

# AN EXPLORATION OF THE CARBON ECONOMY OF THE TOBACCO PLANT

## I. INFERENCES FROM A SIMULATION

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### *Abstract*

The question of whether photosynthesis may frequently be suppressed in the tobacco plant due to lack of demand for assimilates was examined using simulation techniques.

The growth of the tobacco crop of Petrie *et al.* (1939) was first reproduced by use of growth analysis methods. Then the carbon estimated to be required for each day's growth and respiration was compared with that estimated to be potentially available, after allowing for leaf senescence. In making these calculations it was assumed (1) that all leaves were capable of photosynthesis at the nominated rate ( $20 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ ) for the whole period of light saturation, and (2) that light intensity was above saturation level for 10 hr daily, at least for the first 67% of the growth period. (The grounds for these and other assumptions are discussed.) On this basis, the calculated potential photosynthetic capacity exceeded that required by 70–170%, depending on the stage of growth. Input values had to be varied to extreme limits to eliminate this excess.

These calculations, which were intended to stimulate experiment on the carbon budget of tobacco, led to the following conclusions: that rates of photosynthesis of tobacco leaves may commonly be suppressed due to shortage of demand; that photosynthesis cannot therefore be reliably estimated for this crop from environmental analysis unless an effective ontogenetic routine is run concurrently; that accurate prediction of respiration rates will be less important for simulation purposes in tobacco than in the more common cases where the supply of assimilates is limiting; and that many aspects of the physiology of the tobacco plant might be better understood by treating the plant more as an integrated system than has been done previously.

## I. INTRODUCTION

A major aim of crop physiological research is acquisition of the ability to predict yield and quality. Substantial advances have been made in recent years by analysts of the crop environment (e.g. de Wit 1965), but problems are now being met which require solution in physiological terms (Loomis 1970; Monteith 1970). McCree (1970) has suggested that a solution may be achieved through integration of plant physiological principles. By this he is taken to imply that observed phenomena should emerge quite naturally in simulations from the interplay of these principles, whereas little can be expected from correlations or direct mimicking of observations.

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Whilst verbal integration of plant physiological principles has always been prominent in the literature, expression in tangible working forms is an art still to be learnt. This paper takes a very modest step in that direction in the course of examining a question that arose in the Division of Land Use Research, CSIRO, about prediction of photosynthesis in the tobacco plant.

During discussion of the uncommonly small proportion contributed by the root system and inflorescence to the final dry weight of tobacco plants, it was suggested that under conditions of favourable light and water supply the leaves may photosynthesize at rates well below those which would be predicted from environmental measurements. Photosynthesis apparently can be suppressed by lack of use for its products (King *et al.* 1967; Neales and Incoll 1968; Austin 1972; Spence and Humphries 1972), and if this phenomenon occurred extensively in field tobacco it would render invalid the simulation of tobacco growth by techniques now used for many crops.

To help define the questions which should be asked in experiments to test this hypothesis, an estimate of the carbon budget of the plant was made from data in the literature and from the CSIRO Tobacco Research Institute, Mareeba, North Queensland. This paper describes the method followed and the results obtained. The consequential experiments will be described in subsequent papers in the series.

## II. METHOD

The approach adopted was conceptually very simple. The growth of the tobacco plants of Petrie *et al.* (1939) was simulated on the computer by use of growth analysis methods. Then the estimated maximum photosynthetic capacity of the plants was compared each day with that calculated to be required for growth and respiration. Petrie's data were selected for the exercise because they represent the only extensive growth analysis of tobacco which has been published. The thesis of Papenfus (1967) is a valuable source, but the data were of more limited use for the present purpose.

The assumptions made in arriving at the estimates of required and available carbon are clearly all-important, so to help the reader make his own assessments a brief account of Petrie's experiment is given here before the methods of calculation are outlined. The information which does not appear in Petrie's paper has been kindly supplied by Prof. C. M. Donald and Dr. R. F. Williams.

Seeds of a flue-cured variety of tobacco (*Nicotiana tabacum* L. cv. Hickory Prior) were germinated in mid-November 1935 in a glasshouse at the Waite Agricultural Research Institute, Adelaide. After transplanting (day 23), there were 240 plants in the experiment, grown singly in cylindrical pots about 30 cm deep by 20 cm in diameter. The root medium was sand, and the plants were arranged on benches in pairs of north-south rows, with about 120 cm between the benches and about 45 cm between plants on the benches. This arrangement is to be compared with the single-row arrangement in the field at Mareeba (120 cm between rows, 60 cm between plants), which permits the basal leaves of the summer crop to be well illuminated.

We are concerned here with Petrie's untopped plants given the second level of phosphorus (treatment II), which proved neither deficient nor excessive. The nutrients were supplied in doses between days 20 and 34. Water was added several times daily, if necessary, to maintain the sand at 70% of its maximum water-holding capacity. Since the pots lacked drain holes, some waterlogging might have occurred but no nutrients would have been lost by leaching. The final height of these plants was about 190 cm.

Figure 1 shows in summary how growth was simulated prior to initiation of the inflorescence. Leaf development was taken as the reference point, and the growth of the stem and root system was derived from allometric relationships with the relative leaf expansion rate (RLER) calculated over all leaves. Once the inflorescence had been initiated no simple system of this nature appeared to fit Petrie's data, so the stem, root system, and inflorescence were given constant relative growth rates (RGR) for the periods between Petrie's harvests to obtain the dry weight actually recorded for these plant parts.

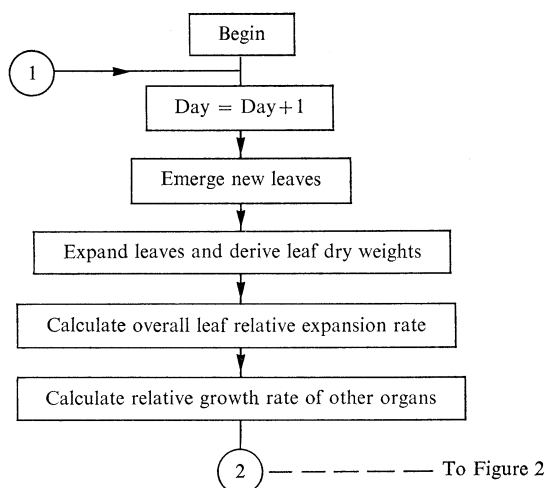


Fig. 1.—Summary of the method of simulating the growth of the plant parts.

The input used for the growth simulation is given in Table 1. Petrie supplied no data on seedling growth, and because the leaves were accounted for in groups it was not exactly clear which leaf position belonged to which group. Data from Hopkinson (1968, 1969a, 1969b), Mareeba, and the present author in one case, were drawn on to complete the picture.

The leaves were regarded as individuals in the simulation, and the method used to expand them was as follows. An initial leaf area was nominated, common to all leaves. Then, drawing from Hopkinson (1968), a final area was nominated, assuming the plants bore 26 leaves in all. This number is low for plants given pre-transplanting drought at Mareeba but is typical of those carefully watered and tended from germination. Expansion developed according to the autocatalytic growth formula, using the expression for RLER given by Richards (1969):

$$\text{RLER} = k \times \frac{(\text{final leaf area} - \text{current leaf area})}{\text{final leaf area}}$$

where  $k$  is a constant. The data of Hannam (1968), based on microscopical analysis, suggest that the Gompertz formula (Richards 1969) would give more realistic leaf expansion, but it was found that the total leaf areas recorded by Petrie could not

TABLE 1

INPUT USED IN SIMULATING THE GROWTH OF THE TOBACCO PLANTS OF PETRIE *ET AL.* (1939) AND  
IN ESTIMATING THEIR CARBON BUDGET

Input		Source or comment or both
<b>Emergence</b>		
Time	Day 4 from wetting	Direct observation
Cotyledons		
Total area at emergence	1.0 mm <sup>2</sup>	Direct observation
Total dry weight at emergence	20 µg	Area × initial SLW
<i>k</i> in autocatalytic formula	0.7	Empirically determined
Total maximum area	10 mm <sup>2</sup>	Direct observation
Stem dry weight	4 µg	Extrapolation from observations on older plants
Root dry weight	4 µg	Extrapolation from observations on older plants
<b>Vegetative growth</b>		
Total No. of leaves	26	Characteristic of plants not droughted as seedlings
Appearance of first leaf	Day 6	Direct observation
Rate of leaf emergence subsequently	1 per 2 days	Values between 1.5 and 3.5 days per leaf are observed
Initial area of leaf	1 mm <sup>2</sup>	Arbitrary value
<i>k</i> in autocatalytic growth formula	0.34	Empirically determined
Initial SLW	20 µg mm <sup>-2</sup>	Petrie <i>et al.</i> (1939), but somewhat arbitrary owing to importance of midribs in early stages of expansion
Carbon as percentage dry weight (all plant parts)	43%	Penning de Vries (1972)
Final leaf area (mm <sup>2</sup> ):		
Leaf No.	Area	Leaf No. Area
1	5 × 10	10 46 × 10 <sup>3</sup>
2	25 × 10	11 70 × 10 <sup>3</sup>
3	10 × 10 <sup>2</sup>	12 78 × 10 <sup>3</sup>
4	25 × 10 <sup>2</sup>	13 78 × 10 <sup>3</sup>
5	50 × 10 <sup>2</sup>	14 90 × 10 <sup>3</sup>
6	75 × 10 <sup>2</sup>	15 90 × 10 <sup>3</sup>
7	10 × 10 <sup>3</sup>	16 94 × 10 <sup>3</sup>
8	17 × 10 <sup>3</sup>	17 107 × 10 <sup>3</sup>
9	26 × 10 <sup>3</sup>	18 115 × 10 <sup>3</sup>
Root RGR : leaf RLER	1.10	Empirically determined
Stem RGR : leaf RLER	1.08	Empirically determined

TABLE 1 (*Continued*)

Input		Source or comment or both
<b>Growth in reproductive stage</b>		
Start of floral development	2 days after initiation of last leaf	Day 58, which is approx. correct for a non-droughted plant
Dry weight of inflorescence at emergence	100 $\mu\text{g}$	Arbitrary value
Final dry weight of inflorescence	$22 \times 10^6 \mu\text{g}$	Petrie <i>et al.</i> (1939)
RGR ( $\mu\text{g } \mu\text{g}^{-1} \text{ day}^{-1}$ ):		} Calculated from Petrie <i>et al.</i> (1939)
	Days	
	58–76    77–90    91–108    109–124	
Inflorescence	0.310    0.310    0.133    0.077	
Stem	0.190    0.073    0.027    0.005	
Root	0.125    0.065    0.015    0.008	
<b>Other inputs</b>		
Photosynthesis period	10 hr	See text. Dark period = 14 hr
Rate of net photosynthesis	20 mg $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$	See text
Rate of respiration:		
Growth respiration ( $R_g$ )	25% carbon in growth increment	
Maintenance respiration ( $R_m$ )	1.5% of carbon in total dry matter	Based on Penning de Vries (1972). No leaf respiration during photo-period—see text
Minimum rate of leaf thickening	0.07 $\mu\text{g C mm}^{-2} \text{ day}^{-1}$	Estimated from Petrie <i>et al.</i> (1939)
Maximum rate of leaf thickening	0.70 $\mu\text{g C mm}^{-2} \text{ day}^{-1}$	Estimated from Petrie <i>et al.</i> (1939)
Maximum SLW	60 $\mu\text{g mm}^{-2}$	

be simulated with this formula without introducing new assumptions for which there is as yet little basis.

The major difficulties encountered in simulating growth in the manner described were in allowing for changes in specific leaf weight (SLW, e.g.  $\text{mg cm}^{-2}$ ) and for senescence. Direct copying of Petrie's SLW data on the computer would have been possible, but the meaning of the results would have remained uncertain because increases in SLW were due at times to thickening and at others to shrivelling. The leaves were therefore thickened and aged according to rules for which some theoretical basis could be found in the literature. Since their operation depended on the current estimated carbon status of the plant, these rules will be given after the description of the method for estimating the carbon status.

The carbon required for growth was estimated by multiplying the growth increment by the assumed carbon content of the dry matter. Hesketh *et al.* (1971) indicate that 40% is a reliable value, but 43% was used to help avoid weighting the results in the direction predicted.

To calculate respiratory losses, it was assumed that growth respiration ( $R_g$ ) and maintenance respiration ( $R_m$ ) could be distinguished (McCree 1970; Hesketh *et al.* 1971; Penning de Vries 1972).  $R_g$  was taken to be equivalent to 25% of the

day's carbon increment and  $R_m$  as equivalent to 1.5% of the carbon in the total dry matter. It will be established later in this paper that these values yielded rates of respiration per unit of dry matter comparable with published data. For the leaves, respiration was entirely discounted during the light period, since net and not gross rates of photosynthesis were used in the calculations.

Day length in Adelaide in midsummer is about 14.5 hr, so a value of 10 hr was set in the simulation as the photosynthesis period, during which time light intensity was assumed to be above saturation for all leaves [which is about one-quarter of full sunlight for tobacco (Hesketh and Moss 1963)]. To estimate the carbon potentially assimilable by the leaves a maximum rate of net photosynthesis ( $P_n$ ) was set, which was multiplied by the photosynthesis period and the area of each leaf and then summed over all leaves. Peak rates of  $P_n$  in tobacco are rather low by comparison with some other  $C_3$  plants: for upper leaves of tobacco values of between 18 and 25 mg  $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  are given by, or can be inferred from, Hesketh and Moss (1963), Papenfus (1967), Tatemichi and Ono (1969), and Turner and Incoll (1971). The value adopted was 20 mg  $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ . Rawson (unpublished data) observed constant rates of  $P_n$  in tobacco during the day when the light level remained above saturation. Neither the stem nor the inflorescence was allowed to assimilate carbon in the simulation, although in tobacco these are green and presumably photosynthetically active.

It will be asked whether the leaf environment was as favourable for photosynthesis as has been assumed in these calculations. With respect to temperature, Petrie's data (his Fig. 15) show that the daily maxima ranged between 27 and 37°C with very few exceptions. Since the rate of  $P_n$  of flue-cured tobacco is not very sensitive to temperature between 22 and 35°C (Tatemichi and Ono 1969), the rate of  $P_n$  in Petrie's plants was probably only rarely limited by temperature. Judging by Petrie's watering regime, water stress can probably be discounted until the later stages of growth, although it is impossible to know how far radiation load and internal resistances might have influenced  $P_n$ . The influence of nitrogen deficiency also has been considered. Watson and Petrie (1940) reported that leaf nitrogen content fell from about 6.5 to 1.5% over approximately 60 days from each leaf's emergence. Whilst the simulated leaves possess low rates of  $P_n$  after about 30 days from emergence, it may be that the potential photosynthetic capacity of the actual leaves would not have been as high as assumed when the lowest nitrogen content was reached. The most serious doubt is about light intensity. Use of a 10-hr photosynthesis period is not unreasonable, given that the average number of hours of bright sunshine per day during each month of the experiment was 7.8–8.8 hr (Waite Agricultural Research Institute records), but once the plants were about 90 cm tall (at about day 80) light intensity at the surface of many basal leaves would have been below saturation early and late in the photosynthesis period, due to the arrangement of the plants. In addition, it has emerged that the glasshouse was approximately 60% shaded by slats throughout the experiment (R. Funder née Watson, personal communication). Because of the low light intensity at which photosynthesis is saturated in tobacco (Hesketh and Moss 1963), it will be assumed in this paper that shading can be neglected up to day 80, but this is clearly a matter to be given early attention in experimental attempts to validate the conclusions reached below.

The final portion of the simulation operated when excess carbon was available. Figure 2 shows the main sequence of events. Firstly, an increment of leaf thickening was permitted over all non-senescent leaves. The necessary alteration to the respiratory load was made, and the comparison with available carbon made again. Passage around this loop was repeated until either no excess carbon was available or the maximum permitted daily increment of thickening had been reached. (Leaves also had a maximum permitted SLW.) If excess carbon was still potentially available, photosynthesis was assumed to be suppressed in the following manner.

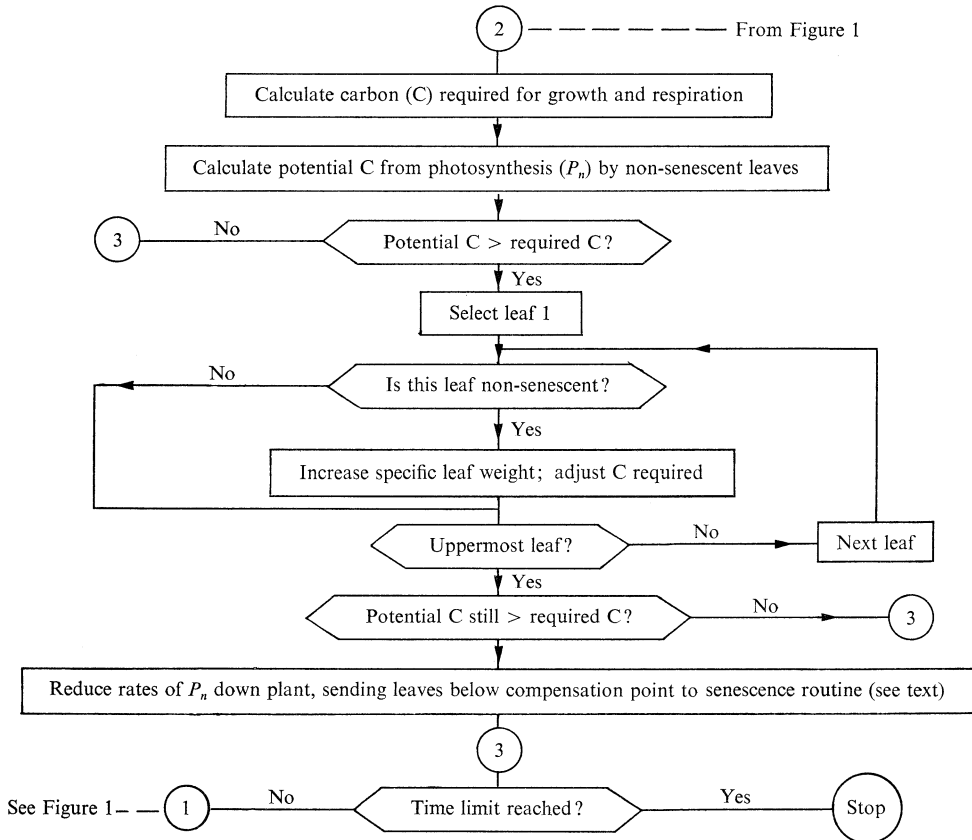


Fig. 2.—Summary of the method of comparing the carbon required and potentially available and of thickening and senescing the leaves.

The uppermost leaf was always given the maximum permitted rate of  $P_n$ . A stepwise decrease in the rate of  $P_n$  was then imposed leaf-by-leaf down the plant, with the decrement being initially very small. If after the first passage around this loop excess carbon was still available, the decrement was increased and the process repeated. Passage around the loop ceased when the carbon assimilated approximately equalled that required. If in the course of these operations the rate of  $P_n$  for a leaf reached zero, the leaf was deemed photosynthetically redundant, was transferred irreversibly to the senescence routine, and was made independent of the plant's

carbon budget thereafter. Such leaves were then permitted no further photosynthesis and they respired their own dry matter (24 hr per day) until their SLW fell to 67% of their maximum, when they were deemed dead. Non-redundant leaves were assumed to be capable next day of photosynthesizing at the maximum rate permitted if the demand was there.

TABLE 2

COMPARISON BETWEEN THE DEVELOPMENT (UNITS PER PLANT) OF THE TOBACCO PLANTS OF PETRIE *ET AL.* (1939) (*ITALIC FOUNT*) AND THE SIMULATED PLANTS (*ROMAN FOUNT*)

Day No.	No. of leaves emerged*	Leaf area (100 mm <sup>2</sup> )	Leaf weight (mg)	Stem weight (mg)	Root weight (mg)	Inflorescence weight (mg)
10	3	0.17	0.36	0.056	0.058	—
20	8	1.4	3.1	0.45	0.48	—
30	13	12	28	4.4	4.9	—
40	18	81	200	35	40	—
50	23	380	950	180	220	—
54	25	660	1700	330	390	—
54†	‡	<i>650</i>	<i>1400</i>	<i>330</i>	<i>400</i>	—
60	26	1500	3700	850	870	0.22
70	26	4500	12000	4800	2800	3.3
77	26	7600	21000	15000	6100	22
77	‡	<i>7000</i>	<i>19000</i>	<i>15000</i>	<i>6000</i>	—
80	26	9000	26000	18000	7300	50
90	26	13000	40000	37000	14000	740
91	26	13000	41000	38000	14000	840
91	‡	<i>12000</i>	<i>40000</i>	<i>38000</i>	<i>14000</i>	<i>1000</i>
100	26	13000	44000	48000	16000	2600
109	26	13000	46000	60000	18000	7600
109	‡	<i>13000</i>	<i>47000</i>	<i>60000</i>	<i>18000</i>	<i>8000</i>
110	26	13000	46000	60000	18000	8100
120	26	13000	50000	63000	20000	18000
123	26	13000	51000	64000	20000	21000
123	‡	<i>12000</i>	<i>48000</i>	<i>65000</i>	<i>20000</i>	<i>22000</i>

\* Initial size = 1.0 mm<sup>2</sup> (Table 1). Leaves counted from cotyledons.

† Data of Hackett from plants of about this age—used to establish relationship between organs, because Petrie's data lie very close to the abscissa.

‡ Petrie referred only to groups of leaves.

This sequence of rules may appear entirely arbitrary at first sight, but this is not the case. Jones *et al.* (1959) considered the deposition of starch in a tobacco leaf (which would increase SLW) to be the leaf's first response to having excess carbon available. Ushijima and Tazaki (1968) report rates of  $P_n$  for different leaf positions on corn, sunflower, and mulberry which, with the exception of the 1–2 uppermost leaves, fit a linear regression of rate upon leaf position. Further, several authors (Woolhouse 1967; Hodgkinson *et al.* 1972; Gifford and Marshall 1973) have found that leaves having low rates of  $P_n$  can be reactivated if the demand for carbon is suddenly increased. It is acknowledged to be erroneous to give the uppermost leaves the maximum rate of  $P_n$ , but no better system could be devised without better data. However, the area of these leaves is very small and their absolute requirement for carbon is also small. Finally, authors already quoted are of the view that



photosynthesis can in some way be suppressed to match demand; and there are indications that this suppression can lead to leaf senescence (Lovell *et al.* 1972). The simulation has attempted to integrate these findings.

Finally in this section it is important to stress that any excess of carbon which emerged in the calculations was not carried forward, except as increased SLW. Growth and respiration were always assumed to depend on current photosynthesis.

### III. RESULTS

The input values adopted as standard for the program yielded the leaf area and dry weights of organs shown in Table 2. Direct comparison is made in the table with the data from Petrie's harvests on days 77, 91, 109, and 123. A harvest had been taken also on day 54, but the points lay so close to the abscissa that the relationship between plant parts at this time had to be obtained from unpublished experimental data of Hackett.

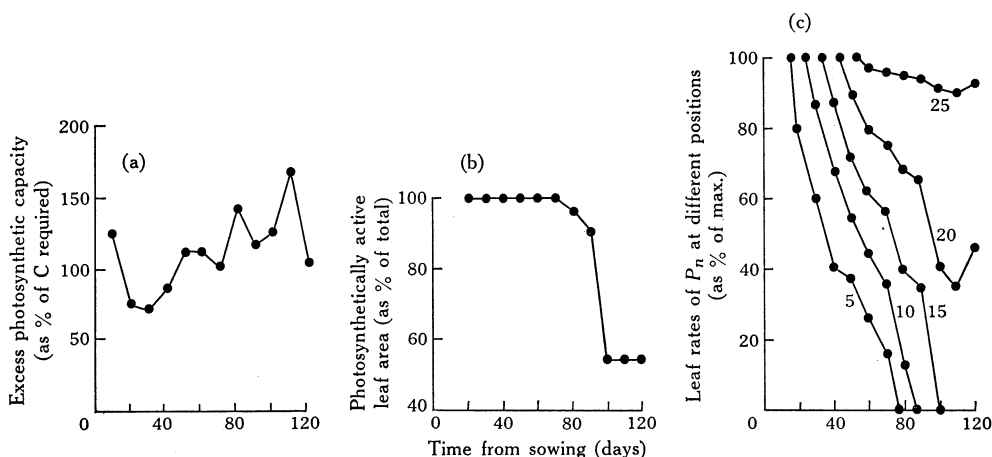


Fig. 3.—(a) Estimated excess photosynthetic capacity as percentage of that required; (b) proportion of photosynthetically active leaf area remaining on the simulated plant; (c) photosynthetic life histories of selected leaves.

Given the “tuning” opportunities in the program, the agreement between the simulated and actual plants was not remarkable except with respect to leaf dry weight. The good agreement here was gratifying because the outcome depended on the rules for thickening, senescing, and killing the leaves.

The chief question asked in this exercise, however, was whether the photosynthetic capacity of the plants exceeded that required to satisfy growth and respiration. The results are shown in Figure 3(a). Throughout the period of growth there was an excess capacity of between 70 and 170% of that required, the actual amount depending on the time from germination. Except for the point at day 10, there was a tendency for the excess capacity to increase with age. This occurred despite the fact that leaf senescence became substantial in the simulated plants after day 90 (Fig. 3b), when, indeed, Petrie's SLW data began to increase sharply, indicating the shrivelling and death of the lower leaves. The fluctuations in Figure 3(a) after day 70 are due to the sudden changes in growth rate of the stem, root system, and inflorescence, due to the method of calculation.

Photosynthetic histories of selected leaves of the simulated plants are shown in Figure 3(c). The rates of  $P_n$  are those obtained after total plant  $P_n$  had been reduced to that required. The basal leaves declined in photosynthetic activity fairly steadily and were found to have a working life of about 55 days. Once the absolute growth of the inflorescence became substantial (e.g. an increment of 500 mg dry weight between days 109 and 110—see Table 2), the upper leaves maintained a more constant rate of  $P_n$ , which was essential because only 10 photosynthetically active leaves were left on the simulated plant after day 92.

This pattern of leaf activity is in error in that a preliminary rise should appear early in the life of each leaf; otherwise it is remarkably like that seen in published data for various species. Hopkinson (1964), Papenfus (1967), and Ludlow and Wilson (1971) show that the rates of  $P_n$  of middle and lower leaves normally decline approximately linearly with time, whilst upper leaves responsible in part for the growth of an inflorescence show much more constant rates of  $P_n$  until maturity (Evans and Rawson 1970). It is also noteworthy in Figure 3(c) that the curve for leaf 20 rises over the last 10 days of growth. This illustrates that the model allows the rate of  $P_n$  of a leaf to rise if the demand is there. Steeper rises could have occurred, for example if a leaf-picking facility had been included in the model.

TABLE 3

RATE OF RESPIRATION OF SIMULATED TOBACCO PLANTS AND PERCENTAGE ATTRIBUTED TO GROWTH RESPIRATION ( $R_g$ )

Respiration rate expressed as  $\text{mg C (g C)}^{-1} \text{ hr}^{-1}$  ( $\text{rate}_1$ ) or  $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  ( $\text{rate}_2$ ). Multiply  $\text{rate}_1$  by 1.58 to obtain rate expressed as  $\text{mg CO}_2 \text{ (g dry wt.)}^{-1} \text{ hr}^{-1}$

Day No.	Photosynthetically active leaves (dark respiration)			Stem		Root		Inflorescence	
	$\text{Rate}_1$	$\text{Rate}_2$	$\%R_g$	$\text{Rate}_1$	$\%R_g$	$\text{Rate}_1$	$\%R_g$	$\text{Rate}_1$	$\%R_g$
10	2.2	0.74	79	2.3	77	2.3	79	—	—
20	2.7	0.94	78	2.7	79	2.7	80	—	—
30	2.5	0.94	76	2.6	79	2.7	79	—	—
40	2.3	0.89	74	2.4	76	2.4	76	—	—
50	2.0	0.79	69	2.0	71	2.0	72	—	—
60	1.9	0.74	68	2.2	74	1.7	66	3.0	81
70	1.6	0.65	61	2.2	74	1.7	66	3.0	82
80	1.2	0.57	52	1.3	54	1.2	51	3.0	82
90	0.9	0.46	36	1.3	56	1.2	51	3.0	82
100	0.5	0.45	26	0.9	31	0.8	20	1.8	55
110	0.6	0.52	22	0.7	8	0.7	12	1.3	55
120	0.6	0.58	20	0.7	8	0.7	12	1.3	55

The respiration rates of the various parts of the simulated plant fell within the range quoted by Schäfer (1971) until vegetative growth began to cease (Table 3). They also agreed with his finding that stem and root respiration rates are roughly equivalent to leaf dark respiration rates. The disagreement between  $\text{rate}_1$  and  $\text{rate}_2$  after day 60 is due to leaf thickening. The possible influence of any errors in estimating respiration are explored later.

Summarizing thus far, it was found that the simulation copied the increase in leaf area and dry weight of Petrie's plants and that the internal workings of the model seemed acceptable, as judged by the photosynthetic histories and the respiration rates of the plant parts. It was then considered whether the estimate of excess photosynthetic capacity arrived at could be false due to fortuitously favourable selection of certain input values.

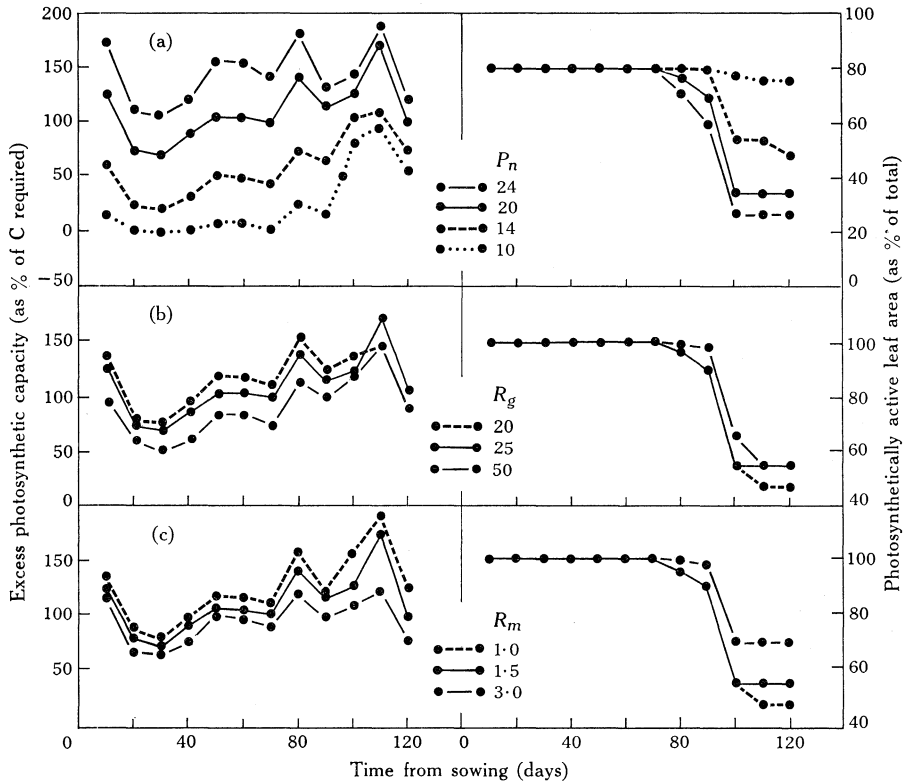


Fig. 4.—Effect of varying the rate of (a)  $P_n$  (net photosynthesis, expressed as  $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ ), (b)  $R_g$  (growth respiration, expressed as percentage of carbon in growth increment), and (c)  $R_m$  (maintenance respiration, expressed as percentage of carbon in dry matter) on the estimate of excess photosynthetic capacity and on the proportion of photosynthetically active leaf area. The solid line corresponds with the standard rate (Table 1) used to calculate Figure 3.

The simplest test of this possibility was to determine the effects of varying the rates of  $P_n$ ,  $R_g$ , and  $R_m$ . These rates have the most obvious influence on the result, and by making large variations in their values effects of errors in less important inputs, such as percentage carbon, would be swamped. The result of varying the rates of  $P_n$ ,  $R_g$ , and  $R_m$  is shown in Figure 4. It required halving the maximum permissible value of  $P_n$  to eliminate excess photosynthetic capacity. Senescence was then almost eliminated too. Doubling the rates of respiration had much smaller effects on the estimated excess photosynthetic capacity and on leaf senescence. Since it is most unlikely that Petrie's plants had a maximum  $P_n$  rate of only  $10 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$

(or a 21 % carbon content, etc.), it was concluded that the estimate of excess photosynthetic capacity originally obtained (Fig. 3a) was not due to the use of favourable input values, although, as has already been indicated, errors could have arisen due to other assumptions in constructing the model.

#### IV. DISCUSSION

The primary purpose of this work was to map out a dynamic whole-plant view of the carbon economy of tobacco, and in doing so, to make a preliminary estimate of whether potential supply of carbohydrate in this species exceeds demand under favourable conditions. Since the method involved new approaches, and only one set of data has been examined so far, the conclusions have been cautious but are thought worthy of attention nevertheless.

Taken at face value, the calculations suggest that Petrie's plants had spare photosynthetic capacity throughout their life, even after senescence had been allowed for. As already explained, this estimate is thought to be reasonable up to about day 80. Afterwards, the questions which arise about the shading of his plants make the conclusions progressively less reliable. However, this exercise was carried out also with Mareeba field conditions in mind. There, where spacing is greater than that used by Petrie, where irrigation is supplied, and light intensity is higher in the summer growing season than in Petrie's glasshouse, it is reasonable to suspect that potential supply of carbohydrate can exceed demand from transplanting to maturity. It is therefore legitimate to point to the consequences should this finding be supported by subsequent work.

Firstly, attempts to predict crop photosynthesis in tobacco under such conditions will founder if the methods rely largely, as has been customary, on environmental analysis. An effective ontogenetic simulation will probably be an essential accompaniment. This would have to predict not only the timing of certain events, such as floral initiation, but also the number of organs and their carbohydrate requirement. Only one example exists at present of an ontogenetic simulation run in parallel with a simulation of carbohydrate availability and consumption. This is for cotton (Duncan *et al.* 1971) and has yet to become widely available and widely tested.

The second inference is that, if photosynthesis in tobacco is often suppressed by lack of demand, there may be less need to determine respiration rates as accurately for simulation purposes as is necessary for supply-limited species. With the latter, errors in estimating carbon losses lead directly to errors in estimating growth, but with tobacco and any species like it, it is probable that respiratory demands will usually be met without retarding growth.

The third inference is that understanding of leaf senescence might be furthered by viewing it much more in the context of the plant as a whole than has been customary. In the present work the leaves are thought of as belonging to a population whose members are all sensitive to the needs of the entire plant but stand in a hierarchical arrangement to one another as suppliers of carbohydrate. Coupling this concept with that of leaf photosynthetic redundancy leading leaves towards senescence provides a more flexible and realistic approach than that based on leaf age alone, which de Wit *et al.* (1970) felt forced to use for ELCROS.

Before concluding, reference must be made briefly to other aspects of the calculations. The use of  $R_g$  and  $R_m$  proved to be a convenient means for estimating respiration, but, due to the nature of the exercise, the results cannot be considered to support the work of McCree (1970), Hesketh *et al.* (1971), and Penning de Vries (1972). The leaf photosynthetic histories agreed with the observations available. The view that the histories were determined mainly by demand for photosynthesis was supported by results of Turner and Incoll (1971), who opened the canopy around a tobacco plant setting seed in the field and found that the increased illumination of the basal leaves did not increase their rate of photosynthesis, despite the fact that they were green and their stomatal conductance was high. The leaf thickening rules also worked satisfactorily, but there is little theory with which to compare them. More needs to be known about this phenomenon if carbon usage is to be predicted accurately. The demand limitation, if it does exist, is presumably due to the strong apical dominance in tobacco and the lack of heavy accumulation of primordia on the stem apex (Hopkinson and Hannam 1969).

This exercise has been based on a linkage of physiological principles such as McCree (1970) suggested should be attempted widely in crop physiology. The results bear out the implication drawn from his remarks that, if the correct relationships between the operating principles can be found, the observed phenomena will appear straightforwardly from the simulation. Whilst the correspondence in the present paper between simulated and actual observations does not validate the physiological assumptions, the outcome and means of achieving it are sufficiently explicit and plausible to provoke worthwhile experimentally based responses. Such interaction between simulation and whole-plant physiological research could benefit both disciplines. Experimental work now under way in this Division with tobacco may help to justify this view.

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