CHEMICAL ECOLOGY OF PLANT-ANIMAL INTERACTIONS

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Summary

Despite that most bacteria, yeasts, fungi, and lichens are essential to higher organisms, the two most visible life forms on earth are plants and animals. Collectively, they concentrate the vast majority of the carbon associated with life. Of the two, plants accumulate the greatest portion of biomass and their organic chemical constituents are

self accrued and assembled from the inorganic medium by virtue of complex photosynthetic and biosynthetic processes in an autotrophic fashion. As opposed to plants, animals acquire the chemicals of life from other living or recently deceased organisms in a heterotrophic manner, and the vegetation is the basic source of these materials. Therefore, a close association between terrestrial plants and animals has evolved over geological time that is based on the controlled transfer of compounds and energy from one to the other across one or more trophic levels of interaction. If plants have progressed to their present status as dominant life forms in terms of biomass and covered land, efficient mechanisms to prevent over-exploitation by animal populations must have emerged over evolutionary time. Thus, herbivore pressure eventually caused the demise of the more edible species and in doing so favored the survival of those plant species exposing physical barriers against phytophagy such as spines, scales, waxy cuticles, lignified or woody tissues, and sheer size under the constraints of their own physiological needs and capabilities. In turn, the evolution of animal traits to circumvent these deterrents became constantly renovated selective pressures over plants that responded with increasingly sophisticated defenses which evolved beyond morphology into a varied and complex array of chemicals to confront the assault of herbivores. But the plant-animal interaction has developed into other more constructive forms than simple attack-defense strategies, as it involves mutual services such as pollination, seed dispersal, and defense that animals provide to plants lured by attractive colors and scents, seeking nutrient gifts and physical protection offered by plants, or through more sophisticated multitrophic levels of interaction. At present, the rapport of the vegetation with invertebrates and vertebrates has grown into one of extraordinary complexity in which a vast set of organic phytochemicals and a highly elaborated sensory, digestive, physiological and behavioral response of animals interact in extremely dynamic forms. This article explores the evolution and diversity of this vital combination of permanent arms race and mutual collaboration between these two advanced life forms: animals and plants.

1. Introduction

Life, no matter how ubiquitous and apparently prosperous, is a fierce struggle to capture the necessary resources from the environment, and to prevail in ecological and evolutionary time scales. At the very base, life can be appreciated as a vastly complex conglomerate of chemical and energy transport processes. According to this view, living organisms may be classified in two general groups: those who can extract all they need from the inorganic medium and physical sources of energy, called autotrophs, and those who cannot, the heterotrophs. Most vascular plants belong to the first group thanks to their photosynthetic apparatus and root system whereas all animals are heterotrophs who need to devour plants and other living or decaying things to procure the chemicals and energy of life they require. Thus, life on earth totally depends on current or past photosynthetic activity, with the sole exception of isolated ecosystems in deep sea volcanic vents and some specialized bacteria in hot springs.

Figure1: Some plants take many years to bloom and seed, such as this rare tropical highland rosetta, *Ruilopezia flocosa* from the Venezuelan Andes, whose first and only inflorescences appear after 17 years. Then the plant dies. Inset: flower bud covered by thick layer of protective wool-like hairs against nightly frost.

Within this duality, plant forms appear to support one way or the other the whole of heterotroph life and therefore are seemingly at a disadvantage when examined in the ecological and evolutionary time scales. Plants have long generation times and low recombination rates as compared with many herbivore species, especially among the arthropods, so herbivores should be better prepared to become adapted and overcome the defenses put up by plants to deter herbivory. Also to the advantage of insects and many other herbivores is the large number of offspring per unit time they are capable of producing and the fastness with which they reach sexual maturity. As opposed to them, annuals require several months to seed and perennials even several years, as is the case of many large trees and some highland rosetta bushes of the genus *Ruilopezia*¸ endemic monocarpic plants of the northern Andes that bloom only once after 17 years before dying shortly after (see Figure 1).

However, plants are by far the dominant life forms on earth and several hypothesis have been proposed and tested to explain this. Among the various theories put forth, the production and accumulation of a vast array of organic compounds in plants that has evolved to establish a dynamic set of communication signals between individual plants and other members of the community, be these other plants or animals, is the most widely accepted tenet. The science that studies these chemically based relationships among organisms is chemical ecology. This article describes how the need to survive under heavy herbivore pressure has led plants to produce these compounds and illustrates some of the very complex forms of rapport between autotrophs and heterotrophs, from small invertebrates to large mammals and man.

2. Why plants apparently play the losing role

The branching of life forms in autoprophs and heterotrophs started early in their history, about 600 million years ago, and a close and exceedingly complex relationship between terrestrial plants and animals has developed ever since. Herbivores need abundant plant tissue to survive. On average, more than 10% of the plant production in natural habitats is consumed by phytophagous animals each year. Such loss only to herbivory is greater than the average effort plants allocate to reproduction. Not all vegetated habitats experience the same pressure from herbivores, however. For example, insects remove from 0.0003 to 0.8% of the existing leaf area per day in the tropical rainforest, depending on tree species, whereas tundra and boreal forests may sustain from zero to 100% losses if occasional animal outbreaks occur. Large vertebrate ruminants also exert considerable pressure on plants, for they eat regularly 10 % and more of their body weight of plant fodder for their daily sustenance. Individual plants on their part grow new tissue only slowly under various constraints such as temperature, light, water and soil nutrients, adding between 0.3 and 32 % of their biomass each year, 40% of which is carbon from atmospheric carbon dioxide. In many ecosystems, this is not enough to support an elevated number of herbivores. For example, a small bush typically occupying 1 m^2 of land and having 0.1 m^2 of leaves may fix a total of 0.6 g of carbon per day under ideal conditions. In the same time period, a 800 kg bull eats around 32 kg of carbon from plant origin. This is equivalent to the combined daily production of over 53 hectares of this bush in times of maximum carbon fixation. Although commercial grasses have been genetically selected to fix greater quantities of carbon dioxide, their productivity as much as of wild plants is strictly dependent on soil chemistry, weather conditions, and the pass of seasons. This productivity is at its lowest during the long months of autumn, winter and early spring in temperate climates, and the dry season in the tropics of the world. If one takes into account that only about 10% of the plant carbon eaten by ruminants at best becomes part of their own biomass, and that the bodyweight development curve of dairy cattle reaches a plateau in less that two years, it is easy to conclude that wild plants must endure considerable pressure from large herbivore herds. Therefore, temporary scarcities of fodder must have limited the size and viability of these flocks, so plant and animal populations have coexisted in a long and unstable equilibrium.

In spite of being at the dinner plate of most moving organisms on the planet, plants as a group somehow have managed to prevail as a dominant guild. For one, chlorophylls, which are compounds of plant and bacterial exclusiveness, can be seen with the naked eye of an observer on the surface of the moon as vast dark land areas over the continents, covering some 149 million square kilometers, whereas not a single common animal product such as uric acid can be detected even with modern spectrometric techniques from the same distance. The contribution of plants to earth's biomass (Table 1) is several orders of magnitude greater than all heterotrophs combined and the several mass extinctions that have endangered all life forms so severely during earth violent geological history were not powerful enough in all their destructive capacity to reduce significantly plant diversity.

Ecosystem	**Area (millions km^2)**	**Biomass (10^9 tons C)**	**Relative Growth Rate/year**
Tropical rainforest	17.0	340	0.045
Tropical seasonal forest	7.5	120	0.042
Temperate evergreen	5.0	80	0.037

forest			
Temperate deciduous forest	7.0	95	0.040
Boreal forest	12.0	108	0.040
Woodland and shrubland	8.0	22	0.100
Savanna	15.0	27	0.175
Temperate grassland	9.0	6.3	0.321
Tundra and alpine meadow	8.0	2.4	0.217
Desert scrub	18.0	5.4	0.107
Rock, Ice and sand	24.0	0.2	---
Cultivated land	14.0	7.0	0.580
Swamp and marshland	2.0	13.6	0.165
Lake and stream	2.5	0.02	22.5
Marine plants	361	1.8	14.1
Total Continental plant (%)	**149 (29.22)**	**827 (99.76)**	**0.058**
World total (%)	**510**	**829**	**0.088**

Table 1: Estimates of biomass and primary production of plant ecosystems.

At present an estimated 270,000 plant species exist in a wide variety of terrestrial ecosystems. Some of these habitats are formed by plant communities of only a few species such as rocky and sandy deserts, pastures and cropland but others contain a much greater number. This is the case of some pristine forests of the western Amazon basin, where over 300 species of trees with 10 cm diameter trunks at chest height –an arbitrary measurement used by field botanists-, not including a myriad undergrowth plants, epiphytes, parasites, and vines, can be recognized in just one hectare. Given enough time without perturbation, these communities become highly organized under the constraints of density, sunlight, and soil nutrients, and constitute a complex mosaic of niches of great variety, even in apparently uniform forests. If animals have been unable to achieve the upper hand in terms of biomass, they have responded to this niche variety extraordinarily well by diversifying into an enormous number of species. If on the one hand it is true that there are only about 6,300 species of reptiles, 4,200 of amphibians –mostly carnivores-, 12,000 of birds, and 4,000 of mammals –mostly herbivores -, on the other, arthropods have diversified themselves into over five million species by some estimates. Such awesome diversity has allowed them to seemingly exploit almost every possible niche created by plant and animal communities worldwide. The case of insects is not only delimited by wholesome diversity but species density as well. For instance, a single tree in the Peruvian east board forest yielded 43 species of ants, which is about the entire ant diversity found in the isles of the UK. Similarly, over 8,000 species of beetles sharing a single tree canopy were collected near Manaus, Brazil. Why and how is this possible, and how plants can resist the impact of herbivory so successfully, are still open questions to science, but some insights can be gained from the in-depth study of present ecosystems and evolutionary theory.

3. How plants survive under a herbivore dominated world

3. 1 Carnivore pressure on herbivores

Anyone visiting a wild meadow in the summer will notice that most plants are not only plentiful but remain largely without damage in spite of a relative abundance of insect herbivores such as caterpillars, beetles, grasshoppers, thrips and the like. Only certain plants appear more attacked by herbivores than others but generally most remain nearly intact. A paradox emerges in considering what stops these herbivores from depleting the nutritious leaf stock available to them as it occurs in severe insect outbreaks. In fact, introduced species in a given habitat and not local residents are often found responsible for such devastations as it occurs with the migratory phenotypes of the desert locust *Loccusta migratoria* in parts of equatorial Africa, South America and elsewhere, the European gipsy moth *Lymantria dispar* and the Japanese beetle *Popilla japonica* in North America. In the early sixties it was suggested that herbivore populations rather than being food limited, were controlled by their natural predators. Introduced species faced new habitats without predators effective against them and thus quickly dominated the community, even temporarily. Supporting evidence came from experiments in which, by selectively killing predatory insects and parasites, the resurgence of populations of phytophagous insects was observed. Conversely, these populations plunged after the release of contingents of predators and parasites in the field, a technique widely used nowadays to control agricultural insect pests.

If it was partly well based, there were also flaws to this theory, as it assumed that all plants were equally edible to all herbivorous insects. And they were not. As it turns out, plant foliage is exceedingly variable at the community level and time scale (see Figure 2). As an example, young leaves and buds are soft and rich in nitrogen, but appear only in early spring when insect populations have not reached yet their maximum phytophagous potential. When they do, most foliage has hardened by accumulation of lignins and mineral deposits in some cases. A similar strategy is observed in many tree species of the deciduous forests of tropical America, which sprout their new foliage a few weeks prior to the onset of the monsoon rains, thanks to sizable water reserves stored in their trunks and roots from the previous wet season. By the time rains bring soil moisture to adequate levels for insect eggs to hatch, leaf growth will have reached sufficient toughness and/or size to sustain insect attack without compromising its function. Most importantly, obnoxious chemicals are also stored in larger quantities in older leaves making it more difficult for insects to exploit this tissue. From this stand, an entirely new view on the plant-animal relationship emerged, whose basis was essentially chemical in nature, and genetic in its control. How this came to be could only be explained in evolutionary terms.

Figure 2: Plants in the same community may or may not be attacked by herbivores, depending on physical characters or obnoxious chemicals as this selectively eaten fern frond illustrates. Feeding deterrents contained in higher amount in segments near the rachis stopped the attacker in its tracks. Meanwhile, the tender leaves of nearby *Passifloras* (inset) remain untouched by herbivores in the area.

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Biographical Sketch

Miguel E.Alonso-Amelot, was born in Caracas, Venezuela in 1946. After receiving his BSc in chemistry at Central University of Venezuela in Caracas (1968) and earning a Ph.D. in organic chemistry from Indiana University (US) in 1974, he joined the National Institute of Research (IVIC) in Caracas to investigate synthetic applications and reaction mechanisms of cycloadditions and other processes. Upon moving to Los Andes University in Mérida, Venezuela in 1986, following a one year tenure in professor Jerrold Meinwald’s laboratory at Cornell University in 1983-4, Dr. Alonso changed his research interests to chemical ecology, with emphasis on plant toxins affecting animals – vertebrates and invertebrates - and humans, and the chemical adaptations of plants to habitats of extreme weather in the upper Andean mountains. He has published over 75 research papers and book chapters, two books, and several monographs and has earned various academic awards.