

**"It follows from the First Law of Thermodynamics that whatever quantity of energy enters an organism, exactly the same amount, albeit in a different form, is ultimately surrendered by it." (J. Phillipson, 1966)**

**Discuss, and also identify the problems encountered in evaluating energy fluxes and stores at ecosystem level.**

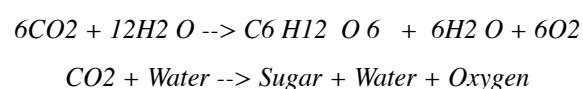
'The ecosystem may be formally defined as the system composed of physical-chemical-biological processes active within a space-time unit of any magnitude', and as the site of interaction between the biological community and its abiotic environment' (Lindeman, 1942). As with all biological entities, these ecological communities require matter for their construction and energy for their activities. The latter - that of energy flux and efficiency within the system - underlies much of the subsequent narrative of this paper. Fundamentally, energetic transfers - between the trophic 'feeding' levels of an ecosystem - accord to the First and Second Laws of Thermodynamics. The former states that 'energy is neither created nor destroyed but can be converted from one form to another.' Energy as such originates from exogenetic, solar radiation before being fixed by photosynthesis into chemical energy and later dissipated as thermal energy through respiration and organic decomposition. The Second Law states that as energy is converted into different forms, its capacity to perform useful work diminishes, and disorder (entropy) of the system increases. Ecosystems are regarded as 'dissipative systems' in that consumers - through respiration or production (growth and reproduction) - continually and progressively dissipate energy up the trophic levels. This observation, that energy dissipates gradually and in multifarious ways, problematises and adds complexity to the evaluation of energy flux and store at ecosystem level. In order to understand these fluxes, transfer efficiencies, which, in essence reveal how energy is partitioned by the actors involved, become significant.

Throughout, I reference and critique Lindeman's law of trophic efficiency which states that the efficiency of energy transfer between the trophic levels is about 10%. As anathema, I suggest that this 10% is an over-simplification and fails to account for the effects of varying physiologies and behaviours between the trophic levels. The main body of this paper thus situates in a discussion of trophic efficiency and its sub-parameters - assimilation, consumption and production. The relations between these parameters are deeply embedded in the complex, energy flux of ecosystems. The preliminary sections of this paper discuss the trophic groupings (producer/consumer) and the processes of energy production (photosynthesis) and net primary productivity. It then logically follows that transfer efficiencies and the equation of Trophic Efficiency ( $CE \times PE \times AE$ ) are explored. Observations of difference between homeotherms and poikilotherms will be used to reveal how physiology and metabolic rate affect the availability of energy for production and thus subsequent energy consumption by the next trophic level. Finally, this paper refers back to the coupling of Thermodynamic Laws in revealing that trophic energy transfer is unidirectional - in contrast to the cyclical behaviour of nutrients - and that this intensity of this directionality increases with maturity. In this sense, ecosystems develop in such a way so as to systematically increase their ability to degrade the incoming solar energy. The more processes or interactions of material and energy that there are within a system (metabolism, cycling, building higher trophic levels), the more the possibility for exergy degradation.

The biosphere functions through the acquisition of energy by organisms and the flow of energy from one organism to another. Organisms are linked together by trophic relationships in food chains and webs. Each stage in the flow of energy is a trophic level and organisms are classified according to the functional trophic level they occupy. Producers

(autotrophs) have the capacity to fix carbon through photosynthesis via green chloroplasts in their leaves or bodies. Examples of these photo-autotrophic organisms are found in green plants and eukaryotic algae. In some cases, chemoautotrophs are said to exist, such as in deep sea vents, wherein organic material is produced without the requirement of sunlight through the oxidation of inorganic compounds. Consumers (heterotrophs) refer to organisms that obtain energy from the tissues of other organisms, either plants or animals or both - herbivores, carnivores and top carnivores (Huggett, 2004). Herbivores are the primary consumers of organic molecules fixed by the producers. Carnivores are secondary consumers, flesh-eaters that live off of the organic molecules of the herbivores. In many ecosystems, there are carnivore-eating carnivores that are thus called top carnivores or tertiary consumers. The final group, that of decomposers and detritivores (saprophytes and saprovores respectively), refers to small animals bacteria and fungi capable of breaking down the complex organic chemicals of dead material and waste products. As such, decomposers dissolve organic matter, whilst detritivores break it into smaller pieces and partly digest it. These trophic groupings are not strictly bound, for instance some 'species of algae can act both as photo-synthesisers (autotrophs) and grazers (heterotrophs).' (Addison et. al, 2008). Thus although each 'packet' of energy follows a linear path along a food chain, actual trophic relationships among species may be more complex, and necessitate a food web. In essence however the producer-consumer-detritivore representation of the ecosystem is independent of the type of ecosystem. Only the amount of carbon, transfer rates, and the factors controlling these rates vary among ecosystems.

The energy within ecosystems originates predominantly from the sun. This solar energy that powers the biosphere is captured through the process of photosynthesis. As such, photosynthesis is the process by which radiant energy is converted into chemical energy. For most plants the radiation used for photosynthesis falls in the red through blue visible light (0.4 - 0.6 micron wavelength) portion of the electromagnetic spectrum. Such light is referred to as photosynthetically active radiation (PhAR) and it provides the energy for photosynthesis. During photosynthesis, autotrophs transform carbon and water vapour into sugar, water and oxygen. These larger structural models facilitate the growth of the plant. The process takes place in chloroplasts that hold chlorophyll, the primary light capturing pigment of plants.



The CO<sub>2</sub> enters the leaves of plants through opening created by specialised sets of cells called stomata. The stomata also allow for the simultaneous release of oxygen and water vapour from the interior of the leaf. There are three different biochemical pathways that green plants use in photosynthesis. Most plants capture energy using the C<sub>3</sub> pathway wherein the CO<sub>2</sub> from the atmosphere is converted into a 3-carbon molecule called 3-phosphoglyceric acid. The C<sub>4</sub> pathway is a further method of energy transfer, common in sugar cane. The cane converts CO<sub>2</sub> into two 4-carbon molecules: malic and aspartic acid. The Crassulacean Acid Metabolism pathway occurs commonly in desert environments, wherein the plant absorbs CO<sub>2</sub> by night and stores it as malic acid, before resuming in the day photosynthesis along the C<sub>3</sub> pathway. In general, C<sub>4</sub> plants have the highest rates of photosynthesis; CAM plants, the lowest. However, these are often obscured by the facet that all plants are relatively inefficient in terms of energy fixation through photosynthesis. As Chapman posits, 'even in the most productive communities, plants trap only about 1-3% of the energy which they receive in sunlight' (Chapman, 1999). Theoretically, photosynthetic efficiency (% of the total energy falling on a field that is fixed in photosynthesis) has the capacity to reach 18%, given the relationships between

light photons and CO<sub>2</sub> (12 photons = the fixation of one CO<sub>2</sub> molecule). In actuality however this ideal is rarely reached, primarily because much of the light misses the leaf chloroplast or is reflected as visible green light.

The photo-autotrophs form the foundations of the trophic hierarchy by producing exploitable organic material. The rate at which this material, biomass, is produced is referred to as gross primary productivity, often expressed in units of energy (joules per square meter per day) or of dry organic matter (kg/hectare/day). Most of this matter is created in plant leaves. Some of it is transported through the phloem to other parts of the plant, especially the roots, to drive metabolic processes. This respiration (R) leads to matter being converted back into CO<sub>2</sub> and water, and thus dry weight is lost. The subsequent productivity of the autotroph is referred to as net primary productivity ( $GPP - R = NPP$ ). Terrestrial observations have shown how gross primary productivity is approximately equal to 2.7 times net primary productivity, whilst in oceans this relationship of difference is 1.5 (Whittaker, 1975). The net primary productivity represents the actual rate of production of new biomass that is available for consumption by heterotrophic organisms. As will be shown later, this partitioning of energy between respiration and production is causal in the dissipation of energy, the rate of which is determined by the dominance of the former.

The total NPP of the planet is estimated to be about 105 petagrams of carbon per year, of which 56.4 Pg are produced in terrestrial ecosystems and 48.3 Pg in aquatic domains. Surface anomalies occur within tropical rainforests and savannas which, as Townsend et. al write, 'account for about 60% of terrestrial NPP, reflecting the large areas covered by these biomes and their high levels of productivity' (Townsend et. al, 2009). The overall global trend is generally latitudinal, with the least productivity in polar, boreal forest and the most in tropical forest. The limiting factors upon primary productivity often equate with levels of solar radiation, carbon dioxide, water and soil nutrients. As such, net primary production is strongly influenced by stand age, species composition and site conditions such that localised manipulations in either three affect plant growth. As Gower et. al discovered in experiments in New Mexico, 'aboveground net primary production increased by 57% in the irrigated plots and 70% in the fertilised plots compared with pretreatment values.' (Gower et. al, 1992) In an environment deficient of these factors, such as underneath a shady canopy, plants may respire more than it photosynthesis. Under such conditions, the autotroph has failed to reach its compensation - the amount of light necessary for a plant to have a rate of photosynthesis equal to its rate of respiration. The plant reacts by losing weight and shedding leaves, thus reducing its leaf area index. These processes of photosynthesis engender the transformation of radiant, solar energy to its chemical, potential forms. There is a general positive relationship between this primary production of energy and the subsequent secondary productivity, performed by heterotrophs.

Transfer efficiencies determine the ecological interactions of energy transfer between the trophic levels. Such efficiencies predominantly refer to the internal workings of organisms in partitioning energy between respiration and production (growth and reproduction). Whilst the former represents lost thermal energy, the latter refers to energy which is available for consumption by the next trophic level. As Lomolino et. al posit, 'the efficiency with which plant or prey organisms maintain biomass per unit of respiration determines how much is available as food' (Lomolino et. al, 1999). These basic relations of energy partitioning are described succinctly through the three sub-categories of efficiency which form trophic efficiency: (i) consumption efficiency; (ii) assimilation efficiency and (iii) production efficiency. Consumption efficiency is the percentage of total productivity available at one trophic level that is consumed by the

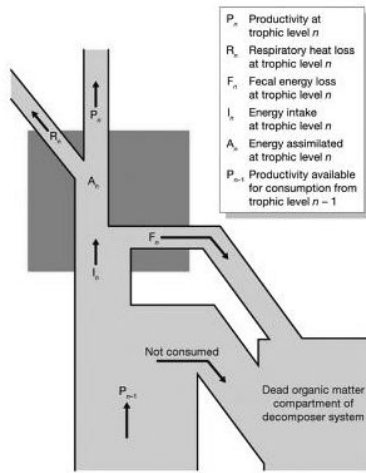


Figure 1: The pattern of Energy flow through a trophic compartment (represented as the maroon box). Note the pivotal moment wherein the assimilated energy is partitioned between  $R_n$  and  $P_n$ . (Townsend et. al, 2010)

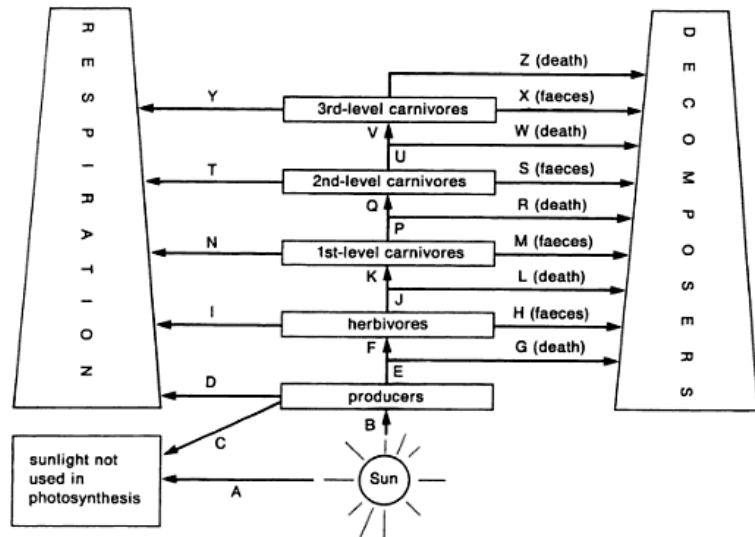


Figure 2: The multifarious ways in which energy is partitioned throughout the trophic levels. (Chapman & Reiss, 2001)

trophic level above ( $I_n$  on figure 1.) Thus for herbivores, CE refers to the amount of net primary productivity that finds its way into their guts. The remainder, dying without being eaten enters the decomposer system. The rates of CE efficiency vary between the trophic groups with carnivorous predators capable of consuming 50%-100% of production from its prey, whilst grazing herbivores in forest communities may only consume 5%.

According to Townsend et. al, 'assimilation efficiency ( $A_n$ ) is the percentage of food energy taken into the guts of consumers in a trophic level that is assimilated across the gut wall and becomes available for incorporation into production/growth ( $P_n$ ) or respiration/work ( $R_n$ ). The remainder - that which is not assimilated - is excreted into the decomposer system ( $F_n$ ). Assimilation efficiencies are often functions of the kind of food eaten, being high for meat eaters (90% in some carnivores) and low for cellulose eaters (as low as 20% in herbivores). Production efficiency is the percentage of assimilated energy that is incorporated into new biomass. In essence, it refers explicitly to the partitioning of energy between metabolism/respiration and production (growth and reproduction). PE varies with the taxonomic class of the organism concerned, particularly between those with differing body heat requirements. As such mammals and birds (ectotherms) have production efficiencies at least an order of magnitude less than poikilotherms. This is due to the fact that much of the assimilated energy has to be partitioned towards respiration and the maintenance of a warm body core temperature.<sup>1</sup> Chapman, however proposes that these metabolic disadvantages are more than made up for by the facet that homiotherms assimilate food at a much faster rate than poikilotherms. On average, a homiotherm assimilates its ingested food 22 times faster than a poikilotherm of the same size.

The overall trophic transfer efficiency from one trophic level to the next is defined as  $CE \times AE \times PE$ . The trophic transfer efficiency of herbivores, for instance, equals the percentage of the net primary production that is converted to herbivore production. This latter stage is pivotal, for it alludes to the time interval in which the complex internal, processes of excretion, assimilation and respiration/production (the purple box above) occur. Thus, rather, than a simple transaction - with no loss in the supply of chemical energy throughout - there becomes a store within the system wherein energy is manipulated and lost as thermal energy. Trophic efficiency is rendered diagrammatically in Figure 2

<sup>1</sup> When in Spain, I pass on the main

to reveal the flow of energy in a generalised food web. The total amount of solar radiation incidental upon the community equals  $A + B$ . However, as was revealed earlier in the low photosynthetic efficiencies of autotrophs, only a small amount  $B$  actually lands on the producers. Much of this energy is further lost, either instantaneously through reflection, or gradually overnight, through respiration ( $C$ ). However, an amount of sunlight equal to  $D + E$  is actually used in photosynthesis (gross primary productivity). In an ecosystem of non-existent plant respiration, the entirety of this would enter the primary consumer trophic level. However plants respire ( $D$ ) and therefore the net primary production equates to  $E$  alone. Some of this net primary production is then consumed by herbivores ( $F$ ), with the uneaten remainder entering the decomposer system ( $G$ ). Of the energy ingested, a further partitioning of energy occurs wherein the unassimilated energy passes directly as feces into the decomposer system ( $H$ ). The assimilated energy is then divided between respiration ( $I$ ) and production ( $J$ ), the amounts of which are dependent upon metabolic rates and respiration requirements.

As Lomolino et. al postulate, the larger an organism, the more energy it requires for maintenance, growth, and reproduction. The rate of energy uptake and expenditure of animals at rest (or, basal metabolic rate,  $m$ ) varies with body mass ( $M$ ), such that:

$$m = cM^{0.75}$$

the constant ( $c$ ) varies among taxonomic groups – animal or plant group having natural relations. There are further complicating factors to the trophic transfers of energy. That energy is unidirectional is revealed through the concept of the energy pyramid. Pyramids of energy can never be inverted, in accordance with the law of the conservation of energy. Thus  $E = F + G$  and  $F = H + I + J$ . As Chapman observes: ‘from these two equations we have that:  $J \leq E$  so that the productivity of the herbivore can never exceed the net primary productivity. Theoretically, herbivorous productivity could equal the net primary productivity, but this would only occur if  $G$ ,  $H$  and  $I$  were all zero. This is an impossibility since herbivore respiration ( $I$ ) cannot be zero. However, whilst the energy pyramid cannot be inverted, Eltonian pyramid of biomass may be and are, in fact, quite a commonality within aquatic ecosystems. This is due to the temporal dimensions often missed when viewing a static pyramid. As such phytoplankton with exceptional rates of photosynthesis may be able to support a biomass of consumer far exceeding their own. This, as Lomolino writes, is possible because ‘the consumer depends on rates of energy transfer (molecules metabolised per unit of time) and not simply biomass’ (Lomolino et. al, 2001).

The high variabilities upon assimilated energy partitioning often lead to energy cascades during period of environmental stress. In a glacial period, for instance, the reduced foraging by primary consumers, and of that assimilated, the increased respiration for warmth, equates to a minimal amount of production and thus little energy for the trophic level of carnivorous mammals. Similarly the low consumption efficiency of certain carnivores may exacerbate this problem. As Gower et. al observed with a pack of wolves on Isle Royale: trophic transfer efficiencies were low and reflected not only the energy respired by moose that was impossible for wolves to consume but also most of the ‘possible’ energy they missed since their consumption efficiency was low. (Gower et. al, 1998). Consumers as such are seen as energy maximisers, programmed to collect available energy efficiently in both temporal and spatial dimensions. However, as Chapman wittily concludes, ‘animals may be [these] efficiency machines, but they are selfish machines also.’ Such devouring narcissism in essence equates to the often low trophic transfer efficiencies experienced in many ecosystems.

That 'useful energy' is gradually dissipated through thermal heat accounts for the often observed maximum of four to five levels within a trophic system.

The trophic transfer efficiency and its sub-parameters are evidently problematic in the study of energy flux and store at ecosystem level. As such, Lindeman's law of trophic efficiency is somewhat damaged by its own universality. That trophic efficiencies equate to 10% fails to account for the various behaviours, both metabolic and reproductive wise, that affect transfer efficiencies. May for instance, writing in 1979, would summarise aptly the complexities of positively identifying these relations: 'what fraction of the net productivity at one trophic level is actually assimilated by creatures at the next level? How do these organisms apportion their assimilated energy between net production (growth and reproduction) and respiration? These interactions of transfer efficiencies lie at the crux of many renewed refutations of Lindeman's 10% law. Recent trophic studies, for instance, revealed that marine and fresh water environments hold trophic level transfer efficiencies that vary greatly between about 2% and 24% (Pauly & Christensen, 1995). It is thus regarded that trophic efficiency rather than a constant is much more of a variable. These interactions further complicate Phillipson's quote: *'It follows from the First Law of Thermodynamics that whatever quantity of energy enters an organism, exactly the same amount, albeit in a different form, is ultimately surrendered by it.'*

In the strictest sense, Phillipson is correct, energy can neither be created nor destroyed, however syntactically perhaps 'surrendered' is too strong a word. This 'ultimate surrendering' suggests a passivity yet if anything, the complex processes of assimilation, respiration and production reveal active, bodily behaviour. Furthermore, 'surrendered' suggests that there is a victor, which instantly places our minds to the consumer. However, as has been revealed, much of this surrendered energy does not fall into the hands of its victor-consumer. Rather, much is equally lost (won) to (by) the atmosphere as thermal energy in respiration and random heat loss. Nevertheless, Phillipson identifies strongly with the facet that whilst energy in terms of quantity never diminishes, in relation to quality this is less so. This paper situates like much of ecological energetics, as both corollary and anathema to Lindeman's revolutionary *The Trophic Dynamic Aspect of Ecology*. Through a discussion of his 'trophic efficiency' and its sub-parameters (consumption, production and exploitation) it has been suggested that energetic transfers between the trophic levels are dually observable/patterned and complex/multifarious. Having explored the 'transfer efficiencies' it is evident that no single ecosystem is the same both in the spatial and temporal dimensions. As such two species may experience over time differing trophic relations amidst a changing scenery of glaciers and spearheads. Ecosystems are thus regarded as fluid manipulators of the coupled First and Second Laws of Thermodynamics. For instance due to the increased consumption efficiency of one particular trophic level - perhaps because of human herding that aids predation - the flux of energy for the whole system changes in a cascading effect. These changes emerge to redefine the partitioning of energy between its potential and thermal forms and as such subsequently alter the intensity and longevity of energy dissipation within the system. Trophic interactions are thus problematised precisely because they are embedded within this deep and chameleonic continuum of energy flux.

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