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Thermochimica Acta 251 (1995) 389–391

thermochimica acta

Calorimetry of plants: a snapdragon's view ☆

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Received 5 September 1994; accepted 5 September 1994

I hate plants! Or, rather, I dislike botany! And have done so ever since my botany schoolmaster perched on a stood and dictated the subject at me. So, it was ironic to find myself chairing a session at the conference on plants; and finding it fascinating! Hence, this statement is more in empathy than would be a snapshot and, thus, more like a snapdragon (*Antirrhinum majus*) than I thought possible some months ago.

The first surprise I had as a casual observer of the discussion on etiolation was to learn that calorimetry of plants had mostly been conducted in the dark where there are, of course, no light reactions. The second surprise was that growth (biomass yield) correlates well with rate of respiration and not the rate of photosynthesis; so I suppose dark calorimetry, with only respiration, photorespiration and the Calvin cycle, is not so bad after all! Still, it was good to learn that the groups in Kazan, Lund and Provo are now equipped with photocalorimeters and making the necessary corrections for heat transformed from light. Of course, the apparatus is more complex and the analysis of thermal events more difficult, but the use of such instruments is necessary if there is to be the fullest contribution of calorimetry to the energetics of plants in, as Ingenhousz put it, their "great power of purifying the common air in sunshine and injuring it in the shade and at night".

Plants go from the small size of unicellular aquatic algae to the giant size of aerial trees, such as redwoods, and studies at both ends of this spectrum were exemplified at the conference. The vast experience of microbiologists studying bacteria and yeast in calorimeters should be a valuable reservoir for phycologists and many of the problems in, say, the marine environment have parallels in

☆ Presented at the Ninth Conference of the International Society for Biological Calorimetry, Berlin-Schmerwitz, 27–31 May 1994.

SSDI 0040-6031(94)02122-8

microbiology, for instance salt stress (in our Institute, phycology is already in the microbiology division! And they bring in kelp!). It came as no surprise that not even our American colleagues had built a calorimeter for an adult redwood tree (or even kelp!), but it was encouraging that many of the studies related to problems of growth and to the search for improvements to it. Experiments of this nature in the dark innards of a calorimeter using "bits" of trees appear to be concerned not with either the dark reactions of the Calvin cycle or the C_4 pathway, both of which fix CO_2 as photosynthate in the "green bits" containing chloroplasts, but with respiration using photosynthate to produce CO_2 in the "brown bits" (meristems of seedlings) containing mitochondria. I suppose that the innards is not a place conducive to photorespiration in the peroxisomes.

To repeat, the rate of photosynthesis does not appear to limit the rate of growth in plants, but the rate of respiration does; and this makes for interest in the thermodynamic model for plant growth, presented at the conference as the Lavoisier lecture. It uses mass and energy balance equations, rather than just the former, to relate specific growth rate (biomass production) to CO_2 and heat production in terms of carbon conversion efficiency. This is why rate of CO_2 production was used instead of the probably more informationally powerful oxygen consumption and no mention was made of nitrogen. There are a number of different difinitions for thermodynamic efficiency of growth with dissimilar system boundaries and balances as well as states of the systems and references. This is an area awaiting clarification but, undoubtedly, the model seems to have value in identifying physiological determinants of plant growth. Changes to cause increased respiratory rate may be the key to improved growth rate in many plants and, as one of the most obvious factors in respiration is the state of the mitochondrion, a target for "improvement" must be that organelle. Because mitochondria are inherited maternally, plant-breeding programmes could be aimed at more "efficient" mitochondria. It may be important also to think beyond energy supply as the only role for catabolic pathways. Many of these supply biosynthetic precurors as well as energy. Their rate may restrict growth by limiting the supply of biomass precursors.

In the animal and animal cellular physiologies, a set of terms has been defined to describe the relationships between respiratory gases and from these gases to other substrates and products. For instance, in respiration there is the theoretical respiratory quotient (RQ) for the CO_2/O_2 ratio which may or may not be the same value as the intracellular (CQ) or bulk phase (R) gas exchange ratios. The experimental flux ratio of heat/O_2 is called the calorimetric–respirometric (CR) ratio, which is directly related to the theoretical oxycaloric equivalent for each carbohydrate (or, for that matter, each amino acid and fatty acid according to Thornton's Rule), $\Delta_k H_{O_2}$; and one could go on .... In Botany, however, the same terms carry different definitions. For instance the CR ratio is of heat produced to CO_2 evolved; and so on. Clearly, there is a need for rationalization.

Photosynthesizing living systems on land and in water are so important in ecology, agriculture and industry that one is surprised that more has not be made of calorimetry in studying them. Technological and computational advances have now ensured progress, if there is the will. As children, we used to call *Antirrhinum* sp., "bunnies" (rabbits). Perhaps one day we shall have a full enthalpy recovery and percentage efficiency (by agreed definition) of *Antirrhinum*. The scientists who accomplish that will not be bunnies!.