

Litter nitrogen release in tropical agroecosystems

Plant litter decomposition based on its physical and chemical composition (quality) and environmental factors could play a key role in determining the productivity of natural and agroecosystems. In a review, Palm and Rowland¹ have suggested a minimum data set for the universal characterization of plant quality for decomposition, nutrient release and soil organic matter formation. Their ultimate aim is to couple indices from the data set with decomposition models in order to recognize a few quality parameters that could replace the need for detailed decomposition studies, in global predictions. Among other parameters, they have included nitrogen (N), because it is essential for microbial growth; but values less than 2% are considered to be associated with net immobilization, due to scavenging of N from the background. They recommend soluble polyphenols as a parameter for the decomposition, but only when the plant N content is greater than 1.8%. Lignin is important for both short and long-term decomposition. They have based these indices on the literature in which researchers have conducted incubation studies with a limited number of observations.

I recently compiled a large, comparable data set (102 observations) for the topics extracted from the literature². I clearly observed that plant materials with less than 2% N concentration show both immobilization and mineralization, irrespective of their type (species), physiological state (fresh and litter) and position in the soil during decomposition. Plant N governs the mineral N release of added plant residues when

their N concentration is between 0 and 2%, but beyond this range carbon (C) and other nutrients determine the rate of the process.

Soluble polyphenols are important determinants of the N release, only when plant N concentration is less than 1%. This was also observed for pine litter that normally contains N concentration of less than 1% (refs 3 and 4). However, plant residues rich in N (i.e. greater than 1%) have also shown significant relationships between polyphenolic contents and the N release⁵. This is attributed to a lack of continuity in the range of data due to relatively small number of observations made in the past incubation studies, as is clearly seen from my data compilation. Lignin is not important as a determinant of the N release. I found that the C/N ratio is the best predictor of plant N release. These observations imply that under low nutrient conditions, it is the nutrients in the added plant residues, which limit the action of diverse decomposer community with varying limiting factors that govern decomposition and N release. Hence, it is clear that the added plant nutrients, which affect microbial enzyme kinetics, are important parameters with respect to decomposition and N release. The critical concentrations of nutrients with respect to decomposition and N release are a function of the species composition of microbial decomposers in any ecosystem, which is determined by the soil, vegetation and climate². Therefore, if these critical levels could be established for different agroclimatic regions, it would help in improving global predictions of N re-

lease from tropical litter. The conclusions should be revised as follows. Plant residue N is a determinant of residue N release when the N concentration is less than 2%. An N concentration of greater than 1.8%, which is considered to be the critical level for the interference of polyphenols in the N release should be replaced by an N concentration of less than 1%. In my study, those indices were independent of litter and soil decomposition properties and hence are universal determinants of the litter N release in the tropics.

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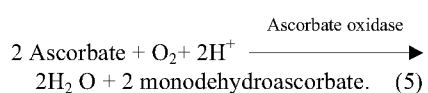
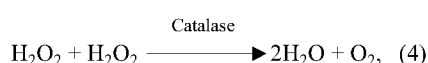
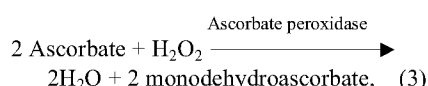
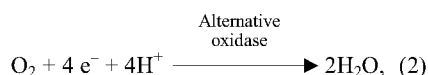
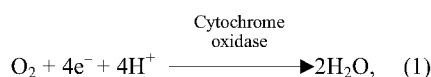
Metabolic synthesis of water in plants and its physiological implications

Plant cells have an array of enzymes to metabolize oxygen using a variety of substrates. The activity of some of these enzymes increases several fold when the plant experiences stress situation(s) or enters a developmental phase^{1–3}. The most

evident being two indirect oxidases, namely cyanide-sensitive cytochrome *a*–*a*₃ oxidase and cyanide-insensitive alternative oxidase, and three direct oxidases, namely peroxidases (ascorbate peroxidase in particular), catalases and ascorbate oxidase.

While cytochrome oxidase is unquestionably an important component of the electron transport chain which is involved in fulfilling the energy demand of the cell by way of oxidative phosphorylation, several roles have been assigned to alternative oxidase

wherein thermogenesis and energy overflow pathway are the most quoted^{4,5}. Direct oxidases mentioned above metabolize hydrogen peroxide (H₂O₂) or oxygen either using an organic substrate or directly. The reactions catalysed by all the oxidases can be written as follows:



The commonality among all the above mentioned oxidases is that water molecules are ultimately synthesized either as a result of reduction of oxygen or as a result of decomposition of hydrogen peroxide. The present communication argues that the metabolic synthesis of water is an important function, although familiar but unclaimed so far, and has immense physiological roles. To explain the physiological implications two diverse processes, namely ripening of the harvested fruits and plants under drought stress will be considered first, followed by expanding the domain of application to other processes and conditions.

It is known that during the unripened to the fully ripened stage, the rate of oxygen uptake or the rate of CO₂ release increases 2 to 10-fold in fruits like mango, tomato, banana, etc. Such an increase is reflected in terms of a similar increase in the activities of some or all the above oxidases⁵⁻⁷. Using eqs (1) and (2) where 2 moles of water are synthesized consuming one mole of O₂, it would be possible to calculate the water synthesized through these reactions. Taking an average value of oxygen uptake of 342.3 nmole O₂ min⁻¹ g⁻¹ dry weight during the unripened to the fully ripened stage⁵, a mango fruit with 15 g mesocarp (pulp) dry weight would synthesize 0.62 mole water in one hour (Table 1). Since it takes approximately 15 days between the unripened and the fully ripened stage, the total water synthesized during the period

Table 1. Estimated quantities of water synthesized metabolically in plant tissues

Plant material	Rate of respiration	Estimated quantity of water synthesized	Remarks
Mango mesocarp [†]	342.3 nmole O ₂ min ⁻¹ g ⁻¹ dry wt	4017 mg	Synthesized by a fruit with 15 g mesocarp in 15 days
Leaf tissue*	15.1 μmole O ₂ m ⁻² s ⁻¹	1957 mg	Synthesized by a leaf with a m ⁻² area in one hour
<i>Tortula ruralis</i> [@]	50 μl O ₂ per 17 mg dry wt h ⁻¹	804 μg	Synthesized by moss (17 mg dry wt) in 10 h.

[†]A mango fruit with 15 g mesocarp (pulp) dry weight would synthesize 342.3 × 60 × 15 × 2 = 0.62 mmole water in one hour (rate of oxygen uptake of 342.3 nmole O₂ min⁻¹ g⁻¹ dry wt during unripened to the fully ripened stage (eq. (5)); 60, conversion factor for minute to hour; 15, weight of the tissue; 2, conversion factor for 1 mole O₂ = 2 moles of water, eqs (1) and (2)). Since it takes approximately 15 days between the unripened and the fully ripened stage, total water synthesized during the period would be 0.62 × 24 × 15 = 223.2 mmole that would be equivalent to 223.2 × 18 = 4017.6 mg of water synthesized by a single fruit with 15 g of mesocarp (18, molecular weight of the water).

*Using the rate of oxygen uptake of 15.1 μmole O₂ m⁻² s⁻¹ (14), leaves with 1 m² area would synthesize 15.1 × 3600 × 2 × 18 = 1957 mg of water in one hour (3600 is conversion factor for second to hour, other factors are the same as used in the calculation above).

[@]Using an average value of 50 μl O₂ per 17 mg dry wt h⁻¹ (23), the moss would utilize (50 × 10)/22.4 = 22.32 μmole of O₂ in 10 h (time period for drying up of the moss). This would lead to 22.32 × 2 × 18 = 803.5 μg of water generated.

would be 4017.6 mg of the water synthesized by a single fruit with 15 g of mesocarp (Table 1). Realizing that the process of ripening occurs when the fruit has been detached from the mother plant, i.e. in the absence of any external source of water, the metabolic source of water would help in sustaining the developmental processes, ripening process in the present case, by furnishing water molecules to water consuming metabolic processes and also compensating for the transpirational losses, thus keeping the fruit turgid and juicy. In fact, data on harvested tomato fruit did show that the juiciness of the fruit increased by 33% at day 7 compared to that at day zero⁸. Similarly pulp analysis of pitaya (*Selenicereus megalanthus*) harvested at the colour break stage showed an increase in the water content by 8.4% when stored at 10°C in 4 weeks time⁹. The interesting point was that when the fruits were stored at 20°C, the water content increased by 14.5%. Although data on the oxygen uptake were not given, it is expected that the respiration rate and the activity of various oxidases would be higher at 20°C compared to that at 10°C (ref. 10). Hence, in the absence of any external source of water, metabolic synthesis of water could explain higher water content at 20°C compared to that at 10°C.

When soil moisture is depleted, the plants experience a situation quite akin to the ripening fruit in that the drought-stressed plants have extremely limited

supply of water either from the soil or from the atmosphere. The leaves of a drought-stressed plant take up more oxygen compared to a control plant¹¹⁻¹³. ¹⁸O uptake studies carried out at a light intensity of 850 μmol photons m⁻² s⁻¹ confirmed a 66% increase in oxygen uptake (9.1 to 15.1 μmole O₂ m⁻² s⁻¹ with change in water potential from -0.7 to -2.6 MPa) by leaves of stressed wheat plants compared to the control¹⁴. It was, therefore, proposed that higher oxygen uptake in stressed plants was due to the acceptance of electrons from the photosynthetic electron transport chain through the Mehler reaction¹⁵ leading to the synthesis of superoxide radical, which upon dismutation would generate hydrogen peroxide. Finally, the increased activity of ascorbate peroxidase would detoxify the hydrogen peroxide as described in eq. (3). Apart from the utilization of oxygen through the Mehler-peroxidase pathway, drought stress enhanced oxygen consumption through photorespiration^{16,17} and through mitochondrial electron transport chain as well^{3,12}. As discussed earlier, the increased oxygen uptake along with the increased activity of cytochrome oxidase, alternative oxidase, ascorbate peroxidase and catalase would certainly lead to increased water synthesis according to eqs (1) to (4). Using the above rate of oxygen uptake of 15.1 μmole O₂ m⁻² s⁻¹, leaves with 1 m² area would synthesize 1957 mg of water in one hour (Table 1). In the drought-stress

situation with substantially reduced availability of soil/atmospheric water, availability of such quantities of metabolic water should be a mechanism for survival and sustenance. Reduced transpiration rate of the drought-stressed plant would further make the metabolically synthesized water more evident and useful to the cell. Metabolic water will provide a locational advantage of immediate availability to osmoticums like proline, which plays a vital role in protecting the enzymes and stabilizing the membranes under stress situations^{18,19}. The proposed metabolic synthesis of water would be crucial even to maintain ultrastructure of important organelles like chloroplasts and mitochondria where ascorbate peroxidase (present in chloroplast and cytosol), catalase (cat-3 present in mitochondria), cytochrome oxidase and alternative oxidase (present in mitochondria) are operative. In fact, chloroplasts and mitochondria maintain their structure and functional integrity and are the last organelles to be destroyed under stress conditions^{1,20}. Chloroplasts from non-stressed and stressed sunflower leaves showed very little difference in the inhibition of their activity. When these isolated chloroplasts were assayed at different water potentials ranging between -2 and -24 bars, the reduction in chloroplast activity was to a tune of only 10% and was reversible²¹. Also, neither grana nor the lamellae was affected at a leaf water potential of -2.6 MPa.

This discussion persuades one to propose that the inherent capability of these organelles to synthesize water metabolically should be one of the important mechanisms to sustain themselves in spite of very low leaf water potential. The hypothesis that 'prokaryote' mitochondria and chloroplast reside symbiotically in a eukaryotic cell appears to be very supportive in the present situation where not only these organelles can protect themselves under adverse conditions by way of synthesizing water, but also would be advantageous to eukaryotic cells as well as in supporting the basic metabolism for sustenance and during recovery from stress.

Data on oxygen consumption in the case of desiccation tolerant moss *Tortula ruralis* showed a very interesting pattern of increase in rate from 25 to ~72 $\mu\text{l O}_2$ per 17 mg dry wt h^{-1} as the moss was subjected to drying²². Showing a peak at 5 h, the rate declined thereafter. Using an average value of 50 $\mu\text{l O}_2$ per 17 mg dry wt h^{-1} , the moss would utilize 22.32 μmole of O_2

in 10 h (time period for drying up of the moss). This would lead to 803.5 μg of water generated within the dried moss (Table 1). Since this moss has a remarkable ability to revive upon rehydration, it is argued that 803.5 μg water synthesized metabolically in a 17 mg dry wt of the moss should be a means to protect the vital machinery of the organism so as to survive the adverse condition of drought.

The metabolic synthesis of water should be a mechanism to save organelles from becoming flaccid in certain situations like the plants growing at high altitudes, where reduced partial pressure would lead to fast escape of water vapours from the leaf²³. This may create a drought-like situation for the leaves and for the vital organelles like chloroplast and mitochondria. It could as well be an adaptive and survival mechanism for the bromeliads belonging to genus *Tillandsia*, in arid plants, e.g. *Prosopis tamarugo*, in poikilohydric angiosperms, e.g. *Myrothamnus flabellifolia*, in poikilohydric ferns, e.g. *Polypodium polypodioides*, in bryophytes, e.g. *Tortula ruralis*, in lichens, e.g. *Cladonia rangiformis*; all the above growing under extremes of drought stress.

It is quite likely that increased activity of oxidases in the plants exposed to low and freezing temperatures²⁴⁻²⁶, is also an adaptive mechanism to provide water synthesized through these reactions. Synthesized water molecules would delay ice formation as well as provide water to osmoticums like proline which, in turn, would protect the enzymes and membrane structures as mentioned elsewhere.

Presence of ascorbate oxidase on cell walls and hence the water synthesized metabolically (e.g. through eq. (5)) would also help in maintaining the water continuity inside the xylem system. Such a mechanism is likely to be useful, particularly for tall trees like *Sequoia* species (reaching to a height of more than 100 m)²⁷.

Although metabolic synthesis of water is common to the animal world with the well-known examples of grizzly bear and camel who oxidize fatty acids to produce water for their survival, this is the first attempt to extend such possibilities to the floral kingdom. Also, I have considered only a few oxidases here for discussion. There are however, other oxidases, monooxygenases (P450, for example) in the cell which would liberate water within the cellular/metabolic compartments. The metabolic synthesis of water is indeed a

powerful means available to the 'immobile' plants and plant parts to survive and sustain under a range of environmental and physiological situations wherein the water-synthesizing enzymes perform a crucial function of water synthesis. Undoubtedly, metabolic synthesis of water is a normal metabolic event; the phenomenon/process becomes evident and has immense implications in situations like limited or lack of external source of water to the plant/plant parts, whether physical or physiological.

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