

**Fig. 2** Inhibition ( $I$ ) of response to motion in small disk plotted as a function of the lower limit,  $F$  (cycles per degree visual angle subtended at cornea), of spatial frequency content of the radial grating pattern. Inhibition  $I$  is defined as  $(NE - NI)/NE$ , where  $NE$  is the number of spikes in the DCMD in response to motion in small disk alone, and  $NI$  is the number of spikes in response to simultaneous motion in disk and rotation of the radial grating pattern. When the number of spikes in response to simultaneous motion  $NI$  is greater than  $NE$ , inhibition  $I$  becomes negative and is, in fact, excitation. In all experiments, these two kinds of trials are interleaved to increase stability of the measurement. ●, Average of means of continuous series of 14 experiments 12 December 1975–14 February 1976 in completely dark surround. ○, Average of means of continuous series of three experiments in light surround, 17–21 February 1976. Light continuous dotted line, negative of response to rotation only of radial gratings from data of acuity studies of 1972<sup>7</sup> to show acuity limits inhibition at high frequencies. △, Data of one experiment (21 February 1976) in light surround; bars indicate  $\pm$  the sum of standard error of  $NE$  and  $NI$ ; each point is the mean of 34 or 68 trials with 30-s ISI and interleaved presentation of disk motion trials with simultaneous disk motion and radial grating rotation. ■, Average of active controls on dark surround experiments. □, Average of active controls on light surround experiments. ▽, Active control on single light surround experiment. (An active control is rotation of the unilluminated radial grating with disk motion.) Stimulus parameters: luminance of a brighter bar of radial grating,  $1,200 \text{ lm m}^{-2}$ ; dark bar,  $\sim 0 \text{ lm m}^{-2}$ ; small disk has luminance equivalent to bright bar of radial grating; light surround luminance approximately  $1.5 \log_{10}$  units below that of bright bar; when the disk is occluded in light surround, the occluded portion has the luminance of the surround, but the excitatory response is approximately the same as in dark surround. The radial grating tangential velocity is  $11^\circ$  (visual angle) per s for most runs of this figure, or  $36^\circ$  per s in pattern plane angle. The velocity of translation of the occluding edge is  $12^\circ$  (visual angle) per s, and the light disk subtends  $5.6^\circ$  (visual angle); the radial grating subtends  $37^\circ$  (visual angle) for all but a few runs of this figure. In all experiments except as noted the disk and grating pattern are directly adjacent along the equator.

themselves. In the locust the latter summation would take place as excitatory synapses at or before the fan of LGMD dendrites in the lobula<sup>4</sup> via interneurons from the medulla, and the former summation as inhibitory synapses from the first set of monopolars on to these interneurons in the medulla. Since the LGMD drives the DCMD directly, this model gives for DCMD response two separate channels selectively responding to high and low spatial frequencies respectively, with an inhibitory cross-connection from the high frequency channel to the low frequency channel. Further tests of these ideas require probing of more peripheral units than the LGMD.

In vertebrate vision the reduction of retinal sensitivity during relative motion of retina and image is known as saccadic suppression. The suppressive or inhibitory effect on human vision (measured with a low spatial frequency test flash) produced by relative motion of gratings<sup>12,13</sup> is parallel to the above results for the locust DCMD. It is of interest that the locust visual system processes high and low spatial frequency image information in the same manner as do some perceptual

channels of the human visual system.

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## Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley

RESERVES of assimilate present in wheat and barley crops a flowering, and available for later translocation to the grains could buffer grain yield against environmental stresses during grain filling. This so-called pre-anthesis assimilate contribution to grain yield can be expressed as a percentage of yield ( $P_1$ ) Archbold<sup>1</sup>, and later Thorne<sup>2</sup>, concluded that  $P_1$  was small being no more than 20%. But only one result (12% for irrigated wheat at Cambridge<sup>3</sup>) refers to a crop in the field as distinct from plants in pots, and no studies considered the effect of stress during grain filling. Recently Gallagher *et al.*<sup>4,5</sup> reported substantial contributions:  $P_1$  averaged 43% over six crops of wheat and barley at Nottingham; this amounted to more than 300 g per m<sup>2</sup> of dry material in two crops and, in the severe drought of 1970, 39% of total dry matter present at anthesis. They assumed, with some supporting evidence from one barley crop<sup>6</sup>, that the pre-anthesis contribution was given by the decrease from anthesis to maturity in dry weight of non-grain parts of the crop. *In situ* labelling with <sup>14</sup>C of the whole crop canopy at frequent intervals before and after anthesis would seem to be the least equivocal way of estimating  $P_1$ . Using this method we have determined  $P_1$  in wheat and barley. It averaged only 12% (watered crops) and 22% (droughted crops), and did not agree with estimates for the same crops obtained by the method of Gallagher *et al.*<sup>4,5</sup>.

Wheat and barley were grown during 1974–75 at the Centro de Investigaciones Agrícolas del Noroeste (CIANO) near Ciudad Obregon in north-west Mexico. There was no rain and crops were either flood irrigated frequently (I) or only until 27th January, about 40 d before anthesis, creating a drought (D) regime. Weather and general experimental procedures were as described elsewhere<sup>7</sup>. Grain yields for regime I were high (Table 1). Significant differences between D and I in leaf water potential arose about 10 d before anthesis and then increased steadily. There were substantial reductions in yield in regime D especially for the wheat cultivars, which were later in flowering (Table 1).

The canopy labelling with <sup>14</sup>C began on 20 February and was repeated on separate 1.08 m<sup>2</sup> portions of the crops every 7–14 d until near maturity. The proportion of total above ground <sup>14</sup>C at maturity found in the grain was slightly greater for any given date of labelling in regime D, but was remarkably consistent between cultivars and species (Fig. 1). The relationship of Fig. 1a agrees with results<sup>2,8,9</sup> obtained in non-crop conditions.

Combining the data of Fig. 1 with information on changes in above ground dry weight,  $P_1$  was estimated to be 12–13% under

frequent irrigation, rising to 27% for droughted wheat (Table 2). But in absolute terms (grain dry weight,  $GDW_1$  in  $g\ m^{-2}$ ), it was similar for regimes I and D. As a proportion of total dry weight at anthesis,  $GDW_1$  amounted to 8.5% (I) and 11.5% (D). Considering that  $GDW_1$  for barley included the husk, already present at anthesis and amounting to 8% (I) and 9% (D) of final grain weight, the true contribution of stored pre-anthesis assimilate was clearly lower for barley than for wheat.

The method used to estimate  $P_1$  in Table 2 assumes that any contribution of carbon from roots, or variation in the proportion of carbon to dry matter in the total crop compared with that in the grain, or fluctuations in crop growth rate within the two key periods, are of minor importance. On the other hand, neglect of the loss of tissue, formed before anthesis, and lost during the post-anthesis period could be important. Such losses seem to be substantial under irrigation, probably due to the saprophytic decay of lower early-formed, and hence unlabelled, leaves. A loss of  $100\ g\ m^{-2}$  would seem probable (R.A.F., unpublished) under the I regime, and correcting  $\Delta TDW_2$  ( $TDW$ , total dry weight) for this would increase  $GDW_2$  by  $75\ g\ m^{-2}$  and lower mean  $P_1$  to 11%. We have also assumed that no assimilate formed before the date of first labelling was later transferred to the grain. Inspection of Fig. 1 shows this to be incorrect, but the small total dry weights at first labelling mean the amounts of assimilate neglected are small. The transfer to the grain of assimilate formed as early as 27 d before anthesis (Fig. 1a) may be associated with the transfer of leaf nitrogen in the form of protein.

Considering this correction to  $GDW_2$  under regime I, the values of  $GDW_1 + GDW_2$  agree closely with the observed grain yield (Table 2). Also the figure of 13% for irrigated wheat is similar to that of 12% for an irrigated wheat crop determined with  $^{14}CO_2$  by Lupton<sup>3</sup>, and to values which can be calculated with our procedure from the extensive results of Birecka and Dakic-Wlodkowska<sup>8</sup>, albeit obtained with wheat grown in pots. An independent upper estimate of the contribution of pre-anthesis assimilate in the case of adjacent irrigated crops of Yecora 70 at CIANO is given by the quantity of sugar stored in stems at anthesis. This amounted to  $50\ g\ m^{-2}$  (15% stem sugar;  $320\ g\ m^{-2}$  stem tissue), to which should be added leaf protein transfer to the grain, for these purposes set equal to the decrease, anthesis to maturity, in leaf lamina dry weight, amounting to  $40\ g\ m^{-2}$  ( $200\ g\ m^{-2}$  of green leaf lamina tissue, 20% decrease in dry weight excluding leaf loss). The total available material thus estimated ( $90\ g\ m^{-2}$ ) agrees well with the value of  $GDW_1$  of Table 2 ( $69\ g\ m^{-2}$ ).

Table 2 makes possible a separate estimate of  $P_1$  based on the decline in non-grain dry weight after anthesis ( $\Delta TDW_2$  less

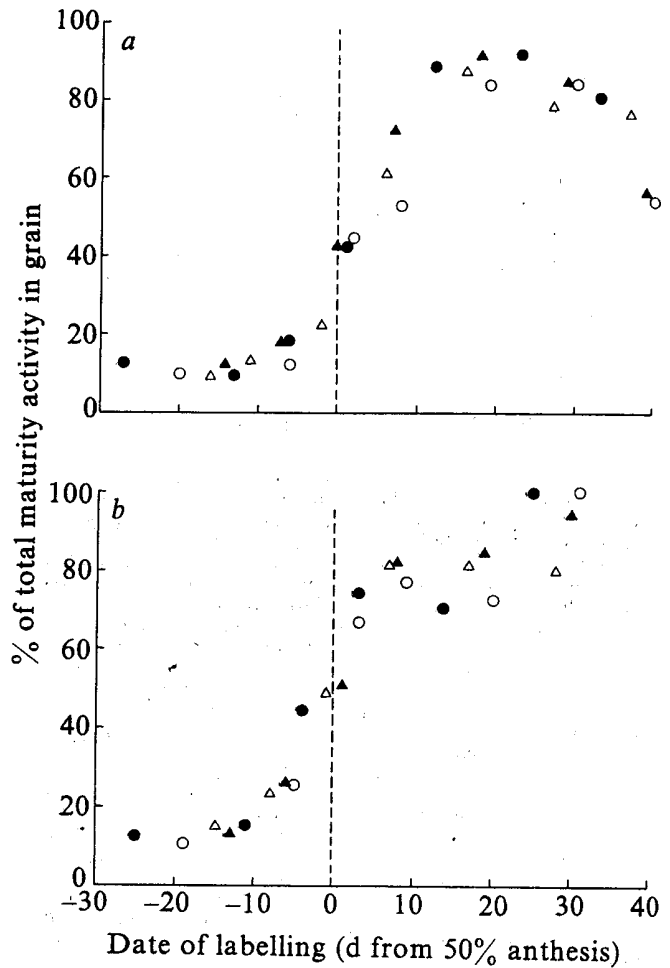


Fig. 1 The fraction at maturity of total crop  $^{14}C$  found in the grain as a function of the time (d from anthesis) when the  $^{14}CO_2$  was assimilated; a, frequently watered, (I); b, droughted, D; Yecora 70 (●), Ciano (▲), CM67 (○) and WI 2198 (△).  $^{14}CO_2$  assimilation involved placing a clear polyethylene chamber over  $1.08\ m^2$  of crop. Into the chamber  $100\ \mu Ci$  of  $^{14}CO_2$  was introduced. The chamber remained closed and was stirred with a fan for 10 min. Labelling was carried out within 3 h of noon. At maturity, a  $0.3\ m^2$  quadrat was cut from each region previously labelled and the specific activity of oven dried subsamples were determined by combustion, trapping of the  $^{14}CO_2$  in a liquid scintillation mixture and counting.

Table 1 Grain yield and yield components in the 1974-75 experiment at CIANO, Mexico

Species	Cultivar	Date of 50% anthesis	Grain yield ( $g\ m^{-2}$ )	Kernel weight (mg)
Frequently watered throughout (I)				
Wheat	Yecora 70	March 17	639	45
	Ciano 67	March 10	563	43
Barley	CM 67	March 4	609	49
	WI2198	March 6	610	54
Droughted during grain filling (D)				
Wheat	Yecora 70	March 15	293	30
	Ciano 67	March 9	293	32
Barley	CM 67	March 3	363	38
	WI 2198	March 5	349	40
		s.e.m.	18	0.5

Plots were sown on 14 December 1974 and received moderate fertilisation ( $75\ kg\ ha^{-1}\ N$  and  $18\ kg\ ha^{-1}\ P$ ). A split plot design (main plot = water regime, sub plot = cultivar) with three replications was used. Each sub plot was  $15\ m \times 1.8\ m$ .

observed  $GDW$ ), as proposed by Gallagher *et al.*<sup>4,5</sup>. But the calculation suggests practically zero contribution in all situations of Table 2. This has been confirmed for irrigated wheat by other experiments with many cultivars at CIANO over several years (ref. 10 and R.A.F., unpublished). The apparent discrepancy when compared to the  $^{14}C$  results of Table 2 probably arises because the absence of net change in the non-grain dry weight after anthesis, does not preclude translocation of pre-anthesis assimilate to the grain, balanced by the accumulation of post-anthesis assimilate in non-grain parts. The fact that the fraction of  $^{14}C$  in the grain from post-anthesis labelling averaged only 0.78 (Fig. 1, Table 2) supports this explanation. Also sampling in other irrigated wheat crops at CIANO showed that from anthesis to maturity the dry weight of the peduncle and chaff increases, while that of the leaves and the remainder of the stem decreases. If these latter decreases are taken to reflect assimilate translocated to the grain, the contribution agrees reasonably well with the 13% value in Table 2.

Our results point to a smaller value of  $P_1$  than that reported by Gallagher *et al.*<sup>4,5</sup>. Notwithstanding the discussion of the preceding paragraph, it is likely that in many situations the method of these authors overestimates  $P_1$ , because the dry

**Table 2** Estimation of the proportion of grain yield derived from pre-anthesis assimilate ( $P_1$ )

Variable	Frequently watered		Droughted	
	Wheat	Barley	Wheat	Barley
Pre-anthesis period				
Start date*	24	15	23	14
Start TDW†	282	410	282	410
Anthesis TDW	760	750	610	655
$\Delta TDW_1$	478	340	328	245
$F_1$	0.14	0.19	0.24	0.27
$GDW_1$	64	65	79	67
Post-anthesis period				
Maturity TDW	1,358	1,367	888	1,038
$\Delta TDW_2$	598	617	278	383
$F_2$	0.74	0.75	0.78	0.83
$GDW_2$	445	465	215	317
Overall				
$GDW_1 + GDW_2$	509	530	294	384
$P_1$	13%	12%	27%	17%
Observed GDW	601	609	293	356

TDW, total dry weight ( $g\ m^{-2}$ ); GDW, grain dry weight ( $g\ m^{-2}$ ). TDW measured by harvests ( $0.30\ m^2$  quadrat per sub plot) at dates corresponding to those when  $^{14}C$  labelling was carried out, and by harvest ( $1.80\ m^2$  per sub plot) at maturity; anthesis TDW estimated by interpolation, and the increase in total dry weight during the pre-anthesis ( $\Delta TDW_1$ ) and post-anthesis ( $\Delta TDW_2$ ) periods was calculated.  $F_1$  and  $F_2$  are the average proportions of total crop  $^{14}C$  at maturity in the grain for labelling in the pre- and post-anthesis periods, respectively, and were obtained from Fig. 1. The contribution to grain yield of pre-anthesis ( $GDW_1$ ) and post-anthesis ( $GDW_2$ ) assimilate in absolute terms ( $g\ m^{-2}$ ) are equal to  $F_1 \times \Delta TDW_1$ , and  $F_2 \times \Delta TDW_2$ , respectively. The pre-anthesis assimilate contribution as a percentage ( $P_1$ ) is given by  $100 \times GDW_1 / (GDW_1 + GDW_2)$ . The data were averaged for the two cultivars of each species.

\*Time (d) before anthesis of first  $^{14}C$  labelling date.

†Average of both water regimes used.

weight change in non-grain parts includes tissue, principally leaves, lost due to decay, wind and so on. At other sites in Mexico,  $P_1$  estimated with this method for various non-droughted wheat cultivars ranged from 12 to 98%<sup>11</sup>, and clearly increased as site rainfall and disease incidence increased. We believe this reflects tissue loss, which even at CIANO with no rain or disease amounted to at least  $100\ g\ m^{-2}$ . Consequently the results from Nottingham<sup>4,5</sup> may have overestimated the importance of the pre-anthesis contribution of assimilate to grain yield. Even in the most suitable conditions for the expression of this contribution in our experiment (well grown wheat crops, post-anthesis drought reducing kernel weight 30%), it amounted to only 27% of final yield or  $79\ g\ m^{-2}$  according to the  $^{14}C$  data.

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## Physiological energetics of cock-crow

ALTHOUGH much is known about bird song in the behavioural context there is no exact information concerning the efficiency of the communication system itself in terms of energy usage. Little attention has been paid to study of energy relationships in animal communications. The domestic fowl (*Gallus domesticus*) is a convenient subject on which to make physiological measurements of the energy involved in sound production, because of its size and its readiness to make calls in the laboratory, and because of the sheer volume of sound it produces. I have made such measurements and report them here.

Cock-crow is visibly and audibly one of the most vigorous and spectacular forms of avian vocalisation. The maximum root-mean-square (r.m.s.) sound pressure level attained during the performance is equivalent to a value of 100 dB at a distance of 1 m (Fig. 1a). This corresponds to a peak value of 103 dB. This very impressive achievement is accompanied by enormous rises in air-sac pressure and air flow in the trachea (Fig. 1c, d). Pressure rises to  $60\ cm\ H_2O = 6 \times 10^4\ dyn\ cm^{-2}$  and averages  $55\ cm\ H_2O = 5.5 \times 10^4\ dyn\ cm^{-2}$ . Air flow reaches  $500\ ml\ s^{-1}$  and averages  $\sim 350\ ml\ s^{-1}$  during the cycle.

Compared with a normal expiration, these values represent increases of  $\sim 100$ -fold and 15-fold for pressure and flow respectively. This indicates that, concomitant with sound production, there is a rise in airway resistance of some 6-7-fold. This rise is attributed to a change in the configuration of the syrinx, the sound-producing organ, involving, amongst other things, a narrowing of the syringeal lumen by the intruding tympaniform membranes<sup>1-3</sup>. In keeping with this idea, Fig. 1b indicates that the pressure changes in the trachea are comparatively small and, therefore, that virtually the whole of the pressure head generated in the air sacs is spent during the passage of air through the syrinx.

The fluid energy losses in the syrinx are accounted for mainly by frictional dissipation, but also to a lesser extent by conversion of a part of the energy into the mechanical vibration of the external tympaniform membranes, and hence into airborne vibrations. It is possible to estimate approximately the efficiency of this conversion process, and therefore of the effectiveness of the lung air sac-syrinx apparatus as an audio-generator, by comparing the total fluid energy losses incurred by the effort with the amount of sound energy finally produced. The work performed in expelling air from the lung air sac system to the atmosphere is estimated by measuring graphically the area enclosed by the pressure-volume curve during a single crowing cycle (Fig. 2d). The volume curve is itself obtained by graphical integration of the linearised flow curve. The final figure is  $\sim 3.5\ W\ s$ . The duration of the crow is 2 s, so the average work rate is 1.75 W. This does not, however, represent total crowing effort since no account has been taken of the internal work of the expiratory muscles lost as contraction heat, and the external work done in moving the viscera enclosing the air sacs.

To calculate the sound energy radiated, the sound pressure level curve given in Fig. 1a is first re-drawn as an equivalent power curve ( $0\ dB = 2 \times 10^{-4}\ dyn\ cm^{-2} = 10^{-10}\ W\ cm^{-2}$ ) which is then integrated over the crowing cycle to yield the total energy per  $cm^2$  (Fig. 3). The resultant value, assuming a maximum r.m.s. sound pressure level of 100 dB, works out at  $\sim 9 \times 10^{-7}\ W\ s$ . This is equivalent to an average sound reading throughout the cycle of 95 dB. The total area