THE PHYSIOLOGY OF GROWTH IN APPLE FRUITS

III. CELL CHARACTERISTICS AND RESPIRATORY ACTIVITY OF LIGHT AND HEAVY CROP FRUITS

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Summary

Cell size, total and protein nitrogen, and preclimacteric respiration have been studied for light and heavy crop fruit of certain Tasmanian-grown apple varieties. Differences in size of fruit from light and heavy crops have been shown to be due mainly to differences in cell size rather than in cell number. Respiration per cell, protein nitrogen per cell, and cell volume were closely intercorrelated but respiration per unit protein is greater in light crop fruit than in heavy crop.

It is suggested that the more rapid senescence and susceptibility to storage disorder of light crop fruit may be related to its higher respiration per unit protein. Though protein synthesis keeps pace with cell enlargement, the respiration per unit protein increases with cell size.

No consistent correlation was found between cell characters of a variety, such as cell size and cell number, and physiological characters such as period or date of maturation.

Attempts to raise the mean fruit size without impairing keeping quality are most likely to succeed if cell number per fruit is increased and cell size is kept small.

I. Introduction

It has long been realized that apples from light crops have a higher susceptibility to cool-storage disorders than those from heavy crops. Carne and Martin (1938) have demonstrated a high degree of correlation between the mean size of the fruit on a tree and the incidence of storage disorders and certain physiological characteristics of the fruit. More recently, Smock (1949) showed that, in gas storage, light crop fruit was more susceptible to brown core and Martin and Carne (1950) demonstrated a similar relation for brown heart. Studies of the differences between light and heavy crops have not been of much assistance in efforts to analyse and improve storage behaviour.

This difference is obviously bound up with differences in respiratory behaviour, but respiration, on a unit fresh weight basis, has shown no consistent difference between large and small fruit (Smock and Gross 1950), and light and heavy crops (Martin, unpublished data). The data given by Hulme (1951) suggested that, in a light crop year (1937), respiration per unit protein was higher than in normal years.

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Similarly, though apple varieties differ widely in characteristics such as mean fruit size for the variety, rate of maturation, storage behaviour, chemical characteristics, and dessert quality, the physiological basis of these differences, and their relation to susceptibility to disorder, have been little studied. Smith (1940, 1950), using English varieties, showed that varietal fruit size was determined by the amount of cell division after pollination, that apples of different varieties differed widely in cellular structure, and that differences in storage behaviour were correlated with cell size. Hulme (1951) considered that in normal years, respiration per unit protein was constant for each variety and was higher in dessert than in culinary varieties.

Bain and Robertson (1951) and Robertson and Turner (1951) have investigated the within-tree relation between fruit size, cell size, cell number, total and protein nitrogen, and respiration rate. This report applies the methods of Robertson and his co-workers to the study of light and heavy crop fruit and extends the work of Smith (1940, 1950) and Hulme (1951) to varieties growing in Tasmania.

II. Materials and Methods

Of the many varieties grown in Tasmania, those whose characteristics are given in Table 1 were selected to provide a suitable range of varietal characters. For crop contrast within a variety a search was made for two adjacent trees of similar growth form and vigour but of contrasting crop. Satisfactory pairs were found for Cleopatra, Cox, Crofton, Democrat, Delicious, Granny Smith, Ribston, Sturmer, and Tasman Pride. For the other varieties fruit was available as follows: Alfriston, trees in different orchards but on the same soil type; Alexander, Geeveston Fanny, and Prince Alfred, one tree of average crop only; Golden Delicious, trees irrigated and crops irregular; Jonathan, crop contrast not marked; and Worcester, no trees of contrasting crop and two adjacent trees of average crop but contrasting fruit size due to different growing conditions used.

From each tree a sample of 20 fruits was selected according to a procedure designed to produce random sampling at a date judged to be close to commercial maturity and before the onset of the climacteric. In Cox, Cleopatra, and Democrat a second picking from the same trees was made 2 weeks later, and with Granny Smith another picking from another source was made 2 weeks later. Each fruit was weighed and measured.

Of these 20 fruits, four of approximately mean size for the sample were selected for cell measurements and 10 were used to determine the rate of respiration at 25°C. by the Pettenkofer method, taking the mean rate for the 8-hour period 40-48 hours after picking. This 10 and the remaining six were later examined for pressure by penetrometer, starch pattern by the starch-iodine method, and soluble solids of juice by refractometer. The mid-cortical tissue was then sliced, dried at 60°C. in an air oven, ground, and stored at 1°C. in sealed jars for analysis.

The four fruits for cell size measurements were halved equatorially and from the two positions on opposite sides of the fruit sections were cut from the mid cortex parallel to the equator. These were fixed and stored in formalin-alcohol (6 ml. formalin in 100 ml. 78 per cent. alcohol). Four sections from each fruit were mounted and 25 cells from each were projected and cell

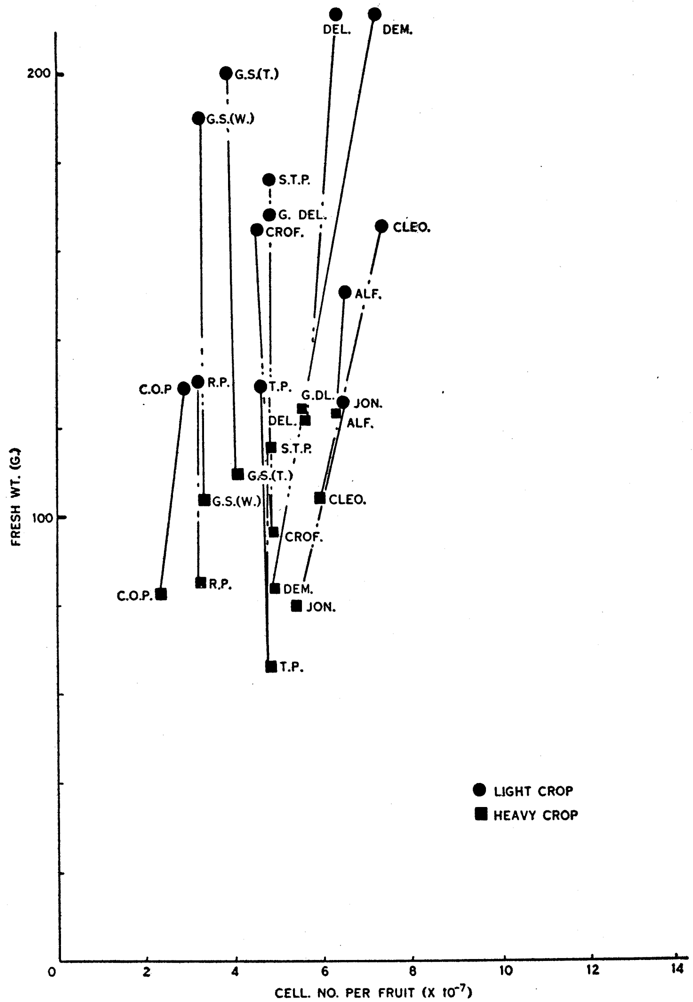

Fig. 1.—Mean weight and cell number per fruit of light and heavy crops of different varieties. Abbreviations used in this and later figures: Alex., Alexander; Alf., Alfriston; Cleo., Cleopatra; C.O.P., Cox's Orange Pippin; Crof., Crofton; Dem., Democrat; Del., Delicious; Eng., English material; G.F., Geeveston Fanny; G. Del., Golden Delicious; G.S., Granny Smith; Jon., Jonathan; P.A., Prince Alfred; P.D.N., Pomme de Neige; R.P., Ribston; S.T.P., Sturmer; T.P., Tasman Pride; W.P.M., Worcester.

volumes and surface areas computed by the method described by Bain and Robertson (1951) and Robertson and Turner (1951). Care was taken to avoid regions of small cells near the vasculars.

TABLE 1

VARIETY CHARACTERISTICS

Variety		Size*	Flowering Order†	Maturation Order‡	Full Bloom to Maturity (days) (tentative only)	Susceptibility to Breakdown§	Susceptibility to Pit§	Storage Life††	Surface Colour**	Acidity
Alexander	C¶	4	3	1	120	2	2	2	2	Medium
Alfriston	C	3	3	1	120	1	2	2	1	Medium
Cleopatra	C	3	2	3	150	1	4	3	1	Medium
Cox	D	1	2	2	140	4	4	1	2	High
Crofton	D	1	2	5	170	1	1	4	3	Low
Democrat	D	4	3	5	170	1	1	4	4	Low
Delicious	D	3	2	4	160	3	1	3	3	Medium
Geeveston Fanny	D	2	2	2	150	3	1	2	2	Low
Golden Delicious	D	3	3	4	150	2	1	2	1	Low
Granny Smith	D	3	2	5	170	1	2	4	1	High
Jonathan	D	2	2	3	150	3	1	3	3	Medium
Pomme de Neige	D	1	1	2	130	3	2	1	2	Low
Prince Alfred	C	5	1	2	140	2	1	2	2	Medium
Ribston	D	3	1	2	130	4	4	1	2	High
Sturmer	D	3	2	5	180	3	3	4	1	High
Tasman Pride	D	3	3	3	150	3	2	2	4	Medium
Worcester	D	2	4	1	110	1	1	2	4	Low

* Range of mean size 2¼-3¼ in.

† Range of mean date 3 weeks.

‡ Range of mean date 3 months.

§ 1, Not susceptible; 2, susceptible in light crops only; 3, susceptible; 4, very susceptible.

†† Very tentative for average crops only and without reference to breakdown.

** 1, No pigment; 2, $< 25\%$; 3, 25-50%; 4, $> 50\%$.

¶ D, dessert; C, culinary only.

Cell number was calculated from fruit weight and cell volume, assuming a specific gravity of 1.1 for the cell, following Smith (1940).

For varietal comparisons, data from Table 1 are used and the mean figure from the light and heavy crop or the figure for the one tree of average crop, when the light and heavy contrast is not available, is taken as representing the mean for the variety.

TABLE 2

VARIETAL CELL CHARACTERISTICS

Variety	Date of Picking	No. of Fruit on Tree	Mean Fresh Weight per Fruit (g.)	Cell No. per Fruit ($\times 10^{-5}$)	Respiration /Cell (mg. CO_2/hr. $\times 10^{-11}$)	*R/P* (mg. CO_2/g. protein N/hr. $\times 10^{-2}$)
Worcester	Feb. 13	375	92.8	479	439	1009
	Feb. 13	420	123.3	545	787	1182
Alfriston	Feb. 13	—	123.6	627	293	530
	Feb. 15	300	151.1	649	—	600
Prince Alfred	Feb. 15	500	317.4	1090	—	—
Pomme de Neige	Feb. 15	650	99.2	307	—	—
Cox—pick 1	Feb. 19	1000	83.0	236	1322	1421
	Feb. 19	400	130.2	280	1743	1760
Cox—pick 2	Mar. 4	—	98.7	246	825	738
	Mar. 4	—	147.0	285	1393	1280
Alexander	Feb. 22	274	143.8	870	—	—
Ribston	Feb. 26	—	85.4	327	786	952
	Feb. 26	—	130.6	321	1586	1438
Jonathan	Mar. 7	820	80.3	542	354	861
	Mar. 7	475	125.7	637	403	925
Cleopatra—pick 1	Mar. 7	900	107.2	593	435	847
	Mar. 7	470	166.3	729	475	910
Cleopatra—pick 2	Mar. 19	—	119.2	564	424	827
	Mar. 19	—	182.4	739	494	968
Tasman Pride	Mar. 14	750	66.4	481	302	703
	Mar. 14	450	130.1	455	503	694
Delicious	Mar. 26	680	125.1	548	573	1282
	Mar. 26	95	213.0	644	1357	1955
Golden Delicious	Mar. 26	670	124.3	553	591	1201
	Mar. 26	470	168.5	487	840	1157
Geeveston Fanny	Mar. 28	—	124.4	498	476	1094
Democrat—pick 1	Apr. 3	900	89.9	461	360	631
	Apr. 3	400	192.1	770	653	1066
Democrat—pick 2	Apr. 25	—	84.0	471	616	1101
	Apr. 25	—	214.1	725	1187	1680
Crofton	Apr. 16	930	97.2	478	519	910
	Apr. 16	175	164.8	447	1137	1055
Granny Smith—source 1	Apr. 16	470	104.4	327	575	711
	Apr. 16	120	191.3	333	1223	1014
Granny Smith—source 2	Apr. 25	500	110.6	412	1204	1559
	Apr. 25	350	200.6	387	2087	1625
Sturmer	Apr. 30	670	116.7	471	762	952
	Apr. 30	315	177.4	461	1718	1627

III. Results

The data are summarized in Table 2.

(*a*) *Cell Number per Fruit*

The difference in fruit size between light and heavy crops was a matter of cell size rather than cell number. As is illustrated in Figure 1 there was no significant difference in cell number between light and heavy crop fruit of the varieties Alfriston, Cox, Crofton, Golden Delicious, Granny Smith, Ribston, Sturmer, and Tasman Pride, and in the others, Cleopatra, Democrat, Delicious, and Jonathan, difference in fruit size was due more to cell size than to cell number.

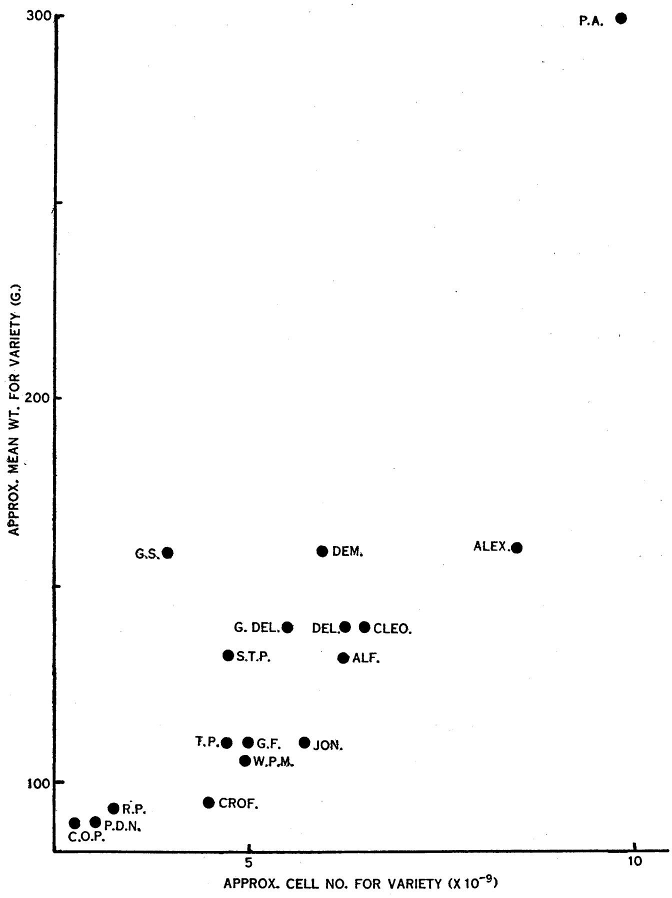

Fig. 2.—Relation between approximate mean fruit weight and mean cell number per fruit for different varieties.

There is probably a characteristic cell number for each variety and if the data available are used to calculate this number, then, as is shown in Figure 2, there is a correlation ($P < 0.01$) between this and the mean fruit weight for the variety, Granny Smith excepted.

This relation between characteristic varietal cell number and fruit weight is independent of rate of maturation and susceptibility to disorder.

(*b*) *Mean Cell Volume*

Again assuming that the data provide an approximate measure of the mean cell volume for the variety, then, as is shown in Figure 3, there is a group of varieties, Golden Delicious, Delicious, Crofton, Democrat, Sturmer, Cleopatra, Tasman Pride, and Jonathan, that does not conform to the relationship between cell size and maturation period established by Smith (1940) for English varieties. It is of interest that the varieties grown in both countries, Cox and Worcester, had similar cell size and growing period in each.

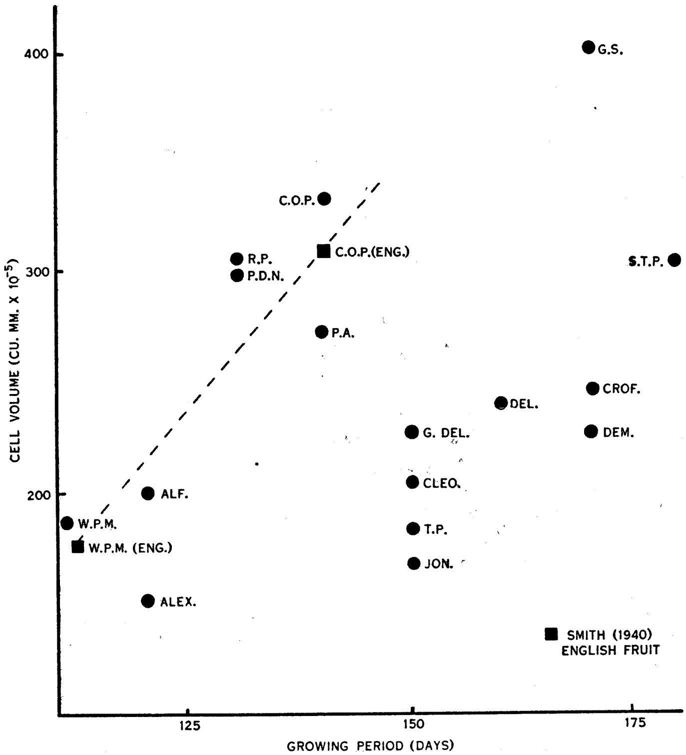

Fig. 3.—Relation between mean cell volume and growing period for different varieties.

(*c*) *Respiration Rate and Protein Nitrogen*

Most varieties can be assumed to be harvested in the preclimacteric stage. The respiration rate per cell was lower for pick 1 of Democrat than for pick 2, which would be expected from the work of Robertson and Turner (1951) and indicates that the latter picking was nearer the climacteric rise. The higher rate of the second picking of Granny Smith may have been due to the same effect. On the other hand, the lower value for pick 2 of Cox was probably due to the peak of the climacteric occurring between the pickings. In all comparisons of varieties involving respiration, second pickings have been omitted. It is again assumed that the data provide an approximation to the varietal mean.

Respiration per cell is closely correlated with cell volume ($P < 0.01$) (Fig. 4), both between light and heavy crops and between varieties. This extends the scope of the relation reported within fruits of the one tree by Robertson and Turner (1951).

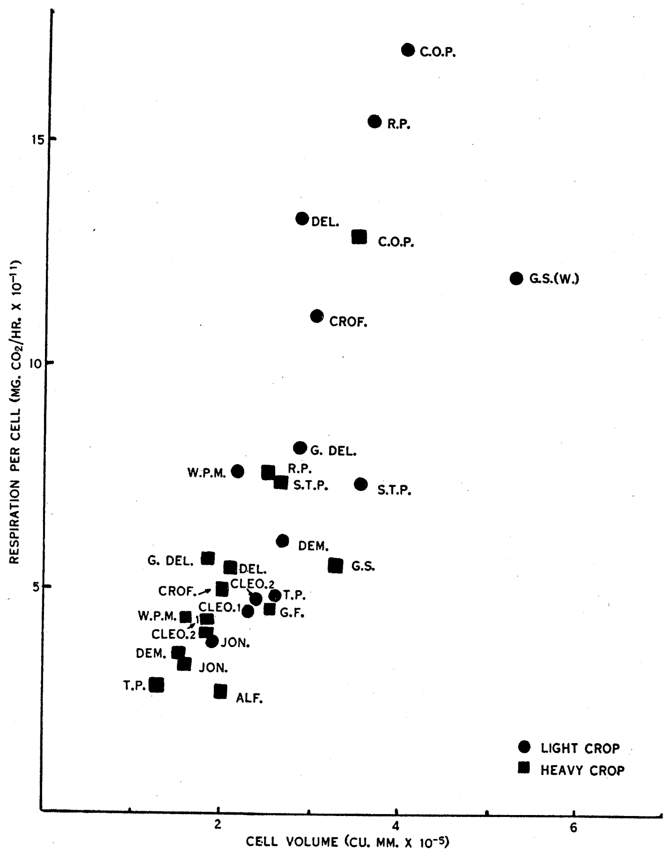

Fig. 4.—Relation between respiration rate per cell and cell volume for different varieties at two cropping levels.

Protein nitrogen per cell is also correlated with cell volume ($P < 0.01$) (Fig. 5) and cell surface ($P < 0.01$) (Fig. 6). This indicates that synthesis of protein keeps pace with increase in cell size. As the latter relation does not depart significantly from linearity, it is probable that the protoplasm is of constant thickness over this range of cell size, again extending the within-tree relation found by Robertson and Turner (1951).

If the data are examined on the basis of Hulme's (1951) conception of the respiration per unit protein, the general pattern is for light crop fruit to have a higher respiration per unit protein than heavy. In the only varieties where this was not so (Tasman Pride and Golden Delicious) there was no significant difference.

There is a significant correlation ($P < 0.01$) between respiration per cell and protein nitrogen per cell but it appears that at higher respiration rates the relationship is not linear (Fig. 7). One possible interpretation of this is that,

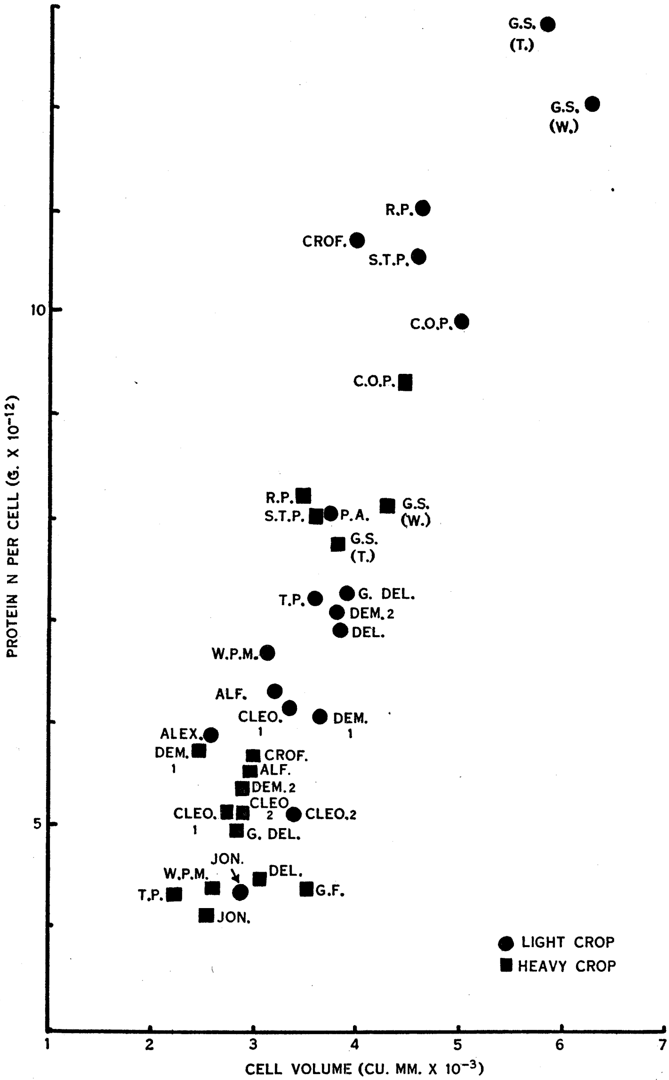

Fig. 5.—Relation between protein nitrogen per cell and cell volume for different varieties at two cropping levels.

with increasing protein content, the respiration necessary to maintain a given amount of protein increases also.

Excluding Granny Smith, correlations ($P < 0.01$) are found between respiration per unit protein and cell volume (Fig. 8) and between preclimacteric respiration rate per unit fresh weight and number of cells per gram; the latter (Fig. 9) is negative in contrast with that found by Smith (1940) between post-climacteric respiration rate and number of cells per gram.

IV. Discussion

The more rapid senescence and greater susceptibility to disorder of light crop fruit may be related to its higher respiration per unit protein. Cells of light crop fruit appear to require more energy from respiration to maintain their protein. Possibly light crop cells are unable to maintain an efficient transfer of energy at the higher rates required and hence show more rapid senescence and greater susceptibility to disorder.

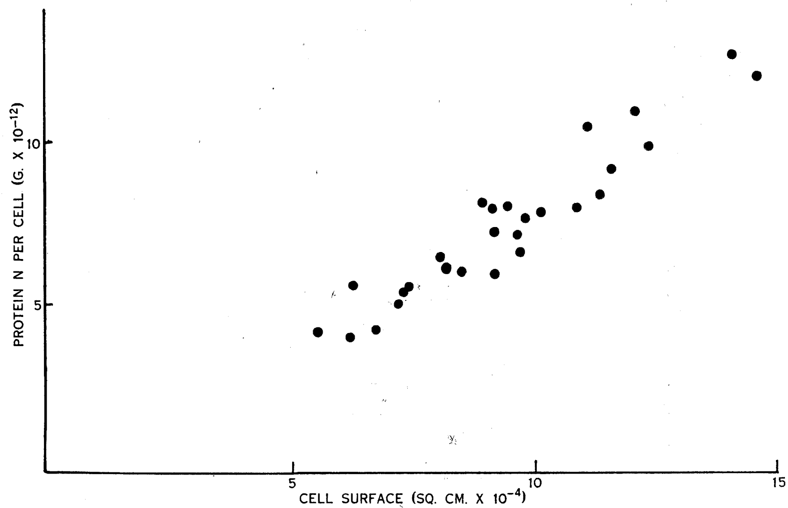

Fig. 6.—Relation between protein nitrogen per cell and cell surface for different varieties.

It is now possible to suggest an explanation why the larger fruit from heavy crops has a lower susceptibility to disorders and a slower rate of senescence than fruits of similar size from light crops, as reported by Carne and Martin (1938). In the former fruit, the large size has been shown by Bain and Robertson (1951) to be due mainly to increase in cell number and in the latter the larger size has now been shown to be due to increased cell size. Respiration per unit protein (*R/P*) would therefore be lower in the former.

The facts presented here support the theory of Robertson and Turner (1951) that the greater the protein concentration in an apple cell, the greater would be the transfer of energy from respiration to protein synthesis for maintenance. If the energy transfers took place through phosphate carriers, the more rapid dephosphorylation of carriers might result in an accelerated respiration since respiration rate depends on the amount of carrier available to accept phosphate. Robertson and Turner thought that large fruit might have difficulty in maintaining cell constituents where high protein contents were making severe demands on the energy distributors of the cells. It has now been shown that though protein synthesis keeps pace with cell enlargement, the respiration per unit protein has increased with cell size.

The comparison of varieties, while of interest, has not shown any consistent correlation between cell characters such as cell size or cell number and physiological characters such as period required for maturation or date of maturation. Lack of any relation between *R/P* ratio and maturation period was unexpected.

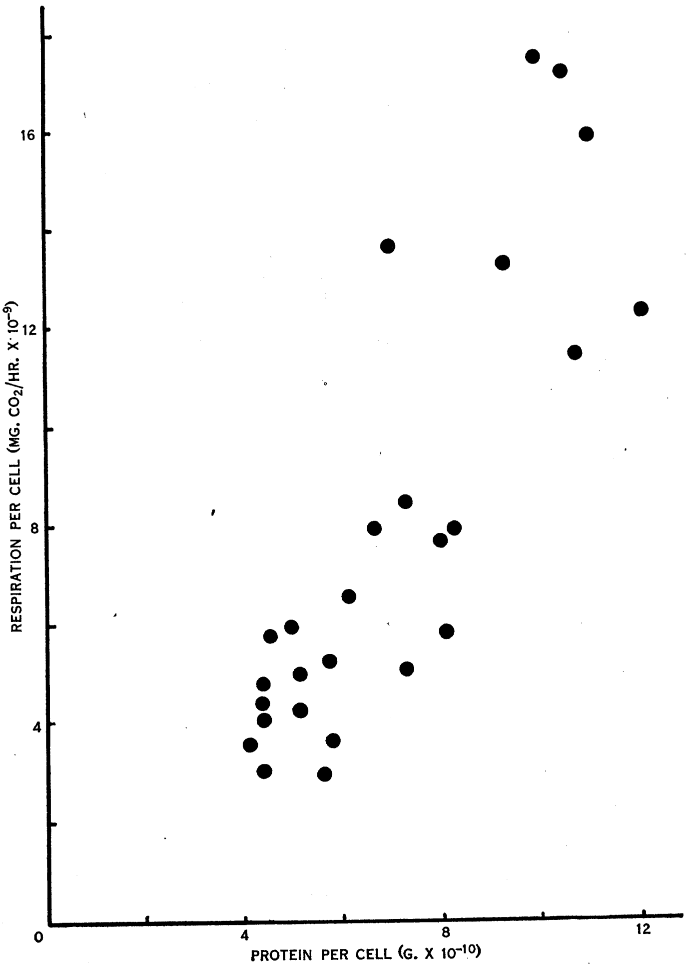

Fig. 7.—Relation between respiration rate per cell and protein nitrogen per cell.

There was a wider range in this value in Tasmanian dessert varieties than in English ones and though the only culinary variety studied (Alfriston) had a low value, it is felt that the transition from purely culinary to purely dessert quality is so gradual over the range of varieties that it is dangerous to assume that culinary quality is linked with *R/P* ratio. Sturmer, with a high *R/P* ratio, has a high culinary quality; Tasman Pride with a low culinary quality a low one. This is the reverse of the relation found by Hulme (1951).

The anomalous behaviour of the variety Granny Smith (Figs. 2, 8, 9) is of interest but no explanation can be offered. Smith (1950) thought certain aberrant characteristics in Bramley's Seedling might be due to its triploidy, but Granny Smith is a diploid and Ribston, another triploid, appears to be normal.

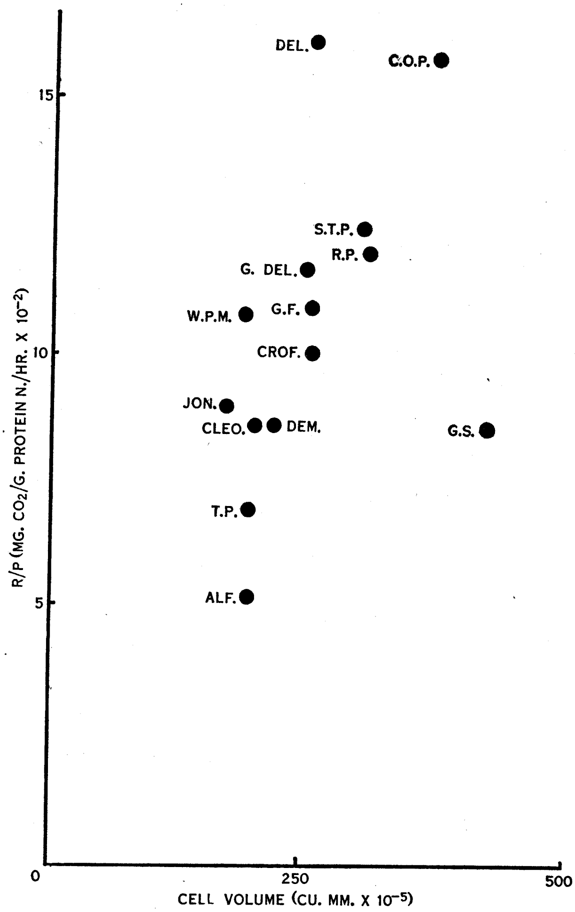

Fig. 8.—Relation between respiration per unit protein and cell volume.

One of the most important problems of the Tasmanian fruit industry is to increase the keeping quality of large fruit for which there is an increasingly strong demand. In the United States large fruit can be cool-stored for periods longer than is possible with Tasmanian fruits of the same varieties. Attempts to raise the mean fruit size without impairing keeping quality seem most likely to succeed if cell number per fruit is increased and cell size kept small.

Cell division normally ceases 3-4 weeks after pollination and therefore horticultural practices that stimulate cell division or prolong this period are likely to be beneficial while excessive increase in cell size must be avoided.

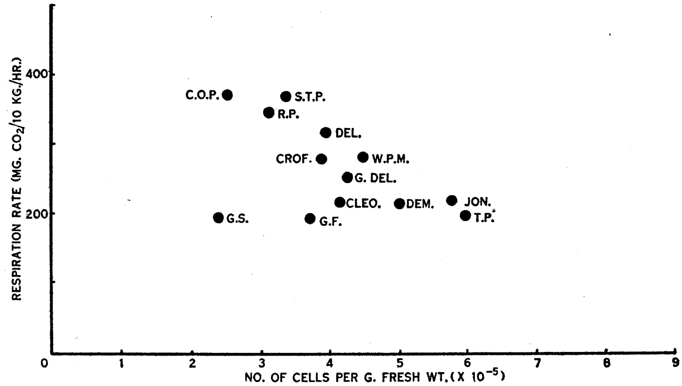

Fig. 9.—Relation between respiration rate per unit weight of tissue and number of cells.

V. Acknowledgments

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