

between plasma membrane electrical resistance and pinoctosis has been noted in *Amoeba*<sup>7</sup>. A similar mechanism may be relevant in stimulated axons.

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## Measurement of Distribution of Photosynthesis in Plant Canopies

ATTEMPTS have been made to measure or calculate photosynthetic activity in various morphological parts or height layers of plant canopies. This has been done by measuring dry weight changes in relation to removal of the parts<sup>1</sup>, carbon dioxide exchange when the parts were enclosed in assimilation chambers<sup>2</sup> and a combination of progressive defoliation and whole canopy carbon dioxide uptake measurement<sup>3,4</sup>. To study the activity in layers of the canopy, Leach and Watson<sup>5</sup> placed phytometers at various points in the canopy to stimulate the photosynthesis of adjacent plant parts, and aerodynamic methods have since been used to estimate the distribution of photosynthesis in canopies<sup>6</sup>. By using photosynthesis response data for leaves and information about the environment in the profile, Monsi and Saeki<sup>7</sup> and others<sup>8,9</sup> have estimated localized photosynthesis.

There have been doubts about the reliability of these methods, however. Removal of parts may upset the balance of plant activities, enclosure of parts may modify their environment to an unacceptable extent and the behaviour of phytometers may not sufficiently parallel that of the plants. The aerodynamic method is in principle the most suitable because it does not interfere in any way with the canopy; but it depends on the assumption that all relevant environmental influences are known and allowed for, that the activity of one plant layer is not modified by its relationship with the activity of other layers or its own immediately previous activity, and that the leaf performance data are applicable to the foliage under study; further, the measurements used may not be sufficiently accurate. The use of <sup>14</sup>CO<sub>2</sub> seemed to offer an alternative method, which we have used in a study of productivity in grain sorghum.

Carbon dioxide labelled with <sup>14</sup>C was injected into an air stream passing uniformly and rapidly (two changes/min) upwards from a distribution system at ground level through a 2 m<sup>2</sup> transparent enclosure of plants in a field stand. Concurrently, the rate of CO<sub>2</sub> exchange was measured with an infrared gas analyser. After 5 min exposure to <sup>14</sup>CO<sub>2</sub> the chamber was removed, the plants collected according to height, stratum or plant parts ("fractions"), killed quickly and dried. The time from the beginning of treatment to the end of the collection was less than 15 min, which is not long enough for significant translocation of <sup>14</sup>C from the fractions. <sup>14</sup>C activity was counted in these fractions.

Photorespiration by the leaves of sorghum seems to be low or zero<sup>10</sup>, the carbon being fixed through the C<sub>4</sub>-dicarboxylic acid pathway<sup>11</sup>. The <sup>14</sup>C activity measured in the photo-

synthetic parts before translocation thus corresponds to true photosynthesis. In turn, the <sup>14</sup>C activity measured in each height stratum or plant part is directly related to true photosynthesis by that fraction, and the summation of these activities directly related to true photosynthesis by the whole canopy. It then remains to convert the <sup>14</sup>C counts for the whole canopy to actual values of true photosynthesis, from which photosynthesis by each fraction follows.

Measured CO<sub>2</sub> exchange is the net result of uptake by the photosynthetic parts, including the inflorescence, less release from the soil and those parts of the shoot which respire in the light, including the inflorescence. This release of CO<sub>2</sub> can be measured in the dark after removal of leaves. Photosynthesis by the whole canopy can then be estimated.

**Table 1** <sup>14</sup>C Activity, Photosynthesis per Unit Land Surface and Leaf Area Index of Canopy Layers

Height in canopy (cm)	<sup>14</sup> C activity in layer		Photosynthesis (mg CO <sub>2</sub> dm <sup>-2</sup> h <sup>-1</sup> )		Leaf area index
	(c.p.m.)	Total %	Measured by CO <sub>2</sub> uptake	Estimated from <sup>14</sup> C activity	
140-160	476	1.8		0.06	(Inflorescence)
120-140	2,647	10.0		3.44	0.2
100-120	8,734	33.0		11.35	0.6
80-100	11,117	42.0		14.45	2.0
60-80	3,494	13.2		4.54	1.4
0-60	0	0		0	0
0-160	26,469	100.0	34.0		4.2

The distribution of photosynthesis down the profile of a sorghum canopy at noon, 26 days after anthesis (a growth stage approaching grain maturity), as determined by our technique is shown in Table 1. Even when photosynthesis cannot be measured by CO<sub>2</sub> exchange because of the difficulty of taking a gas analyser into the field, the profile of relative <sup>14</sup>C activity directly indicates the profile of photosynthesis. In some comparisons between canopies, this may be sufficient.

There are difficulties with Calvin pathway plants, in which there is a relatively high rate of photorespiration, not only in correction for respiration (which cannot be easily measured, at least in the field), but also in knowing to what extent, in the short period of exposure, <sup>14</sup>C may have entered leaf respiratory activity. At least, relative profiles of activity may be established in a fairly satisfactory way. In the case of sorghum, however, as with several other important tropical crops and pasture grasses, the distribution of photosynthesis can be determined with a convenience and precision not previously possible.

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