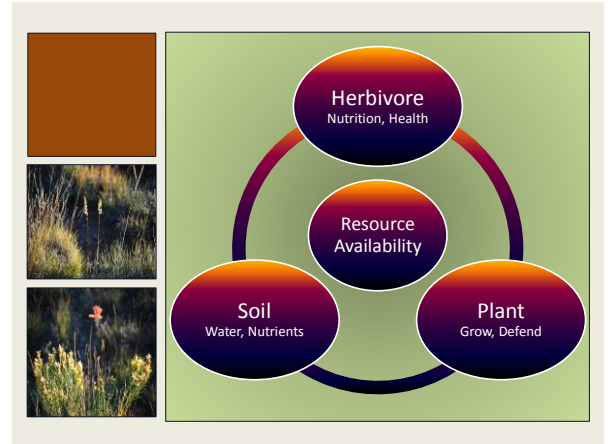


# Plant Behavior



How does resource availability (water, nutrients, sun) influence *evolutionary* responses of plants to herbivory?

**Resource-poor** areas select for low inherent growth rates and high levels of defense.

**Resource-rich** areas select for high inherent growth rates, re-growth, and low levels of defense.

**Resource Availability**  
(water, nutrients, and sunlight)

**Resource Poor**

- ✓ low inherent growth rates
- ✓ less able to grow/regrow
- ✓ higher levels of defense
- ✓ inflexible allocation

**Resource Rich**

- ✓ high inherent growth rates
- ✓ able to grow/regrow
- ✓ lower levels of defense
- ✓ flexible allocation

**Herbivores Influence Resource Availability**

Herbivore Impacts → Resource Availability → Plant Diversity and Chemistry

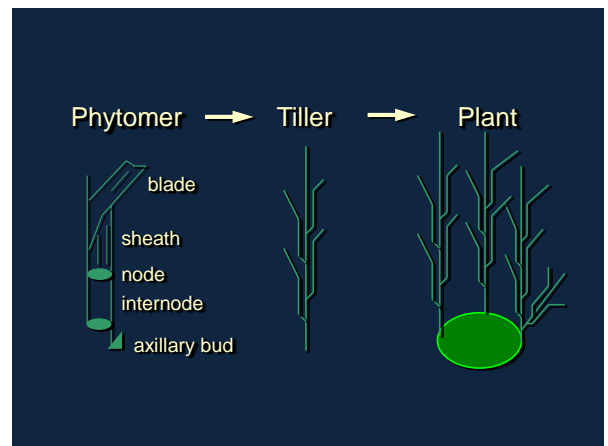
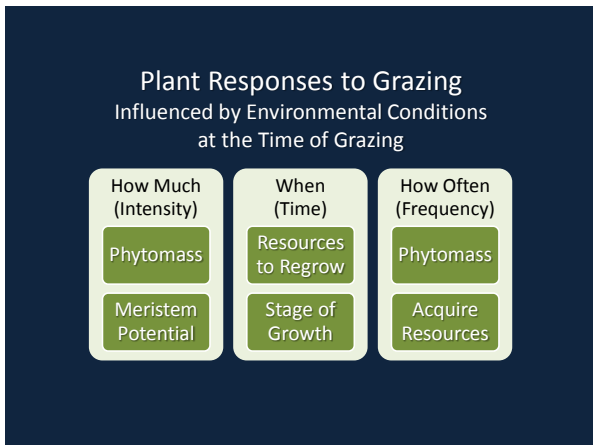
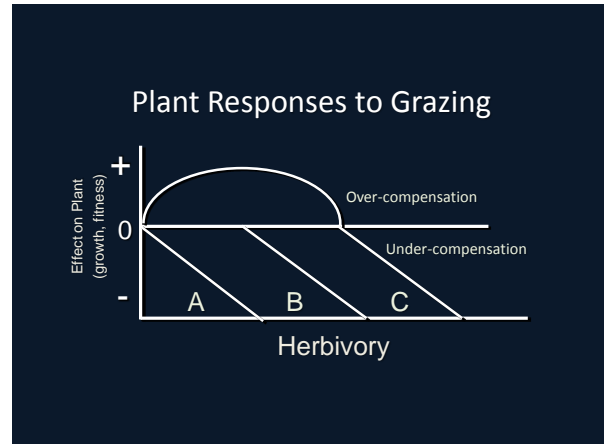
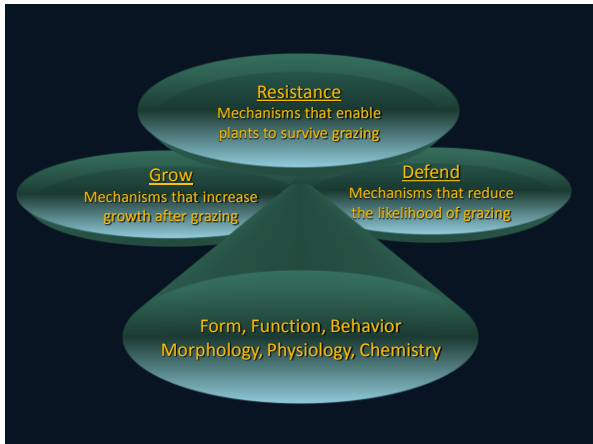
Grazing can either increase or decrease resource availability.

**Intensity Frequency**

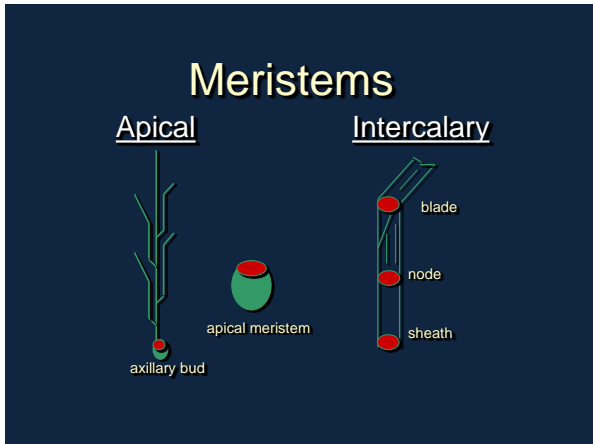
**Time Timing**

- ✓ Soil Organic Matter
- ✓ Soil Temperature
- ✓ Water Infiltration
- ✓ Plant Species Diversity
- ✓ Plant Chemistry

# Plant Behavior



# Plant Behavior



**Short-Shoot Plants**

Don't elongate internodes during vegetative growth.  
Tolerate grazing season-long grazing.

**Long-Shoot Plants**

Elongate internodes during vegetative growth.  
Tolerate grazing early or late in the growing season.

Dandelion  
Kentucky bluegrass

Blue grama

Bluebunch wheatgrass  
Arrowleaf balsamroot

Bluebells

Bitterbrush tolerates fire and grazing better than sagebrush...

Bitterbrush

Sagebrush

...due to the greater number and locations of meristems.

Physiological Characteristics

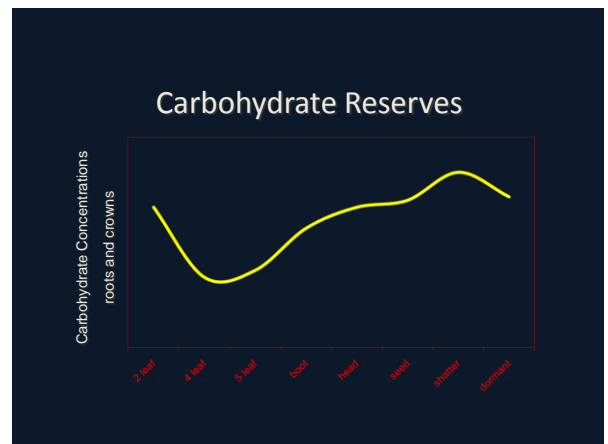
Carbohydrate Reserves  
Competitive Ability

Bluebunch wheatgrass and crested wheatgrass are similar in many characteristics,

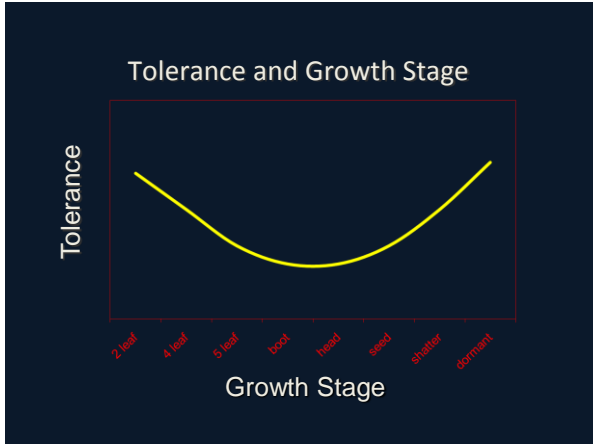
Bluebunch Wheatgrass

Crested Wheatgrass

...but crested wheatgrass tolerates grazing much better than does bluebunch, even though they have similar carbohydrate reserves. Why?



# Plant Behavior



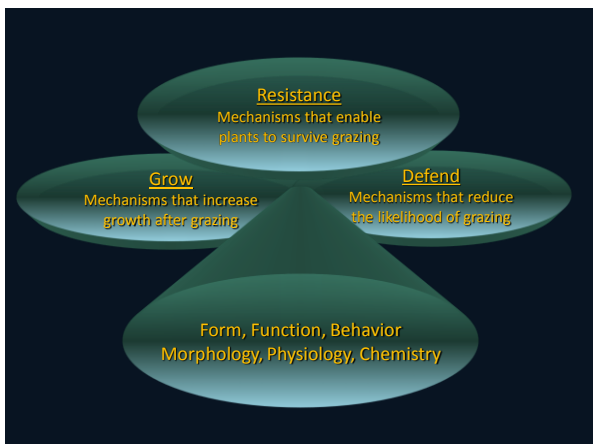
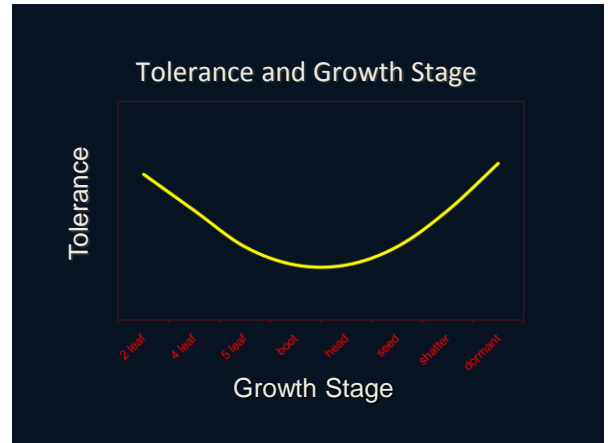
Crested wheatgrass competes better than bluebunch wheatgrass for resources.

Crested Wheatgrass-Sagebrush

Crested wheatgrass regrows much more quickly after grazing.

Bluebunch Wheatgrass-Sagebrush

When is grazing most detrimental to weeds?




### The First Biochemists

Plants produce thousands of organic compounds.


# Plant Behavior

**Primary Compounds**  
Energy, Protein, Minerals




Sagebrush - Terpenes

**Secondary Compounds**  
Phenolics, Terpenes, Alkaloids





Mountain Mahogany - Tannins

Plants produce thousands of primary and secondary compounds that vary in concentrations in time and space.



Phenolics > 8,000  
Terpenes > 25,000  
Alkaloids > 12,000

Primary Compounds in Spinach		Secondary Compounds in Oregano	
<b>Macronutrients</b>		<b>Terpenoids</b>	
Water	Fat (mainly linoleic)	alpha-pinene (0.1-0.2)	beta-pinene (0.1-0.2)
Carbohydrate	Carbohydrate	limonene (0.1-0.2)	gamma-terpinene (0.1-0.2)
Protein (mainly lysine)	Fiber	1,8-cineole (0.1-0.2)	linalyl acetate (0.1-0.2)
<b>Minerals</b>		<b>Phenolics</b>	
Calcium	Sodium	rosmarinic acid (0.1-0.2)	thymol (0.1-0.2)
Iron	Zinc	carvacrol (0.1-0.2)	thymol quinone (0.1-0.2)
Magnesium	Copper	thymol (0.1-0.2)	thymol quinone (0.1-0.2)
Phosphorus	Manganese	thymol (0.1-0.2)	thymol quinone (0.1-0.2)
Potassium	Selenium	<b>Alkaloids</b>	
<b>Vitamins</b>		nicotinic acid (0.1-0.2)	
C (Ascorbic Acid)	B-6 (Pyridoxine)	tryptophan (0.1-0.2)	
B-1 (Thiamin)	Folate	tryptophan (0.1-0.2)	
B-2 (Riboflavin)	A fat (carotenoids)	tryptophan (0.1-0.2)	
B-3 (Niacin)	E (tocopherol)	tryptophan (0.1-0.2)	
<b>Fatty Acids</b>		<b>Other</b>	
14:0 (Myristic acid)	18:1 (Oleic acid)	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
16:0 (Palmitic acid)	20:1 (Eicosenic acid)	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
18:0 (Stearic acid)	18:2 (Linoleic acid)	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
18:1 (Oleic acid)	18:3 (Linolenic acid)	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
<b>Amino acids</b>		<b>Other</b>	
tryptophan	valine	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
threonine	arginine	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
isoleucine	phenylalanine	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
leucine	alanine	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
methionine	aspartic acid	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
cysteine	glutamic acid	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
threonine	proline	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
lysine	serine	isochlorogenic acid (0.1-0.2)	isochlorogenic acid (0.1-0.2)
<b>Phytosterols (mainly beta-sitosterol)</b>		<b>Other</b>	
beta-sitosterol (0.1-0.2)		isochlorogenic acid (0.1-0.2)	

Primary Roles for Secondary Compounds



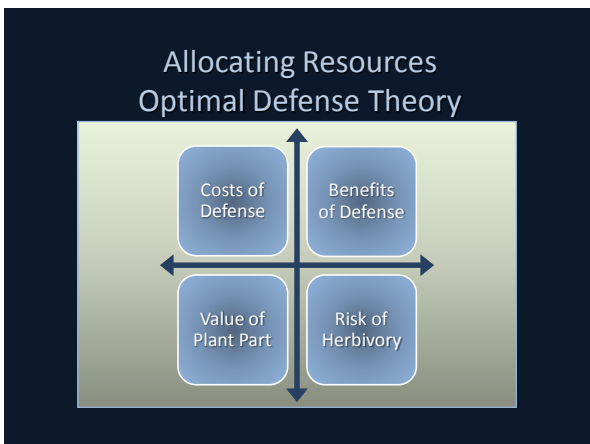
Sun Screen  
Antioxidants  
Adaptive Coloration  
Attract Pollinators  
Fruit Eaters



Allelopathy  
Drought Resistance  
Persistence



Recovery Injury  
Regrowth Grazing  
Defense Grazing



Defenses are costly.  
The cost of defense is due to  
diversion of energy and nutrients  
from other needs.

# Plant Behavior

## Costs of Defense

Synthesis  
raw materials, biosynthetic machinery


Storage  
storage sites, enzymes to degrade secondary compounds

Transport  
extra and intracellular movement

Maintenance  
volatilization, leaching, exudation

Commitment to defense is a positive function of the energy and nutrient budget of a plant and is negatively related to growth and reproduction.

Wild tobacco allocates fewer resources to growth and reproduction when it is allocating resources to defense.



Commitment to defense is decreased when enemies are absent and increased when plants are subjected to attack.

Induced defenses are produced when plants are attacked

Physical



Chemical



Less well defended individuals have higher fitness than more highly defended individuals when herbivores are absent.

# Plant Behavior

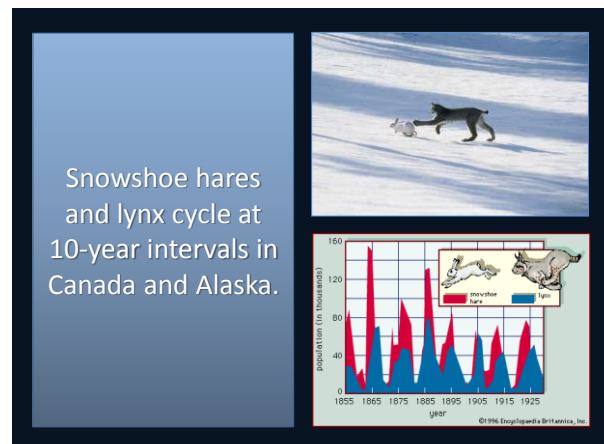
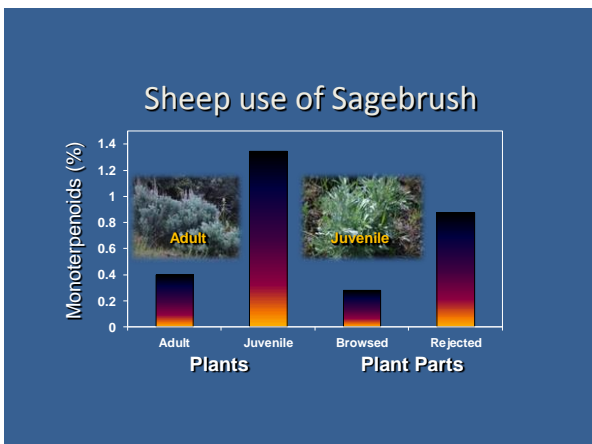
Within species, individuals with low levels of defense outcompete those with high levels of defense in the absence of herbivores.

More valuable plants and plant parts (young vs. mature) are more highly defended than less valuable plants and plant parts.

Young plants and plant parts are more highly defended than older plants and plant parts.

Heavy browsing by goats during winter stimulates production of new twigs that are much higher in tannins.

Juvenile vs. Mature Growth Stages Woody of Plants



# Plant Behavior



Fire → Alaska Paper Birch → Hares → Highly Defended (papyriferic acid) Juvenile Growth Stage in Birch → Hares Crash

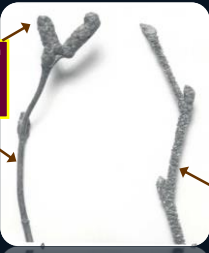
Snowshoe hares prefer mature over juvenile twigs from birch



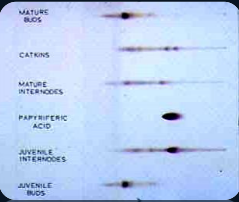
### Winter Dormant Twigs of Alaska Paper Birch (*Betula neolaskana*)

Mature Stage

Juvenile Stage



Note Catkin And The Lack Of Resin Glands




MATURE BUDS  
CATKINS  
MATURE INTERNODES  
PAPYRIFERIC ACID  
JUVENILE INTERNODES  
JUVENILE BUDS

Note Resin Glands




How does the environment where a plant is growing affect concentrations of secondary compounds in real time?



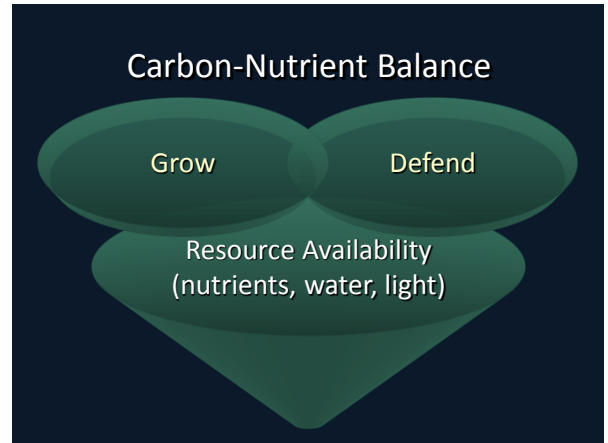
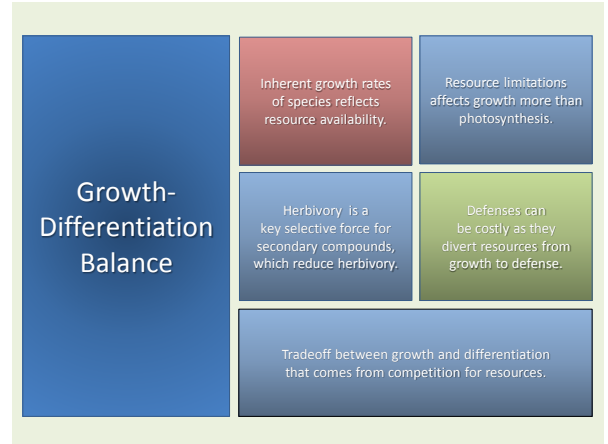
Sunlight, moisture, nutrients, herbivory, other plants...

Under some conditions, some willow genotypes are twice as resistant to insect herbivores as other genotypes. But when fertilizer is added, the formerly resistant genotypes become nearly three times more susceptible.





# Plant Behavior



Carbon-Nutrient Balance  
Carbon-based compounds  
(phenolics, terpenes)

As example of a tannin

Hopginsin      Carotenoid (in Carotenium 1)

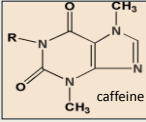
Flavonoid (in plant roots)      Menthol (in mint)

Phenolics in grasses, forbs, and shrubs are higher in plants growing on dry sites than on wet sites and in dry year than in wet years.

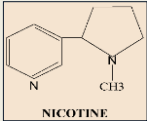
Phenolics in grasses (many species), forbs (Sericea, birdsfoot trefoil), and shrubs are higher in plants growing on infertile sites than on fertile sites.

# Plant Behavior

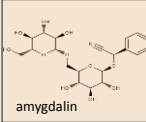
**Carbon-Nutrient Balance**  
**Nitrogen-based compounds**  
 (alkaloids, cyanogenic glycosides)






caffeine



NICOTINE



amygdalin






Alkaloids in lupine, tobacco, fescue and cyanogenic glycosides in sudangrass, sorghum and cassava are higher in plants fertilized with nitrogen than in nitrogen-limited plants.








Alkaloids in lupine, larkspur, hemlock and cyanogenic glycosides in white clover and serviceberry are higher in plants growing on dry sites than on wet sites and in dry year than in wet years.

Plant mixtures can influence concentrations of secondary compounds

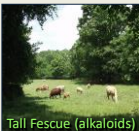


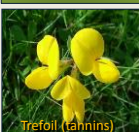

Tall Fescue (alkaloids)

Fescue-Alfalfa increases alkaloids in fescue


Alfalfa (saponins)

Trefoil (tannins)

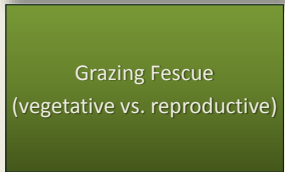
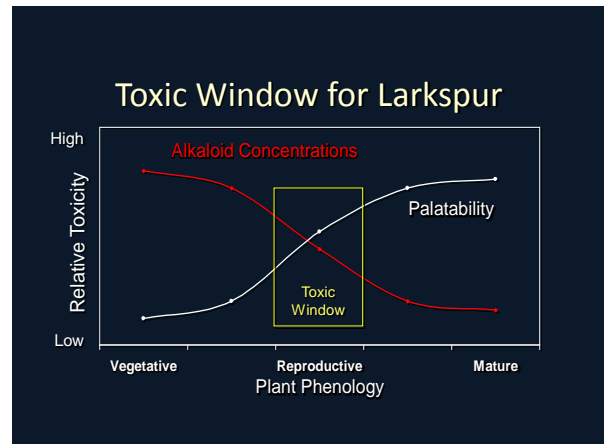
Trefoil-Alfalfa decreases tannins in trefoil

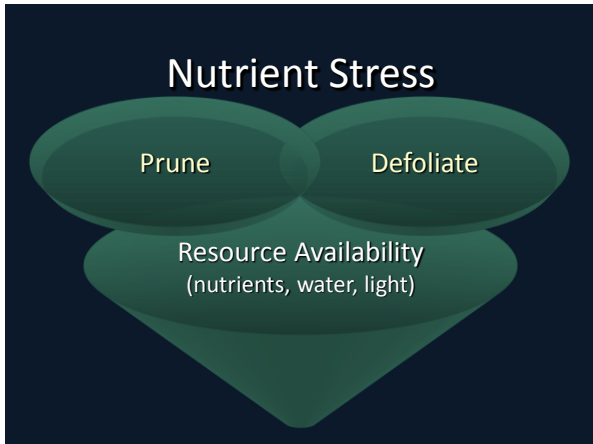
**Endophyte-Infected Tall Fescue**  
 Fertilize: spring/fall



Grazing Fescue  
 (vegetative vs. reproductive)

# Plant Behavior



By removing leaves, *defoliation* can increase nutrient stress

By removing twigs, pruning can decrease nutrient stress

This slide features a dark blue background. On the left, text reads 'By removing leaves, *defoliation* can increase nutrient stress'. To the right is a photograph of a moose eating green leaves. Below this, on the left, is another photograph of a moose eating twigs. To the right of this second photo, text reads 'By removing twigs, pruning can decrease nutrient stress'.

Topping tobacco increases concentrations of alkaloids (nicotine) in leaves.

A photograph shows a person wearing a green hat and a light-colored shirt, working in a field of large green tobacco plants. The person appears to be tending to the plants, possibly performing a topping operation.



The First Biochemists

Plants produce thousands of organic compounds.

A photograph of a single purple flower with yellow centers, growing from a bed of dry, brownish ground cover.

Plants produce thousands of organic compounds.

A goal for the future would be to determine the extent of knowledge the cell has of itself and how it uses that knowledge in a thoughtful manner when challenged.  
Barbara McClintock

The slide features a dark blue background. On the left is the cover of the book 'Plant Behaviour & Intelligence' by Anthony Trewavas, showing a close-up of a plant's root system. To the right of the book cover is a light green rectangular box containing the text: 'A goal for the future would be to determine the extent of knowledge the cell has of itself and how it uses that knowledge in a thoughtful manner when challenged. Barbara McClintock'. Below the book cover, the text 'Plants produce thousands of organic compounds.' is written in white.

# Plant Behavior



Plants communicate via chemical signals.

Plants can 'smell' volatile compounds in the air and they can 'taste' compounds on their bodies.

Plants respond to tactile cues: vines and roots know when they encounter various objects including, for instance, their own shoots and roots or those of other plants.

Plants 'see' different wavelengths of light; they 'breathe' through stomata on the surface of leaves and stems.

Cells and the plants they make up have knowledge of themselves.

Cells receive environmental challenges that lead to changes in form, function, and behavior of cells and plants.

Learning and memory are vital as cells and organ systems interact with one another and the plants they create to address environmental challenges and solve problem.

Plants behave in ways that imply assessment and intelligent behavior.

The game plans of organisms in nature are complex, honed by playing offence and defense with friends and foes alike for eons.



People have been playing these games for decades and the simple game plans we've devised enable our 'foes' to easily resist our attempts to thwart them.



Primary Roles for Secondary Compounds

- Sun Screen, Antioxidants, Adaptive Coloration, Attract Pollinators, Fruit Eaters
- Allelopathy, Drought Resistance, Persistence
- Recovery Injury, Regrowth, Grazing, Defense, Grazing





While some were learning of the values of secondary compounds, others were reducing their concentrations...

- ...increase yields of crops and forages
- ...maximize energy/protein as opposed to total phytochemical richness
- ...make plants more susceptible to environmental hardships





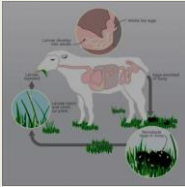
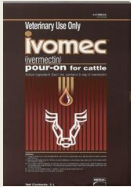


# Plant Behavior





In their stead, we've come to rely on fertilizers, herbicides, and pesticides to grow and protect plants in monocultures.

Fertilizers to Enhance Growth	
	Herbicides to Control Weeds
Pesticides to Control Herbivores	




We've come to rely on antibiotics and anthelmintics to treat diseases and parasites.

People are trying to genetically engineer back into plants resistance they had originally.

	
Plants and herbivores have been playing these games for millions of years	
	Pharm-Ecology Pharmacological Aspects of Ecology

Concerns with Genetically Modified Crops

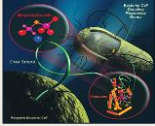
Pesticide-resistant Insects	
	Herbicide-resistant weeds
Pesticide Herbicide Residues	

Research by Séralini and Colleagues on Glyphosate

Two-year study showed deficiencies in liver and kidney function, more severe in males, and female mammary tumors (3.25-times more than controls), which led to premature deaths. This was associated with a 2.4-times increase in pituitary dysfunctions.

In 2014, Elsevier, the publisher of *Food and Chemical Toxicology*, retracted their paper

We've isolated and purified compounds to amplify their effects, but that has simply made resistance easier for bacteria, insects, plants.

Antibiotic resistant bacteria	
	Pesticide resistant insects
Herbicide resistant plants	

# Plant Behavior

## Pesticide-Resistant Insects

Bollworm resistance to first-generation Bt cotton has been confirmed in India, Australia, China, Spain, and the U.S. Monsanto responded by introducing a second-generation cotton with multiple Bt proteins.

## Herbicide-Resistant Weeds

The number and extent of weed species resistant to glyphosate has increased quickly since 1996, with 21 species now confirmed globally (Heap, 2011). There are now 245 species of herbicide-resistant weeds globally (449 unique cases: species x site of action). Weeds have evolved resistance to 22 of the 25 known herbicide sites of action and to 156 different herbicides. Herbicide resistant weeds have been reported in 86 crops in 66 countries.

## Herbicide-Pesticide Residues

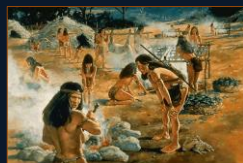
*The Lancet Oncology*, the foremost scientific journal for cancer studies, recently published a review paper by the World Health Organization's International Agency for Research on Cancer (IARC) that has classified glyphosate (the active ingredient in Roundup) as a 'probable carcinogenic,' reviewing studies that show glyphosate causes a range of cancers...



...including non-Hodgkin's lymphoma, renal cancer, skin cancer, and pancreatic cancer.

Category	Item	Residue (ppm)	Limit (ppm)	Compliance (%)
Vegetables	Asparagus	0.01	0.05	100
	Broccoli	0.01	0.05	100
	Brussels sprouts	0.01	0.05	100
	Cauliflower	0.01	0.05	100
	Corn	0.01	0.05	100
	Cucumber	0.01	0.05	100
	Kale	0.01	0.05	100
	Kidney beans	0.01	0.05	100
	Spinach	0.01	0.05	100
	Tomato	0.01	0.05	100
Fruits	Apple	0.01	0.05	100
	Banana	0.01	0.05	100
	Blueberries	0.01	0.05	100
	Cherry	0.01	0.05	100
	Citrus	0.01	0.05	100
	Dragonfruit	0.01	0.05	100
	Grape	0.01	0.05	100
	Pineapple	0.01	0.05	100
	Raspberries	0.01	0.05	100
	Strawberry	0.01	0.05	100

Historically, people used cultural practices like washing and cooking to reduce concentrations of secondary compounds in plants. That had multiple ecological benefits.



Plants resistant to environmental hardships, which contributed to our health, and that of the animals in our care.

'Primitive' Foodscapes (flavor/phytochemical richness trump yield) morphed into 'Modern' Foodscapes (yield trumps flavor/phytochemical richness)



# Plant Behavior

Of the roughly 400,000 species of wild plants on earth...

...only a few thousand are eaten by humans,

just a few hundred of these have been domesticated

and just a dozen account for over 80% of the current annual production of all crops

That constrained crop production to a few plants, relatively productive in a range of environments, rather than broaden diversity to include a wide array of plants valuable in local environments.

As we've moved from complexity to simplicity, we've increasingly been confronted with diseases that thrive on phytochemical simplicity.

Antibiotic Resistance in Bacteria and Parasites

Herbicide Resistance in Plants

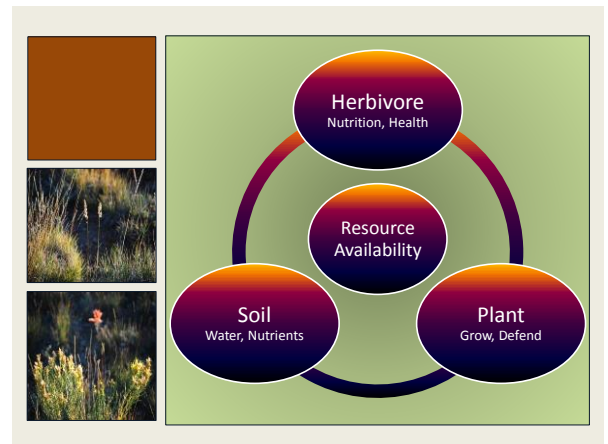
Obesity, Heart Disease and Cancer in People

Phytochemically rich combinations of foods -- not compounds or individual foods -- are etiologic in health.

Individual Compounds

Individual Foods

Combinations of Foods


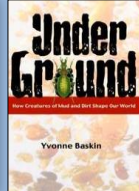


# Plant Behavior

We're all connected...

Resource Availability ↔ Soil Health ↔ Plant Diversity and Chemistry

Health and well-being of people is linked to the health of soil.

We're all connected...

Plant Diversity and Chemistry → Biochemical Richness Diet → Quality Milk, Cheese, Meat





We're all connected...

Soil, Plants → Herbivores → Humans





We're all connected...

Animal Impacts ↔ Plant Diversity and Chemistry ↔ Carbon Sequestration

