Herbivory

Why is the World Green?
- HSS hypothesis

Terminology

Effects on Individuals

Effects on Populations
- EAB
- Granivory
- Biocontrol

Effects on Communities

Plant Defenses
- Physical
- Chemical

Why is the World Green?

This is a non-trivial question that has been pondered for some time. Plants are at the base of the food web and support virtually all life on earth.

Yet, we exist in a world with mostly [uneaten] plants.

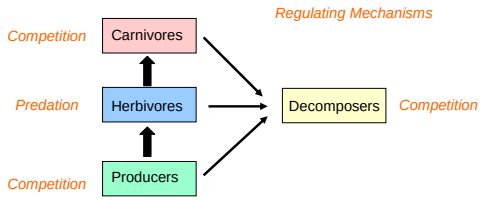
Why is the World Green?

This question was first dealt with in the literature by an elegant hypothesis proposed by Hairston, Smith, and Slobodkin (1960) and is often referred to today as the HSS hypothesis.

First, assume terrestrial ecosystems can be divided into 4 parts: producers, herbivores, carnivores, and detritivores (a simple food chain as it is).

What can we say about the relative importance of competition, predation, and disturbance in regulating these parts?

HSS Hypothesis



Detritivores: are thought to be food limited (dead carcasses rarely accumulate)
Producers (plants): all compete for light, water & nutrients
Herbviores: are surrounded by excess food (therefore not competition)
Carnivores: are at the top of the food chain and therefore not infl. by predation.

Terminology

Herbivory: the consumption of all or part of a plant.

Herbivore: the organism doing the consuming.

Frugivores: consume fruits (may or may not damage seeds)

Granivores: seed predators

Grazers: eat predominantly grasses & low lying veg

Browsers: eat leaves and twigs of woody plants

Herbivory

Herbivores are consumed by organisms from a variety of kingdoms: animals, fungi, bacteria, and even other plants.

Scale remains a major thread. Ecological effects occur obviously at the level of the individual, but there are often ramifications at the population, community, and ecosystem level.

Herbivory often acts as an important selection mechanism in plant populations. Thus, strongly affecting plant evolution (especially in mammalian grazing and insect systems).

Herbivory and Individuals

Herbivores can affect plants differentially. Because a seed is a zygote (and therefore an individual), granivores actually kill individual plants when they consume a seed.

Herbivores can also eat only parts of a plant (damaging, destroying, or removing those parts).

Herbivores can also live in or on a plant and consume some of the plant's resources.

Response to Herbivory

Plant typically respond to herbivory in one of two ways: Resistance or Tolerance.

Resistance to herbivory is the ability of a plant to avoid being eaten.

Tolerance of herbivory is the ability to minimize the impact to fitness.

We will deal with resistance when discussing plant chemistry later. Tolerance is often tested by "clipping experiments" where plant performance and fitness are measured as outcomes. The stage of a plant's life-history will tie closely to the results (e.g., seedling vs. mature plant).

Positive Effects of Herbivory?

McNaughton (1983) hypothesized that some plants might actually respond positively (i.e., growing back vegetatively more aggressively and producing more seed) by being grazed. Sounds counterintuitive and was quite controversial.

This process was termed **overcompensation** and was due to evolution in coevolved systems involving mammalian grazers and grasses. Buffalo saliva and urine was thought to result in overcompensation.

Herbivory & Plant Populations

The extent to which herbivores affect plant population dynamics is a highly controversial and unresolved question.

The "**Top-Down**" school of thought argues that herbivore populations are limited at low densities by their predators and rarely exert negaive influences on plant populations.

The "**Bottom-Up**" school of thought argues that plants are limited by a restricted common set of resources, not by herbivores.

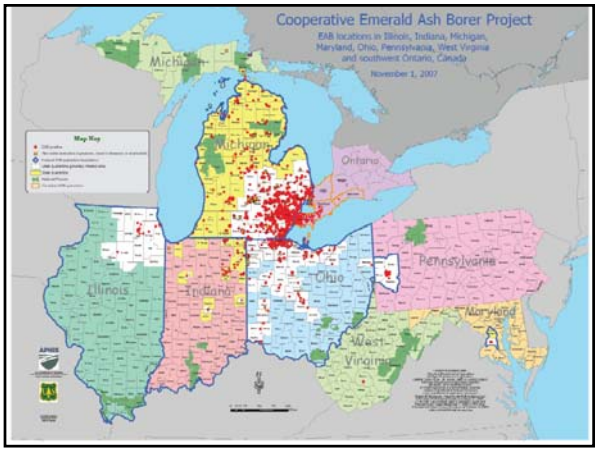
Which perspective is correct seems to be system dependent and requires more data before conclusions can be drawn.

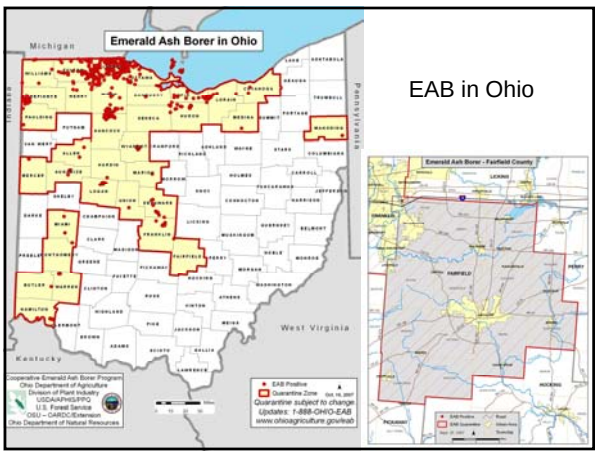
Herbivory & Plant Populations

The best examples of herbivores affecting plants at the population level involve insect herbivores and tree species: EAB, Gypsy Moth, Bark Beetles.

Let's consider the Emerald Ash Borer (*Agrilus planipennis*) in a bit more detail because of its immediate regional influence.

Symptoms of EAB Dieback (100% Fatal, all species of *Fraxinus)*


Cooperative Emerald Ash Borer Project
EAB locations in Illinois, Indiana, Michigan, Maryland, Ohio, Pennsylvania, West Virginia and southwest Ontario, Canada
November 1, 2007
Michigan
Ontario
Illinois
Indiana
Ohio
Pennsylvania
Maryland
West Virginia


Emerald Ash Borer in Ohio
Michigan
Pennsylvania
West Virginia
Kentucky
Emerald Ash Borer - Fairfield County

EAB in Ohio

Herbivory & Plant Populations

In all likelihood, EAB will remove *Fraxinus* spp. as a genus from the North American continent. Similar problems have occurred with Gypsy Moth and oak (East) and Scolytid bark beetles and pine (West), but neither have driven host to extinction.



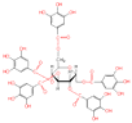
Granivory

Granivory can have important implications for plant populations. Studies of squirrel granivory on oaks (*Quercus* spp.) have provided some interesting insights.

Oaks in the sub-genus Erythrobalanus (red oak group) have acorns with a high tannin content.

Oaks in the sub-genus Lepidobalanus (white oak group) have acorns with a low tannin content.

Given the distastefulness of tannins, the obvious conclusion would be that gray squirrels (*Sciurus carolinensis*) would prefer acorns from the white oak group; thus, affecting plant population structure…

Granivory

However, the interaction is more complicated than this. Acorns of the red oak group remain dormant until spring; those from the white oak group germinate in autumn (and therefore less desirable to cache over winter).

Squirrels will eat white oak acorns when they find them, but, prefer to find and cache red oak acorns for winter food reserves.

(See Smallwood et al. 2001; Steele et al. 2001)

Biological Control

Biological control is the deliberate use of herbivores or pathogens [by humans] to control populations of undesirable plant species. They offer strong examples of how herbivores can alter plant populations.

An excellent recent example is the release of several specialist insects to control the invasive wetland species purple loosestrife (*Lythrum salicaria*).

Several species were released including a root-mining weevil (*Hylobius transversovittatus*) and two leaf-feeding chrysomelid beetles (*Galerucella calmariensis* and *G. pusilla*).

Biological Control

The obvious question here is whether or not this is a safe practice. Do the biocontrol species affect non-target plants? Do the [non-native] biocontrol species create yet a new ecological problem?

Usually this can be safeguarded against by extensive testing and finding species within the native range that are specialist feeders on only the non-native invasive plant species that you are wishing to control.

This being said, there are examples where this has gotten out of control and/or had other than anticipated effects.

Effects of Herbivory at the Community Level

The effects of grazing animals was already discussed in detail under the heading of diversity. Some of the classic studies included Tansley's chalklands and grazing by rabbits as well as grazing studies done throughout the eastern U.S. with cattle, bison, and deer.

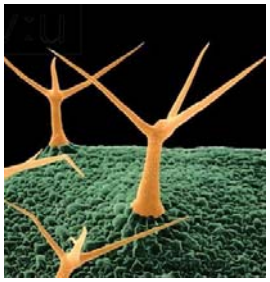
A recent meta-analysis study suggests that generalizations are difficult, but all available data suggests:

1) Herbivores have large effects on plant communities through differential grazing or browsing and significantly impact species richness, composition, and diversity.
2) Invertebrates (insects specifically) have a much greater effect on most plant communities than do large vertebrates.

Plant Defenses Against Herbivory

Because plants cannot move, they have to have to "sit there and take it" from herbivores. This immobility results in natural selection to be able to defend oneself. One may become less palatable either through increasing toughness or chemicals in the tissues.

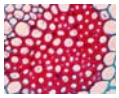
Single-celled plant hairs—trichomes—serve many functions; one of which is believed to be increased protection.

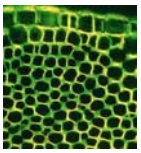


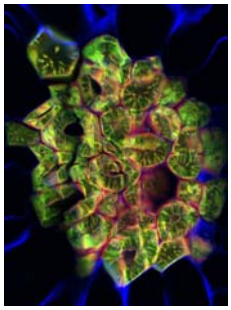
Plant Defenses Against Herbivory

Other physical defense includes tissues that make entry into the plant body more difficult.

This might include thick walled cell types, bark, seed coats, etc.







Plant Secondary Chemistry

Plant chemists differentiate between primary metabolites (e.g., sugars, amino acids, proteins, etc.) and secondary metabolites (e.g., tannins, alkaloids, flavanoids, etc.).

Primary metabolites are chemical compounds which are necessary for the basic functioning of the plant (i.e., respiration and photosynthesis).

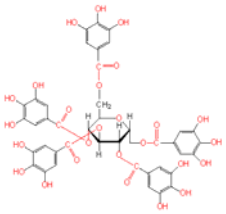
Secondary metabolites represent a broad spectrum of compounds that are often unique to a particular species and may be involved in attraction of pollinators, defense against herbivores, etc.

Plant Secondary Chemistry

The three major categories of defensive secondary chemicals are:

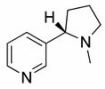
1) Phenolics
2) Alkaloids
3) Terpenes

Phenolics are chemicals consisting of an aromatic ring with an attached hydroxyl group (-OH). Probably the most important group here are the **tannins** which reduces tissue digestibility. **Lignins** are an important second group.



Plant Secondary Chemistry

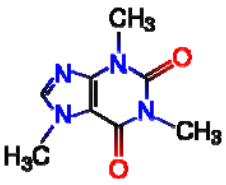
The **alkaloids** are another important group of compounds, many of which have pharmaceutical value. Most have a bitter taste and are toxic to animals. They are usually very species specific.



Nicotine

Nicotiana tabacum

And, Everybody's Favorite Alkaloid…



Plant Secondary Chemistry

Terpenes represent the last major group of secondary compounds. Terpenes are found in all plants, but differ from species to species and play a variety of functional roles in the plant. The latex found in plants of the Euphorbiaceae is poisonous and likely plays a defensive role.

Constitutive vs. Inducible Defenses

Constitutive Defenses: those that are present in a plant regardless of herbivore damage.

Induced Defenses: responses brought on by the plant in response to herbivory.

Both physical and chemical defenses can be induced, although research has largely focused on the chemical aspects. There has been a lot of research in this area in recent years.

It has been argued that chronic herbivory should select for constitutive defenses, whereas low or sporadic rates of herbivory should select for inducible defenses.

Baldwin (1988) provides a nice study of inducible defenses in wild tobacco.