

Chapter 20

SUCCESSION AND STABILITY

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Chapter Concepts

- Community changes during succession include increases in species diversity and changes in species composition
- Ecosystem changes during succession include increases in biomass, primary production, respiration, and nutrient retention
- Mechanisms that drive ecological succession include facilitation, tolerance, and inhibition
- Community stability may be due to lack of disturbance or community resistance

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Definitions

- Succession – Gradual change in plant and animal communities in an area following disturbance
 - ✓ Primary – Succession on newly exposed geological substrates
 - ✓ Secondary – Succession following disturbance that does not destroy soil
- Climax Community – Late successional community - remains stable until disrupted by disturbance

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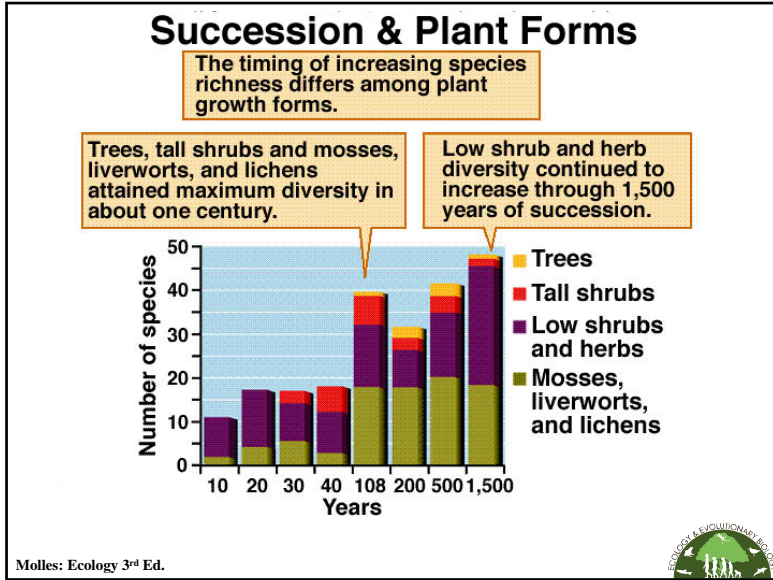
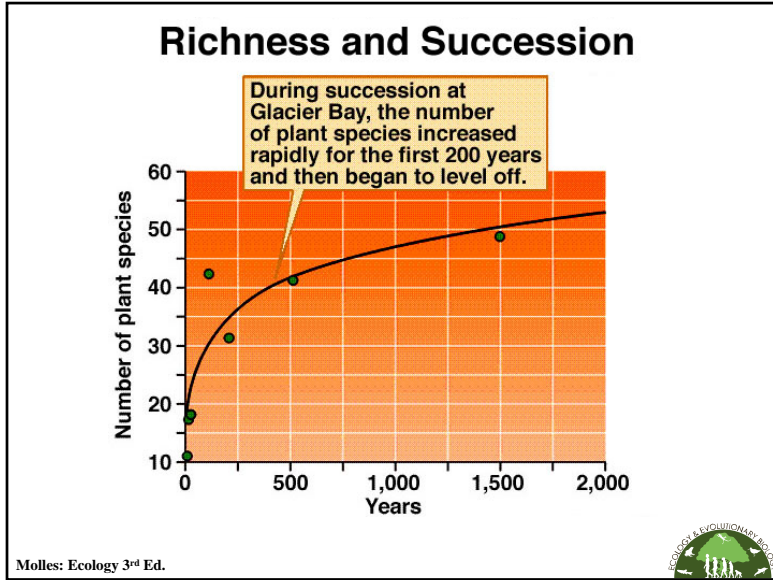


Primary Succession – Glacier Bay, Alaska

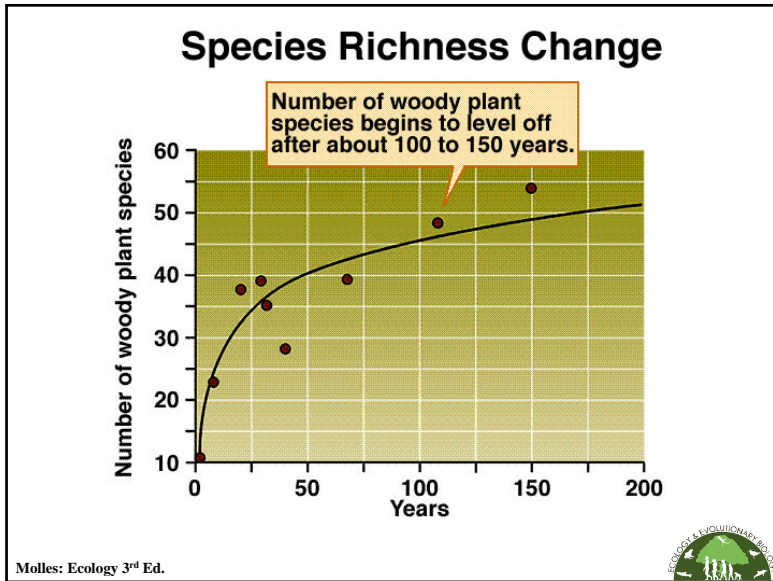
- *Reiners et al.* (1971) studied changes in plant diversity during succession
 - ✓ Total number of plant species (species richness) increased with plot age
 - ✓ Species richness increased rapidly in early years of succession and more slowly during later stages
 - Not all groups increased in density throughout succession (different composition)

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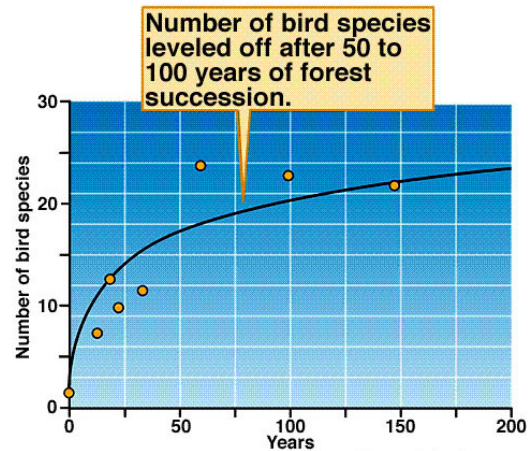




- ### Secondary Succession in Temperate Forests
- *Oosting* (1942) found number of woody plant species increased during secondary succession at Piedmont Plateau
 - *Johnston and Odum* found increase in bird diversity across successional sequence closely paralleled increase in woody plant diversity observed by Oosting
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Succession & Species Number



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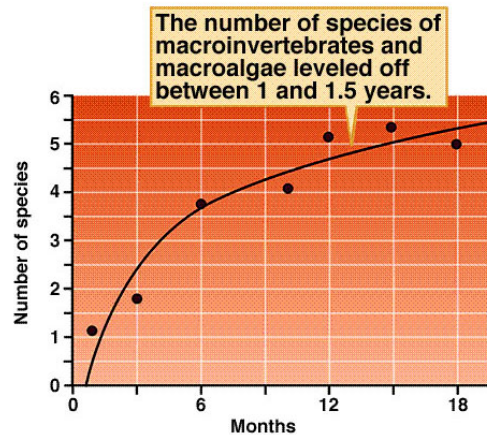
Succession in Rocky Intertidal Communities

- Easy manipulation
- The first species – green alga (*Ulva*) and the barnacle
- The next – perennial red algae
- Finally - perennial red algae (*Gigartina canaliculata*) dominated
- 1.5 years as compared to 1500 yrs in Glacier Bay and 150 yrs in Piedmont Plateau

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Succession in Species Number



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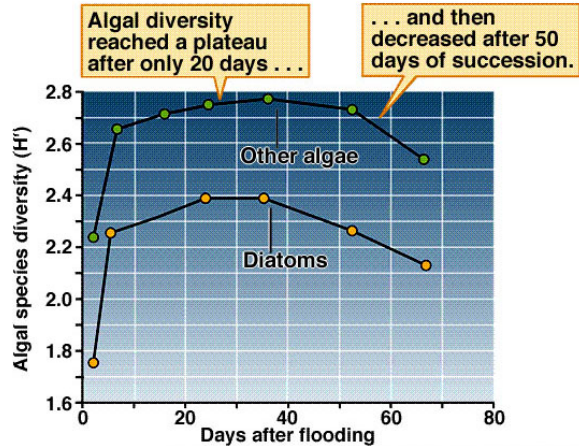
Succession in Stream Communities

- *Fisher et al.* (1982) studied rapid succession in Sycamore Creek, AZ
 - ✓ Evaporation nearly equals precipitation – flows generally low and intermittent
 - Subject to flash floods (disturbance)
 - ✓ Observed rapid changes in diversity and composition of algae and invertebrates
 - Invertebrates found refuge because many adults in aerial stage
 - Re-colonized after flooding

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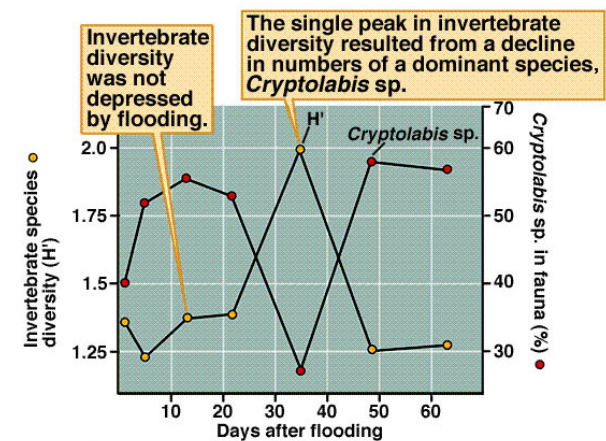
Succession & Species Diversity



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Succession & Invertebrates



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Ecosystem Changes During Succession

- Ecosystem changes during succession include increases in biomass, primary production, respiration, and nutrient retention

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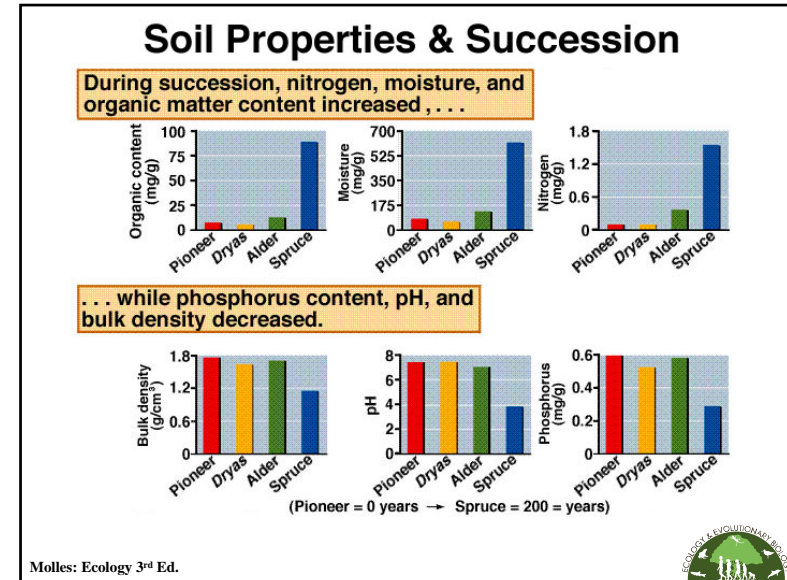
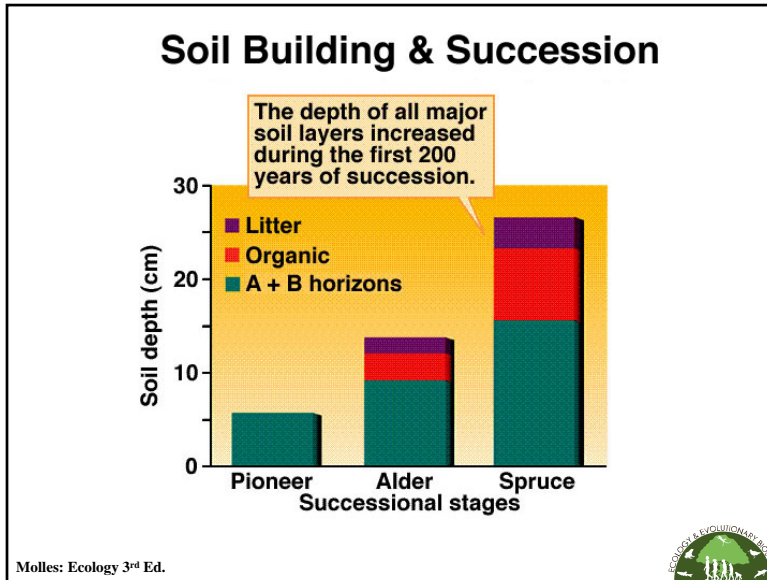


Ecosystem Changes at Glacial Bay

- *Chapin (1994)*, Glacier Bay
 - ✓ Total soil depth and depth of all major soil horizons show significant increase from pioneer community
 - ✓ Soil properties (influencing the kinds of organisms that can grow) also changed during succession, i.e.,
 - Organic content, moisture, and N concentrations all increased
 - Physical and biological systems inseparable

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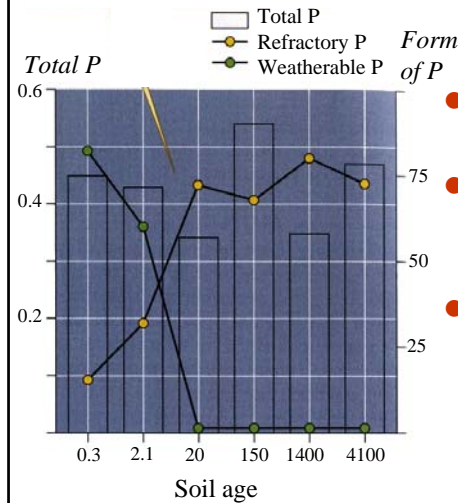
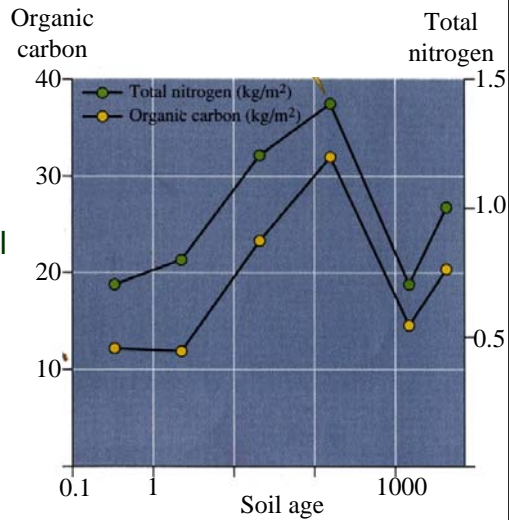




- ### Four million years of changes
- Studies at Glacial Bay
 - Chronosequence – the sequence of ages represented by the study sites
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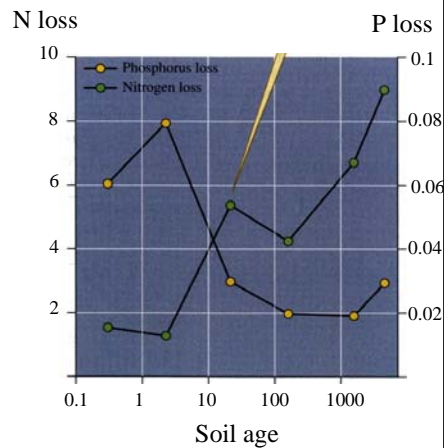
- Hedin et al. (2003) – Hawaii islands, chronosequence of forest ecosystem
 - ✓ Different islands have different historic development (300 to 4,100,000 yrs) in their rocks due to volcanic lava flows
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- Organic matter increased in soils over the first 150,000 years
- Analogous increases in soil organic matter
- Also, the changes in soil N content followed precisely



- Change pattern in P content in soils was different
- No obvious pattern was found
- But, the form of P changed substantially
- Become a limiting factor on primary production when the content is low in older soils

- There are changes in rates of nutrient loss across the chronosequence
- Higher rate of N loss
- Decreased rates of P loss
- Most of the losses are due to leaching to groundwater



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Recovery of nutrient retention after disturbance

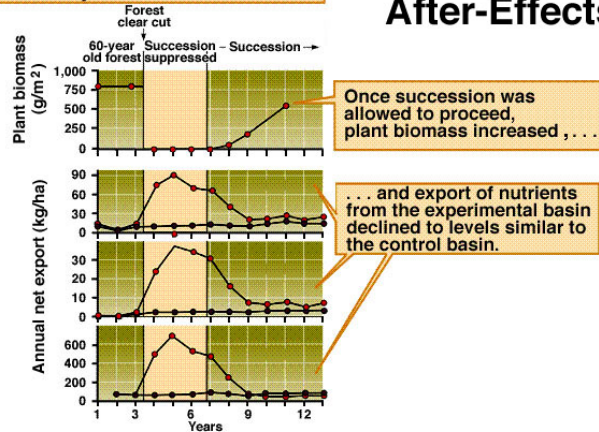
- *Bormann and Likens (1981)* in the Hubbard Brook Experimental Forest
- Cut forest and suppress vegetation growth by herbicides
- High nutrient losses during the suppressed period
- When the herbicide applications were stopped, succession proceeded and nutrient losses decreased dramatically

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The Hubbard Brook deforestation experiment showed that succession can reduce losses of plant nutrients caused by

Deforestation After-Effects



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Model of Ecosystem Recovery

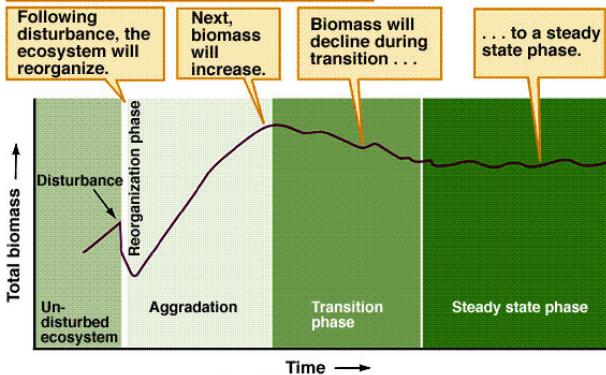
- Bormann and Likens proposed the biomass accumulation model
- Four phases
 - ✓ Reorganization (10-20 yrs)
 - Forest loses biomass and nutrients
 - ✓ Aggradation (100+ yrs)
 - Ecosystem reaches peak biomass
 - ✓ Transition
 - Biomass declines from peak
 - ✓ Steady-State
 - Biomass fluctuates around mean

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Succession & Biomass

According to the biomass accumulation model, disturbing a forest ecosystem will induce a series of distinct recovery phases.



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Succession and stream ecosystem properties

- Sycamore Creek, Arizona
- Succession happened within in 63 days after flooding
- Show similar pattern as proposed by the biomass accumulation model

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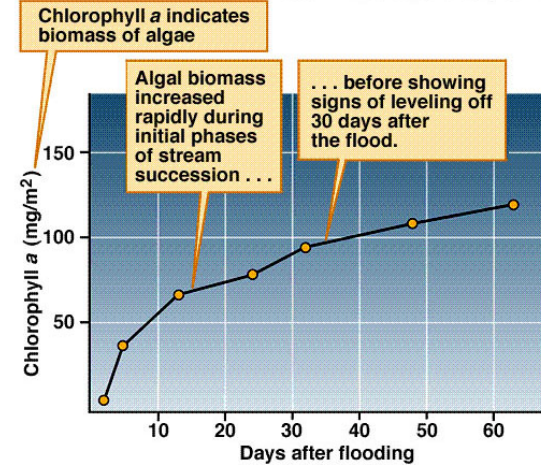
Succession and stream ecosystem properties

- Algal biomass increased rapidly for the first 13 days and then decreased more slowly afterwards
- Ecosystem metabolic parameters (e.g., photosynthetic rate) show leveling off
- The level of retention increased rapidly during succession, then leveling off to eventually 0 (balance state, input = output)

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Biomass & Stream Succession



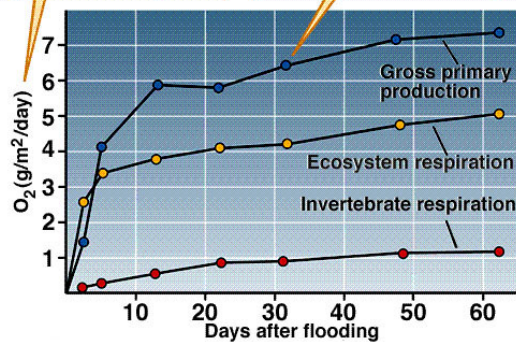
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Succession Processes

Photosynthetic rate measured by oxygen production, respiration by oxygen consumption.

Both primary production and respiration began to level off in less than a month after flooding.



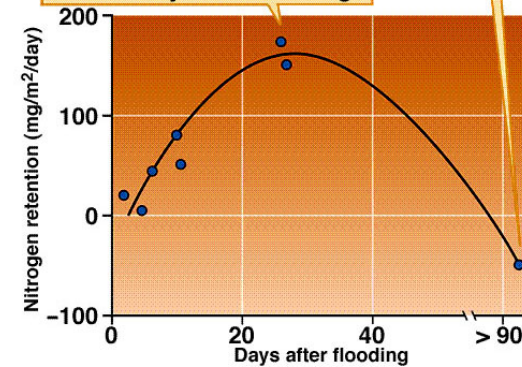
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Stream Nitrogen Retention

Nitrogen retention by the Sycamore Creek ecosystem reached a maximum in less than 30 days after flooding.

By 90 days after the flood nitrogen retention decreased.



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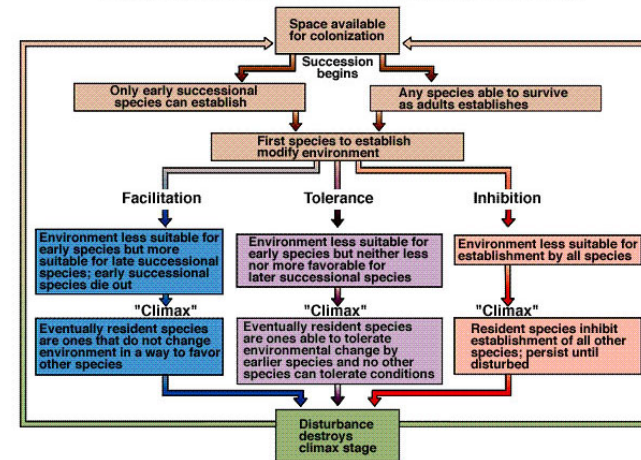
Mechanisms of Succession

- *Clements (1916):*
 - ✓ Facilitation
- *Connell and Slayter (1977):*
 - ✓ Facilitation
 - ✓ Tolerance
 - ✓ Inhibition
- Most of the current evidences support the facilitation model, the inhibition model, or some combination

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Successional Mechanisms



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Facilitation

- Proposes many species may attempt to colonize newly available space
 - ✓ Only certain species will establish
 - Colonizers – “Pioneer Species” – modify environment so it becomes less suitable for themselves and more suitable for species of later successional stages

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Tolerance

- Initial Stages of colonization not limited to Pioneer Species
 - ✓ Early successional species do not facilitate later successional species

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Inhibition

- Early occupants of an area modify env. in a way that makes it less suitable for both early and late successional species
 - ✓ Early arrivals inhibit colonization by later arrivals
 - ✓ Assures late successional species dominate an area because they live a long time and resist damage by physical and biological factors

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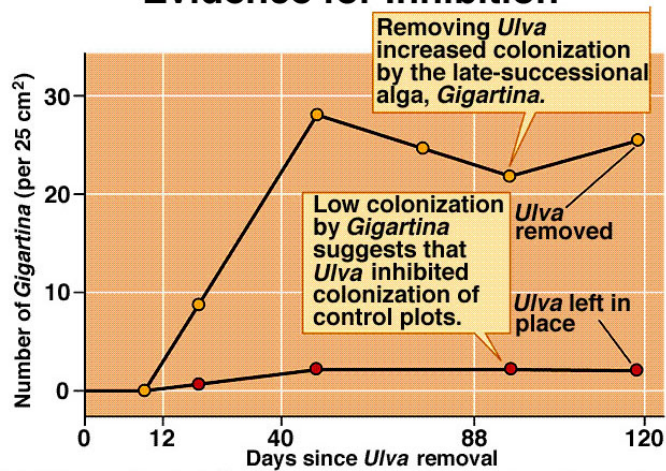
Successional Mechanisms in Rocky Intertidal Zone

- *Sousa* investigated mechanism behind succession of algae and barnacles in intertidal boulder fields.
 - ✓ If inhibition model is in effect, early successional species should be more vulnerable to mortality
 - Results showed early successional species had lowest survivorship and were more vulnerable to herbivores

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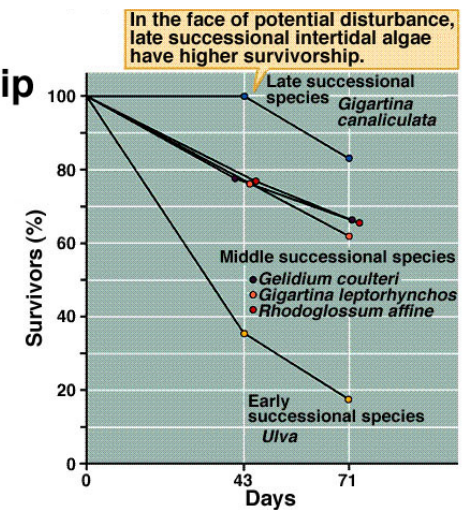
Evidence for Inhibition



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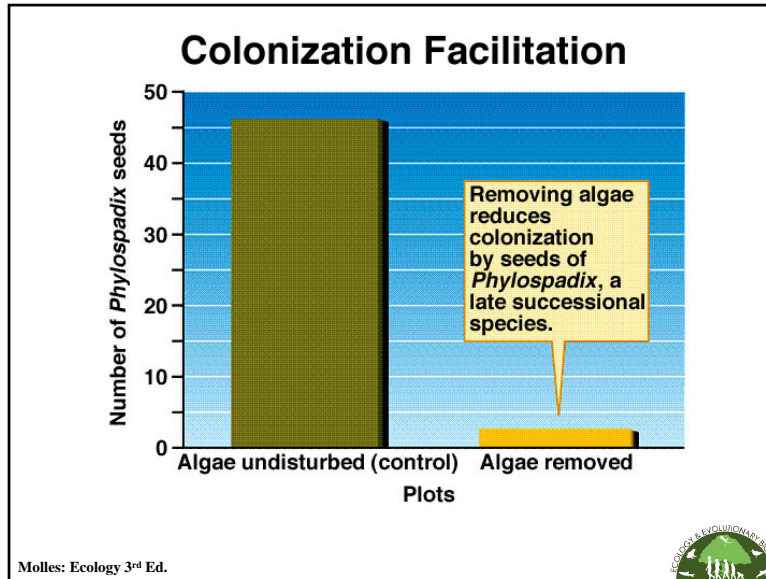


Species Survivorship



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- ### Successional Mechanisms in Forests
- Hundreds of years
 - Old field succession
 - Primary succession on a volcanic substrate
 - Primary succession following deglaciation
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- ### Mechanisms in Old Field Succession
- Keever (1950), Piedmont Plateau
 - What was the causes of early species replacements?
 - Results support the inhibition model and the facilitation model
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- ### Mechanisms in Primary Succession on a Volcanic Substrate
- 1980 - Mt St. Helens, Washington erupted
 - ✓ Disturbance set stage for succession
 - Avalanche debris, hot volcanic ash and pumice killed all plant life
 - *Morris and Wood* studied influences of facilitation, tolerance, and inhibition on early succession on pumice plains
 - ✓ Found complex blend of influences
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Mount St. Helens



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Three pioneering species

- Pearly everlasting (*Anaphalis margaritacea*)
 - Fireweed (*Epilobium angustifolium*)
 - Perennial Lupine (*Lupinus lepidus*) – a N-fixer
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- The first two species disperse by wind and rapidly colonize
 - The third species does not disperse easily

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Pearly everlasting (*Anaphalis margaritacea*)



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Fireweed (*Epilobium angustifolium*)



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Perennial Lupine (*Lupinus lepidus*)



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Experiment results

- Consistent with the inhibition and facilitation models
- Seedling survival during the first growing season was highest on the barren control plot (inhibition)
- But, during the second growing season, the pattern reversed, the survival seedlings was lowest (facilitation)

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Lupine & Colonization

During the early phases of succession, lupine both inhibited and facilitated colonizing plant species.

Lupine

Inhibition
Reduced seedling survival

Facilitation
Increased seedling growth
Increased flower production

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Mechanism of primary succession

- Glacial Bay
- Field observations, field experiments, and greenhouse experiments
- *Chapin* (1994) found no single factor or mechanism determines the pattern of primary succession – complex influences

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Spruce & Succession

Pioneer		Dryas		Alder		Spruce	
Inhibition	Facilitation	Inhibition	Facilitation	Inhibition	Facilitation	Inhibition	Facilitation
Lower germination	Higher survival	Lower germination	Higher nitrogen	Lower germination	Higher survival	Lower growth	Higher germination
		Lower survival	Higher growth	Lower survival	Higher nitrogen	Lower survival	
		Higher seed mortality		Higher seed mortality	More mycorrhizae	Higher seed mortality	
				Root competition	Higher growth	Lower nitrogen	
				Light competition		Root competition	
						Light competition	

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Community and Ecosystem Stability

- Community stability may be due to lack of disturbance or community resistance
- Stability – Absence of change
- Resistance – Ability to maintain structure and function in face of potential disturbance
- Resilience – Ability to recover from disturbance

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- Succession restores a community disrupted by disturbance
- Succession is the basis of resilience
- Take long time to study

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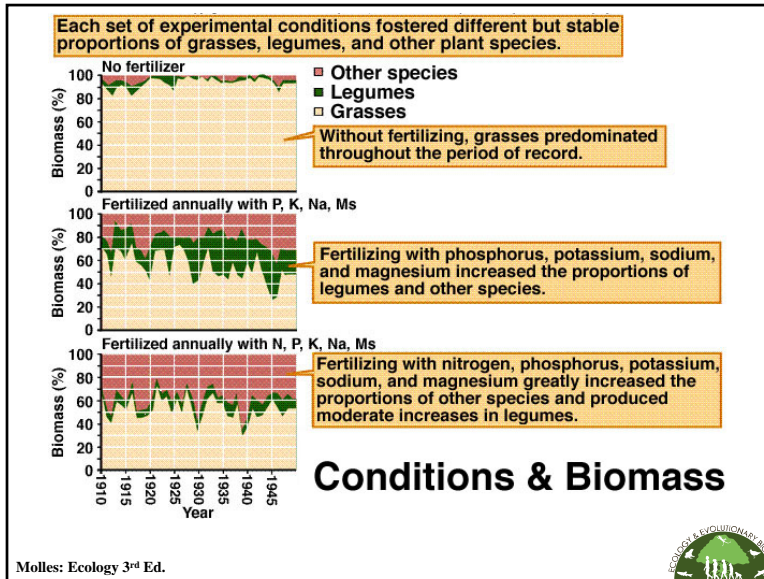


Park Grass Experiment

- Hertfordshire, England
 - ✓ Studied effects of fertilizer treatments
 - Continued for almost 150 years
- *Silvertown* (1987) investigated ecosystem stability
 - ✓ Used community composition variability as measure of stability
 - ✓ Represented composition as proportion of community consisting of each plant form

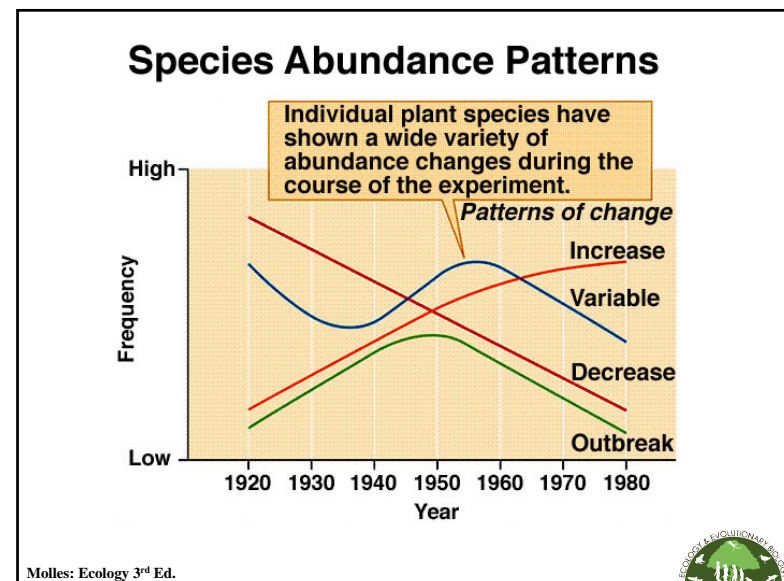
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- The proportions of grasses, legumes, and other species remained fairly constant
 - Mainly affected by precipitation
 - However, population of individual species changed substantially
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- ### Community and Ecosystem Stability
- *Dodd et al. (1995)* showed although community stability is present, populations of individual species can change substantially
 - ✓ Stability depends on spatial resolution an area is investigated at
 - ✓ Landscape, form, and species levels
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Replicate Disturbances and Desert Stream Stability

- Sycamore Creek, Arizona
- *Valett et al.* (1994) tested the hypothesis that ecosystem resilience is higher where hydrologic linkages between the surface and subsurface water increase the supply of N – a nutrient limiting the primary production

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- *Valett* studied interaction between surface and subsurface waters
 - ✓ Flash floods devastated biotic community
 - Spatial relationships of zones stable
 - Geomorphology of landscape

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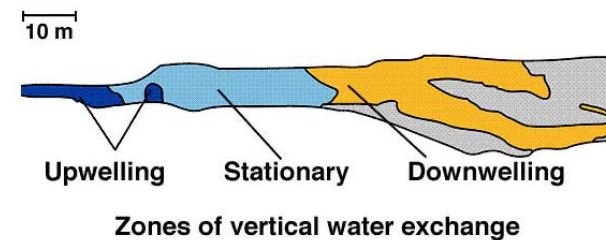


- Measured vertical hydraulic gradient – hydrologic maps
 - ✓ Positive vertical – flow from streambed to the surface – upwelling zone
 - ✓ Negative vertical – flow from the surface to the streambed – downwelling zone
 - ✓ Zero vertical – stationary zone

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Upwelling and Downwelling



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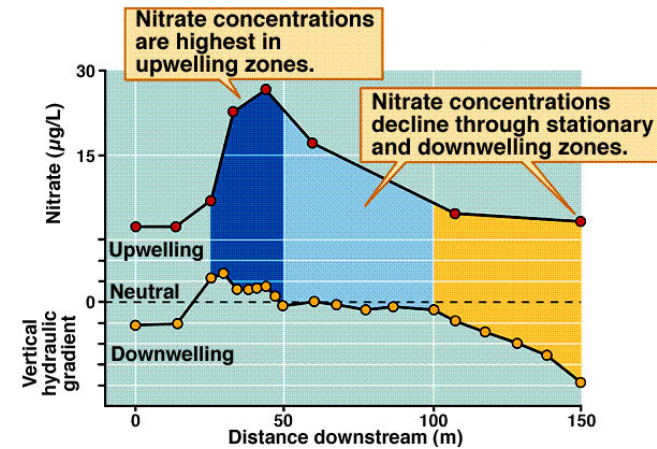


- The concentration of nitrate in surface water varies directly with vertical hydraulic gradient
- Upwelling zones – have the highest nitrate concentration due to upwelling from the sediments
- Nitrate concentrations gradually decline

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Nitrate & Hydraulic Gradient

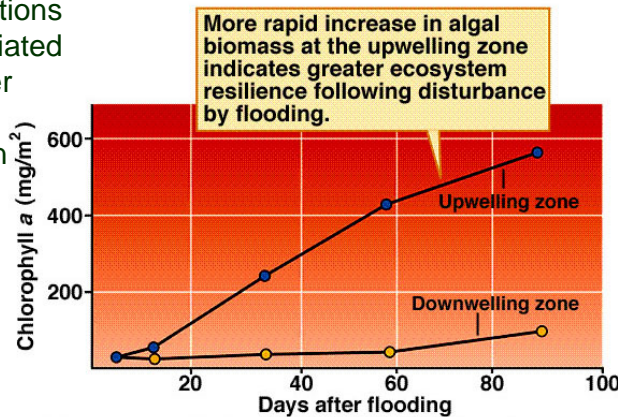


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The higher nitrate concentrations are associated with higher algae production

Chlorophyll a & Flooding



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- The rate of algal biomass accumulation can be used as a measure of rate of recovery from disturbance
- Therefore, the rate of ecosystem recovery is higher in upwelling zones since the rate of algal biomass accumulation is higher in this region
- i.e., algal communities in upwelling zones are more resilient

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Summary

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- Community stability may be due to lack of disturbance or community resistance

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