral inhibition" between receptors of uniform spectral sensitivity in Limulus (Hartline, Ratliff & Miller, 1961) and in a fly (Zettler & Järvilehto, 1972; Zettler & Autrum, 1975), and have indicated inhibition between different colour receptors in various lepidopterans (Swihart, 1968, 1969, 1970, 1972a, b) and in the honey-bee (Menzel, 1974). Electrophysiology of arthropods thus supports the possibility of "central inhibition" which Kennedy deduced in aphids from his behavioural studies, and, furthermore, that this can occur between different colour receptor systems.

Hypothetical neuronal "wiring" diagrams of lateral inhibition in arthropod visual systems have been given by several workers who considered the integration of achromatic (Ratliff, Hartline & Miller, 1963, cited by Ratliff, 1965), unspecified (Kennedy, 1966a), or chromatic stimuli (Burkhardt, 1964; Swihart, 1969). Features of these have been incorporated in the hypothetical diagram, opposite, (Fig. 30) to illustrate the possibility of selective chromatic stimulation and reciprocal lateral inhibition between the homopteran flight and alightment reflexes.

This diagram would be consistent with Kennedy's (1961) statement that "The basic difference between migratory and non-migratory behaviour is a difference of relative thresholds", and with his flight chamber demonstration that the phototactic responsiveness changes during flight (Kennedy & Booth, 1963b; Kennedy, 1966b) and that descending aphids are still responding positively, though less strongly, to a light from above (Kennedy & Fosbrooke, 1973), if the hypothesis of Kennedy et al. (1961) (alternative (ii) on p.58) were modified slightly, as follows:

> The change in phototactic responsiveness of homopterans during flight, is due to a decrease in the response thresholds to UV and/or yellow-green light (which stimulate alightment and perhaps inhibit flight), relative to that to blue light (which inhibits alightment and perhaps stimulates flight).

Such an hypothetical relative change in thresholds could involve either a raising of the response threshold to blue light, or a lowering of that to yellow-green and/or UV light, or both. The response threshold to blue light could be raised due to adaption to, or selective fatiguing of the blue receptor system by,

the blue light of the sky (the possibility of such a phenomenon having been demonstrated in insect behaviour (Hamilton, 1922) and in electrophysiology (Goldsmith, 1960)). The response threshold(s) to UV and/or yellow-green light could be lowered due to some factor associated with energy utilization during flight, which would result in increasing stimulation of an innate or learned response of phototaxis to leaf green specifically for feeding. This seems plausible in view of the fact that, in Aphis fabae, bouts of walking are normally followed by probing (Ibbotson & Kennedy, 1959), and flight progressively lowers the threshold of settling (Kennedy & Booth, 1963b, 1964), on which grounds Kennedy (1966b) suggested that it was a general phenomenon that locomotory activity lowers the threshold of feeding responses.

Neuronal integration of achromatic photic stimuli (not included in Fig. 30) could conceivably reinforce that of the chromatic stimuli in eliciting behavioural responses. If inputs from receptor systems sensitive to light polarization and to total intensity were neuronally "wired" in the same manner as the input from the blue receptor system (Fig. 30), this could account for any possible initial but decreasing preference for (polarized) incident (as opposed to (non-polarized) reflected) light which could be involved in the initial strong flight towards the sky and the subsequent "plant-dodging" movements of the majority of flying aphids observed in the field (Kennedy, Booth & Kershaw, 1959a, b), and for the initial but decreasing preference for bright lights in the laboratory flight chamber (Kennedy & Booth, 1963a).

The knowledge of T.erytreae's trichromacy, and the effect of each of the primary colours on alightment, provided the basis for the evaluation (i.e. explanation and/or prediction) of the relative attractiveness of any surface to the psyllids for alightment, attempted in the following chapter (6).

6. CORRELATION OF ALIGHTMENT WITH PARAMETERS OF SPECTRAL REFLECTANCE

In order to describe behavioural preferences, and to draw attention to a possible causative stimulus, Moericke (1952 *et seq.*) pointed out that there was a visual (i.e. not mathematically-treated) correlation between frequency of alightment of aphids in general and the "purity" of the basically yellow target stimuli presented. When Moericke's (1952) data were treated mathematically (Walker, 1974) it was found that the linear regression of relative alightment frequency (expressed as a percent of the catch on the yellow surface) against target purity (expressed as percent yellow mixed with white) did indeed indicate, above a certain threshold, a very high degree of correlation ($r = 0{,}994$) between these variables. In an attempt to link aphid alightment to something more physiologically relevant to aphids (than the human colour parameter, purity), Kennedy *et al.* (1961) formulated a new colour parameter, the "long/short ratio" (as described in the introduction to Chap. 3). They found good visual correlation between relative frequency of aphid alightment and the relative magnitude of the long/short ratio of leaf surfaces.

Visual and mathematical comparison of graphical trends of the alightment frequency of *T.erytreae* on series of surfaces, with the trends of surface colour parameters (Chap. 3) indicated that alightment frequency and the colour parameters "purity" and "long/short ratio" were always positively correlated, though sometimes highly, and at other times rather poorly. (The full results of the mathematical testing of these comparisons are reported in this chapter). The inconsistency of correlation cast doubt on the possibility that either purity or long/short ratio might be the causative stimulus of *T.erytreae*'s alightment preferences, and necessitated the gathering of fundamental information on the visual physiology and behaviour of *T.erytreae* (done in Chaps 4 and 5).

The opinion was expressed by a visual physiologist (Ratliff, 1965) that "... the behavior of the entire neural network from [optical] stimulus to [behavioural] response conceivably might be represented in a purely mathematical model by a single transfer function ... the ... terms [of which] ... should be ... physiologically sound as well as mathematically succinct." It was necessary, therefore, to examine whether or not the colour parameters, purity and long/short ratio, were "physiologically sound" as regards *T.erytreae*. Purity was not physiologically sound because *T.erytreae* did not respond to bandwidth *per sé* (Fig. 25). Long/short ratio was not physiologically sound as regards *T.erytreae* for a number of reasons: (i) the "shortwave" region was sensed by not one, but two, receptor systems, differently neuronally "wired", so that UV light was not alightment-inhibitory but alightment-stimulatory (Figs 28 & 29); (ii) the response was not a linear function of energy (within relevant wavebends), but a logarithmic function of quantum flux (Figs 24 & 29a); (iii) the response to each colour occurred only above a relevant colour threshold (Figs 24 & 29a).

Kennedy et al. (1961) formulated the long/short ratio, to explain relative alightment preferences of aphids, with (attractive) longwave energy (above 500 nm) in the numerator and ("repellent") shortwave energy (below 500 nm) in the denominator. The placement of the UV fraction of the light in this formula was problematical. Kennedy et al. included UV light with the blue in the "... short-wave region that tends rather to turn them away ..." on the grounds that: (i) Moericke's finding that UV stimulated alightment of aphids in general, probably did not apply to the "yellow-sensitive" species with which they were working; (ii) the UV emission is a very small fraction of that from leaves in daylight; and (iii) omitting the UV fraction from the denominator of the long/short ratio, or even transferring it to the numerator, did not alter the sense in which the ratios differed. They noted that the ratio was "strictly provisional" in the absence of measurements of the relative sensitivity of each aphid species to different wavelengths, and would call for correction if the aphids were especially sensitive to UV light.

Trioza erytreae's responses fell into the basic homopteran behaviour pattern elucidated by Moericke; the species was clearly one of the "yellow-sensitive" Homoptera, yet UV light was as strongly alightment-stimulatory to T.erytreae as YG light, above the relevant colour threshold (Fig. 29a), and would apparently be more strongly alightment-stimulatory than YG light at low light intensities (Fig. 29a). A new alightment formula was, therefore, required: one which would firstly take into account, in a "physiologically-sound" manner, the basic knowledge of the visual responses of T.erytreae. A formula recently developed for predicting the relative attractiveness of different lamps to house flies (Thimijan & Pickens, 1973) involved integration of the product of the emission spectrum of each lamp and the phototactic action spectrum of the house fly. Such a formula is unsuitable for predicting the relative alightment preferences of T.erytreae for several reasons, the most important of which is that not all the peaks of the phototactic action spectrum of T.erytreae (Fig. 23) were associated with alightment stimulation: at least one peak was shown to be linked to alightment inhibition (Chap. 5). It was hoped that a new formula could be derived, which would not only be physiologically sound, but would provide a more accurate and a more consistent correlation with the observed alightment frequency of T.erytreae than was provided by "purity" and by "long/short ratio".

Materials and Methods (correlation).

The new alightment formula, called the "relative alightment stimulus -" or "RAS equation", was derived as explained in Section 6.1.

Frequency of alightment of T.erytreae on several series of coloured surfaces was tested (by means of the coefficient of determination, r^2, explained in the Materials and Methods (General) p.11) for degree of correlation with five parameters of the spectral distribution of light from those surfaces. The slope of each linear

regression of alightment frequency against colour parameter values was also noted. The colour parameters tested were "purity" and "reflectance" (human-based, used by Moericke), "long/short ratio" and "total energy" (aphid-based, formulated by Kennedy et al., 1961, and evaluated with respect to environmental illumination), and various modifications of the "RAS equation" (which was formulated here). (It is appreciated that Moericke attached little importance to "reflectance" alone, and Kennedy et al. to "total energy" alone, as suitable parameters to use in the description of aphid alightment preferences. Nevertheless, these parameters are included in Tables 7 and 8 for comparison and completeness.) The coefficient of variation (also explained on p.11) was employed for the purpose of comparing the overall variability of the "goodness of fit" (r^2) values calculated in connection with different colour parameters.

Finally, an attempt was made to see whether or not the different alightment distributions of "yellow-sensitive" Aphis fabae and "non-yellow-sensitive" Hyalopterus pruni aphids on leaves and painted surfaces, observed by Moericke (1955a, 1969), could be theoretically explained by the basic "RAS equation" developed here for T.erytreae.

6.1 Derivation of "Relative Alightment Stimulus" ("RAS") Equation.

The statement of an insect neurophysiologist/behaviourist (Roeder, 1967 p.128) that "The output of the motor neuron is a function of the sum of facilitation and inhibition from all the inputs ..." can be expressed in the form of the following proportionality:

$$m \propto e - i \qquad (1)$$

where m is the motor output, and e and i are total excitatory and inhibitory stimuli (respectively). Proportionality (1) can be broken down into

$$m \propto s \qquad (2)$$

where s is the net stimulus, and

$$s = e - i \qquad (3)$$

Excitatory chromatic alightment stimuli for T.erytreae are produced by ultraviolet (UV) and yellow-green (YG) light (Figs 28-30), and their effect on alightment is one of summation (as demonstrated by the optical mixing of the light from colour filters UV_3 and YG_4 (recorded in Fig. 29a), so that

$$e = YG + UV \qquad (4)$$

The only known inhibitory chromatic alightment stimulus for T.erytreae is produced by blue (B) light (Figs 28-30), thus

$$i = B \qquad (5)$$

Substituting equations (4) and (5) in equation (3), we have

$$s = YG + UV - B \tag{6}$$

which may be written

$$RAS = YG + UV - B \tag{7}$$

where "RAS" is an abbreviation for the apparent chromatic "relative alightment stimulus" for T.erytreae, and YG, UV and B are the stimuli resulting from neural integration of the photic inputs to the YG, UV and B receptor systems, which are described more fully in equations (14a-c). Only values $\geqslant 0$ are permitted for each of the four terms of equation (7) because they refer ultimately to neurone impulse frequencies, which cannot be negative; if the values work out (in equations (14a-c) or (14d-f)) to be negative, they are taken as zero.

Photic inputs must be dealt with in quanta, because photochemical processes are quantum phenomena (Seliger & McElroy, 1965). The physiologically-important quantum flux emitted by the target, and which impinges on each receptor system, is given by

$$q = \int_{300}^{700} Q(\lambda)d\lambda \tag{8a}$$

where q is the total absolute UV+visible quantum flux, expressed in the units quanta.s^{-1}.mm^{-2} , and $Q(\lambda)$ is the absolute spectral distribution of quanta, which, in practice, is expressed as a step-function (of wavelength) in quanta.s^{-1}.mm^{-2}.$10nm^{-1}$ (where the "10nm" refers to a wavelength interval) and is evaluated as a finite sum of areas over 10-nm waveband intervals, e.g. over the wavelength range 300-700 nm

$$q = \sum_{i=0}^{39} Q(305 + 10i) \ . \ (10) \tag{8b}$$

where the "10" refers to the 10-nm waveband interval. The spectral distribution of quanta emitted by the target comes from

$$Q(\lambda) = I(\lambda) \ . \ D(\lambda) \tag{9}$$

where $I(\lambda)$ is the absolute spectral distribution of quanta in the illuminant (quanta.s^{-1}.mm^{-2}.$10nm^{-1}$) calculated as demonstrated in Table 4 (facing p.15), and $D(\lambda)$ is the diffuse reflectance spectrum of an opaque surface or the transmittance spectrum of a translucent surface illuminated from behind (%.10^{-2}). Substituting equation (9) in equation (8a) we have

$$q = \int I(\lambda)D(\lambda)d\lambda \tag{10}$$

The incident quantum flux, q, (of equation (10)) is modified by integration with the spectral sensitivity, $R(\lambda)$, of each receptor. Thus, the quantum flux that can be sensed by that receptor, q', is given by

$$q' = \int I(\lambda)D(\lambda)R(\lambda)d\lambda \tag{11}$$

A logarithmic transformation is necessary, because phototaxis of T.erytreae (like retinal electrophysiological responses generally) is a linear function of the logarithm of incident quantum flux (Figs 24 & 29a). In his contribution to a symposium on the Mechanisms of Colour Discrimination, Rushton (1960) noted that "... quite early in the electrophysiological process there is this logarithmic transformation and it is only after that, that the various interactions occur." The potential response, p, of the receptor system, therefore, is given by taking logs of equation (11) :

$$p = \log \int I(\lambda)D(\lambda)R(\lambda)d\lambda \qquad (12)$$

Phototactic responses of T.erytreae are subject to thresholds (Figs 24 & 29a). Thus, the actual response, r, of a receptor system is given by the value of equation (12) above the log of the threshold, i.e.

$$r = \log \int I(\lambda)D(\lambda)R(\lambda)d\lambda - \log T \qquad (13)$$

where T is the threshold of that receptor system, expressed in the same units as q and q' (not Q) i.e. quanta.s^{-1}.mm^{-2} .

The contribution to the net neuronal stimulus, s, (of equations (3) and (6)) that is produced by each receptor system, s', is described by the product of the actual receptor system response (equation (13)) and a weighting factor, which takes into account the different relative slopes of the intensity response functions of the different colour receptor systems (which might be due to different numbers of the receptor types or their axon terminals, leading, through neural integration, to different amounts of "gain" as demonstrated, for example, by Menzel (1974) in the neurones proximal to the retinula cells of the honey-bee). The product of the weighting factor, W, and equation (13) yields

$$s' = W \left(\log \int I(\lambda)D(\lambda)R(\lambda)d\lambda - \log T \right) \qquad (14)$$

Applying equation (14) to the three colour receptor systems of equation (7), we have

$$YG = W_y \left(\log \int I(\lambda)D(\lambda)R_y(\lambda)d\lambda - \log T_y \right) \qquad (14a)$$

$$UV = W_u \left(\log \int I(\lambda)D(\lambda)R_u(\lambda)d\lambda - \log T_u \right) \qquad (14b)$$

$$B = W_b \left(\log \int I(\lambda)D(\lambda)R_b(\lambda)d\lambda - \log T_b \right) \qquad (14c)$$

where the subscripts, y, u and b, refer to the (spectral sensitivity curves, thresholds and weighting factors of the) YG, UV and B receptor systems. Equations (14a-c) may be substituted in equation (7) to describe the apparent stimulus more fully.

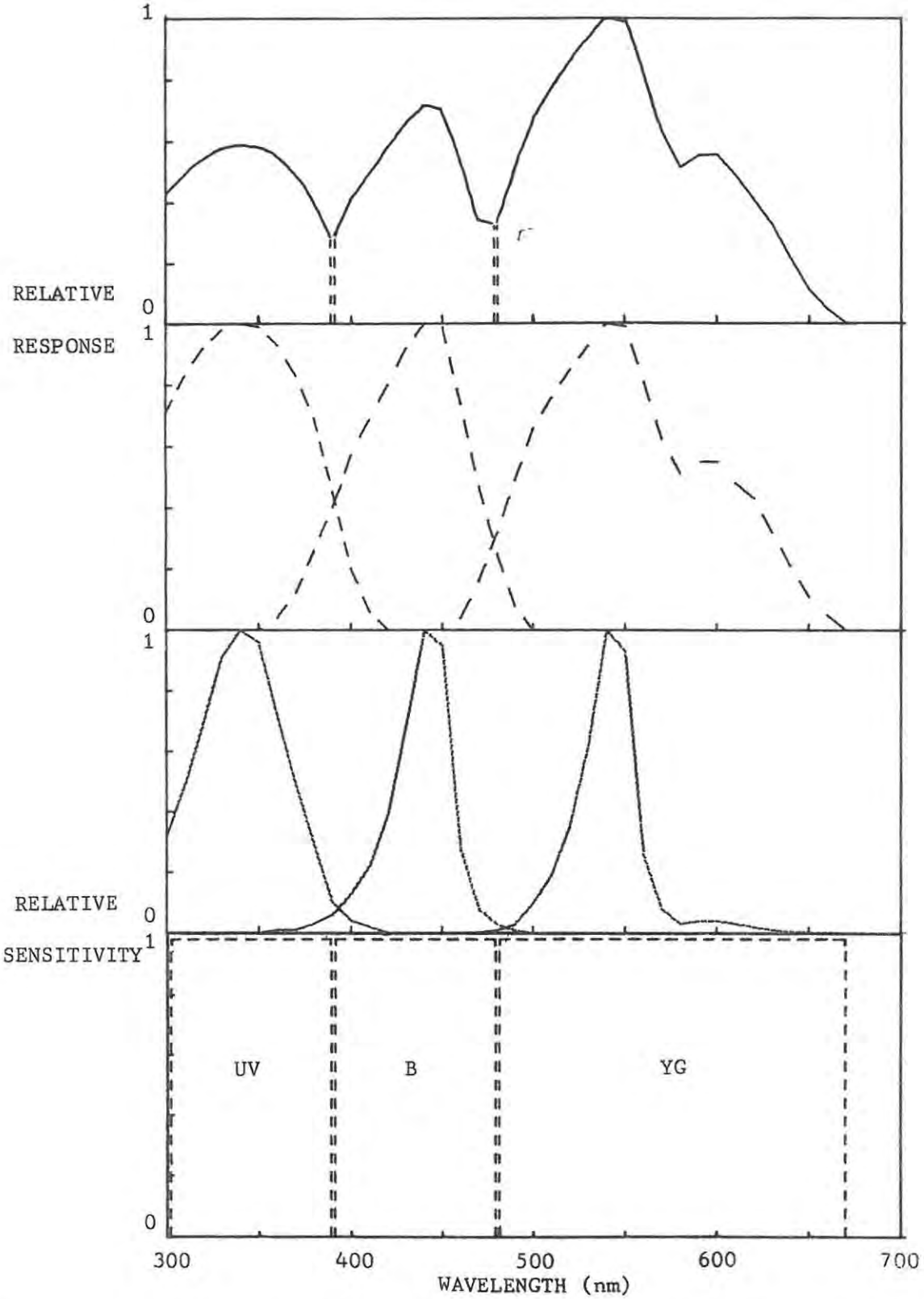

Fig. 31. Receptor spectral functions used in variations (listed in Table 8) of the "relative alightment stimulus" (RAS) equation. (a): Segments of the photo= tactic action spectrum (PAS) of T.erytreae (reproduced from Fig. 23a). (b): Extrapolated PAS peaks, with maxima of equal height. (c): Hypothetical receptor sensitivity curves, calculated from (b) and the intensity-dependence function (Fig. 24) as described in the text. (d): Square-wave receptor sensitivity functions used in the basic RAS equation.

Spectral sensitivity is defined as the reciprocal of the quantum flux necessary to produce a response of uniform magnitude at different wavelengths, expressed as a percentage of the maximum sensitivity (e.g. Autrum & von Zwehl, 1964). The closest approximation that could be obtained to the spectral sensitivity curves of the colour receptors of T.erytreae in the present work, was (i) that given in Fig. 31c. These hypothetical curves were obtained by the method of Autrum & von Zwehl (1964) from the extrapolated peaks (Fig. 31b) of the phototactic action spectrum (PAS) (Fig. 31a) (which is a graph of "relative effectiveness" of photic stimuli of uniform size) and the intensity-dependence function (Fig. 24). (This procedure sharpens the peaks but does not reduce the total wavelength range of receptor sensitivity). The curves are hypothetical because the procedure requires response spectra of individual receptor cells (not of populations of animals as in Fig. 23 = Fig. 31a), and intensity-dependence functions of each receptor type (not only of one type as in Fig. 24). The hypothetical receptor sensitivity curves calculated here were used to compute the RAS equation values of series of surfaces for conditions 9 and 14 of Table 9. Other spectral functions used as receptor sensitivity approximations were (ii) spectrally-contiguous segments of the PAS (shown in Fig. 31a) (used for Table 9 conditions 7, 8, 12 & 13); (iii) spectrally-overlapping PAS peaks (Fig. 31b) (Table 9, conditions 2 & 4); and, usually, (iv) spectrally-contiguous square-wave segments of the spectrum (Fig. 31d), which, in effect, assumed the spectral sensitivities of the receptors to be maximal and their ranges to be constricted (and was used in Table 9, conditions 1, 3, 5, 6, 10 & 11). Trioza erytreae's visible spectrum effectively covered the wavelength range 300-670 nm (Fig. 23). (Receptor sensitivity below 300 nm was not dealt with because it has no ecological relevance: that part of sunlight is absorbed before reaching the earth's surface (Robinson, 1966, cited by Goldsmith & Fernandez, 1968b)). On the grounds of the PAS (Fig. 23 = 31a), the usual ranges of the square-wave "receptors" were UV: 300-390 nm; B: 390-480 nm; YG: 480-670 nm (Fig. 31d) (though YG: 480-640 nm was also tested, because phototaxis at wavelengths greater than 640 nm was not statistically significant (Fig. 23b)). Weighting factors were all taken to be 1,0 in the case of the citrus psylla because the intensity response functions of T.erytreae were of apparently equal slope in the case of the UV and the YG receptor systems (Fig. 29a) (and there was no information on the relative slope of the intensity response function of the B receptor system). In the case of targets evaluated under the "usual" receptor conditions (Table 9, condition 5) the relevant stimuli described by equations (14a-c) were, therefore,

$$YG = \log \int_{480}^{670} I(\lambda)D(\lambda)d\lambda \quad - \log T_y \qquad (14d)$$

$$UV = \log \int_{300}^{390} I(\lambda)D(\lambda)d\lambda \quad - \log T_u \qquad (14e)$$

$$B = \log \int_{390}^{480} I(\lambda)D(\lambda)d\lambda \quad - \log T_b \qquad (14f)$$

Table 6. Example of calculation of the "relative alightment stimulus-" ("RAS-") equation value of a surface. In this example, the surface is lead-white (PbW) inside the choice-chamber in lab 1, and the component equations (14d-f) of the RAS equation (7) are evaluated in the manner of equation (8b) under the "usual" conditions (given in Table 9, condition 5). Column 1: For purposes of calculation, the spectrum was divided into 10-nm waveband segments; 2: Step-function AQ1 of Fig. 5, calculated as shown in Table 4 (opposite p.15); 3: Curve "100 PbW" of Figs 13d, 14d and 15d, determined by spectrophotometer; 4 = 2.3; 5 = Σ4.(10 nm) in relevant colour range (given); 6 = log 5; 7: From Fig. 29a, assuming alightment response threshold to blue light, T_b, is midway between T_u and T_y, and that all vary in direct proportion to log total ambient light intensity at the intensities used (therefore thresholds in choice-chamber in lab 1 = the Fig. 29a values minus 0,45); 8: Value $\geq$0 of 6-7, and final calculation of "RAS equation" value.

Wave-length, centre of 10-nm band (nm)	Absolute quantum flux in chamber ($.10^9$ quanta $.s^{-1}.mm^{-2}.10nm^{-1}$)	Diffuse reflectance of PbW surface (%=10^{-2})	Absolute quantum flux reflected ($.10^7$ quanta $.s^{-1}.mm^{-2}$) per band ($.10nm^{-1}$)	Absolute quantum flux reflected in colour range	Absolute quantum flux reflected (log of light intensity measured in quanta.$s^{-1}.mm^{-2}$)	Threshold (T) of response to colour	Flux above threshold
1	2	3	4	5	6	7	8
305	0,000	3,43	0,00				
315	0,027	3,43	0,09				
325	0,000	3,51	0,00				
335	0,022	4,03	0,09				
345	0,022	14,13	0,31	300-			
355	0,022	32,36	0,71	390nm			
365	0,187	41,98	7,85	(UV	(in UV	T_u=	
375	0,125	50,70	6,34	range)	range)		UV=
385	0,258	57,81	14,91	30,30	8,481	9,19	0,000
395	0,627	63,68	40				
405	7,308	68,87	503				
415	4,977	72,11	359				
425	5,267	74,13	390				
435	33,864	76,74	2599	390-			
445	10,480	77,63	814	480nm			
455	13,967	79,43	1109	(blue	(in blue	T_b=	
465	17,036	81,28	1385	range)	range)		B=
475	19,741	81,85	1616	8815	10,945	9,54	1,405
485	21,796	82,22	1792				
495	23,455	82,22	1928				
505	24,687	83,18	2053				
515	26,609	83,56	2223				
525	30,332	84,33	2558				"Relative alightment stimulus" RAS= YG+UV-B = 2,000 + 0,000 - 1,405 = 0,595
535	34,300	84,72	2906				
545	85,048	84,14	7156				
555	65,365	83,18	5437				
565	78,323	83,18	6515				
575	98,259	83,18	8173				
585	89,496	83,18	7444				
595	87,797	83,18	7303				
605	74,844	83,18	6226				
615	57,439	83,18	4778	480-			
625	40,460	83,18	3365	670nm			
635	32,044	83,18	2665	(yellow-			
645	26,533	82,22	2182	green	(in YG	T_y=	
655	20,292	81,28	1649	range)	range)		YG=
665	15,875	81,28	1290	77643	11,890	9,89	2,000

The threshold of the B receptor system was evidently below $10^{11,3}$ at an ambient light intensity (within T.erytreae's visible spectrum) of $10^{12,56}$ quanta.s^{-1}.mm^{-2}, because of the full alightment inhibition obtained by optical mixing of light from filter B_2 at this intensity, with that from filter YG_3 (Fig. 29a). In the absence of more accurate information, the threshold of the B receptor system was taken to be either midway between those of the UV and YG receptor systems demonstrated in Fig. 29a (Table 9, conditions 1, 2, 5-9) or equal to that of the UV receptor system (Table 9, conditions 3, 4, 10-14). Another point concerning thresholds is their variation with ambient light intensity. The logarithm of the test flash intensity required to produce an arthropod retinal electrophysiological response of constant magnitude, was found to increase approximately linearly with log of adapting light intensity (Ruck, 1958), which indicated that the threshold rises in linear relation to the adapting light intensity, when both are expressed in log units. It was usually assumed, therefore (Table 9, conditions 5-14), that the retinal thresholds of T.erytreae, expressed in log terms, vary in direct proportion to the log of the total ambient light intensity (in the psyllid's visual spectrum) at intensities near those of Fig. 29a (and, therefore, to be 0,45 lower in the choice-chamber in lab 1 than in that in lab 2). (It was appreciated that the thresholds would also presumably alter with the physiological state of the psyllids, e.g. with the amount of energy they have recently expended in flight, as discussed in Chap. 5).

A worked example of the method of calculation of the "RAS equation" value of a surface is presented in Table 6. In this example, the RAS equation value is calculated under the "usual" conditions (Table 9, condition 5), namely using equations (14d-f) for substitution in equation (7), each of the integrals being evaluated as a summation as shown in equation (8b).

The RAS equation values of series of target surfaces calculated in this manner were tested for degree of correlation with the alightment distributions of T.erytreae on those surfaces, as described in the following section.

6.2 Coefficients of Determination.

Listed in Table 7 are the signs of the slopes and the goodness-of-fit (r^2) values of the linear regressions of T.erytreae alightment frequency against various colour parameters of series of target surfaces presented. In spite of the fact that Moericke and Kennedy did not consider reflectance and total energy (respectively) suitable colour parameters to use in the description of homopteran alightment preferences, they are included in Table 7 for comparison and completeness.

In the case of colour filter targets (Table 7, part a) goodness of fit of alightment both with purity and with reflectance was very poor (r^2 = 0,177 and 0,018). Human-based colour assessment of these stimuli was inappropriate because

Table 7. Sign of slope of linear regression of T.erytreae alightment frequency against each of 5 colour parameters (listed below) of several choice test series of (a) colour filters, (b) leaves, and (c) painted targets, and coefficient of determination (r^2) of regression. (f): Also given, in the case of 3 colour parameters, is the coefficient of variation (CV) of the r^2 values. Colour parameters were: PUR = purity, REFL = reflectance, (human colour parameters, used by Moericke); L/S = long/short ratio, T.E. = total energy (aphid colour parameters, formulated by Kennedy et al., 1961); RAS = relative alightment stimulus equation (derived in the present study, Section 6.1) and evaluated for condition 5 of Table 8. CF = colour filter; Y = yellow; G = green; R = red; PbW = lead-white; Blk = black; LH = leaf hue; Kodak = visible spectrum print.

Part	Target choice or test statistic	Fig.	Sign of slope of linear regression and coefficient of determination (r^2) of alightment frequency of T.erytreae against the following colour parameters of the series of surfaces presented.				
			Moericke		Kennedy		Present study
			PUR.	REFL.	L/S	T.E.	RAS
a	9CF's "basic"	26a & 28	+ 0,222	+ 0,002	+ 0,290	+ 0,002	+ 0,882
	10CF's "mixer"	26b & 29	+ 0,132	+ 0,034	+ 0,002	+ 0,001	+ 0,684
	Mean r^2 for CF targets		+ 0,177	+ 0,018	+ 0,146	+ 0,002	+ 0,783
b	Flush vs. mature	8	+ 0,718	+ 0,515	+ 0,672	+ 0,503	+ 0,649
	YG versus R flush	10	+ 0,586	+ 0,441	+ 0,793	+ 0,0003	+ 0,768
	Mean r^2 for leaves		+ 0,655	+ 0,480	+ 0,730	+ 0,250	+ 0,709
c	Kodak spectrum	11	+ 0,323	+ 0,837	+ 0,618	+ 0,815	+ 0,606
	G-to-Y	12	+ 0,825	+ 0,983	+ 0,995	+ 0,979	+ 0,949
	G-to-PbW	13	+ 0,581	- 0,655	+ 0,539	- 0,654	+ 0,796
	Blk-to-Y-to-PbW	14	+ 0,545	+ 0,169	+ 0,574	+ 0,126	+ 0,651
	Y-to-PbW	15	+ 0,956	- 0,948	+ 0,726	- 0,980	+ 0,984
	LH series	16	+ 0,723	+ 0,039	+ 0,944	+ 0,017	+ 0,814
	Mean r^2 for paints		+ 0,659	-------	+ 0,733	-------	+ 0,800
d	Mean r^2 leaves & paints		+ 0,657	-------	+ 0,733	-------	+ 0,777
e	Mean r^2 overall		+ 0,561	-------	+ 0,615	-------	+ 0,778
f	CV (%) leaves & paints		29,4	-------	22,9	-------	17,9
	CV (%) overall		47,3	-------	48,1	-------	16,9

it did not take into account the UV light (sometimes a major portion of the colour filter stimulus (Figs 28b & 29b)) to which the insects were highly responsive (Figs 28a & 29a). Correlation of alightment with long/short ratio and total energy of colour filter targets was also very poor (r^2 = 0,146 and 0,002). It was noted earlier (consideration of Fig. 28) that alightment frequency was completely unrelated to intensity of the group of assorted colour filter stimuli. The long/short ratio was unsuitable because it takes the UV light to be "repellent" rather than attractive (as well as for other reasons mentioned in the introduction to this chapter). Correlation of alightment with values of the "relative alightment stimulus-" or "RAS equation" was comparatively good (r^2 = 0,783). The comparatively good correlation of T.erytreae alightment frequency with RAS equation values of the colour filter targets, however, was open to the serious criticism that it could possibly simply have been a result of circular reasoning, because the RAS equation itself was partly derived from the colour filter results. It was essential, therefore, to test the RAS equation on the results of leaf and paint choice tests performed earlier.

In the case of leaf and painted targets, the alightment frequency of T.erytreae was sometimes highly positively correlated with reflectance and total energy (e.g. the Kodak spectrum : r^2 = 0,837 & 0,815 ; the G-to-Y paint series : r^2 = 0,983 & 0,979 ; Table 7 part c), but the slope of the regression was actually negative in two series (G-to-PbW, Y-to-PbW), with fair to high correlation, which indicated that neither reflectance alone, nor total energy alone, could have been T.erytreae's alightment stimulus. Alightment was positively correlated with purity, long/short ratio and RAS equation values in all series; the "goodness of fit" of alightment frequency against these colour parameters averaged, respectively, at 0,657 , 0,733 and 0,777 (Table 7 part d) considering leaf and paint targets only, or at 0,561 , 0,615 and 0,778 (Table 7 part e) when colour filter targets were included.

Coefficients of variation of the r^2 values (Table 7 part f) showed that the degree of correlation was highly variable (17-48 %). The variability using the RAS equation, however, was 0,68 (considering leaf and paint targets) or 0,35 (including colour filter targets) as great as the variability using purity or long/short ratio; i.e. correlation of alightment frequency was most consistent with the RAS equation colour parameter.

Correlation of the alightment distribution of T.erytreae on leaf choices and paint series with the RAS equation values of those surfaces did not vary markedly in the variety of conditions for which the RAS equation values were calculated (Table 8). The correlation was slightly less good than average when the alightment thresholds derived from the colour filter experiments in lab 2 (Fig. 29a) were applied to the alightment experiments done in lab 1 without any allowance for the lower environmental light intensity in the choice-chamber in lab 1 (Table 8, conditions 1 & 2). When

Table 8. Mean coefficient of determination (r^2) of linear regressions of T.erytreae alightment frequency against the "relative alightment stimulus-" i.e. "RAS equation" colour parameter values of several leaf choices and paint series, given in Table 7, calculated for various conditions, 1-14. All regressions treated here were of positive slope. Alightment thresholds are expressed in log of light intensity measured in quanta.$s^{-1}.mm^{-2}$. PAS = phototactic action spectrum (Fig. 23 reproduced as Fig. 31a); Extrapolated PAS peaks (Fig. 31b) had overlapping ranges. Hypothetical receptor sensitivity curves (Fig. 31c) were obtained from extrapolated PAS peaks and the intensity-dependence function (Fig. 24) as explained in text. The square-wave receptor curves are given in Fig. 31d. Weighting factors (see Section 6.1) were taken always to be 1,0 . The results listed in Table 7 are from the RAS equation values calculated for condition number 5.

Condition number	Details of conditions for which RAS equation values were calculated						r^2 value, mean of leaves & paints, alightment against RAS
	Lab	Threshold			Red end wave-length (nm)	Receptor curves (see Fig. 31)	
		T_u	T_b	T_y			
1	1 & 2	9,64	9,99	10,34	670	Square-wave	0,605
2	"	"	"	"	"	Extrapolated PAS peaks	0,603
3	"	"	9,64	"	"	Square-wave	0,800
4	"	"	"	"	"	Extrapolated PAS peaks	0,807
5	1	9,19	9,54	9,89	"		
	2	9,64	9,99	10,34	"	Square-wave	0,777
6	1 & 2	As condition 5			640	"	0,781
7	"	"	"	"	"	Segments of PAS	0,754
8	"	"	"	"	670	" " "	0,752
9	"	"	"	"	"	Hypothetical sensitivity	0,764
10	1	9,19	9,19	9,89	"		
	2	9,64	9,64	10,34	"	Square-wave	0,738
11	1 & 2	As condition 10			640	"	0,746
12	"	"	"	"	"	Segments of PAS	0,767
13	"	"	"	"	670	" " "	0,774
14	"	"	"	"	"	Hypothetical sensitivity	0,796

the hypothetical response threshold to blue radiation (T_b) was taken as being the same as the UV threshold (9,64 in lab 2) rather than midway between the UV and YG thresholds (i.e. 9,99 in lab 2), the correlation was slightly better than average (Table 8, conditions 3 & 4). Both possible positions of the B threshold were tested in subsequent conditions (5-14) in which all thresholds were taken to vary in direct proportion to total ambient light intensity. Receptor sensitivity curves were taken, under different conditions (described in Fig. 31) to be either flat, or to vary according to those segments of the phototactic action spectrum, or to have a form as calculated by the method of Autrum and von Zwehl (1964) from the extrapolated peaks of the phototactic action spectrum and the intensity-dependence function (taken to be applicable to all receptors). All the conditions (1-14) under which the RAS equation values were calculated yielded coefficients of determination of approximately 0,75 , i.e. about 75 % of the observed variation in alightment frequencies could be attributed to the variation in the RAS equation values of the surfaces presented.

The theoretical applicability of the basic RAS equation to other Homoptera was examined using data published by Moericke (1955c, 1969), on alightment distributions of a "yellow-sensitive" (Aphis fabae) and a "non-yellow-sensitive" aphid species (Hyalopterus pruni) on leaf and painted surfaces in relation to the diffuse reflectance spectra of those surfaces. Because Moericke's experiments were conducted in the field, colours were evaluated with respect to the spectral emission curve of average European spring sunlight (given by Kennedy et al., 1961, from Moon, 1940). In addition, it was assumed that the colour filters used by Moericke were 2 mm thick and had transmission spectra as given in the relevant catalogue (Schott, 1970). Moericke's data are re-presented in Figs 32b, c & 33b, c , along with the RAS equation values of the surfaces (Figs 32a & 33a) calculated under the trial threshold and weighting factor conditions specified for each species in Table 9A. The trial threshold values were chosen as follows. The wavelength ranges relevant to the aphids' colour vision were taken to be the same as for T.erytreae, on the grounds of the hypothesis of qualitative homogeneity of homopteran colour response (the evidence for which was cited on p.56). The log of the quantum flux reflected in each of the 3 spectral regions was calculated for selected surfaces, and the log values of the trial thresholds were chosen empirically so as to adjust the size of the (log intensity - log threshold) values in a manner which resulted in RAS equation values that were approximately proportional to the published relative alightment frequencies on those surfaces.

The linear regressions of alightment frequency of each species of aphid against the calculated RAS equation values of the target surfaces all had positive slopes. From Table 9B it is seen that the different observed alightment distributions of A.fabae and H.pruni were each about 78 % "explained" by the RAS equation values

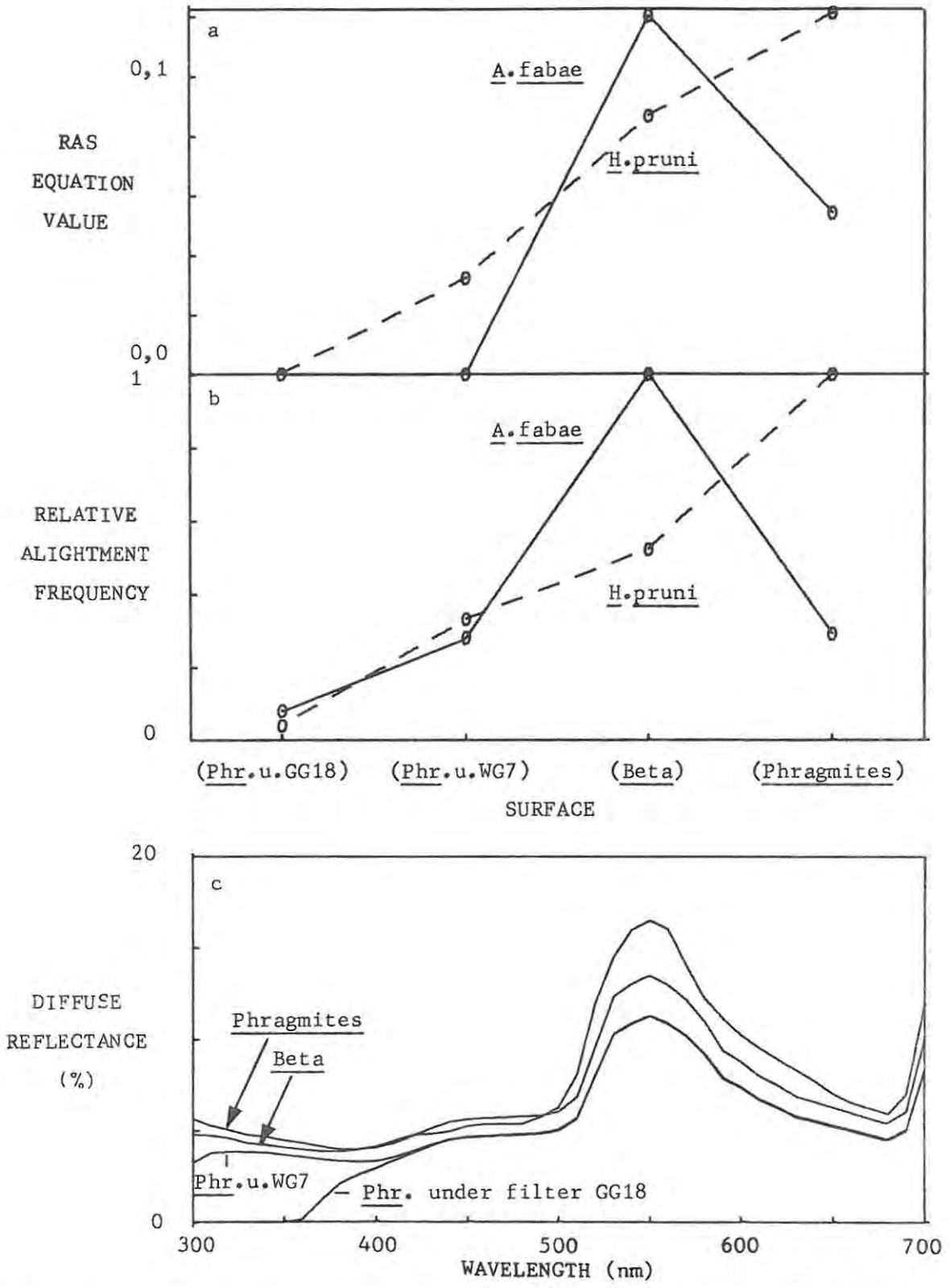

Fig. 32. (b): Relative alightment frequency of Aphis fabae and Hyalopterus pruni on Phragmites or Beta leaves presented either fully exposed or under (u.) Schott colour filter WG7 or GG18, in relation to their diffuse reflectance spectra (c) (b and c from Moericke, 1955c, 1969). (a): "Relative alightment stimulus" (RAS) equation values of the surfaces, calculated under the sunlight spectrum (given by Kennedy et al., 1961, from Moon, 1940) and hypothetical threshold and weighting factor conditions for each species (given in Table 10a) in an attempt to "explain" the different experimentally-determined alightment distributions.

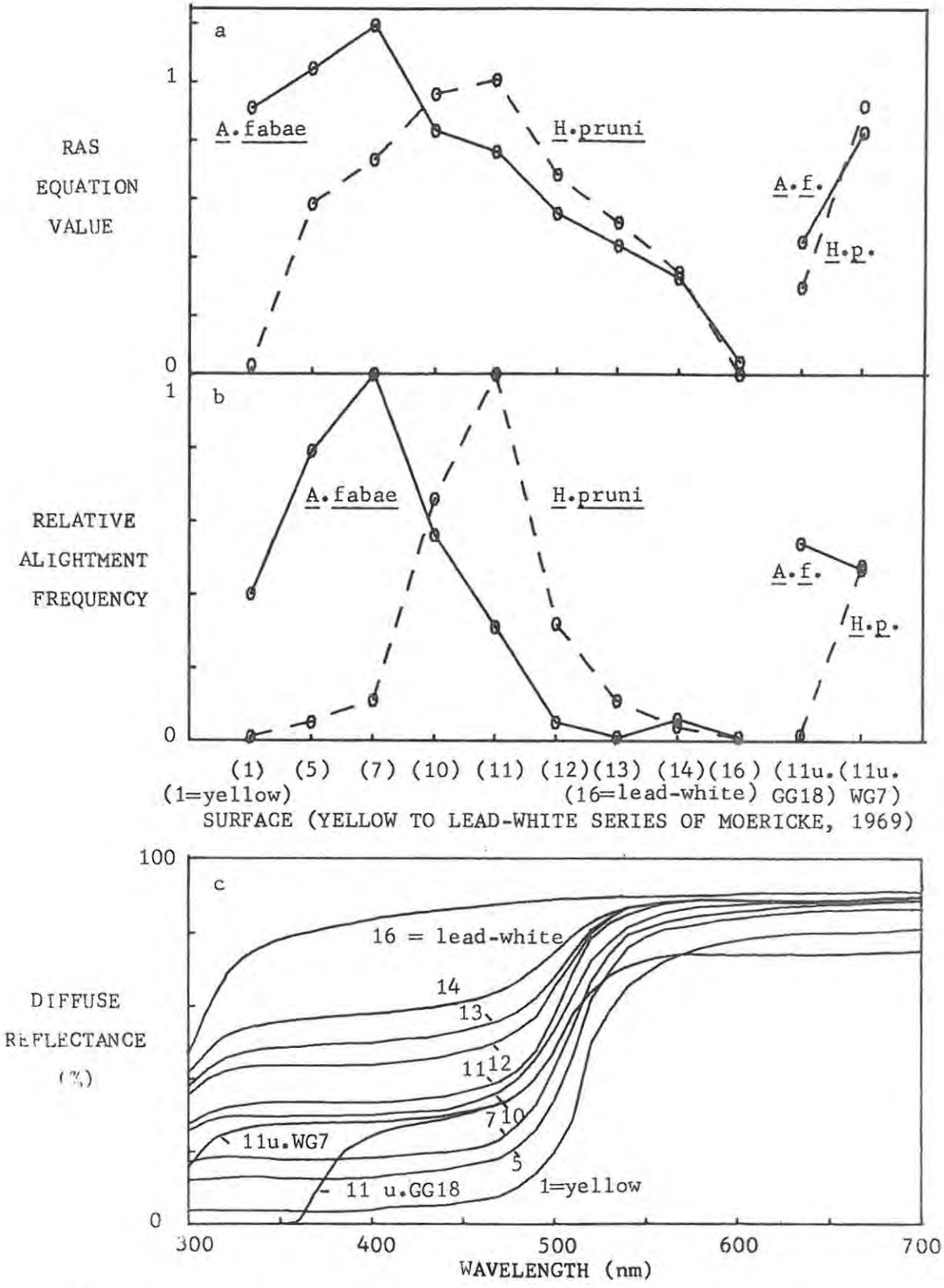

Fig. 33. (b): Relative alightment frequency of Aphis fabae and Hyalopterus pruni on a series of painted surfaces ranging in colour from yellow (surface number 1) to lead-white (16) presented either fully exposed or under (u.) Schott colour filter WG7 or GG18, in relation to their diffuse reflectance spectra (c) (b and c from Moericke, 1969). (a): "Relative alightment stimulus" (RAS) equation values of the surfaces calculated under the sunlight spectrum (given by Kennedy et al., 1961, from Moon, 1940) and hypothetical threshold and weighting factor conditions for each species (given in Table 10a) in an attempt to "explain" the different experimentally-determined alightment distributions.

Table 9. A: Details of trial conditions, chosen as described in the text, used for calculating "relative alightment stimulus-" i.e. "RAS equation" values of surfaces exposed to "yellow-sensitive" Aphis fabae and "non-yellow-sensitive" Hyalopterus pruni in alightment preference studies by Moericke (1955c, 1969). Thresholds (T) are in log of light intensity measured in quanta.$s^{-1}.mm^{-2}$. u = ultraviolet; b = blue; y = yellow-green region of the spectrum. Weighting factor (W) was applied to log of light intensity minus log of threshold.

B: Coefficient of determination (r^2) of aphid alightment frequency against RAS equation values of the surfaces presented. Slope of linear regression was always positive.

A Species	Details of conditions for which RAS equation values were calculated					
	Threshold			Weighting factor		
	T_u	T_b	T_y	W_u	W_b	W_y
Aphis fabae	14,40	15,50	15,70	1,0	3,0	1,0
Hyalopterus pruni	13,90	15,75	16,70	1,0	4,0	1,0

B Target	r^2 value			
	A.fabae conditions		H.pruni conditions	
	A.fabae alightment	H.pruni alightment	A.fabae alightment	H.pruni alightment
Leaves + Filters	0,856	0,247	0,230	0,935
Y-to-PbW paints	0,707	0,055	0,109	0,650
Mean for leaves & paints	0,782	0,151	0,170	0,793

calculated for the trial threshold and weighting factor conditions (Table 9A) applic= able to that particular species. At the same time, an average of only ca. 16 % of the observed alightment distribution of each species could be attributed to the RAS equation values calculated for the other species, i.e. using "fabae" thresholds for examining H.pruni's alightment distribution, and vice versa (Table 9B). This sup= ported the indication from Figs. 32 and 33 that RAS equation values can, theoreti= cally, possess a considerable degree of species specificity.

Discussion (correlation).

Merits of the "RAS" equation. One of the most valuable contributions by Kennedy et al. (1961) was their indication of the manner in which a colour parameter relevant to Homoptera could be derived from a knowledge of homopteran colour responses. The "relative alightment stimulus-" or "RAS equation" alightment colour parameter was (i) physiologically sound as regards T.erytreae, and perhaps other Homoptera, because it was derived from the fundamental knowledge of T.erytreae's visual physiology as related to alightment behaviour (produced by this study). Consequently, the RAS equation provided a (ii) more accurate and (iii) more consis= tent description (i.e. explanation and/or prediction) of the alightment distributions of T.erytreae than that provided by previously-available colour parameters. Use of the RAS equation rather than other colour parameters lead to slight improvement of correlation between alightment frequency and target colour parameter value in the case of leaves and paints (Table 7, part d), which did not reflect physiologically-sensible amounts of UV light in the choice-chamber environment (as is apparent from the lead-white surface in this situation, given in column 8 of Table 6), and to marked improvement in the case of colour filter targets (Table 7, part a), which did emit physiologically-sensible amounts of UV light (as is apparent from Figs 28 & 29). About three-quarters of the observed variation in alightment frequency of T.erytreae was accounted for by the linear regression of the RAS equation values of the targets; the explanation and/or prediction value is, therefore, fair, although there is still much scope for refinement.

The possibility of refinement of the RAS equation by incorporation of (i) a saturation intensity effect was tested briefly. The alightment results of Figs 17 , 28a and 29a suggested that under a given set of environmental conditions, each of the photoreceptor systems might be subject not only to a threshold intensity but also to a saturation intensity, the latter approximately 1,2 log units above the former. This possibility was tested on 2 paint series exposed in lab 1: these were evaluated under condition 5 of Table 8 (including appropriate saturation intensities), and compared with the evaluation under the unmodified condition. The coefficient of determination (r^2) of the linear regression of alightment frequency against colour parameter changed from 0,993 to 0,9901 in the case of the yellow-to-lead-white series, and 0,842 to 0,8415 in the case of the leaf-hue series. Thus a saturation

intensity effect, which had not appeared in walking phototaxis experiments (Fig. 24), did not seem to be involved in alightment responses. The light coming from the colour filter targets (as observed with the environment room lights switched off) was in the form of a (spatially-restricted) cone, rather than a (spatially-unrestricted) hemisphere: alightment frequency saturated at 30-40 psyllids (more than during the control) in the "basic" apparatus (Fig. 28a) in which the cone of light was rather narrow (Fig. 26a), compared with 40-50 psyllids in the "colour-mixing" apparatus (Fig. 29a) in which the cone was about 3 times as broad due to the light diffuser being closer to the target (Fig. 26b). "Saturation" effects, therefore, appeared to be an artifact of the experimental set-up.

Other possible points of refinement of the basic RAS equation would be the incorporation of (ii) the electrophysiologically-determined spectral sensitivity curve of each type of colour receptor; (iii) the behaviourally-determined weighting factor, i.e. intensity response function, of each receptor type; (iv) the effect of ambient light intensity (which affects the strength of a colour preference (Fig. 17) and suggests that the threshold of response to different colours might not rise in direct proportion to total ambient light intensity); (v) the effect of angle subtended by the targets (which also affects the strength of a colour preference (Fig. 18)); (vi) the optomotor stimulus (which is a factor influencing the alightment responses of homopterans to surfaces (Kennedy et al., 1961; Kennedy & Ludlow, 1974), which was seen in the "edge effect" of alightments by T.erytreae (Section 2.2), and which depends upon visual contrast between the object and its surroundings); and (vii) the flight stimulus (of the (incident) environmental lighting, which competes with the alightment stimulus of the (light reflected from) coloured targets, flying homopterans being in a state of "... uneasy balance between the upward pull of the sky light and the downward pull of the ... light from plants and soil ..." (Kennedy et al., 1961; Kennedy & Fosbrooke, 1973)).

Applicability of the RAS equation to other Homoptera. The basic (unrefined) RAS equation is, nevertheless, evidently theoretically able to explain the different alightment distributions both of "yellow-sensitive" and of "non-yellow-sensitive" Homoptera, under threshold and weighting factor conditions applicable to each species in the test situation (Table 9). It should be stressed that only further research, in particular the experimental determination of species-specific thresholds of the alightment response to UV and to YG light and of alightment-inhibition by B light under measured environmental intensity, could support or disprove this hypothesis of general homopteran applicability of the RAS equation as a description of the alightment colour stimulus.

DISCUSSION (GENERAL)

A short resumé is necessary at this point, to draw together the main findings presented and discussed in the previous sections.

Choice-chamber experiments demonstrated that the colour of light green (Class B) flush leaves stimulated flying T.erytreae to alight about 2-3 times as frequently as did the colour of dark green mature leaves (Fig. 8c). Young (Class A) flush, to which T.erytreae's oviposition is restricted, was much the same colour as expanded (Class B) flush (Fig. 7a, b), but would present a weaker alightment stimulus due to its smaller size (Fig. 18). It was therefore hypothesized that, in the field, T.erytreae in dispersal or trivial flight probably use Class B flush as a visual "flare" en route to the Class A flush oviposition site. Pest control techniques for the citrus psylla involving alightment and colour could be rationally designed only after understanding the basis of such alightment colour preference behaviour.

The mechanism underlying T.erytreae's alightment colour preferences was not immediately clear, because the relative alightment frequency of the citrus psylla was not consistently highly positively correlated with any of the human or aphid colour parameters which had been used previously in describing the alightment colour preferences of Homoptera. Alightment frequency was sometimes correlated negatively with "dominant wavelength" (Fig. 10), and "reflectance" and "total energy" (Figs 13 & 15; Table 7 part c) which rules out the possibility that any one of these parameters alone was responsible for T.erytreae's alightment preferences. Alightment frequency was always correlated positively with "purity" and "long/short ratio", but sometimes very well (Figs 12, 15 & 16; Table 7 part c) and at other times rather poorly (Figs 11, 13 & 14; Table 7c) which cast doubt on the possibility that either of these colour parameters alone accurately described the alightment stimulus. To formulate a colour parameter of more reliable explanatory and/or predictive value for alightment of T.erytreae, it was therefore necessary to investigate fundamental aspects of T.erytreae's visual physiology as related to alightment behaviour.

Trioza erytreae showed peak phototactic responsiveness, by walking, at 3 wavelengths in its visible spectrum (Fig. 23). When light stimuli of these 3 colours were presented individually or in various combinations, it was found that UV and yellow-green (YG) light both stimulated alightment, above different thresholds, in an additive manner, and that blue (B) light inhibited alightment in combination with either of the former colours (Figs 28 & 29). These results demonstrated that T.erytreae has trichromatic colour vision. The above information was used to formulate a new colour parameter, the "relative alightment stimulus-" or "RAS equation", to describe the relative alightment-inducing strengths of coloured targets:-

$$RAS = YG + UV - B$$

where each colour refers to a weighted logarithm of the quantum flux (because phototaxis of T.erytreae was a linear function of the logarithm of the stimulus quantum flux (Fig. 24)) in the appropriate waveband of the spectrum, minus the logarithm of the relevant colour threshold.

The RAS equation values (part c of Figs 8 & 10-16) of leaf and artificial surfaces presented in choice tests, obtained by evaluating the diffuse reflectance spectra (part d of Figs 8 & 10-16) under the absolute spectral distribution of quanta in the choice-chamber light (Fig. 5), "explained" about 78 % (Table 7 part d) of the variation in the alightment frequency of T.erytreae. Compared with the human and the aphid colour parameters, the RAS equation colour parameter had a more sound physiological basis as regards T.erytreae, and the "goodness-of-fit" with the observed alightment distributions of the citrus psylla was, on average, slightly improved (Table 7 part d) as well as more consistent (Table 7 part f). Marked improvement in goodness-of-fit was obtained in relation to (colour filter) targets which emitted physiologically-sensible amounts of UV light (Table 7 part a).

By suitable choice of (hypothetical) species-specific thresholds and weighting factors, it was shown that the same basic RAS equation derived for T.erytreae was able, theoretically, to explain alightment distributions (recorded in the literature) both of a "yellow-sensitive" and of a "non-yellow-sensitive" species of aphid (Table 9), which suggested that the RAS equation could have general homopteran applicability as a description of the alightment colour stimulus.

The economic relevance of this research is the topic that remains to be considered. Does the understanding of the basis of T.erytreae's alightment colour preferences suggest any possible alternative method(s) of citrus psylla control? In brief, the work suggests that 2 techniques merit consideration. The reasoning behind these techniques, as well as their likely pros and cons (i.e. factors in favour and factors against), are discussed below. It is important to appreciate at this stage that the greening mycoplasma is probably spread by psyllid carriers in the same manner as plant viruses are spread by winged aphids (as described by Kennedy, 1950), namely in a succession of take-off, flight, alightment and probing, repeated many times. Key considerations in the spread of such diseases are, therefore, the abundance and activity of the vector (Kennedy, loc. cit.). The present study has relevance to control methods based (as described by Kring, 1972) on reducing the numbers of the vector alighting on its economically-important host plants.

The first alternative method of pest control suggested by the work could be termed "flush-masking". By this is envisaged spraying flushing citrus trees a colour which is highly unattractive to psylla for alightment, so as to retard the rate of flush colonization and thus of flush infection and of subsequent psylla multiplication. Flush is visually preferred to mature leaves because of its greater RAS equation

value, assisted by its contrast with the background. The greater RAS equation value of flush is due to its greater reflectance in the yellow-green range (480-670 nm). Folsom (1927) and Moore (1935) found that treating crops with white dusts increased the infestation by two species of aphid, and that this was due to the increased intensity of reflected light (Moore, 1937). Moore (1937) found that it was possible to reduce the aphid infestation of cabbage, and the proportion of unmarketable heads, by 30-36 % , by adding carbon black to his insecticide dust. He concluded that "... present dusting and spraying practices on crops infested with aphids may be profitably modified by the use of dyed materials to produce a reduction in the intensity of light reflected from the treated surfaces."

At least 4 colour pigment treatments could reduce the RAS equation value of flush. (i) A coating of carbon black reduced the reflectance in the yellow-green range, which reduced the RAS equation value of a "leaf-hue" surface to 55-75 % and reduced alightment of T.erytreae to ca. 30 % (Fig. 16). (ii) A dark red pigment would presumably have a similar effect, because T.erytreae see poorly in the red (Fig. 23); thus red leaves had 35-55 % the RAS equation value of yellow-green leaves and elicited alightment ca. 55 % as strongly as the latter (Section 2.3). Similarly, red artificial surfaces compared with yellow-green (Fig. 11: Kodak axis positions 610, 650 & 690 compared with 555 "mμ") had ca. 83 , 78 & 38 % (respectively) the RAS equation value of the latter, and elicited ca. 36 , 21 & 18 % (respectively) as great an alightment frequency of T.erytreae as the latter. (iii) A blue pigment would presumably also have a similar effect, as blue light alone does not elicit alightment, and is alightment-inhibitory in combination with (leaf-like) yellow-green light (Figs 28 & 29); thus blue surfaces compared with yellow-green (Fig. 11: Kodak axis positions 485 , 450 & 410 compared with 555 "mμ") had ca. 12 , 0 and 9 % (respectively) the RAS equation value of the latter, and elicited alightment of T.erytreae ca. 16 , 13 & 9 % (respectively) as frequently as the latter. A reduction in alightment frequency, however, to ca. 50 % that on yellow-green might be more likely to result from a coating of blue pigment on the alightment-stimulatory yellow-green background of leaves. (iv) A white pigment that does not reflect UV light should decrease the RAS equation value of flush because the combination of blue and yellow-green light which this pigment would reflect, does not stimulate alightment (Figs 28 & 29). The white pigment used in the experiment with surfaces of "leaf hue" was magnesium oxide, which had a strong diffuse reflectance in the UV (Fig. 16d) but nevertheless did not reflect a physiologically-sensible amount of UV in the choice-chamber (not even the lead-white surface did so: Table 6, column 8), because the lab light contained virtually no UV (Fig. 5). A coating of white pigment, therefore, reduced the RAS equation value of a "leaf-hue" surface, and the alightment thereon, to ca. 30 % (Fig. 16c).

Possible adverse effects on the citrus tree, however, could arise from flush-

masking with pigments of various colours. It is commonly stated that a leaf coating of sooty mould, growing on the "honeydew" excreted by Homoptera, adversely affects photosynthesis (e.g. Hart et al., 1973), but this statement seems to be intuitive. In experimental studies, a reduction in light intensity to 13-30 % was found to make citrus leaves grow bigger, thinner, and lighter in weight per unit area and in colour (Monselise, 1951a, b), though the assimilation rate, which is presumably highly important for the fruit production rate, was not significantly altered. Citrus leaf assimilation rate reached saturation at an illuminance of ca. 25 000 lx (Kriedemann, 1968); bright sunlight is ca. 100 000 lx (Seliger & McElroy, 1965) which explains why a reduction in light intensity to ca. 25 % was found to not affect the assimilation rate. Of course, the dye coating would retard or halt the assimilation rate if it reduced light penetration to below 25 % or 1 %, respectively, because the compensation point of citrus is 1 000 to 2 000 lx (Possingham & Kriedemann, 1969). This problem seems unlikely to arise, however, because the heavier of the two carbon black coatings tested (Fig. 16: LH+C) did not reduce total reflected energy to quite 30 % .

Deleterious effects of flush-masking on leaf physiology seem more likely to arise from over-heating, particularly as a result of coating leaves with blue or black pigments. Diffuse reflectance of near-infrared radiation (700-1 400 nm) by citrus leaves is decreased markedly (from ca. 56 to ca. 33 or 16 %) by a sooty mould deposit (Hart & Myers, 1968). Resultant increased heat absorption seems likely to lead to excessive water stress, and might also completely inhibit growth because the upper temperature limit for growth of citrus is 38 ^{o}C (Webber, 1948, cited by Mendel, 1969), a temperature which in Africa can be reached in the shade during the spring and summer season of citrus flush production.

Another problem associated with flush-masking is anticipated from the experience of previous workers. A liquid whitewash (hydrated lime) "... with the same formula as that commonly used on citrus trees to prevent sunburn ..." was used to render groves unattractive to a leafhopper pest emigrating from dying herbaceous summer host plants in search of evergreen winter quarters (Woglum & Lewis, 1940). Initial results were promising: new growth and crop-setting appeared normal and the percentage of damaged fruit was reduced. Subsequently, however, drawbacks were noticed (Lewis, 1940). As the spraying programme in central California increased, leafhopper infestations in untreated groves increased. It was concluded that "Treating part of a grove is of no value generally since whitewashing forces the leafhoppers into untreated areas or into other untreated groves."

Compared with the massed, seasonal "invasion" of Californian citrus groves by this leafhopper, immigration of the African citrus psylla appears to be more akin to "infiltration", and, therefore, considerably more difficult to cope with. It has been hypothesized that citrus groves are infested continually by T.erytreae from the

reservoir population on their indigenous host plant species (van der Merwe, 1940; Moran, 1967). Field studies with yellow sticky traps and a suction trap (Catling, 1970) certainly did not detect any mass "invasion" by T.erytreae, and did indicate small numbers dispersing in spring and summer during the period of peak population density. When T.erytreae, which have left their indigenous host plants and dispersed with the wind, alight by chance on citrus, they will be more strongly arrested than on their indigenous hosts (Moran, 1968) and will be able to survive on the mature leaves for an average of about 2 months (Catling, 1970). Only 1-2 % of the field population of T.erytreae are carriers of the greening pathogen (Catling, 1970). Nevertheless, with a fecundity of about 600 (Moran, 1968), a single gravid female carrier could presumably cause a greening epidemic in a citrus grove by transmitting the mycoplasma to numerous offspring through location and infection of and oviposition on any flush available at the time of her arrival in the grove, or that subsequently appears whilst she is living on the mature citrus leaves. Psyllids which develop on infected flush would presumably acquire and spread the greening pathogen. Although there is a definite flushing rhythm of citrus in areas susceptible to psylla, a variety of other factors (such as fertilizer treatments, hail and rain) result in unseasonal flush production (Catling, 1970). It would surely be impracticable to attempt to use flush-masking to prevent T.erytreae already on citrus from locating and multiplying on unseasonal flush, because this would require continual spot treatment or uneconomically-frequent overall treatment (even if it was not physiologically damaging to the tree). Flush-masking of unseasonal or seasonal flush could, at best, only retard the rate of flush colonization. As a method of pest control, therefore, flush-masking holds little promise.

The second alternative method of pest control suggested by the work is the use of coloured sticky traps. This would entail setting up, close to the canopy of each tree, several small adhesive-coated rectangles or cylinders, painted a colour highly attractive to citrus psylla, so as to continually cull psylla as they fly around, vectoring the greening mycoplasma. Of the presently-available colours, saturated yellow would be best for use on sticky traps because it has the greatest RAS equation value (Figs 11 , 12 , 14 & 15), due to its high reflectance in the wavelength region 480-670 nm and simultaneously low reflectance in the region 390-480 nm. The reason for using many small traps rather than a few large ones of equivalent area, is that yellow trap efficiency (i.e. number of homopterans caught per unit trap area) decreases with increasing trap size (Costa & Lewis, 1967), so the former arrangement is more effective for trapping when the population of vectors is sparse.

The main vector of tristeza virus of citrus in southern Africa is the citrus aphid, Toxoptera citricidus, (McClean, 1963), which competes directly with Trioza erytreae for the utilization of citrus flush (Catling, 1972). Like Trioza, Toxoptera is highly responsive to yellow: from the ratio of yellow water tray to nearby suction trap or sticky net catches, Toxoptera was found to be the most

"yellow-sensitive" species of aphid in 2 studies (Eastop, 1955; O'Loughlin, 1963). Yellow sticky traps thus seem likely to be of value in controlling not only citrus psylla but also citrus aphid.

In spite of the common use of yellow traps to monitor the aerial density of Homoptera (e.g. Dickson et al., 1956, on the aphid vectors of tristeza virus of citrus), attempts at aphid control by means of coloured traps have been limited in number, as was pointed out both by Kring and by Roach and Agee in 1972. At that time, partial reduction in fruit infestation by apple maggots had been obtained through the use of sticky red spheres in apple trees (Prokopy, 1968, and Maxwell, 1969, cited by Prokopy, 1975), and this has since been repeated (Prokopy, 1975) with a reduction in infestation from more than 80 to less than 3 % . Yellow sticky traps placed by Remund (1971, cited by Prokopy, 1975) and by Russ et al. (1973) on the canopy of cherry trees (2-8 traps/tree, depending on tree size) reduced the infestation by the cherry tephritid from an expected 30-35 % to 3,6 %. Airborne tephritid flies, however, presumably have a far greater ability than homopterans to cope with breezes and wind eddies, and this raises the important question of whether or not homopterans have a sufficiently strong flight ability to respond to coloured stimuli in the field to an extent that would be of use in pest control.

In connection with aphids, initial attempts at manipulation of pest populations in the field, based on their colour responses, employed non-sticky materials. Reductions in the incidence of crop infection with aphid-borne viruses were obtained using non-sticky aluminium foil and white polythene, either as strips between gladiolus plantings (Johnson, et al., 1967) or as mulches in fields of watermelons (Adlerz & Everett, 1968; various authors cited by Kring, 1972). In a more recent trial, successful crop protection from aphid-borne diseases was obtained using sticky yellow polythene sheeting around fields of peppers (Cohen & Marco, 1973). Coloured stick traps have thus already shown promise in field trials as a feasible technique for the control of various pests, including Homoptera.

A conceivable drawback of coloured sticky traps is their possible attractiveness to beneficial insects, such as parasitoids, predators and pollinators. A trichogrammatid (Zdarek & Pospisil, 1966b) and an icheumonid (Hollingsworth et al., 1970) parasitoid of phytophagous lepidopteran pests showed peak phototactic responsiveness to UV (wavelengths 379 and 365 nm, respectively) and to green or yellow-green (517 and 560 nm, respectively), which is remarkably similar to that of the citrus psylla and suggests that the parasitoids' process of host location might involve an initial response to the host's habitat i.e. foliage. If this were true, hymenopteran parasitoids of phytophagous homopterans could be expected to react similarly. Yellow was preferred to light of other colours by a braconid parasitoid of an aphid pest (Bridges & Pass, 1969), and parasitoids of aphids and of aleyrodids were more strongly attracted to yellow-coloured stakes than to ones of other colours (Kring,

personal communication, cited by Weseloh, 1972). Aphidophagous syrphids have been attracted to UV (Chernyshev, 1959) and to green (Dixon, 1959) and yellow surfaces (Schneider, 1969) (although yellow was less attractive than blue or white in some studies (Sol, 1966)). An aphidophagous coccinellid responded positively to UV light in the laboratory (Chernyshev, 1959). In one field operation, yellow traps were successfully used to monitor not only various homopterans but also "their potential predators": syrphids, dolichopodids, empidids and coccinellids (Duviard, 1973). Yellow traps aimed at apple maggot flies attracted tachinids (Moore, 1969), and in another study, they attracted far more honey-bees than the pest (Japanese beetle) target species (Wellso & Fischer, 1972). From the above it is clear that lack of specificity could be problematical: coloured sticky traps could disrupt natural control if the parasitoids and predators were more active and/or responsive to the traps than the host. In the case of T.erytreae this might not matter, because the parasitoids are relatively ineffective in natural psylla population control anyway (McDaniel & Moran, 1972). Numerous species of citrus-infesting insects are, however, under successful biological control in the Ethiopian region (Greathead, 1971), so it would be important to determine whether or not the use of coloured sticky traps would significantly upset this balance. Jimenez (1972) has gone so far as to claim that the use of yellow sticky traps is compatible with the biological control of citrus blackfly (Aleurocanthus woglumi), but he did not consider the colour responses of the parasitoids. Clearly, in field trials of coloured sticky traps for the control of homopteran pests, the attractiveness of the traps to parasitoids and other beneficial insects must be carefully monitored.

Optimization of trap colour is obviously desired. As is evident from the RAS equation, a surface more attractive to T.erytreae than pure yellow, would be one reflecting a maximal amount both of yellow and of UV light, and simultaneously, a minimal amount of blue light. Because this colour comprises light from both ends (but not the middle) of the insects' visible spectrum, it was called "Bienenpurpur" i.e. "bee-purple" by Daumer (1956). "Insect-purple" sticky traps would have a definite advantage over yellow traps at low light intensities (Fig. 29), and perhaps also at normal light intensities if (as seems possible) the apparent saturation effect in Fig. 29 is simply an artifact of the experimental set-up. "Insect-purple" colouration does exist in nature, e.g. in the petals of numerous species of flower in Europe (Daumer, 1958) and in North America (Kevan, 1972). It could have as its basis either a single pigment reflecting both yellow and UV strongly, and blue weakly, or a mixture of 2 pure pigments reflecting yellow light and UV light respectively. Research into the production of an "insect-purple" pigment for use in paints and polythene sheeting for sticky traps could yield considerable economic benefits in terms of control of citrus psylla and other homopteran crop pests.

SUMMARY

1. Fundamental knowledge was gathered about the visual physiology underlying alightment colour preferences of the African citrus psylla, Trioza erytreae, vector of greening disease, in the hope of it suggesting alternative methods of pest control.

2. T.erytreae had a significant alightment preference for flush rather than mature leaves, and this was found to be the result of its high sensitivity to the wavelength of peak reflectance of leaves, combined with its increasing rate of phototaxis to increasing light intensity, the reflectance of flush being approximately double that of mature leaves.

3. Alightment distributions on artificial (printed and painted) surfaces demonstrated that T.erytreae was most responsive to pure yellow. Alightment correlated well with surface "purity" and "long/short ratio" in some situations, but poorly in others, indicating that the causation of T.erytreae's colour preferences was not adequately described by colour parameters previously used in work on Homoptera.

4. Monochromator studies revealed that T.erytreae's phototaxis peaks at 3 wavelengths: ca. 550 nm (yellow-green: YG), ca. 450 nm (blue: B), and ca. 350 nm (ultraviolet: UV). Phototaxis was a linear function of the logarithm of light intensity over 6 orders of magnitude, and was not related to bandwidth of the stimulus.

5. Colour filters were used to test the influence of each of the above 3 spectral regions, individually or in combination, on T.erytreae's alightment response. Alightment was stimulated by YG alone and by UV alone, above different thresholds, and the combined effect of YG and UV light was approximately additive. Alightment was not stimulated by B light alone, and was inhibited by B in combination with YG and with UV light. This demonstrated that T.erytreae has trichromatic colour vision.

6. A new colour parameter incorporating these findings was formulated, to describe the "relative alightment stimulus" of coloured targets to T.erytreae: the "RAS equation" :-

$$RAS = YG + UV - B$$

where the colour terms were, in the simplest case, taken to refer to the weighted logarithm of the quantum flux from the target in the wavebands: YG = 480-670 nm, UV = 300-390 nm, B = 390-480 nm, minus the logarithm of the relevant colour threshold, the thresholds depending on colour receptor type and environmental light intensity.

7. Previously-determined alightment distributions of T.erytreae on colour filter targets, leaf choices, a printed spectrum and various paint series were found to be more consistently, as well as slightly more accurately (namely about three-quarters) "explained" by the RAS equation values, than by the values of previously-available colour parameters.

8. By empirical choice of hypothetical thresholds and weighting factors for each species, it was found that the same basic RAS equation could "explain" about three-quarters of the different alightment distributions (recorded in the literature) both of a "yellow-sensitive" and of a "non-yellow-sensitive" speices of aphid on leaf and artificial surfaces. This suggested that the RAS equation might have general homopteran applicability.

9. Two alternative methods of T.erytreae control were suggested by the fundamental knowledge gathered: "Flush-masking" with a black, red, blue, or non-UV-reflecting white pigment; "Sticky-trapping" with several yellow or "insect-purple" traps close to the canopy of each citrus tree. Possible pros and cons of these techniques were discussed. The review of relevant literature indicated that the latter technique holds considerable potential for homopteran pest control.

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