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Permalink

<https://escholarship.org/uc/item/023434pv>

Journal

Annals of Botany, 117(7)

ISSN

0305-7364

Author

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Publication Date

2016-06-01

DOI

10.1093/aob/mcw061

Peer reviewed

REVIEW

Plant defences on land and in water: why are they so different?

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Received: 9 February 2016 Accepted: 22 February 2016

• **Background** Plants (attached photosynthesizing organisms) are eaten by a wide variety of herbivorous animals. Despite a vast literature on plant defence, contrasting patterns of antiherbivore adaptation among marine, freshwater and land plants have been little noticed, documented or understood.

• **Scope** Here I show how the surrounding medium (water or air) affects not only the plants themselves, but also the sensory and locomotor capacities of herbivores and their predators, and I discuss patterns of defence and host specialization of plants and herbivores on land and in water. I analysed the literature on herbivory with special reference to mechanical defences and sensory cues emitted by plants. Spines, hairs, asymmetrically oriented features on plant surfaces, and visual and olfactory signals that confuse or repel herbivores are common in land plants but rare or absent in water-dwelling plants. Small terrestrial herbivores are more often host-specific than their aquatic counterparts. I propose that patterns of selection on terrestrial herbivores and plants differ from those on aquatic species. Land plants must often attract animal dispersers and pollinators that, like their herbivorous counterparts, require sophisticated locomotor and sensory abilities. Plants counter their attractiveness to animal helpers by evolving effective contact defences and long-distance cues that mislead or warn herbivores. The locomotor and sensory world of small aquatic herbivores is more limited. These characteristics result from the lower viscosity and density of air compared with water as well as from limitations on plant physiology and signal transmission in water. Evolutionary innovations have not eliminated the contrasts in the conditions of life between water and land.

• **Conclusion** Plant defence can be understood fully when herbivores and their victims are considered in the broader context of other interactions among coexisting species and of the medium in which these interactions occur.

Key words: Sexual selection, visual signal, trichomes, spines, herbivory, defence, freshwater, terrestrial, marine, specialization, animal guards.

INTRODUCTION

The world, or at least the sun-exposed part of it, is green (Hairston *et al.*, 1960). This statement might seem too obvious for serious discussion, but its implications are profound and in many ways still unexplored. It means that plants – here defined as attached photosynthetic organisms – have not only persevered over hundreds of millions of years, both on land and in water, but have likely increased their collective productivity despite their exposure to legions of herbivorous consumers ranging in size from tiny mites, aphids and snails to huge elephants, dinosaurs and sea cows. The success of plants is in no small part due to the evolution of an astonishing variety of physical, chemical and animal-assisted defences (Farmer, 2014).

The intensity of herbivory, as measured by the amount of photosynthetic tissue lost to herbivores per year varies widely among species, among growth forms and among ecosystems. The consensus among researchers holds that herbivores take an average of 10 % to as much as 20 % of plant biomass annually on land, and 51 % to nearly 100 % (mean 68 %) of attached aquatic (marine and freshwater) vegetation (Lowman, 1984; Cyr and Pace, 1993; Hay, 1997; Shurin *et al.*, 2006; Poore *et al.*, 2012; Farmer, 2014). A mean of 5.3 % of terrestrial leaf biomass is consumed when averaged among species from all growth forms and categories (Turcotte *et al.*, 2014), apparently

by insects, although the source of herbivory was not stated. Terrestrial estimates might be biased towards the low end because of the underrepresentation of grasslands and savannas, where high-intensity herbivory by vertebrates predominates, whereas aquatic estimates are perhaps too high because consumption of photosymbiotic animals was not considered. Regardless of these estimates, terrestrial plants and herbivores are globally and regionally far more diverse than their aquatic counterparts, and host specialization there is greater (Hay and Fenical, 1988; Hay and Steinberg, 1992; Coley and Kursar, 2014; Forister *et al.*, 2015).

Despite the vast literature on herbivory, little is known about how plant defence differs between the realms of land and water. Lodge and colleagues (1998) noted that trichomes and tough cuticles are largely absent as potential defences in freshwater plants, and suggested that this absence reflects the importance of reducing the boundary layer for gas exchange and nutrient uptake in water plants. Most comparisons between land and aquatic plants concern carbon and light gain and trade-offs between antiherbivore resistance and whole-plant or leaf lifespan (Leigh *et al.*, 1987; Pierce *et al.*, 2012; Maberly, 2014). Mean longevity is said to be shorter for water plants than for those on land (Smith, 1981), but there is great variation in both realms, with warm-water corals and cold-water coralline red algae living as long as many trees on land (Frantz *et al.*, 2005; Farjon, 2015). Long-lived plant parts tend to be more resistant to attack

by insects (Southwood *et al.*, 1986; Reich *et al.*, 1992; Coley and Barone, 1996; Caldwell *et al.*, 2016), but this tendency cannot explain the differences in herbivore-related traits between land plants and those living in the much denser, more viscous medium of water.

Aquatic herbivores were thought to be less mobile and more generalized in their diets than terrestrial species (Hay and Fenical, 1988), but this characterization applies only to small consumers. Both aquatic and terrestrial realms support large, highly mobile herbivores at high and low latitudes. Comparisons between realms from the perspective of the herbivores have been little explored.

My aims in this review and synthesis are threefold. First, I consider how plant and consumer performance is influenced by the medium in which herbivory and other interactions take place. Second, I evaluate predictions stemming from this analysis by assessing the incidences of several kinds of mechanical plant defence, the role of visual and olfactory cues emitted by plants to their animal helpers and herbivores, and the extent of host specialization by small herbivores on land and in water. Finally, I set these findings in a broader ecological and historical context, highlighting the importance of innovations and of the properties of the surrounding medium in which interactions among organisms occur.

DEFINITIONS AND THEIR IMPLICATIONS

I use the term ‘plant’ in a broad functional and ecological sense to mean any primarily photosynthesizing multicellular or coenocytic organism. This definition is not synonymous with any one clade and therefore has no taxonomic or phylogenetic connotations. It encompasses land plants (embryophytes), lichens, seaweeds (chlorophytes, rhodophytes and phaeophytes) and sedentary photosynthetic animals, including sponges, cnidarians, bivalves and tunicates.

This broad conception of plants is justified on the grounds that most multicellular, attached photosynthesizers represent symbiotic relationships, whether they be between an animal and a single-celled guest or between an alga or embryophyte and a fungus or bacterium. What matters is that the organism fixes carbon by means of energy from the sun.

In this paper I focus on attached plants and do not consider phytoplankton floating freely in water. There is no real equivalent to phytoplankton on land, and the modes of life of both the unattached photosynthesizing organism and its enemies cannot be compared with those of attached aquatic or land-dwelling plants. It would be interesting to compare multicellular free-floating tracheophytes and algae (mostly found in freshwater) with co-occurring attached plants, but that is beyond the scope of this paper. I also exclude the relatively small number of mobile photosynthesizing animals, such as some flatworms, opisthobranch gastropods and cardiid bivalves.

The terms ‘herbivore’ and ‘plant consumer’ are used interchangeably to refer to an animal that feeds on photosynthetic tissues. With this restricted definition, I exclude animals that eat flowers, spores, pollen, seeds, fruits, roots and wood, but I include animals that consume symbiont-containing coral polyps, photosynthetic tissues of other animals (sponges, clams and tunicates), as well as sap-feeders.

A TAXONOMY OF DEFENCE

An attack on a plant comprises two phases. For herbivores, the first phase consists of searching for and recognizing a plant as edible and desirable, whereas the second involves overcoming the plant’s resistance. From the plant’s perspective, these phases are first to prevent being found or recognized, and second to facilitate the herbivore’s quick exit or to slow the herbivore’s consumption. If these options fail, a plant must tolerate and replace extensive tissue loss. Many plants, of course, thrive in places where herbivores are rare or ineffective, as on subtidal sand plains seaward of tropical reefs (Hay, 1981). I do not consider such refuges further here.

To elude herbivores, plants must be rare or unpredictable (Feeny, 1975). This option, which is enabled by long-distance dispersal of gametes or propagules like pollen, spores and seeds, works best against taxon-specialized herbivores such as insects (Janzen, 1970; Leigh *et al.*, 2004; Vermeij and Grosberg, 2010). Plants can also employ long-distance signals that advertise inedibility or danger. As with warning signals in animals (Edmunds, 1974), long-distance communication of danger in plants must be accompanied by effective defences when the herbivore makes contact, and the herbivore must learn to associate the signal with real risk of being injured by spines, toxins or trichomes.

The contact defences of plants fall into two categories: those that minimize contact with the enemy and those that slow the rate of consumption. The first category comprises three options: (1) preferentially shedding herbivore-attacked parts and rapidly replacing them, a possibility open only to fast-growing plants; (2) dislodging a herbivore, effective mainly against small animals; and (3) ushering, directing or guiding a small herbivore away from vulnerable parts. Slow consumption involves (1) toxins or other chemical deterrents that attack the nervous system or interfere with digestion; (2) immobilizing attackers with hairs, spines or sticky surfaces; and (3) establishing a barrier between palatable tissues and the consumer with a mineralized or tough outer layer, hairs or spines that must be removed before feeding begins, latex that must be isolated from the plant parts being consumed, and meristems hidden in places inaccessible to the herbivore. Damage due to herbivores can be mitigated by functional redundancy afforded by multiple branches, small leaves and network venation (Vermeij, 2004; Sack *et al.*, 2008). Although wound plugging is known in plants, repair and restoration of damaged parts apparently is not. Finally, plants can employ aggressive means to minimize herbivory either by injuring attackers directly with spines or stinging hairs or by bringing in animal guards. Many of these defences can be combined and in some cases coalesce into continuous syndromes. Two of these syndromes in savanna sapling trees are spinescent plants, which reduce access to vertebrate herbivores, and plants with a low nutrient content for large consumers (Tomlinson *et al.*, 2016).

Plant defence is influenced by the capacities of herbivores and by the medium in which plant consumption takes place. Some defences work against a wide variety of large and small herbivores, whereas others target particular categories, as is the case for toxins against insects or spines and a prostrate habit against vertebrates. The primary consumers in open landscapes are ground-dwelling vertebrates (McNaughton, 1984; Didiano

et al., 2014). In the rain forest at Barro Colorado Island, Panama, vertebrates and insects each account for about half the leaf consumption (Coley and Barone, 1996). Coral-reef algae are largely eaten by fishes and sea urchins (Hay, 1981, 1997), reflecting the low-growing turf morphology of many species (Bellwood *et al.*, 2014). It cannot be assumed, however, that the herbivores with the largest appetites or representing the highest diversity of species are the only, or even the most important, selective agents for plant defence. Anti-herbivorous secondary compounds are under intense selection because they work well even though consumption rates on plants with these defences are low (Agrawal and Weber, 2015). Moreover, the primary agents of selection and adaptations to them change over the lifespan of a plant or even a leaf (Coley and Barone, 1996; Barton and Koricheva, 2010; Henríquez *et al.*, 2011).

Plant defence and the effects of herbivores are strongly affected by patterns of selection on the herbivores themselves, especially by the risks herbivores face from predators. Selection for multiple plant toxins can be imposed by herbivores that sequester these compounds for their own protection or that seek refuge from enemies on noxious plants (Brower, 1958; Hay and Fenical, 1988; Hay *et al.*, 1989, 1990a, b; Cimino and Ghiselin, 1998). Chemical defences are the only form of protection that can be transferred from one trophic level to another. Plants also offer spatial refuges where predators' abilities to find herbivorous prey is diminished. Palatable caterpillars are often restricted to the undersides of leaves (Heinrich, 1979; Heinrich and Collins, 1983), where birds are less apt to find them, consistent with the presence of defensive hairs or prickles only on the lower leaf surface of some species. Host specialization and counter-defences occur on large seaweeds, where predators and scraping sea urchins cannot easily forage (Vermeij, 1992; Sotka, 2007; Long *et al.*, 2013). Herbivores can also hide in self-made tunnels or mines in the plant (Kobayashi *et al.*, 2015). In short, plant defence reflects not just the interaction between a plant and its herbivores; instead it is shaped also by selection imposed by other agents.

SEARCH, SIGNALS AND THE ROLE OF SEXUAL SELECTION

One of the hallmarks of angiosperms, cycads and some Carboniferous seed ferns is animal-assisted pollination, the transfer of male gametes to female egg-containing structures by motile animals drawn in their search by plant-produced rewards. To be effective, this form of internal fertilization requires that the plant advertises these rewards with an odour or visual signal to which faithful pollinators are attracted from afar. Animal-assisted dispersal of spores or seeds, especially when the structures containing them are nutritious, also entails cues for long-distance attraction.

The evolution of attractive signals operating at a distance has two important implications for plant defence. One is that, by attracting animal vectors essential for reproduction, the plant also advertises to its enemies. Selection for defence, especially resistance, should therefore be more intense in species that employ long-distance signals than in those in which gamete fertilization and propagule dispersal do not depend on animals (Vermeij, 1987). A second consequence is that animal-directed

signalling opens the evolutionary door to crypsis, camouflage, mimicry, deceit and warnings, i.e. to adaptations functioning during the initial phase (detection and recognition) of an encounter between a plant and its herbivores. Involvement of animals in plant reproduction has therefore led to more intense selection for both contact and long-distance defences in plants.

If a plant and its primary consumers rely on external fertilization, in which gametes are broadcast outside the body before zygote formation, neither party would be subject to selection for long-distance signals influencing mate choice. This situation is the rule in algae and corals and for such major herbivores as echinoids, asteroids (sea stars, including coral-feeding species of *Acanthaster* and *Culcita*) and the majority of chitons, patello-gastropods (true limpets), haliotids (abalone) and trochoidean vetigastropods (topshells). Effective defences in externally fertilizing plants would be chiefly in the form of general resistance and a high tolerance of herbivore-induced damage. The likelihood of evolving long-range, defence-related signals rises when one or both parties engage in active direct or indirect mate choice.

Animal-assisted pollination and dispersal of plants is an almost entirely terrestrial phenomenon (van der Hage, 1996; Vermeij and Grosberg, 2010). Seagrass pollination and seed dispersal might be aided by some vertebrates with very generalized diets (Sumoski and Orth, 2012; van Tussenbroek *et al.*, 2012), but neither party in these interactions appears to be specialized. All animals that pollinate and disperse plants practise internal fertilization themselves and, like animal-pollinated plants, use long-distance signals to attract or choose among potential mates. In animals, signalling involves vision, olfaction or hearing. The evolution of animal-assisted pollination was facilitated by the potential for high-speed, long-distance locomotion (especially flying) and the long-range, rapid dispersal of attractive scents in the thin medium of air. The high density and viscosity of water constrains such movements and perceptions in small animals (Vermeij and Grosberg, 2010; Weissburg, 2011; Martens *et al.*, 2015). Small amphipod crustaceans, for example, react to olfactory stimuli in water at distances of half a metre or less, and even large predatory crabs and spiny lobsters respond at distances of at most 3 m (Weissburg, 2011). Selection for long-distance signalling should therefore be weak for freshwater and marine plants.

All terrestrial herbivores – arthropods, vertebrates and gastropods – exhibit mate-choice behaviour and have therefore been substantially influenced in their adult sensory capacities by the imperative to attract and distinguish among mates. With the exception of land snails and slugs, which often use mucus trails to track potential mates, many of these animals rely on long-distance signals to find suitable partners (Hansson and Stensmyr, 2011; Reeves, 2011), an ability that is readily applied to the remote detection of plant food. Remote sensing is especially important to flying adult insects that must locate appropriate plants on which to lay eggs, so that the non-flying larvae are well situated to begin feeding (Bruce *et al.*, 2005). It should be noted, however, that long-distance mate choice does not automatically imply remote food choice: adult scale insects are dispersed by the wind and do not employ dedicated searching to locate suitable host plants (Hardy *et al.*, 2015). Food discrimination from afar is likewise unfeasible for terrestrial herbivorous molluscs. Land plants have adapted to remotely sensing

herbivores by appearing to be dead or inanimate, being visually cryptic, displaying a visual or olfactory warning of toxicity or spininess, or displaying spots resembling prior damage or insect eggs (Benson *et al.*, 1975; Brown *et al.*, 1991; Lev-Yadun, 2001, 2014; Lev-Yadun *et al.*, 2009; Bond *et al.*, 2004; Cooney *et al.*, 2012; Gianoli and Carrasco-Urra, 2014; Yamazaki and Lev-Yadun, 2015). Blue, red, brown, black or grey leaves and stems confuse herbivores (Thomas *et al.*, 2010; Queenborough *et al.*, 2013; Strout *et al.*, 2013; Niu *et al.*, 2014), while the colour or brightness of yellow and red autumn leaves could indicate inedibility to aphids (Hamilton and Brown, 2001; Döring and Chittima, 2007; Reeves, 2011).

Aquatic herbivores in which sexual selection and the potential for long-distance sensing of mates and food exist include vertebrates, crustaceans and many gastropods. For other marine herbivores, however, it is often the small larvae or juveniles rather than the larger adults that must locate suitable food plants (Hay and Fenical, 1988; Pawlik, 1992), so that the challenge of finding food is separate from that of securing mates. The sensory world of very small aquatic animals is spatially limited (Martens *et al.*, 2015), implying that food-specific cues must be detected either through direct contact or over centimetre-scale distances. Even for larger, more mobile aquatic herbivores, olfaction may be unimportant. Herbivorous sirenians (sea cows) lack colour vision (Marshall *et al.*, 2015) and rely mainly on tactile sensing to locate plants (Marshall *et al.*, 2003). Long-range detection of dimethylsulphide released by phytoplankton and seaweeds enables ocean-going birds to find food (deBose and Nevitt, 2008; Savoca and Nevitt, 2014), but this air-dispersed signal is not species-specific and is not known to be used by herbivores. Sea urchins are said to detect large brown algae at distances of at least 30 m (Leighton *et al.*, 1965), but how they do so is unknown. Underwater olfaction at a distance is well developed in predatory sea stars, gastropods and crustaceans, and spectacular in predatory fishes (deBose and Nevitt, 2008; Weissburg, 2011). Larvae of some reef fishes can detect the odour of algae and corals by olfaction at a distance (Dixson *et al.*, 2008; Lecchini *et al.*, 2013), but the cues, which remain unidentified, are not species-specific.

The best documented case of plant-food choice at a distance under water by adults comes from internally fertilizing sacoglossan gastropods (Rasher *et al.*, 2015). Other examples might be found in coral-feeding gastropods and in small, host-specialized, seaweed-feeding amphipods, chitons and gastropod limpets, but the sedentary habits of these species means that long-distance olfaction is unlikely to be important. Many marine herbivores, including large host-specialized limpets, fertilize externally and rely on chemical cues from food plants during the larval settlement phase (Hadfield, 1984; Rahmani and Uehari, 2001; Huggett *et al.*, 2005; Williams *et al.*, 2008; Hayakawa *et al.*, 2009), when detection is feasible only by contact or over centimetre-scale distances.

To my knowledge, no examples have yet come to light of aquatic plants confusing, warning or misleading herbivores with underwater visual signals. For aquatic angiosperms with animal-pollinated, air-exposed flowers, the potential for such visual cues above water does exist, but it does not seem to be realized for the submerged parts of the plants. Insect-pollinated water lilies (Nymphaeaceae) are targeted by many specialized insect herbivores (Cronin *et al.*, 1998), but there is no evidence

that underwater vision plays a role in food-plant choice by these insects. At least some reef-associated fishes can learn to associate rewards or unpalatable foods with colour (Siebeck *et al.*, 2008; Miller *et al.*, 2013), but again there is no indication that their algal or coral food species provide any visual assistance in the choices these fishes make.

The apparent absence of visual signalling by submerged plants contrasts with the great abundance of visual crypsis, mimicry and warning colours and patterns in marine animals. Although the intensity of selection by predators may be less in aquatic ecosystems than in those on land (Agrawal and Weber, 2015), many marine vertebrates and crustaceans use colour and pattern to detect prey animals and mates. Why this capacity does not carry over to the interaction between food plants and marine herbivores remains a puzzle.

HERBIVORE LOCOMOTION AND ATTACHMENT

Herbivores that are much smaller than the plants on which they feed must in many cases move along and cling to the plant surface. For small surface-moving herbivores, there are two available methods of locomotion, one using appendages (legs), the other relying on a self-produced sheet of mucus for gliding. The former method characterizes arthropods and small vertebrates, whereas the latter typifies molluscs.

I have suggested elsewhere that anisotropically disposed hairs and scales on plant leaves and stems serve either to prevent small arthropods from ascending plants or to hasten the departure of these herbivores by guiding them to leaf tips (Vermeij, 2015a). There is also evidence that asymmetrically oriented features entangle arthropods' appendages (Eisner *et al.*, 1998; Vermeij, 2015a). Travelling on a thin film of mucus would make such a defence ineffective.

Plants can dislodge small herbivores in two ways. One is to present edible parts that are highly mobile, such as leaves fluttering in the wind or fronds flapping in the surf (Bernays, 1991; Sotka, 2007; Yamazaki, 2011). The other is to make the plant surface slippery with a glossy, waxy or mucilaginous coating (Jeffree, 1986; Voigt *et al.*, 2007; Ferrenberg and Mitton, 2014). Countermeasures by herbivores include excavating a tunnel or cavity in the plant, constructing a shelter that is permanently attached to (and often made from) the plant, tightly gripping the plant with jaws or appendages, or forming a temporary attachment with a thread of mucus or silk. These defences and herbivores' adaptive responses to them work both in water and in air.

Instead of dislodging prey, plants can immobilize and entrap intruders with trichomes, spines, sticky surfaces, or leaves or vesicles that enclose small animals. Entrapment can have the added benefit of using the victim either as a nutritional source for the plant or, especially in sticky plants, of attracting animals that not only eat the dead arthropod but also the plant's herbivores that are unaffected by the adhesive surface (LoPresti *et al.*, 2015). Variations on these methods occur in terrestrial and freshwater angiosperms and resinous gymnosperms and in nematocyst-bearing corals, but appear to be absent in marine and freshwater algae (Vermeij, 2015b) as well as in terrestrial spore-bearing plants.

DISTRIBUTION OF DEFENCES

Interesting and hitherto unrecognized contrasts exist in the types and incidences of mechanical and animal-assisted defences in plants from the principal habitat domains of land, freshwater and the sea. Below I discuss many of these defences, especially mechanical and animal-assisted ones, and largely overlook the vast literature on chemical defence. Toxins and other chemical deterrents appear to be nearly universal even if certain types are unique to particular taxa or environments. Defences induced by herbivores are also extremely widespread and are likewise not considered explicitly. The defences discussed below are qualitatively summarized in Table 1.

Spines, prickles and thorns are common on the leaves and stems of land plants, especially in dry climates and in the lowest 1–2 m of vegetation in forests. They are effective largely against ground-dwelling mammals, birds and tortoises (Cooper and Owen-Smith, 1986; Eskildsen *et al.*, 2004; Palmer *et al.*, 2008). My analysis of the monograph on Dutch flora of tracheophytes (Heimans *et al.*, 1960) shows that the 50 plant species with sharp projections on stems and leaves account for 4.4 % of the 1137 native land-dwelling species. This incidence is lower than that in the drier vegetation of Israel (294 of 2600 species, 11 %; Ronel and Lev-Yadun, 2012). In tropical rain forests, spines are confined to the lower parts of some trees and to vines that climb into the canopy with hooks.

Although sharp-tipped leaves (needles) are well known in some wind-pollinated conifers (especially some species of *Pinus*, *Picea*, *Abies* and *Araucaria*) and in grasses, spiny stems and leaf veins and margins are uncommon in plants that are not animal-pollinated. These plants are still frequently animal-dispersed, but at least in the case of grasses this often happens as a consequence of casual contact with the fur of passing mammals. It is therefore plausible that the infrequent development of spiny surfaces and margins in wind-pollinated plants reflects a lower evolutionary priority for long-distance visual recognition.

In freshwater, spines and prickles are known in two species of Hydrocharitaceae, the European *Stratiotes aloides* and the widespread *Najas marina* (Haynes, 1979; Cook and Urmikönig, 1983), and in two genera of water lilies, the South American *Victoria* and the South Asian *Euryale* (Borsch *et al.*, 2008). The two temperate species constitute 1.7 % of the 118

native freshwater plants in the Dutch flora, and the four prickly species together constitute just 0.2 % of the global freshwater spermatophyte flora, estimated by Chambers and colleagues (2008) to number 2614 species. Spines are absent in the 18 aquatic plant species studied by Ostrofsky and Zettler (1986) in Pennsylvania.

A few large marine algae carry very short, sharp projections on their blades. They include the kelps *Ecklonia radiata* and *Pelagophycus porra* and the tropical western Pacific fucoid *Turbinaria ornata* (Abbott and Hollenberg, 1976; Bittick *et al.*, 2010; Wernberg and Vanderklift, 2010). Calcified turf-forming red algae of the genus *Amphiroa* have spiny tips. These prickly species account for a negligible proportion of the approximately 9400 multicellular red, green and brown algae and vascular plants in the sea as compiled by Appeltans and colleagues (2012). Many photosymbiotic corals have notably rough skeletal surfaces, but neither they nor other photosymbiotic marine animals can be said to bear spines.

Trichomes (hairs) on stems and leaves are common in land plants (Levin, 1973; Johnson, 1975), in which they have various deterrent functions against small herbivores such as insects. The Dutch flora of terrestrial tracheophytes (Heimans *et al.*, 1960) contains 247 trichome-bearing native species, which account for 21.7 % of the total; for woody shrubs and trees (80 species) this incidence climbs to 38 % (30 species), a figure somewhat lower than the 47 % reported for the subtropical woody species of Wuhan, China (36 of 76 species; Chen and Huang, 2013).

Hairy surfaces are rare among freshwater plants. They are best developed in some water lilies (Nymphaeaceae), buttercups (Ranunculaceae) and water ferns (Salviniaceae) (Borsch *et al.*, 2008; Vasco *et al.*, 2013). In the ferns and in the aquatic aroid genus *Pista* (Araceae), hairs function to repel water from photosynthetic surfaces (Schenck, 1886; Vasco *et al.*, 2013). Only four of the 118 native freshwater spermatophyte species of the Netherlands (3.4 %) have trichomes on submerged parts of the plant. In *Polygonum amphibium* (Polygonaceae), submerged leaves lack trichomes, whereas emergent parts of the plant are hairy.

Some marine algae have marginal hairs on the fronds (Abbott and Hollenberg, 1976), but no marine plant can be said to be hairy. This statement holds for all major groups of seaweeds, marine angiosperms and photosymbiotic animals. Some

TABLE 1. Qualitative occurrence of plant defences

Defence	Marine	Freshwater	Land
Spines, thorns, prickles	Rare	Rare	Common
Envenomation	Common	Absent	Rare
Toxicity	Common	Common	Common
Pubescence/hairiness	Rare	Rare	Common
Anisotropic surfaces	Absent	Absent	Common
Mineralization	Common	Common	Common
Visual crypsis	Absent	Absent	Common
Visual aposematism	Absent	Absent	Common
Slippery surface	Common	Rare	Common
Animal guards	Rare	Absent	Common
Tough cuticle	Common	Rare	Common
Long-distance olfactory signal	Absent	Absent	Common
Sticky surface, entanglement	Absent	Absent	Common
Deciduousness	Absent	Absent	Common

high-shore, low-growing algal turfs have a hairy appearance, but this effect is a collective one caused by many tiny plants growing together in a mat. A similar effect is seen in mosses on land.

The near absence of spiny and hairy surfaces in aquatic plants contrasts strikingly with their frequent occurrence in mobile and sedentary animals. Spines are almost the rule in sea urchins, but they are also common in sea stars, shell-bearing gastropod and bivalve molluscs, decapod crustaceans, fishes, and fossil cephalopods, brachiopods and trilobites. A hairy (but almost never anisotropic) periostracum characterizes numerous gastropods and bivalves as well as crabs and annelids. Projections from the cuticle, shell or appendages do not interfere with nutrition, whereas in marine photosynthetic animals and algae they would substantially reduce the uptake of nutrients from the water as well as the ability to absorb light.

Asymmetrically disposed (anisotropic) trichomes occur commonly in land plants, perhaps as a means of ushering small arthropods off leaves or preventing ascent of the plant by arthropods (Vermeij, 2015a). I know of no freshwater or marine plant with such anisotropic surface structures. By contrast, anisotropic features are extremely common in mobile marine and land animals (Hancock *et al.*, 2012). As with normal trichomes and spines, anisotropic features perhaps interfere with light and nutrient absorption in aquatic plants. Moreover, many small marine herbivores move on a film of mucus, rendering anisotropic surfaces ineffective deterrents to their locomotion.

Protection by animal guards is much more common on land than in water. Highly mobile animals (especially ants and mites) patrol plant surfaces and remove or repel herbivores (Davidson and McKey, 1993). Guards living in specialized housing provided by the plant occur in 681 vascular plant species, representing at least 158 independent land-plant lineages (Heil *et al.*, 2001; Chomicki and Renner, 2015). Another 3541 plant species have extrafloral nectaries that feed less specialized guards, in this case representing at least 457 plant lineages (Chomicki and Renner, 2015). All these associations apparently evolved during the Cenozoic, beginning in the Early Eocene (Parker and Grimaldi, 2014). Together, these animal-defended land plants account for about 4.5 % of living vascular plant diversity. In addition, many land plants release volatile compounds that attract predators of herbivorous arthropods (Jürgens *et al.*, 2006; Loivamáki *et al.*, 2008).

As noted above, sticky plants have been shown to be protected by casual predators that are attracted to arthropods immobilized on the adhesive surface (LoPresti *et al.*, 2015). The 110 genera containing sticky species listed by LoPresti and colleagues (2015) are all land plants and are probably a mere fraction of terrestrial species that could benefit from this form of animal-assisted defence.

The only marine photosynthesizers known to maintain specialized herbivore-removing guards (mainly decapod crustaceans and some gobies) are some branching corals and sea anemones (Glynn, 1983a, b; Godwin and Fautin, 1992; McKeon *et al.*, 2012; McKeon and Moore, 2014). At least in some cases, the corals provide a nutritional reward in the form of mucus as well as physical refuges for the guards (Stimson, 1990). Photosymbiotic cnidarians have a well-developed in-house defence in the form of nematocysts (stinging cells) and tentacles that effectively discourage intruding consumers. It is ironic that

intrinsically well-defended cnidarians should also host animal guards. Animal-assisted defence and sources of nutrition for such guards are unknown in algae. No freshwater plant appears to employ animal guards either. The reasons for these absences are obscure. The incidence of guarding in marine plants (in 100 out of more than 10 000 species) is 1 % or less.

HOST SPECIALIZATION

Few comprehensive data on host specialization exist for either terrestrial or aquatic herbivores. Most small terrestrial arthropods are host-specific, at least locally (Ehrlich and Raven, 1964; Dixon *et al.*, 1987; Dyer *et al.*, 2007; Futuyama and Agrawal, 2009; Forister *et al.*, 2015). Nevertheless, generalized diets are known in many caterpillars (Dethier, 1988) and most attine leaf-cutter ants (Howard, 1987) and tropical sternorrhynchan scale insects (Hardy *et al.*, 2015). To my knowledge, no terrestrial or freshwater gastropods have taxonomically restricted plant diets. Most terrestrial herbivorous vertebrates also have a broad diet, although the bamboo-feeding giant panda and the eucalyptus-feeding koala – animals with very low metabolic rates (Nie *et al.*, 2015) – are exceptions.

Marine herbivores tend not to be host-specialized. With the exception of coral-feeding fishes and sea stars and seagrass-feeding vertebrates, most specialists are small animals living protected within toxic algae, or in self-made excavations and shelters (Lewis and Kensley, 1982; Hay *et al.*, 1989; Conlan and Chess, 1992; Poore *et al.*, 2014). My review of herbivorous crustaceans indicates that 20 of 52 studied species (39 %) are host-specialized.

To assess the host use of herbivorous marine molluscs, I surveyed intertidal and shallow-subtidal shell-bearing species (mostly excluding the generally tropical, often host-specific sacoglossans) from literature sources and my field notes and collections. The highest incidences of host specialization occur in cold waters (Table 2); lower incidences cluster in the tropics despite the presence there of specialized coral-feeders. These data support previous suggestions that feeding specialization is less common for small marine herbivores than for those on land.

TRADE-OFFS BETWEEN HERBIVORY AND OTHER FUNCTIONS

Herbivory is only one of several agencies affecting the lives of plants. These other demands can conflict with defence, and often differ markedly between water and land.

One of these demands is nutrient acquisition. Most water plants take up dissolved and particulate organic matter and minerals directly from the surrounding water. Their surfaces are often finely divided, cuticles are thin, and blades and stems are flexible (Schenck, 1886; Corner, 1964; Maberly, 2014). Algae with large fronds increase their surface area and disrupt boundary layers with wavy blade margins, raised assimilatory structures and bullate or wrinkled surfaces (Hay, 1986; Koehl and Alberte, 1988; Stewart and Carpenter, 2003). Defences such as a thick cuticle, non-absorptive trichomes and spines could interfere with photosynthesis and nutrient uptake in water, where plants are often carbon-limited and sometimes light-limited

TABLE 2. Numbers and percentages of species with host specialization (S) compared with the total number of herbivores (N) in marine shell-bearing molluscs.

Location	N	S	Percentage	Source
Aleutian Islands	40	10	25	Vermeij <i>et al.</i> , 1990
Northern New England	8	2*	25	Vermeij collection
Washington State	86	12	14	Kozloff, 1987
Isefjord, Denmark	14	3	21	Rasmussen, 1973
South-central Chile	44	2	4.5	Aldea and Valdovinos, 2005
Jamaica	55	6	11	Vermeij collection
Western Panama	46	1	2.2	Vermeij collection
Guam	103	9	8.7	Vermeij collection
Palau	81	7	8.6	Vermeij collection

*Includes the recently extinct eelgrass-associated limpet *Lottia alveus* (Carlton *et al.*, 1991).

(Leigh *et al.*, 1987; Maberly, 2014). Nutrient uptake from the sediment complements acquisition from water in some siphon-lean green algae and in aquatic vascular plants. In land plants, nutrient uptake tends to be restricted to roots, freeing up aerial parts for support, photosynthesis, and defensive structures that do not contain chlorophyll.

Fouling by surface colonists poses an additional complication. Colonists such as fungi, lichens, bryophytes and algae on land plants and epiphytic algae and sedentary animals in aquatic settings reduce exposure to light, interfere in water with nutrient uptake and weaken plant parts structurally (Coley *et al.*, 1993; Coley and Kursar, 1996; Krumhansl *et al.*, 2011; Anderson and Martone, 2014). Plants therefore benefit from small herbivores that scrape colonists from surfaces, but they also run the risk that these same consumers will eat the plants. Defensive hairs, spines and sticky surfaces could promote settlement by, and impede the removal of, colonists; these features would therefore be inappropriate for plants that are susceptible to fouling. Slippery or chemically repellent surfaces could prevent some settlement and discourage herbivory without compromising photosynthesis. Plants on land and in water often use mobile animals to keep surfaces clean of colonists (Putz, 1984; Stachowicz and Hay, 1996, 1999; Dixson and Hay, 2012). For plants with ephemeral parts, antifouling protection might be unimportant, but for long-lived algal crusts and sclerophyllous land-plant leaves, selection for traits that prevent settlement by colonists should be intense. Many dry-adapted and montane woody plants have thick leaves with convex upper and concave lower surfaces that, like drip-tips on the leaves of tropical rain-forest trees, can expel water, dust and potential colonists and prevent their accumulation (Vermeij, 2015a).

Many terrestrial epiphytes and desert plants collect water from the air and convey it to where it can be absorbed (Hill *et al.*, 2015). Micrometre-scale anisotropic features on cactus spines enhance this capacity even against the force of gravity (Ju *et al.*, 2012). These functions could also have a defensive function, although their size is small compared with the anisotropic trichomes typical of many plants that are not under obvious water stress.

HISTORICAL ASPECTS

In addition to the contrasting effects of air and water on plant defence, where land plants clearly have more scope than their aquatic counterparts, there is a historical dimension to the

adaptive chasm in plant defence between the two realms. Herbivory appears relatively late in the history of Phanerozoic ecosystems. The earliest indication in land plants is in the Middle Devonian (Labandeira *et al.*, 2014), but abundant evidence of herbivore-caused damage dates from the latest Carboniferous and Early Permian (Labandeira, 2006a, b; Pinheiro *et al.*, 2015). Plant defences, including glandular and anisotropic trichomes and network leaf venation, appeared during the Late Carboniferous (Krings *et al.*, 2002, 2003; Boyce and Knoll, 2002). Pollination of some seed ferns by flying insects emerged in the Late Carboniferous (Labandeira, 2006a, b), implying that visual signals of defence could also have existed at that time. The discovery that some mosses release volatile compounds to attract collembolans (Rosenstiel *et al.*, 2012) could mean that olfactory cues acting at a distance were used even earlier. Amber (fossilized stickiness) is known back to at least the Triassic in land plants (Schmidt *et al.*, 2006; Sidorchuk *et al.*, 2015).

Herbivory and adaptations to it lagged in the sea. Indiscriminate rock-grazing likely extends back to the Early Cambrian, but herbivores that in the modern fauna tear, bite, grind or pierce marine plants can be traced back only to the Triassic (Vermeij and Lindberg, 2000). Suctorially feeding gastropods (sacoglossans and some neritids) are known with certainty only from the Cenozoic era (Jensen, 1997) and marine herbivorous vertebrates are no older than the Late Cretaceous.

CONCLUSIONS

In this paper I have explored the hypothesis that the variety of remotely sensed and contact defences is much greater in plants living on land than in plants submerged in water. Much of this difference is attributable to the greater locomotor and long-distance sensory range of herbivores in the thin medium of air than for animals in the denser, more viscous medium of water. Although the limitations of water on defence and other functions apply to large and small plants and animals alike, they are most starkly expressed in small organisms. The result is much less host specialization by small herbivores in water than on land, especially at tropical latitudes. The direct effects of the medium on plant functions are magnified by the role that animals play in plant reproduction and dispersal on land. Evolutionary time has not eliminated these contrasts, and in many ways perhaps has made them even more dramatic, with the Late Mesozoic and Cenozoic rise of host-specialized

pollination, dispersal and herbivory of plants on land and the critical role that sexual selection has taken in the evolution of flowering plants and the animals associated with them.

Throughout, I have emphasized the importance of considering not merely the interaction between plants and their herbivores, but also the role of other agents – pollinators, dispersers, mates, surface colonists, and predators – in defining the milieu in which adaptation takes place. Still others not considered here (microbial pathogens and symbionts) are apt to be just as important.

Advances in understanding plant defence will come from several lines of enquiry. These include: (1) local and regional surveys of the incidences of various types of defence in different growth forms and habitats; (2) quantification of degrees of host specialization by herbivores in relation to plant growth form, climate, habitat, and herbivore size; (3) investigation of the sensory capacities of herbivores, especially those in freshwater and the sea, in relation to the role sexual selection plays in the reproduction of these herbivores; and (4) studies on how purported defences function against particular enemies. With respect to this last category, it will be important to go beyond preference choice tests, in which plants with contrasting defences are offered to herbivores. Much more needs to be done on how herbivores find, move on and eat plants and how these capacities are influenced by plant traits. Finally, although chemical defences have figured prominently in the study of herbivory, more attention must focus on physical deterrents and on potential long-distance signals.

The study of interactions like herbivory will succeed fully only if they are placed in the broader context of other interactions that plants have with the species living with them. As Agrawal and Weber (2015) also emphasize, different plants will have evolutionarily found different solutions to the selective agency of herbivory. In the abstract, we can speak of a single agency of herbivory, but in reality there are many agents, each with its own capacities and limitations to which a plant must evolutionarily (or inductively) respond according to the importance of that herbivore in the overall pattern of selection to which the plant is subjected. The heterogeneity introduced by these herbivores, by differences in growth form and habitat, by predators, parasites and symbionts, and by evolutionary legacy, is a central attribute in any assemblage of species, whether these species coexist in an ecosystem or are all members of a particular taxon or clade. We ignore this heterogeneity at our peril.

ACKNOWLEDGEMENTS

I thank Alyssa Henry for technical assistance, and Edith Zipsper and Eric LoPresti for useful discussions.

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