Expl Agric. (1978), **14**, pp. 1–5
Printed in Great Britain

REASSESSMENT OF MAXIMUM GROWTH RATES FOR C_3 and C_4 CROPS

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(*Accepted* 18 *September* 1977)

SUMMARY

Figures for maximum crop growth rates, reviewed by Gifford (1974), suggest that the productivity of C_3 and C_4 species is almost indistinguishable. However, close inspection of these figures at source and correspondence with several authors revealed a number of errors. When all unreliable figures were discarded, the maximum growth rate for C_3 stands fell in the range 34–39 g m^{-2} d^{-1} compared with 50–54 g m^{-2} d^{-1} for C_4 stands. Maximum growth rates averaged over the whole growing season showed a similar difference: 13 g m^{-2} d^{-1} for C_3 and 22 g m^{-2} d^{-1} for C_4. These figures correspond to photosynthetic efficiencies of approximately 1·4 and 2·0%.

In bright sunshine and at temperatures which are optimal for photosynthesis, the leaves of most plants belonging to the C_4 group assimilate carbon dioxide faster than the leaves of most C_3 plants. Because this difference is well established, it is widely accepted that stands of C_4 crops such as maize and the tropical grasses, which grow well only in warm climates, are likely to have faster maximum growth rates than C_3 crops growing either in warm or in cool climates. Records compiled by Gifford (1974), however, purport to demonstrate that C_3 and C_4 crops have a range of maximum growth rates which are indistinguishable and Evans (1975) claimed that crop yields display 'no consistent advantage of the C_4 pathway'. The purpose of this note is to suggest that errors and uncertainties in the figures used by Gifford and Evans make their conclusions untenable.

The maximum growth rate (C) of a plant stand is generally determined by sequential harvests at intervals of 1–3 weeks and published figures are prone to several types of error. *Random sampling error* is often between ±5 and ±10% and tends to be positive when a figure for the maximum growth rate of a crop is selected from a set of field measurements. *Systematic experimental error* is sometimes suspected on circumstantial evidence but is hard to quantify. *Numerical error* is difficult to detect but can sometimes be corrected retrospectively.

Two numerical errors were identified in the sources of Gifford's Table 5. First, the value of $C = 53$ g m^2 d^{-1} for *Typha latifolia* was taken from Table 3 of a paper by Penfound (1956) quoted by Williams *et al.* (1965). The same table contains harvest dates and weights from which the correct figure for the period appears to be 31 g m^{-2} d^{-1}, less than the next entry in the table which is 34 g m^{-2} d^{-1}. Second, for *Agrostemma githago*, Gifford cites 57 g m^{-2} d^{-1} from Britten and from Blackman (1968) who gave a range of 37–57 g m^{-2} d^{-1}. However, the number 57 was a typographical error not detected in proof (Blackman, private communication). Newton (1968), who continued Britten's work at Oxford, obtained consistent values of $C = 37$–39 g m^{-2} for this species.

At least two of Gifford's figures came from experiments in which significant amounts of light were intercepted laterally by tall plants grown in small plots. For *Helianthus annuus*, values of C measured by Hiroi and Monsi (1966) are often quoted as 68–76 g m^{-2} d^{-1}. Critical reviewers have rejected these figures because the linear dimensions of the plot ($1{\cdot}8 \times 1{\cdot}8$ m) were comparable with maximum plant height (Loomis and Gerakis, 1975). In each plot, the vertical surface of the canopy was approximately four times its horizontal surface, so even allowing for some mutual shading between plots, plan area was not an appropriate basis for calculating C. Similarly, for *Phragmites communis* growing in a circular tank containing culture solution, Dykova (1971) reported $C = 57$ g m^{-2} d^{-1}. Her paper includes a photograph showing that the tanks were well separated and that the maximum plant height exceeded the tank diameter. The author herself admits that 'the very high values of C may be attributed to the marginal effect, namely, the large amount of incident radiation received by the spheroidal surface of the stands'. Although her comparison of treatments may be internally consistent, her figures should not be compared with the maximum productivity of other species.

When the figures already discussed are removed from Gifford's table, two anomalously large values remain for maize and for rice. Exceptionally fast rates of maize growth were reported by Haggar and Coupar (1972) from a density trial in northern Nigeria. For a sowing density of 430,370 seeds/ha, $C = 78$ g m^{-2} d^{-1} was achieved at a leaf area index of $L = 12$, whereas at 107,590/ha, $C = 26$ g m^{-2} d^{-1} when L was 4. From published figures for the extinction of light in maize canopies, it can be estimated that the less dense stand intercepted about 90% of incident light compared with almost 100% intercepted by the denser stand. It is inconceivable that a 10% increase of available energy would increase growth rate by a factor of 3. According to Coupar (private communication) many of the plants in the densest stand died as a result of competition, so the anomalous value of C is probably the result of combining nominal—and greatly exaggerated—plant densities with mean dry weights which were determined from ten plants at each harvest. Loomis and Gerakis drew attention to a similar error attached to a record growth rate for carrots.

A figure of $C = 55$ g m^{-2} d^{-1} for rice was obtained at the International Rice Research Institute, Philippines, by Tanaka *et al.* (1966). Their original report does not contain experimental details but according to correspondence with Professor Tanaka, a record value of C was obtained over a period of 8 days during panicle development when isolation was $23{\cdot}6$ MJ m^{-2} d^{-1} (implying almost continuous sunshine) and plants were harvested from 'the central positions of a reasonably large plot where no border effect was expected'. However, in many later experiments at the same site, C was much less than 55 g m^{-2} d^{-1} and the maximum reported by Yoshida and Cock (1971) is about 30 g m^{-2} d^{-1}. This lower value is comparable with the maximum of 36 g m^{-2} d^{-1} reported for IBP trials at eight stations in Japan between 1967 and 1970 (Murata and Togari, 1975). If the possibility of systematic error is discounted, the anomalous figure quoted by Tanaka *et al.* may be distorted by an unusually large sampling error.

In summary, there are grounds for correcting or rejecting eight of the eleven entries in Gifford's Table 5 and five of the fourteen entries in Table 11.3 of Evans. Two other figures cited by Evans need comment. The values of $C = 60$ g m^{-2} d^{-1} for *Pennisetum purpureum* (Arias and Butterworth, 1965) is exceptionally large even for a C_4 plant. Fast growth was possibly a result of the lateral interception of light by plants in plots only 3·1 m wide, a dimension comparable with maximum stand height. On the other hand, $C = 37$ g m^{-2} d^{-1} for *Saccharum officinarum* (Borden, 1942) is well below the figure for other C_4 species. Unlike the other short-term growth rates in Evans's table, it is a mean rate over a period of 3 months and probably underestimates the true maximum rate for sugar cane.

When all figures regarded as unreliable are eliminated, the four highest rates of dry matter production for C_3 plants fall in the range 34–39 g m^{-2} d^{-1} compared with 50–54 g m^{-2} d^{-1} for C_4 plants (Table 1).

Table 1. *Maximum short-term growth rates*

Group	Species	C (g m^{-2} d^{-1})	Reference
C_4	*Pennisetum typhoides*	54	Begg (1965)
	Zea mays	52	Murata and Togari (1975)
		52	Williams *et al.* (1965)
	Sorghum vulgare	51	Loomis and Williams (1963)
C_3	*Agrostemma githago*	39	Newton (1968)
	Sozanum tuberosum	37	Lorenz (1944)
	Oryza sativa	36	Murata and Togari (1975)
	Typha latifolia	34	Penfound (1956)

The difference between the two groups is of the order that might be expected from laboratory measurements of photosynthesis and from the loss of carbon by photorespiration from C_3 species. Part of the difference may be environmental however: C_4 plants growing in the tropics are generally exposed to greater insolation than C_3 plants in temperate latitudes. The photosynthetic efficiencies of the C_4 crops, calculated from available radiation records, range from 3·0% for *Zea mays* at 31 MJ m^{-2} d^{-1} (total solar radiation) to 4·5% for the same species at 20 MJ m^{-2} d^{-1}. The corresponding figure for rice is 3·1% at 20 MJ m^{-2} d^{-1}. Radiation records are not available for the other C_3 crops in the table, but assuming the same level of insolation as rice, their efficiencies would lie between 3 and 3·4%.

On the basis of these incomplete figures, it appears that in sunny, but not cloudless summer weather (20 MJ m^{-2} d^{-1}), the maximum growth rate of C_4 crops is substantially faster than the C_3 rate. There is no evidence for faster growth rates in cloudless weather (30 MJ m^{-2} d^{-1}), possibly because photosynthesis is then restricted by the effects of light saturation or water stress or both.

The difference between C_3 and C_4 crops is not confined to maximum growth rates: it is manifest for seasonal mean growth rates $\bar{C}$ defined as standing dry weight at harvest divided by the length of the growing season. Records tabulated by Loomis and Gerakis and by Cooper (1975) include five C_4 species for which $\bar{C}$ exceeded 17 g m^{-2} d^{-1} and six C_3 species for which $\bar{C}$ exceeded 11 g m^{-2} d^{-1}. Figure 1 shows that the final dry weight of the crops in each group was strongly correlated with the length of the growing season, presumably because this period is a good measure of the amount of radiation intercepted by the foliage.

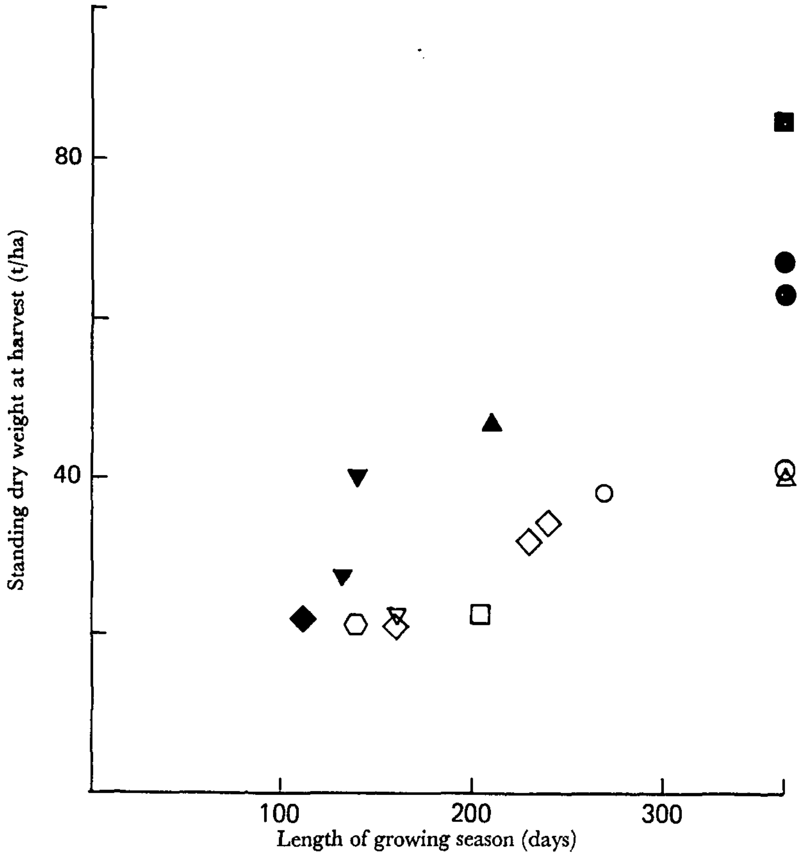

Fig. 1. Standing dry weight of crops at harvest in relation to length of growing season.

C_3 kale	○	C_4 bulrush millet	◆
potatoes	▽	maize	▼
sugar beet	◇	sorghum	▲
rice	□	sugar cane	●
cassava	○	napier grass	■
oil palm	△		

The mean value of $\bar{C}$ for the C_4 group is 22·0 ± 3·6 g m^{-2} d^{-1} or 0·42 times the mean maximum in Table 1. Corresponding figures for the C_3 group are 13·0 ± 1·6 g m^{-2} d^{-1} and 0·36. Although Figure 1 and Table 1 relate to different species and are therefore not strictly comparable, the ratio of about 0·4 for mean to maximum rates of dry matter production is consistent with the incomplete interception of light at the beginning of the growing season and with senescence before harvest. The mean photosynthetic efficiency for the C_4 group is 2·0% of total solar radiation compared with 1·4% for the C_3 group. The ratio of mean efficiencies (1·4:1) is smaller than the ratio of mean $\bar{C}$ values (1·7:1) because the tropical plants received more radiation.

Compared with the very large biochemical and physiological differences between C_3 and C_4 species, their growth rates are *similar*— and this was the main point of Gifford's paper. However, reassessment of the evidence shows they are *distinguishable* and differences of 40% in the efficiency of solar energy conversion are certainly significant in terms of food production.

Acknowledgement. I am grateful to all the authors whose correspondence I have quoted and to Dr J. N. Gallagher for comments on a draft of this note.

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