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Plant Antiherbivore Defense in Diverse Environments

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Abstract

Herbivores can damage plant productivity and fitness; plants have improved defensive traits, such as chemical defenses. Plant species produce specific defensive traits in response of diverse risk factor generated by herbivores. In this chapter, we analyze and compare the defensive traits used by plants in different habitats: aquatic ecosystems, temperate forest, and rainforest. In aquatic environments, the number of herbivores is scarce, and plants develop biomass and restrict defensive compound production. At the terrestrial environment, plants need to accumulate defensive traits for an eventual attack. But the number and quantity of those traits depend on biotic and abiotic factors. In temperate forest, plants have a low growth, and herbivore diversity is low, because there are a few number of defensive traits but in great quantity to guarantee plant survival. In contrast, at tropical forest there is a great herbivore diversity, and plants have a quick growth; thus they develop a great variety of defensive traits. There are substantial differences in plant defensive strategies at different environments. Usually, the aquatic plants use water-soluble and diffusible compounds; plants in rainforest use a plethora of chemical defenses, and in temperate forest, plants utilize physical barriers, resins, and terpenes.

Keywords: aquatic environment, terrestrial environment, temperate forest, tropical forest, plant defenses

1. Introduction

Photosynthetic organisms are the primary producers; they are essential for correct function of all ecosystems; nevertheless, these organisms are susceptible to be attacked by different herbivores, and they can perform various defensive measures: allocate resources to protect

themselves from microbes, competitors, ultraviolet (UV) rays, and predators [1], reduce plant tissue quality, and produce chemical and mechanical defenses [2, 3].

Throughout 350 million years, plants and insects have been keeping a close relationship [4] resulting in an efficient defense system in plants that can recognize signals from herbivore and activate the plant immune response against them. To arrest herbivore attack, plants produce specialized metabolites with negative physiological effects against herbivores, such as toxins, deterrent, dissuasive, and/or no nutrition [5].

Metabolites that implicate in defense against herbivores can be modified by biotic and abiotic factors, such as humidity, altitudinal gradient, nutrient availability, herbivores diversity, etc., [6]. Then, we asked: at distinct environments, are plant defense mechanisms the same? If they are different, are there some recognizable patterns at separate environments?

To answer, we select three very distinct ecosystems to compare plant defense traits: the first great difference is between aquatic and terrestrial environments, and the latter we divide in tempered and tropical forest. The objective is recognizing the ecological and evolutionary diversification of plant defense traits at distinct environments.

2. Aquatic environments

In aquatic environments, there is a great diversity of photosynthetic organisms that interact and maintain complex ecological relationships with herbivores. In aquatic habitats, these interactions are considered very important since they affect the nutrient cycle and energy flows of food chains [7, 8].

Generally, when a plant is attacked, its defense mechanisms are activated through the production of diverse compounds generically termed plant secondary metabolites (PSM) [9]. It has been recognized that the secondary compounds may either serve as feeding deterrents or attractants in terrestrial plant-animal interactions or function as allelopathic chemicals or antibiotics; the same evolutionary pressures responsible for the many biologically active compounds found in terrestrial vegetation have been predicted to have parallels in marine [1, 10] and freshwater vegetation [11]. However, it is possible that the constraints in aquatic habitat lead to some differences in the production and action of these natural compounds.

2.1. Marine environments

The primary producers most widely distributed in marine habitats are the seaweeds (red, brown, and green algae); these photosynthetic organisms have developed several defenses in response to herbivores, for example, by having a resistant or unpalatable physical structure or a morphology that makes the feed difficult for the herbivore or by having spatial and temporally diverse stages of life cycle and by the production of chemical defense against herbivores ranging from unpalatable to toxic. Marine algae are known to produce a wide range of secondary metabolites with various biological actions [1], many of them with medicine and agriculture human uses [12].

On the sea, the most common grazers are generalist such as fishes, sea urchins, gastropods, polychaetes, and a great variety of marine crustaceans [7], which usually feed on the stalks of seaweed. Over 2400 natural products have been isolated from marine red, brown, and green algae, the majority are terpenoids and acetogenins; very few nitrogenous compounds have been isolated. In general, these compounds occur in relatively low concentration (0.2–2.0% dry mass), even so several ecological roles have been documented, and some of them are produced as protection against grazing [13, 14].

Brown algae produce about 1000 secondary metabolites, terpenoids and acetogenins are the most frequent, and they are the only seaweeds that produce polyphenolic compounds [12]. Polyphenolic compounds may function like terrestrial tannins, but they are structurally different so they are often termed phlorotannins to distinguish from them [12, 15, 16]. Phlorotannins are usually associated with a chemical defense: protection against grazing, pathogen attack, epiphytism, microfouling, and ultraviolet (UV) damages [16]. In red algae, the greatest variety of secondary metabolites is found, about 1240 reported; in Rhodophyta, all classes of compounds except phlorotannins can be found; most of them are halogenated (methanes, haloketones, phenolics, and complex terpenes) [15] recognized as antibacterial, antifungal, antiviral, anti-inflammatory, antiproliferative, antifouling, antifeedant, cytotoxic, ichthyotoxic, and insecticidal activity [17]. In contrast, the green algae are the ones with the least secondary metabolites isolated; about 290 are known and most of them are sesquiterpenes and diterpenes; only few species produced halogenated compounds [18].

These diverse compounds are consumed directly by the herbivore when it feeds algae, but many of them may be released into the aquatic environment during algal growth or at cell lysis. In the last cases, chemical information is transmitted by diffusion and advective lamina flow [19]; a major problem in the aquatic environment is dilution of the secreted products, so small molecules are favored because of their faster diffusion.

As we see, the natural compound production differs among seaweeds, as well as between and within species [7, 20], these differences suggest separate historical origin [11]. In the same way, the type and quantity of secondary compounds in algae differ from vascular plants; in algae, the absence of alkaloids and the presence of halogens compounds have been detected, contrary to terrestrial plants [7].

In marine environments, sea grasses are the only true submerged angiosperm, and as vascular plants, they are more complex morphologically and physiologically than algae; they produce some secondary compounds against herbivores, such as phenolic acids, phenolic acid sulfate esters, and sulfated flavonoids [21].

2.2. Freshwater and continental environments

In continental and freshwater environments, angiosperms are more abundant than macroalgae; therefore, they contribute significantly to primary productivity, and they maintain numerous interactions with aquatic consumers such as birds, mammals, fishes, crayfish, insects, and mollusks [22, 23]. For a long time, it was considered that the herbivory on freshwater macrophytes was infrequent and with minimal impact [24, 25]. Contrary to this point

of view, a growing body of evidence suggests that the evolutionary and ecological importance of herbivory occurs in an aquatic context as in terrestrial habitats [9, 11]. Interactions between herbivores and aquatic plants have been reported in a wide range of habitat types, including freshwater lakes, rivers, estuaries, wetlands, and shallow seas [26, 27]. Accordingly, interactions between herbivores and aquatic plants have global distribution, and herbivores are present wherever submerged, floating, or emergent plants are present [27]. It is a fact that aquatic herbivores have a strong impact on aquatic plant biomass, productivity, and species composition [22, 28]; thus, like in terrestrial angiosperms, selection may favor aquatic plants that have chemical and other types of antiherbivore defenses [9].

Defense and resistance mechanisms against herbivores have been poorly understood in freshwater; even so we now know that freshwater plants are frequently chemically or structurally defended from consumers [29–31]. Structural defenses are more commonly found among upland plants than wetland plants [22]; in some cases, we can find thorns or tough leaves [32]. Chemical defenses are more widespread in macrophytes [23, 31] as well as in various algae, cyanobacteria [22].

Diverse groups of chemical compounds are known in aquatic plants, including alkaloids [33, 34], flavonoids, steroids, saponins, phenolics (including tannins), cyanogenic glycosides, glucosinolates [23, 29], quinines, and essential oils [32]. The different types of chemical defenses can vary between species, localities, time, and environmental conditions [31]. Many of them have not been identified; some studies have found multiple dissuasive components in the chemical extracts analyzed, but the low concentrations or their unstable state makes their identification difficult and therefore their correlation with the dynamics of the aquatic community [35].

In the aquatic environment, plant-herbivore interactions are different from terrestrial ecosystems because water provides different physicochemical conditions compared with air or soil, which should affect the herbivore access and the dispersal of released compounds [36].

2.2.1. Macrophyte growth adaptations

The growth forms of macrophytes are the most significant adaptation to freshwater environments and have important consequences for aquatic plant-herbivore interactions. The structure of the macrophytes and the presence of leaves and flowers above or below the water level determine the access and type of herbivores [36], so structures above the water surface can be consumed by terrestrial herbivores while the submerged parts by aquatic herbivores. Therefore the growth forms may have different mechanisms to prevent herbivory. Compared with terrestrial vegetation, freshwater aquatic plants produce less phenolic compounds, and a different phenolic amount in the aquatic growth forms has been observed. Lodge [22] indicated that the rank of mean phenolic content in wetland plants is tree > floating leaves plants > emergent > submersed > algae. Submerged macrophytes have much lower content than emergent or floating leaved macrophytes [37]. These differences are because emergent plants need more structural tissue, thicker cell walls, and a more complex cuticle to limit evapotranspiration and provide stability; therefore they present structural defenses, while submerged

macrophytes are less structurally defended because they have little lignification, thin cuticles to facilitate gas exchange with water, and less exposure to ultraviolet light [36]. As a consequence, interactions with herbivores are modified, fully aquatic leaves of amphibious species and submersed plants exhibited higher grazing rates than aerial leaves, possibly due to a lower structural defense [38].

It is considered that in freshwater plants, constitutive chemical resistance against herbivores are frequent [31, 39, 40] presumably because of a high and lengthy exposure to mostly generalist herbivores [34]. Plants, which would be attacked by generalist herbivores, tend to be defended by a diverse collection of toxins in small concentrations, whereas plants attacked by specialist herbivores tend to employ higher levels of compounds, which reduce digestibility, as it happens in numerous terrestrial plants that are consumed by specialist herbivores.

Aquatic plant-herbivore interactions are highly variable across aquatic ecosystems [11], and we have little information about the presence, levels, types, and function of PSMs; thus we require further analysis in order to make suitable generalizations.

3. Terrestrial ecosystems

The ancestors of terrestrial plants are closely related with charophytes. Plant terrestrialization was preceded by terrestrial algae after aquatic algae, with adaptive mechanisms to live in terrestrial environment such as drought, resistance to UV radiation. In addition, land plants need to increase its body size and cellular differentiation [41].

Another important topic is defensive mechanisms. Aquatic plants have only a few defensive compounds, and their structural defenses are limited because its biomass is constantly renewable. By contrast, terrestrial plants have a plethora of both chemical and structural defensive traits elaborate and accumulate by long-time periods [42]. Nevertheless, at different environment conditions, plants can accumulate diverse molecules or develop distinct structural mechanisms.

Abiotic factors, such as altitude, drought, and nutrient availability, can control defensive traits in plants. At altitudinal gradient, it has been hypothesized that the plant species growing at lower elevations need to invest more in defensive traits because they have greater herbivore pressure, whereas high-elevation plants need less defensive traits [43]. So, as expected at tropical forest, there are more defensive traits than at temperate forest.

Drought slows growth to decrease photosynthetic rate and, in moderate drought, an increase in secondary metabolites is possible, including defensive compounds and structures [44]. In tropical forest, the humidity remains relatively constant, then that factor is not significant.

Plant defense mechanisms are partially due to resources availability; at high resource availability, there are more photosynthesis and growth; but at low resource environments, plant increased defense allocation, because with herbivore attack, it is much more difficult to replace tissue [6, 45, 46].

3.1. Temperate forest

In temperate perennial forest, dominant plants are gymnosperms (see **Figure 1** for distribution). Conifers are dominant vegetation since 200 million years ago, and they appeared 300 million year ago, and during their evolution, they have had few changes. Currently, there are 630 species, which dominate many terrestrial ecosystems, principally in the Northern Hemisphere [47].

Gymnosperms are the major plant lineage with less leaf herbivory, only 0.9%. Low percentage can be explained to tough needle tissue and the presence of terpenoid resins [48]. Herbivory is low in temperate forest tree canopies, and the highest foliar damage occurs in high-quality leaves as youngest [49], it is more probably that the trunk is attacked by bark beetles [3].

At conifer communities, the primary compounds in defense are principally phenolics, terpenoids, and alkaloids, which lay up in the bark [50]. Another line of defense is resin ducts, which confer resistance to insect attack by resin production, flow, and chemical content (**Table 1**) [51].

There are two defense kinds: constitutive, which are expressed all time, even when they are not suffering from damage and induced defenses that enhanced after damage [50, 52]. Among constitutive defenses are resin canals, chemical compounds such as phenolics and therpenes, and the mechanical properties of the cortex that act as a barrier [50, 53]. Those constitutive compounds are nonselective against herbivores, but chemicals produced by induced defense

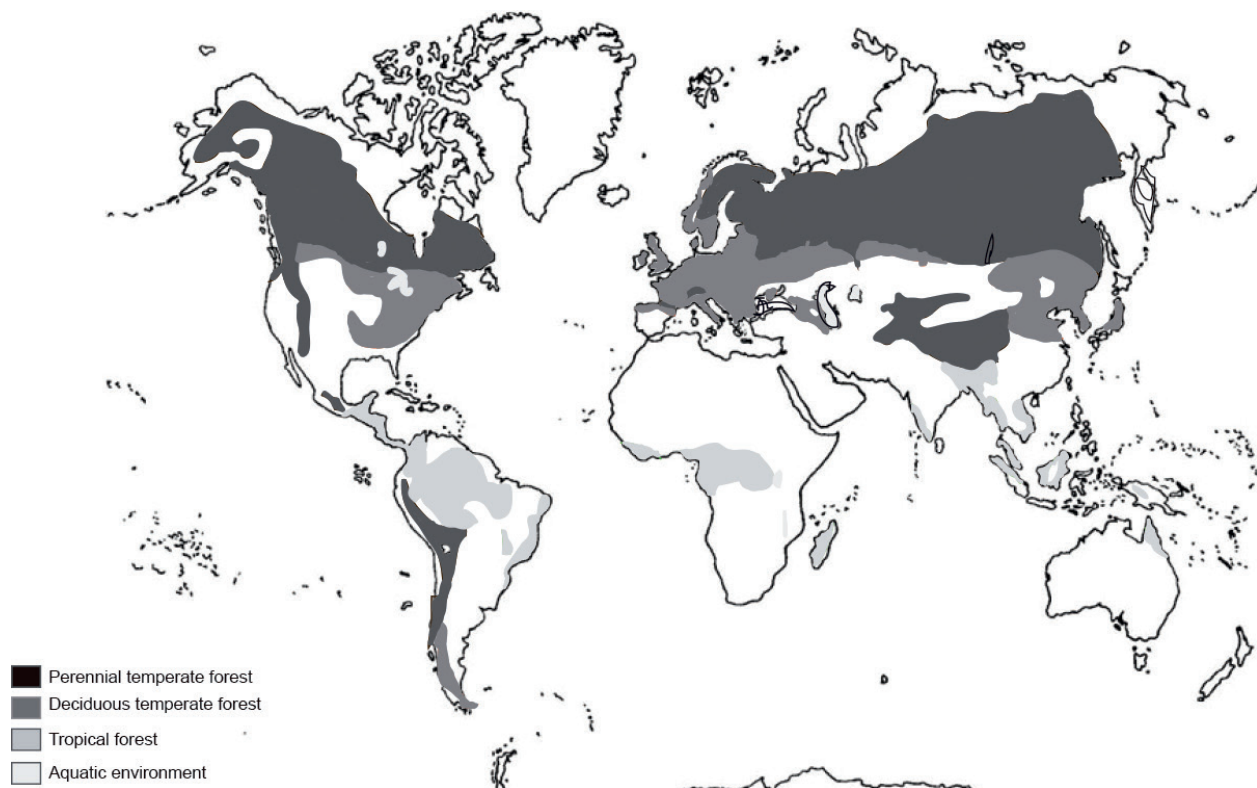


Figure 1. General distribution of different ecosystems in the world.

Environment	Principal plant	Chemical compounds produced
Aquatic environment		
Marine	Red, brown, and green algae	2400 products, the majority terpenoids, acetogenins, phlorotannins (polyphenolics), and halogens
Freshwater	Angiosperms submerged, floating, or emergent	Alkaloids, flavonoids, steroids, saponins, phenolics (including tannins), cyanogenic glycosides, quinines, and essential oils
Temperate forest		
Perennial	Conifers	Terpenoid resins, phenolics, tannins, and alkaloids
Deciduous	Subclass Hamamelidae	Condensed tannins and phenolics
Tropical forest		
	The most diverse plant ecosystem	Great variety of chemical compounds, principally blends, which include phenolics, saponins, amino acids, amides, alkaloids, azoxy glycosides, and terpenes

Table 1. Chemical compounds produced by principal plant types at different environments.

have a wide spectrum and form specific compounds, so they are very diverse and cover a great variety of herbivores [54, 55]. Among induced defenses include phenolic compounds, resin terpenoids, enzymes, PR proteins, and reactive oxygen species [50].

In conifers, resin terpenoids are produced during and after attack of insects, when constitutive duct is active and produces resin, which can flow at great quantity [54, 56].

The bark of conifers has abundant phenolic compounds [57–59]. When phenolics and tannins join to amino acids and proteins, both of them reduce the nutritional value and the ability of insects to digest plant tissues [60]. Constituent phenols can be converted in polyphenolic compounds after herbivore attack, and they are more toxic and specific against herbivores [61].

There are proteins that act as chemical defenses, such as enzymes that degrade components of herbivores such as glucanases and chitinases [62]. Generally, chemical defenses have multiple strategies overlapping that result in a chemical toxic cocktail that stops or destroys an aggressive or virulent attack.

At gymnosperms, multiple overlaying defense systems provide an efficient barrier against a wide range of possible insect attacks. However, conifers remain susceptible to certain organisms that have evolved strategies to overcome the defenses or avoid them. Nevertheless, the remarkable longevity of conifers is a proof to the success of their defense strategies (**Figure 2**) [53].

Another plant community at temperate environment is deciduous forest, particularly the oak forest (distribution in **Figure 1**). In *Quercus robur*, phenolic concentration in leaves increases toward higher elevations with a decrease in leaf damage in comparison with organism at same species that grow in lower altitude [43] that suggest that temperate oak forest is less susceptible to insect damage than tropical forest. In the same way, *Quercus variabilis* total phenolic and total condensed tannin concentration decreases to higher elevation and is more concentrated in juvenile individuals [63].

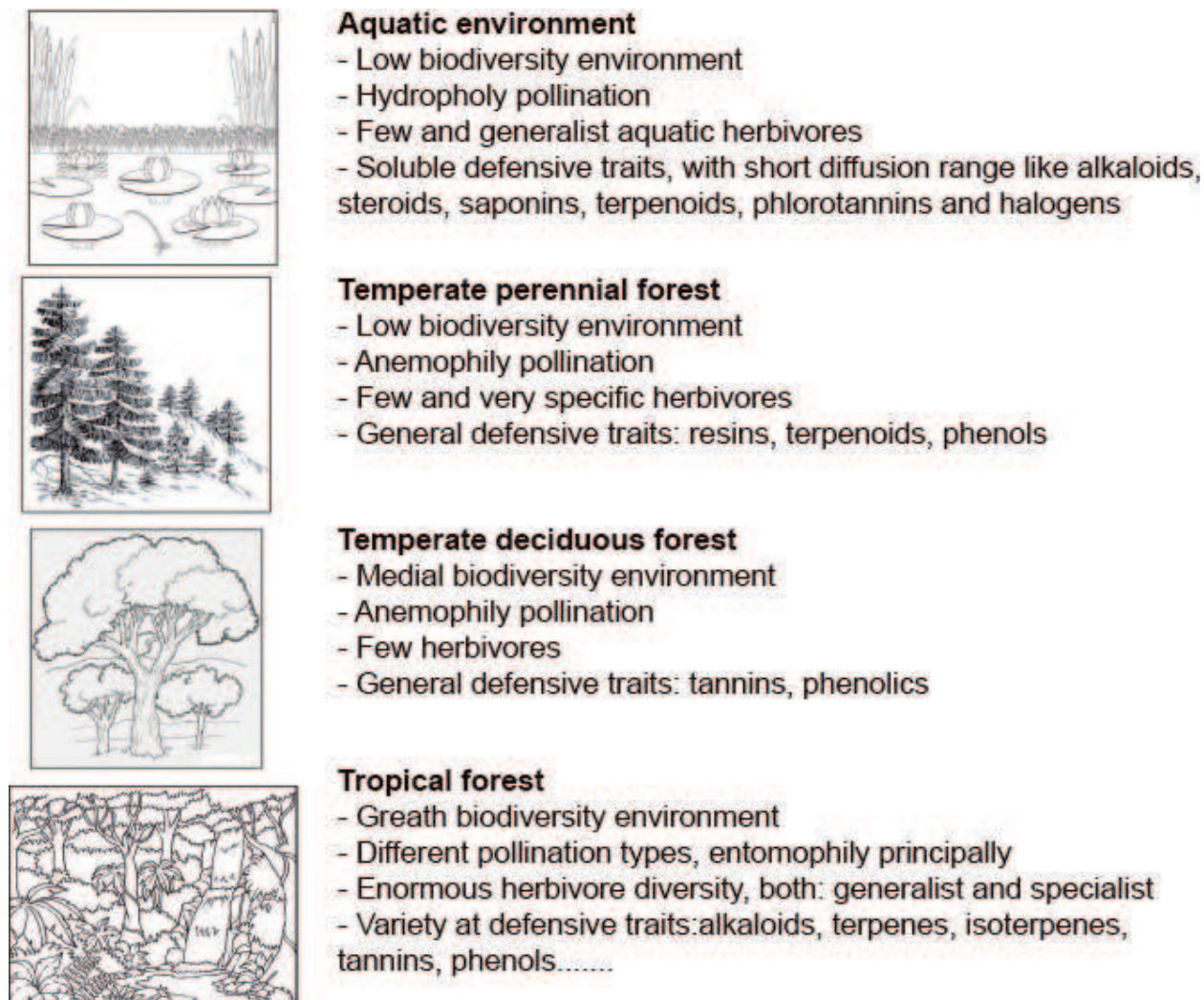


Figure 2. Characteristics related to defense mechanisms in plants of different environments.

In a temperate deciduous forest at Powdermill Nature Reserve, the leaf damage caused by herbivores and in majority of individual had a low rate than 2% that can be due to low herbivore densities and poor degrees of specialization thereof [64].

Also, in stressful environment like high-elevation alpine plant communities with low temperatures, plant species have asexual reproduction by rhizomes resulting in clones. Clonal species have developed a tolerance strategy against herbivores and reduced investment in chemical defense [65].

3.2. Tropical forest

The most recent plant community is the tropical forest (see distribution in **Figure 1**), which originates toward of the end of Cretaceous period when angiosperms take over the plant diversity [66]. In general, plants at tropical forest have a great variety of chemical compounds for defense, principally blends (**Figure 2**, **Table 1**).

In tropics, there is a high herbivory variation explained by multiple syndromes in plant defense strategies, driven by leaf nutritional quality, in relation to nutrition defense [67], where most extreme plants can combine high chemical defense, low nutritional quality and asynchronous leaf expansion, reduces to minimal its vulnerability [68].

At tropical forest, chemical plant defenses have diverged recently and increased their diversity, because there is a high herbivore pressure due to high insect diversity [69]. Tropical forest may hold more than 650 tree species per hectare, in that species interact each, and pests may promote plant diversity including that in leaves of a unique tropical tree, there are hundreds of different chemical defensive compounds. In addition, herbivore diversity and abundance, rates of herbivory, and host specificity are higher in the tropical than temperate plants (see **Table 1** for comparison) [70]. For example, in Amazonian forest canopy, there are concentrations of one to two orders of magnitude in value of foliar phenols, lignin, and cellulose [71].

Tropical forest has been considering an unproductive habitat where plants need investment in defensive traits because they cannot utilize molecules and energy simultaneously to defense, growth, and replacing loss tissues [6, 45, 72]. Then, synergistic interactions among various defensive traits offer an effective resistance, which is reflected with an increase in the simultaneous expression for direct and indirect defenses [73]. When plants exceed the capacity to store, constitutive secondary metabolites could avoid autotoxicity [74].

Mixtures of defensive compounds allow plant increase resistance, including attack from new herbivore-related congeners, considering that species interactions are stronger in tropics [75].

In general, plant species in tropical forest have a high defensive diversity, in which plant species are chemically unique in their communities [76]. It should be noted that chemical compounds implicate in defensive traits, and different interactions between molecules to perform defenses are equally distributed at family, genus, and species level [71].

For example, in tree genus *Inga*, there are a great variety of defensive traits, like phenolics, which includes polygalloylated compounds, polymers of flavan-3-ols with different substitutions, triterpene saponins, and the amino acid tyrosine. Moreover, plant can identify the agent, amount, and timing of damage and produce a particular induced response, and its response differs in low- and high-risk environments [77].

Amino acid tyrosine can be redirected into other primary and secondary metabolites, and its accumulation in excess in young leaves may not be adaptive as they would persist once the leaf was full size and protected by toughness [78].

Another genus well characterized about its defensive chemical compounds is *Piper*, which is broadly represented at tropical forest in the world [79]. The most bioactive compounds reported by *Piper* are amides, a group nitrogen-based compounds stored at leaves and fruits to defend that genera against herbivores [80]. In *Piper*, prenylated benzoic acid, chromene, and dimeric chromane at concentrations higher than 10% of dry weight of leaf material that compounds have synergistic or additive effect against herbivore attack also have been reported. In addition, concentration of these metabolites is correlated with increasing elevation in relation

with UV exposure and photoactive properties, and more toxic plants support a lower diversity of specialist herbivores [81].

Sometimes, plant species can respond locally to different herbivores, as *Datura stramonium*: the plant can be eaten by generalist and specialist herbivores at great geographic range and produces the alkaloid atropine and its derivative, less toxic, scopolamine. The secondary plant compound is more effective against herbivores specialist, but the precursor is still effective against generalist. Then, when there is a community of generalists, *D. stramonium* produces atropine [82].

Another example is *Zamia stevensonii*, which produces azoxy glycosides (AZGs), highly toxic with mutagenic and carcinogenic properties. AZGs are an excellent defense against generalist herbivores, but are not sufficient to specialist [83].

Another important group of chemical compounds, relevant in defensive plant traits, is phenols, including tannins, which at media concentration reduces herbivory, through reduction of digestibility of plant tissues, and increases immune responses [84].

Terpenes also are present at plants in tropical forest; in that, these compounds protect against abiotic factors such as light, heat, and drought and against herbivores. In Borneo rain forest, foliar terpene presence in 73 of 75 plant species has been analyzed (97%), 15 monoterpenes and 65 sesquiterpenes. This suggests that terpenes can be a favorable selective trait in rainforest [46].

Currently 25,000 structures of terpenes approximately have been reported; some of them are volatile and can be synthesized de novo or are stored in leaves, stems, and trunks and are released in response to attack [85]. One plant can release a highly complex blend, which can include up to 200 volatile terpenes, and its effect is due to direct toxicity, repulsion to herbivores, or attraction of herbivore enemies [85, 86].

Among defensive traits in tropical forest, some are strongly correlated with herbivore damage: leaf size, shearing resistance, cellulose, and ash content. Then, large leaves are more susceptible to herbivory. Other three factors—shear toughness, cellulose content, and ash, which is a mixture of calcium oxalates and phytoliths—reduce herbivore damage acting as structural defenses. These strategies are very efficient and have a relatively low energetic cost [45].

Interestingly, lianas have increased cover and abundance. That plant forms are genetically predisposed to reduce structure and defense traits for investment more in chemical implicates in growth and light capture, wherewith lianas response to stress conditions, like warmer and drier conditions [87].

At tropical forest are common indirect defenses to reduce herbivore attack. In that way, plants provide house, nourish or attract organisms like ants or parasitoids [88], by production of refuges or nesting sites, extrafloral nectar, food bodies or/ and volatile compounds (VOCs) [89].

For example, extrafloral nectar production increases in herbivory and diminishes in the herbivore absence, because that is the secret to attract predators like ants, who defend their food sources and parasitoids. Extrafloral nectar consists in sugars, proteins, lipids, mineral nutrients, and antioxidants and can attract organisms like mites, ladybird beetles, wasp, lacewing larvae, and spiders [90, 91].

VOCs also attract other organisms to improve defense, can attract pollinators, repel herbivores, and are used by plants for communication among them [92, 93] to alert of a possible future attack [94].

4. Conclusions

Every ambient has their own biotic and abiotic selective pressures, and plants are able to respond differentially. In general, there are a great variety of defensive traits in plants, and they are different at distinct environments. In aquatic environment, the principal defensive traits must be water soluble and diffusible, but their action time and range are short, because aquatic plants need to produce this constantly. For aquatic plants, biomass production is more relevant than defensive traits outlay, then they prefer investment in growth and photosynthesis.

In terrestrial environments, plants need to accumulate defensive compounds for an eventual attack, but the quantity depends on biomass replacement rate. If ambient conditions allow rapid biomass formation, plant accumulates less defensive compounds; in contrast, slow accumulation in biomass induces the great defensive compound accumulation. Because at temperate forest, plants accumulate greater quantity of defensive compounds, particularly resins and phenolics.

Herbivore diversity and pathogens also contribute in plant chemical production. In places, with high herbivore diversity, plants produce a plethora of compounds for defense so much for generalist such as specialist; then at tropical forest, there are a greater variety of chemical defensive compounds, especially complex chemical mixtures.

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