JE
Bio149
9/19/89

EXPERIMENTAL PLANT ECOLOGY
Biology 149

Harvard University
Fall Term 1989

Instructor: Fakhri A. Bazzaz Rm 387 Bio Labs 495-0916
Teaching Fellows: Rosie Crabtree Rm 391 Bio Labs 495-8791
Peter Wayne Rm 394 Bio Labs 495-8791
Meeting Times: Tuesday and Thursday 11:30-1:00; Room 258 Bio Labs
Lab/Discussion Session TBA

Course Requirements:

Mid-Term Hourly Exam	200
Final Exam	350
Experiment + Research Paper	300
Class Mini-Presentation	150
Total	1000

Field Trip - Sept/Oct - Harvard Forest

SYLLABUS

Date	Topic
9/19	1. Plants, Environments, and their Relationships: An Overview (FAB)
9/21	2. Global Climate and Vegetation Patterns in Space and Time (FAB)
9/26	3. Solar Radiation: Physical Principles and Considerations (FAB)
9/28	4. Solar Radiation: Plant Biophysical Responses (FAB)
10/3	5. Photosynthetically Active Radiation (PAR): Physiological and Whole Plant Responses (FAB)
10/5	6. Photosynthetically Active Radiation (PAR): Physiological and Whole Plant Responses (cont.)
10/12	7. Temperature, Light, and Seed Germination (FAB)
10/14	8. Water: Physical and Chemical Principles (SM)
10/19	10. Ecophysiology of Plant Water Relations (SM)
10/24	11. Atmospheric CO2: Direct and Indirect Effects on Plants and Plant- Herbivore Interactions (EF)
10/26	12. NOx/SOx/O3 Ecophysiological Effects of Atmospheric Pollutants (JC)
10/31	13. Midterm
11/2	14. Soils: Origins, Development, and Classifications (FAB)
11/7	15. Soils: Physical and Chemical Properties and Processes (FAB)
11/9	16. Ecological Aspects of Plant Nutrition (RC)

Syllabus (cont.)

11/14 17.✓ Demography: Population Structure and Dynamics in Contrasting Environments (FAB)

11/16 18.✓ Plant Plant Interactions: Classifying and Quantifying the Effects of Neighbors (PW)

11/21 19.✓ Plant Plant Interactions: Neighbors as Resource Modifiers (PW)

11/28 20.✓ Niche Breadths, Ontogenies, and Evolution (FAB)

11/30 21.✓ Resource Heterogeneity and Plant Plasticity (FAB)

12/5 22.✓ Disturbance, Succession, and Physiological Ecology (FAB)

12/7 22.✓ Disturbance, Succession, and Physiological Ecology (FAB)

12/12 24.✓ Scaling Up from Organelles to Ecosystems: An Example from the Harvard Forest (TWS)

Lecturers: FAB= Fakhri A. Bazzaz; SM= Dr. Suzzane Morse; EF= Eric Fajer; JC= Dr. Jim Coleman; RC= Rosie Crabtree; PW= Peter Wayne; TWS= Timothy Sipe

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(B+)

Biology 149 Midterm Exam October 31, 1989

Please answer all 5 questions concisely; outline format is acceptable as long as points are clear. Use diagrams and examples where appropriate. Each question is equally weighted. You have 1 hour 20 minutes. Good Luck, Live Long and Prosper.

Name: Jonathan A. Eisen

33/40

2

Name: Jonathan Eisen   Bio 149

1. From the seedling's eye view, the forest is extremely heterogeneous with respect to light availability. Conditions may range from deep, shaded understories to exposed canopy gaps. Seedlings of many species such as birch, however, successfully occupy a range of these environments. This may be due in part, to their developmental and physiological plasticity.

a) Describe two whole plant and two leaf level anatomical/morphological traits characteristic of sun and shade plants.

b) Draw photosynthetic light response curves for equivalently aged and positioned leaves on sun and shade seedlings. List and define the key variables derived from these response curves. Compare these variables from sun and shade seedlings.

c) Give two biochemical/physiological mechanisms that may underlie these differences in light response curves for sun and shade seedlings

a) whole plant differences ✓

① leaf arrangement ✓

- sun plants may tend to stack their leaves more than whorling them. In other words, they may have a higher degree of overlap. (LAI)
- shade plants would tend to space their leaves as evenly as possible so that self-shading is reduced.

height too - plants may reach for the sun more in low light environments and will therefore be taller than high light buddies

② root: shoot ratio ✓

- plants in higher light will likely need more water and thus may focus a higher proportion of energy on roots than shade plants would.

b) leaf level differences 2

① ~~[illegible] surface area~~

. surface : volume ratio ✓

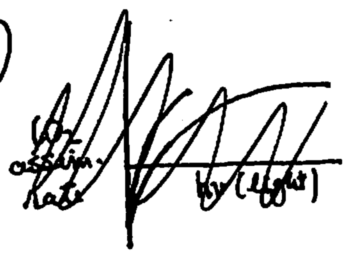
- shade plants would tend to have higher surface areas per unit volume so that they maximize photon capture

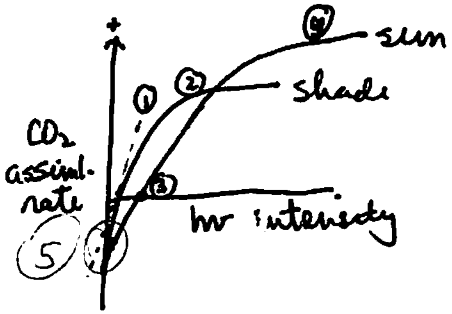
Specific Area / leaf wt.

② cuticle thickness ✓

- sun plants have thicker cuticles - possible to protect from UV damage ✓

b)





✓ ① - slope is quantum yield : ~~[illegible]~~ $\frac{CO_2}{I}$

- but this is only a measure of light projected on plant and not light absorbed.

Sun = ✓

✓ ② light saturation pt

- point at which some other factor (such as CO_2) becomes limiting

✓ ③ ~~point at~~ light compensation pt.

- the pt at which photosyn. balances with respiration
- for shade plants this tends to occur at lower light levels - possibly due to lower respiration rates.

3 - Respiration

✓ ④ max Photosynthesis rate

c) 1) chlorophyll a:b ratio

✓ . shade plants may have lower a:b ratios so that more Chl. b will lead to incr. photon capture

also - see point 3 above

(-2)

2) resistance to light damage

- sun plants may have enzymes and structures more resistent to damage (esp. by UV) and may therefore do better in high light.

N # Rubisco in Sun plants
- more total Chl. [illegible]

(30)

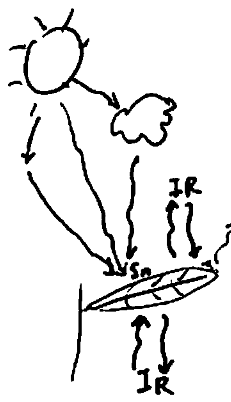
Name: Jonathan Eisen Bio 149

2. In a Halloween ecophysiological hallucination, SWAMP THING, a plant-like comic strip creature from wet, dark environs, kidnaps you. It and its kind now wish to invade high radiation environments, yet these leaf covered, chlorophyll brained creatures do not understand the biophysical differences between dark and sunny environments, and the needed "adaptations" required for living in the sun. Your life is threatened unless you accept a position as Swamp Thing Leaf Energy Budget Director.

a) What is the equation for the energy budget of a single leaf? Define all terms.

b) Can you come up with suggestions for how Swamp Thing should alter its leaves so that it can operate more efficiently under the new exposed conditions?

c) How would you change your recommendations if the new, high radiation environments, are also water limited?



a) $S_n + T_n + LE + H + P = 0$

S_n = net solar radiation

T_n = net thermal radiation

LE = latent heat of evaporation = energy absorbed by H_2O as it evaporates

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H = convection + advection

P = photosynthesis & other methods by which a plant may convert external energy (esp. S_n) to internal potential energy (chem. bonds)

b) yes - there are many ways to do this

-since swamp thing wants to adapt to the sun, each factor in the above formula could change.

- S_n is increasing but this incr. can be modified by

① changing angle with the sun (the swamp things could stand upright at noon, and ~~tilt in~~ maintain a 90° angle to the sun all day - this would reduce S_n ($I = I_o \cos\theta$)

② put a coat of reflective material on - this would reduce the Sn by increasing reflectance ✓

③ reduce the amount of light absorbed by incr. transmittance - less chlorophyll - or clearer leaves. ✓ 6

<u>Tn</u> - Tn is probably going to incr. somewhat due to a few factors - such as incr. soil reradiation. ✓ 2

<u>LE</u> - the swamp things could ~~incr~~ modify their energy budget so that LE increases (and takes more energy away from them things) This can be done by
① incr. conductance ✓ 4
② decr. boundary layer by.... ✓ 2
reducing lf size?
behavioral modifications - wave in wind

1 H changes ③

c) <u>However</u> - this incr. in water loss may cause other problems which could be compensated for by
① drinking more
② further reducing Sn & Tn so that water loss doesn't need to be increased much. How?

∴ I would recommend C4 or CAM metabolism of these swamp things could switch. These would incr. the water-use efficiency of the swamp things. 5

The swamp things could also try the following in H_2O limiting situation
① water storage
② dormancy until H_2O around 2

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Experimental Plant Ecology (Biology 149) September 18,1989

Plants, Environments, and their Interaction
Outline for Lecture # 1

What is Plant Ecology: The Plant and its Environment

The Physical Environment: Resources and Controllers; The Principle of Reciprocity

The Biological Environment: Neighbors, Pollinators, Herbivores, Pathogens, Decomposers, Mutual Associates

The Nature of Plant Resources:
- a. Spatial Patterns: Continuous; Patchy; Resource Foraging (growth)
- b. Temporal Patterns: Diurnal and Seasonal; Excesses and Shortages through Time.

Plant Attributes Relevant to Resource Capture

Sessile

Modular Construction

Indeterminate Growth-development and death of parts

Developmental Plasticity and Physiological Flexibility

Plant Growth: The Serach for More Resources!

Plant Architecture; Clonality; "Phalanx" and "Guerilla" Modes of Growth (species specific); Reiteration (branching flexibility *Abutilon* vs *Ambrosia*);

Neighbors as Resources Modifiers and Removers

Positive, Negative, and Neutral Interactions

The Principle of Allocation

Allocation to Growth, Defense, and Reproduction; Allometric Relations and Ratios; The Economics of Resource Capture and Utilization

Scaling Up: Individuals, Populations, Communities/Ecosystems, Landscapes, the Globe

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Bio 90r
SA-11
(LAC)

Tim Jim
Eng CAR

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Experimental Plant Ecology -

Introduction
- no textbook - books in biolabs and Cabot

Ecology -
How do we define ecology?
① study of relationship betw. plant/envir.
ⓐ physical envir. - total of resources
- resources - things consumed
light, H_2O, CO_2, nutrients
- other - modify but not consumed
T°, wind, light ("controllers")

plant design - to use resources and adapt to controllers

each part has many functions

ⓑ biological environment
- neighbors - usu. related
- pollinators - have to "recruit"
- herbivores

can be both a resource & controller

Resources.

- plant resources are generally continuous (supply)
- all plants basically require same resources

① continuous (not packaged)

② patchy - in time, space (both phys. & biol)
- patchiness for one resource doesn't match others
- whereas animals - mouse = prot, fat, H_2O, N, P,

capacitance - storage of resource til other time so that they can be mixed

foraging strategies

② temporal - flowers grow before trees have leaves change life history

10 → 350

③ levels are important - shortage → optimal → excess
- toxicity
- each species responds differently
  - ONE MAN'S FOOD IS ANOTHER MAN'S POISON.
  - PLANT'S EYE VIEW

Resource Capture - what plant attributes are important?

Billings. *

- environment is very complex and always changing

① sessile

② modular construction — animals - born - grows → reproduce → die; plants - add same pieces, parts die
- above/below ground - in direction of resources
- death of parts

③ Indeterminate growth - very big range

④ Morphology not constant -
- are some constraints (ie - architecture)

Resource Capture

Plant Growth

clonal - modules connected

branching

- influenced by barriers, resources

genet - whole plant

ramet - each part

- distance between ramets varies
- phalanx - short ramets separation

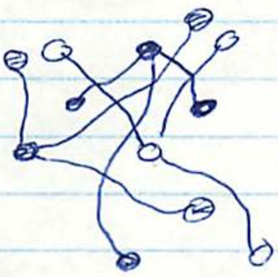
guerilla - spread out

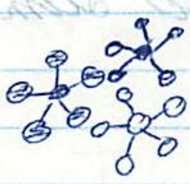
Independence vs. Integration of foraging parts

- Integration - share resources

∴ must allocate appropriately

Phalanx vs. Guerilla

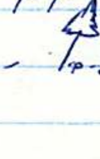




v. big differences in neighbors

Neighbors - resource modifiers - usu. "removers"

- negative
- neutral -
- positive - ↑-shade plant



Growth leads to aquisition

Allocation-

Growth - leads to more aquisition
Reproduction - leads to future growth
Defense - prevents "growth" from being set back

- can't allocate one resource to two things
- need to balance - some rules

Allometry

RT/SHT   SA/diam

Resource Use

- determines most of plant life

Integration

- several hierarchical levels
- not direct sum -

Experimental Plant Ecology (Biology 149) September 21,1989

Global Climate and Vegetation Patterns in Space and Time
Outline for Lecture # 2

I. Differential Distribution of Energy on the Earth's Surface and the Creation of Winds

II. Differential Distribution of Precipitation and the Resulting Patterns of Evapotranspiration

III. Climate Influences Soils and Plants: The "Climate, Soil, Vegetation Triangle"

IV. Modification of Climatic Patterns by Ocean and Mountain Ranges: Orographic Effects and Rain Shadows

V. Examples of Vegetation Types with Different Patterns of Temperature and Moisture
  a. Low Temperature, Low Precipitation-- The Tundra
  b. Seasonal Temperatures--The Deciduous Forest; The Grasslands
  c. Low Precipitation, High Temperature--Hot Deserts
  d. High Precipitation, High Temperature--Tropical Rainforests

VI. Unusual Large Scale Climatic Events: e.g. El Nino

VII. Climate in the Past and Species (Vegetation) Migration
  a. Carbon Dioxide Levels
  b. Glaciation and Deglaciation

VIII. Global Change and Future Climate: The Human Impact
  a. Greenhouse Gases
  b. Rise in Mean Global Temperature
  c. Change in Rainfall Patterns
  d. Land Clearing
  e. Ecological Consequences

This Week's Readings

1. MacArthur R.H. (1972) Climates on a Rotating Earth (Chapter 1, pp 5-14) in Geographical Ecology: Patterns in the Distribution of Species.

2. Schneider, S. 1989. The Changing Climate. Scientific American (9-89)

Next Week's Reading

1. Larcher, W. 1983. Physiological Plant Ecology (Chapter 2: Radiation and Temperature: Energy, Information, and Stress. pp 5-27). Springer Verlag

2. Chiariello, N.R., Field, C.B., and Mooney, H.A. 1987. Midday wilting in a tropical pioneer tree. Functional Ecology 1; 3-11.

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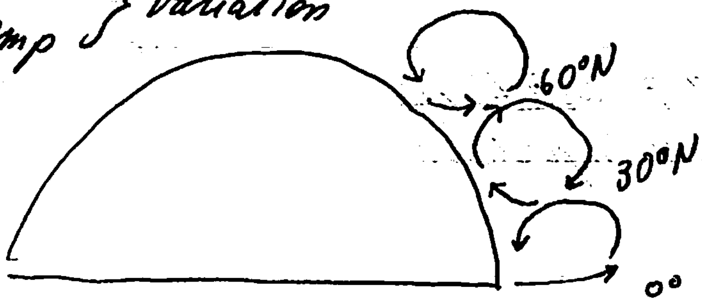
Global Climate & Vegetation Patterns · Space & Time

NB
① insolation varies from 0° → 90° LAT.
② " " " w/ seasons, day ...

variation in insolation/energy leads to
wind } variation
temp }



30°N/30°S
· wind/air descends & warms → ∴ dry

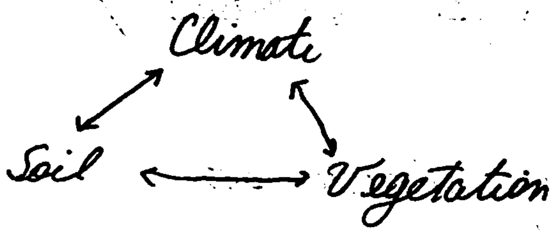
Amount of radiation depends on
① atmosphere (dust, angle, clouds ...)
② seasons...

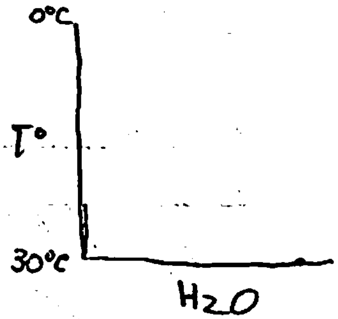
Winds, T°, determine climate

Oceans & Mountains · molders of climate
- continents - higher range of T°
- mountains
  · air forced up & H_2O lost
  - on other side - descends - picks up H_2O
    · "rain shadow"
    - in N.A. - deserts extend further North

oceans - Water source; T° balance;

date nearing a close.





<u>Climate</u> → <u>vegetation</u>

① <u>temperature</u>

② <u>moisture</u>

<u>amount</u> & var<u>iability</u>
very importent

Examples

- <u>Tundra</u> - low H_2O ; low T°
  - <u>temp</u> is important
  - H_2O not limiting bec. low evap.
  - grass, lichens
  - high diversity
  - <u>soil</u> - frozen except for 20-50cm during growing season
    a lot of organic debris buried/frozen
  - <u>adaptations</u>
    small SA; short growing season

<u>Alpine Tundra</u>
- no permafrost ∴ more nutrients

- <u>Deciduous Forest</u> - seasonal T°; moder. H_2O
  - <u>soil</u> - better drainage
  - high diversity
  - Spring flowers in understory (canopy open)
    use stored 'C' to burst out

that was amazing. thank you.

Grassland - seasonal T°; lower H_2O

- less rainfall is main difference
- grasses & broad leaf species (forbs)
- v.v. diverse
- fire adapted - need fire to keep out trees

Desert - high T°; low H_2O

high T°, low precip. - highly seasonal

two life forms

① Shrubs - deep roots - to H_2O source

∴ can remain active throughout year

② rain dependent species

- sea of annuals
- v. quick lifestyle

Tropical rainforest

- ++ H_2O, ++ T°
- big variation betw. forests in rain
- seasonality in rainfall
  - leads to growth seasonality
- buttresses, climbers (leonas)
- epiphytes
- herbivory enormous
- fragile → erosion
  - diff. soils - highly weathered, leached
    - Fe near surface
    - "laterization"

① small (relative) amt of wght. to roots

② nutrients ~~in~~ ~~biomass~~ up higher

③ layer of leaves/biomass decaying roots on top

Paleocene
Eocene
35mya Oligocene - trop. shifted N
Miocene
Pliocene
60,000 Pleistocene - ice age
Present
Future

species & vegetation vary w/ climate
- decoupling of associations
- diff. species move at diff. rates

Correlations
- levels of CO_2 in ATMOS w/ T°
  high CO_2 = high T°
  - today - $\Delta[CO_2]$ is very fast
    burning forests } → ↑CO_2
    - fossil fuels
    - ↑CH_4 - more efficient greenhouse gas from termites
  - oceans absorb about 50% of CO_2

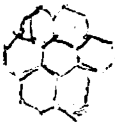
↑CH_4
- termites
-

future
- Temperature - mean global T° will incr. w/ CO_2
  - where incr. T° occurs is disputed
  - if ↑T° v. high in tundra
    - soil active zone will incr.
    - organic matter will decompose → ↑CO_2
      or will be a sink

VENUS - runaway greenhouse

Incr. in CO_2 →

① incr. T°
② Δ wind → Δcloud → ΔT°
③ Δ H_2O fall → Δcloud



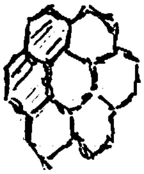
EPS-30

What does this do?

① Crops - corn belt - T° may change but soil doesn't so decoupling of traditional methods

② Social -

③ Political - location of croplands



~~④ Dispersal~~
④ Diversity - no time for dispersal

Problems
- need to incorporate vegetation models

Scientific American

incr CO_2 → incr T° → Δ wind
Δ H_2O
↓
pol. -
social -
diversity - Δ C_3, C_4, insect,

9/26

$4H \rightarrow He + e$

$4 \times 1008 = 4032$ $He = 4003$

$\therefore e = mc^2 = 29c^2$

Energy of sun emitted as radiation

- every body emits radiation

$I = \sigma \overset{K^\circ}{T}^4 \longrightarrow$ Boltzman formulation

photon flux density 8.13×10^{-11}

①for a perfect body "black body"
-perfect emission/absorption

②most bodies depart slightly due to "imperfection"
"emissivity"
$I = \varepsilon\sigma T^4$

for plants $\varepsilon = .97$ ∴ almost irrelevant

①bodies emit radiation based on T (& ε)

②energy in various frequencies
-Planck's Distribution Law
-can calculate w/ T°

③wien's law - maximum wavelength λ_{max}

Experimental Plant Ecology (Biology 149) September 26-28,1989

Solar Radiation: Physical Considerations and Plant Biophysical Responses

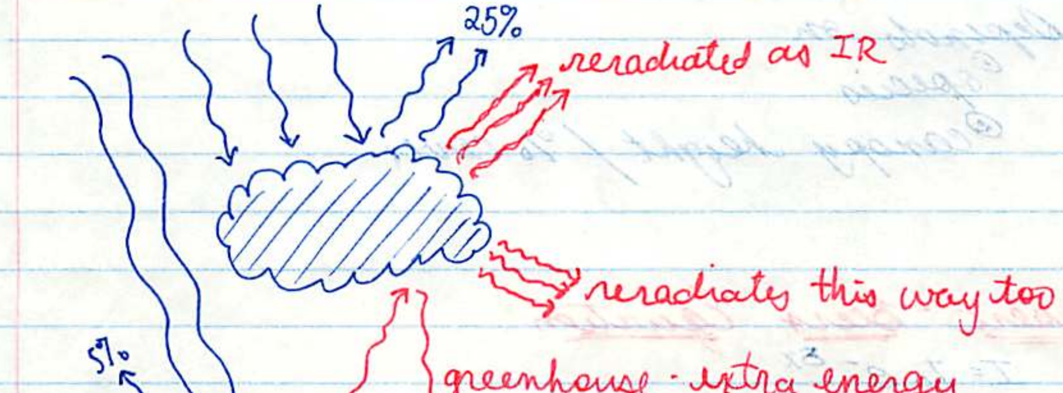
Outline for Lecture 3 and 4

- The Source of Radiation--The Sun
  - Electromagnetic Waves and Photons
- The Radiation Spectra
  - 0.29-5.0 microns
  - Black Body Radiation
  - Emmissivity
- Boltzman's Law; Planck's Distribution Law, Wien's Law and Peak Energy
- Fate of Radiation in the Atmosphere:
  - Duration
  - Reflection
  - Scattering
  - Absorption
  - Transmission
- Radiation at the Biosphere Level
  - Seasonal Changes
  - Angle of Incidence
  - Thickness of Atmosphere; Lambert's Law
  - Lag Times
- Radiation Through Plant Canopies
  - Changes in Quantity (Beer-Lambert's Law); Monsi-Sakai attenuation formula
  - Leaf Area Distributions
- Light Quality in the Understory: IR/R ratios
- Energy Budgets of Plants
  - Solar
  - Thermal
  - Latent Heat
  - Sensible Heat
  - Boundry Layer

so sun emits max at .4 → .7 (visible)
earth " " " 10 (IR)

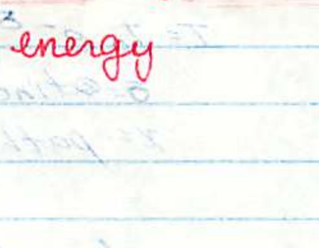
Different gases absorb diff. λ

O_3 absorbs UV
H_2O " " IR
CH_4 CO_2 " " IR



absorbed
scattering
transmission
reflection
reradiation

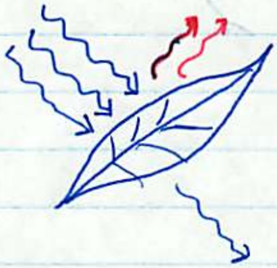
Radiation Absorbed depends on
① Duration
② Angle of incidence
more absorbtion
higher area of contact



Lambert's Law
$I = I_0 \cos\theta$
I_0 = irradiance perpend. to source

Radiation

What happens when it hits vegetation

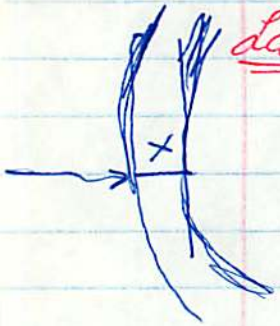


Slides

Depends on

① species

② canopy height / % cover



Lambert - Beers Equation

$I = I_0 e^{-\delta x}$

δ = extinction coefficient · depends on material travelling through

x = path length

- some forests / fields ...
- amt of I received at floor depends on type / density

If vegetation were uniform then could use Lambert-Beer equation

But

① material not uniform - quantity / distribution

- can get around this by using

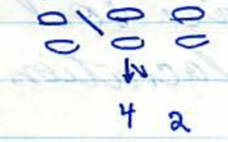
Monsi - Saeki Equation

$I = I_0 e^{-\delta(LAI)}$

Leaf area index - leaf SA per unit ground area

- Tropical rain forest ≈ 5
- crops LAI ≈ 5-7

Monsi-Saeki problems
①LAI not uniform
②LA distribution (separation betw levels) is v. important
③Angle of sun change theoretical LAI



Quality of radiation changes:
①Ratio of visible to ~~far~~ far red

example - take leaf

red → far red → IR

Leaf absorbs
①red - in chlorophyll
~~②far red - absorbed by H_2O~~
② IR - absorbed by H_2O
③ far red - not touched

∴ → cooler

Forest floor
①T° lower
②far red/red higher

① atmospheric absorbtion
② patchy
③ quality * V. IMPORTANT TO GERMINATION

Leaves
①absorb photosyn. wavelength
②let red (heat) through

Diff. canopies do diff. things
hairs, thickness, ...

Satellite Imagery is based on how diff. "types" reflect radiation

Reflection

Albedo - reflection in all wavelengths
- this occurs in ice and bare soil
- positive feedback for glaciation

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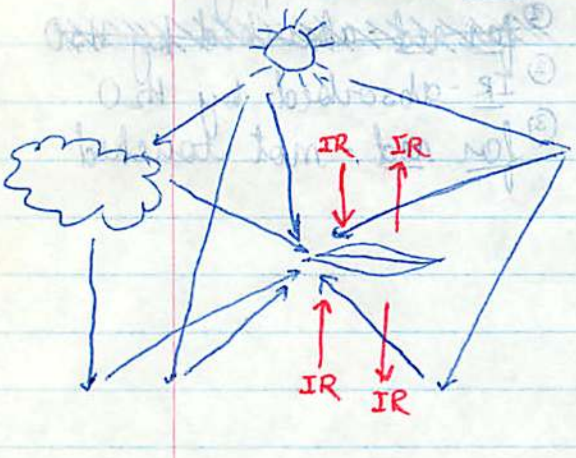
Energy Budgets

solar radiation: radiation from the sun - direct or indirect
thermal radiation: usu. in longer wavelengths coming from a body - reradiation.



conductance
~~win~~ ① osmosis = convection C
② wind assisted = G

H = sensible heat transfer

L = constant = latent heat
E = evaporation

S_N = solar (Net) radiation = received - transmitted - reflected
T_N = thermal " "

$$S_N + \overset{\text{-reradiation}}{T_N} + \overset{\text{-so}}{LE} + H + P^{=\text{photosynthesis }(1\%)} = \emptyset$$

H ↙ advection (wind assist) ↘ convection } warming up molecules

① laminar ⇉
② turbulent ↻↻↻

boundary layer - v. important

moving
still

boundary layer - thin layer of air where DIFFUSION is #1.
air movement is "more turbulent" if surface is rough

① wind speed } influence thickness of boundary layer
② position

Definition of thickness is very ~~arb~~ arbitrary

thickness = constant $\sqrt{\frac{\text{length mm}}{\text{wind velocity (m/s)}}}$

$\delta = 4.0\sqrt{\frac{l}{v}}$ (leaf)

l = length of "pathway" of wind

$\delta = 5.8\sqrt{\frac{l}{v}}$

$$\begin{tikzcd}[column sep=tiny] S_N + T_N + LE + & H \arrow[dl] \arrow[dr] & + P = 0 \\ C & & G \end{tikzcd}$$

$-\frac{H}{LE} = \beta$ = bohn ratio

plants spend energy/time to try and maximize relationship w/ T_N & S_N

boundary layer

-Grilli -BUG
-RMBL marathon - -Tutor select.

Leaf Temperature
- can depart significantly from air T°

- depends on species

example
- alpine species in Color.
- leaf temperatures are much higher than air
- boundary layer v. important

- PLANTS ARE NOT PASSIVE!

Regulated T°
① diff parts need diff T°

How do plants regulate T°
① boundary layer
② morphology
③ follow sun (mvmt) → flowers & leaves

Can reduce SN
① turning
② color (hairs)
③ phenology

Events are at very short time scale also.

Soil has energy budget also.

- color
- H_2O
- organic
- graininess
- cover

all influence

Conduction - occurs downward
- but deeper down soil is cooler, less variable
- relative temperature (diff. betw surface) depends on time of day

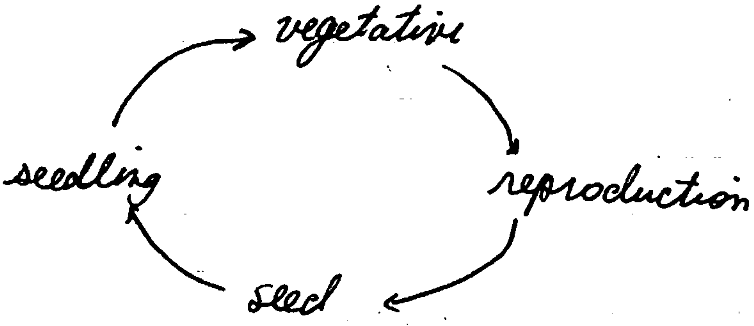
lag phase
- temp. takes time to move ∴ the root system temp. may be out of synch with roots. Depends on season.

Enorgnous variability between plant parts.

Experimental Plant Ecology 10/3

Plant Response to Radiation Environment

10/3



-each stage has different response

I) Seed Germination
- time at which embryo begins to grow

❶ giberellic acid → enzyme (breaks down starches)

→ sugars → growth

① temp dependent
② light enhances this cascade
but differential sensitivity
- ⓐ light NOT required "light insensitive"
- ⓑ light sensitive
  - ① required
  - ② enhanced
- ⓒ light inhibited

- but v. difficult to NOT expose to light (bec when flowering)

- what type of light?
  - ① red: far red ratio important
  - ② far red inhibits in light sensitive
    but it is reversible

- so forest floor has lots far red and many species only germinate in gap.

①

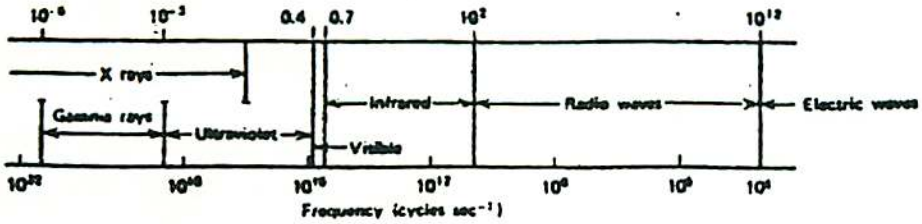
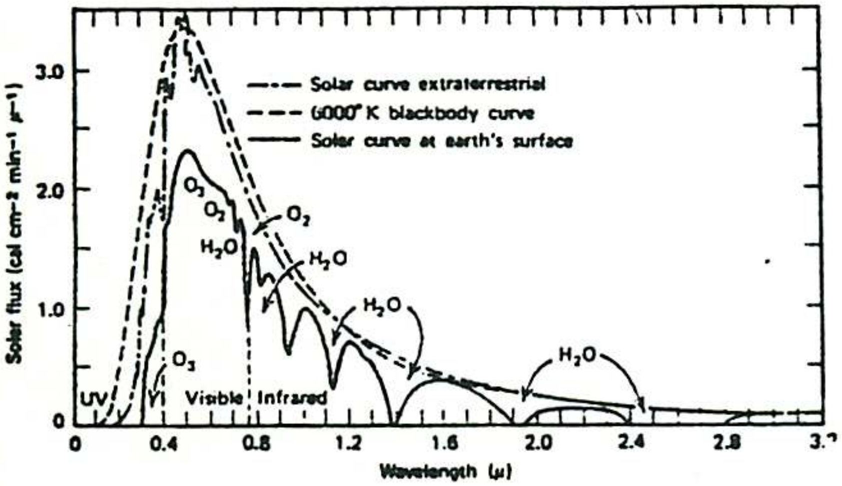


Figure 1.1. Electromagnetic spectrum on logarithmic wavelength and frequency scales (after Lapp and Andrews, 1954).



.50% betw. .4 & .7 (visible)
Ochloro range

Figure 1.3. Theoretical and actual spectra of solar radiation at the top of the atmosphere and the actual spectrum at the earth's surface (after Gates, 1962).

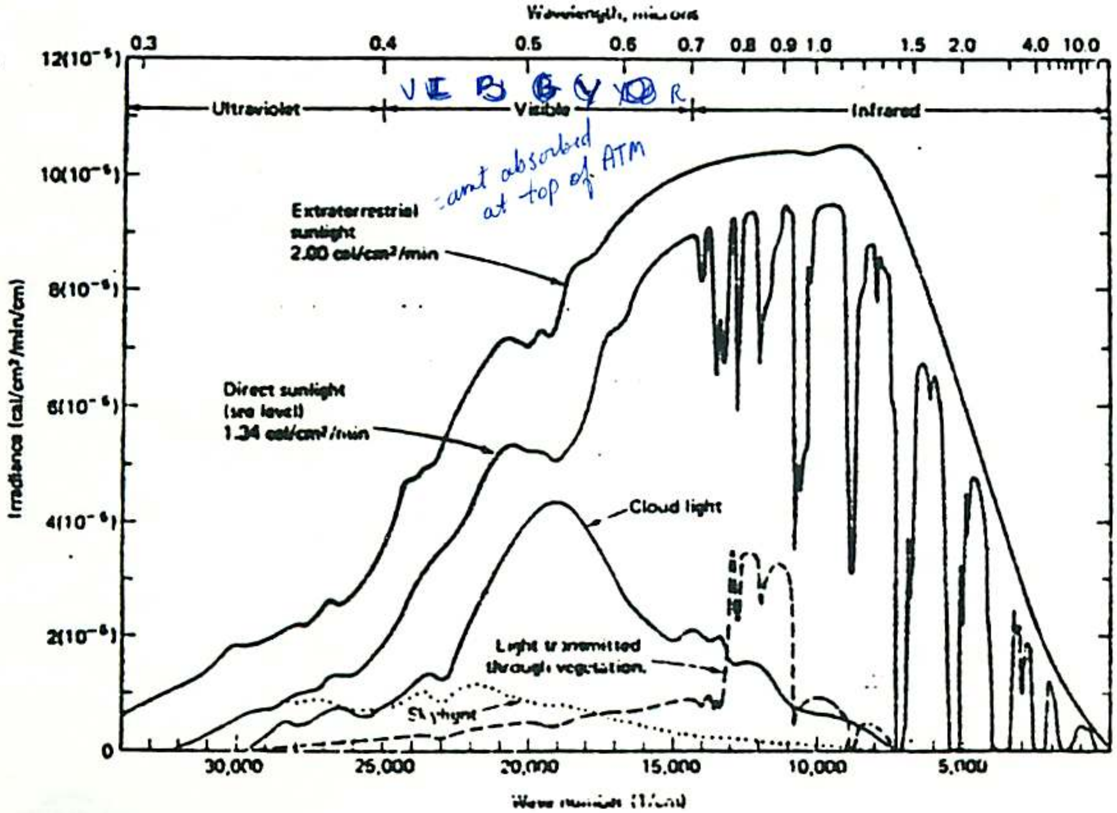


FIGURE 3–15. Spectral distribution of extraterrestrial solar radiation, of solar radiation at sea level for a clear day, of sunlight from a complete overcast, and of sunlight penetrating a stand of vegetation. Each curve represents the energy incident on a horizontal surface. (From Gates, 1965a.)

STEFAN-BOLTZMANN EQUATION

$$I = \varepsilon \delta T^4$$

$\varepsilon \doteq .97$ for plants

where

I = irradiance
ε = emissivity varies w/ diff. bodies
δ = constant [8.13×10^{-12} Cal cm^{-2} min^{-1}]
T = temperature

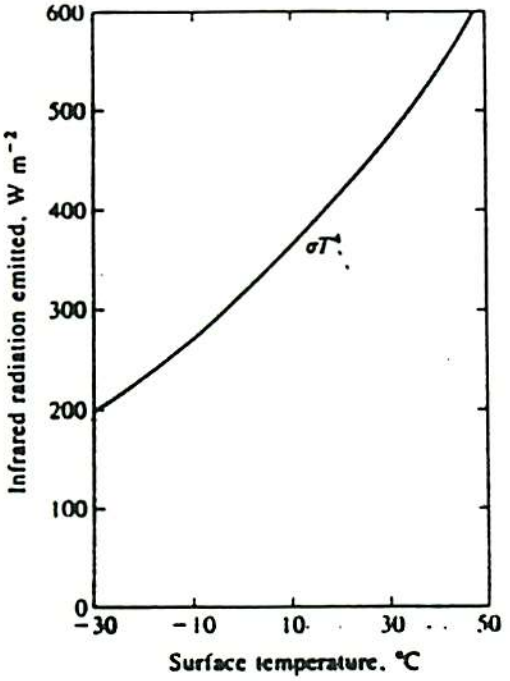


Figure 7.3
Rate of emission of infrared (longwave) radiation per unit area by a blackbody (e_{IR} = 1.00) as a function of its surface temperature.

PLANCK'S DISTRIBUTION LAW - energy at various frequencies

$$\frac{dR}{d\lambda} = \underset{\overset{\downarrow}{\text{constant}}}{c_1}\ \underset{\downarrow}{\lambda^{-5}}\ \left(e^{\overset{\overset{\text{constant}}{\uparrow}}{\frac{c_2}{\lambda T}}} - 1\right)^{-1}$$

WIEN'S LAW - peak λ

λ_{max} : λ at which max E.

$$\lambda_{max} * T = 2897\ \mu$$

$$\lambda_{max} = \frac{2897}{T}$$

sun λ_{max} = .5 = visible

earth λ_{max} = 10 = IR

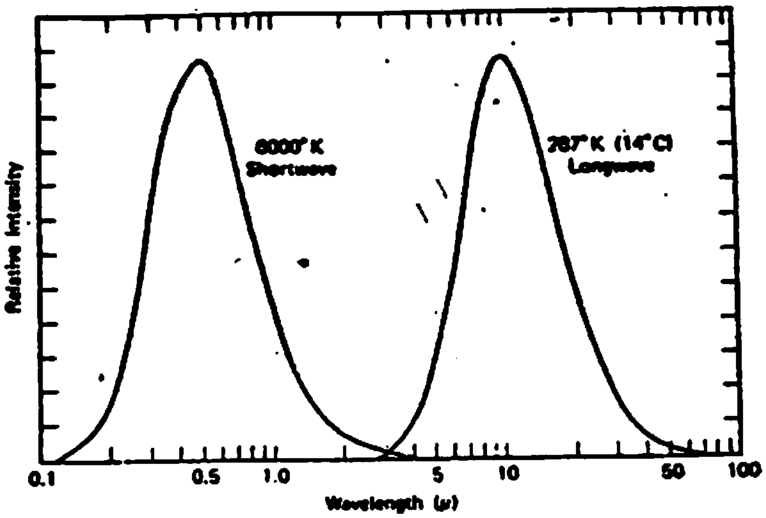


Figure 1.4. Spectra of solar and terrestrial radiation, both normalized with respect to their peak intensity (after Reifsnyder and Lull, 1965).

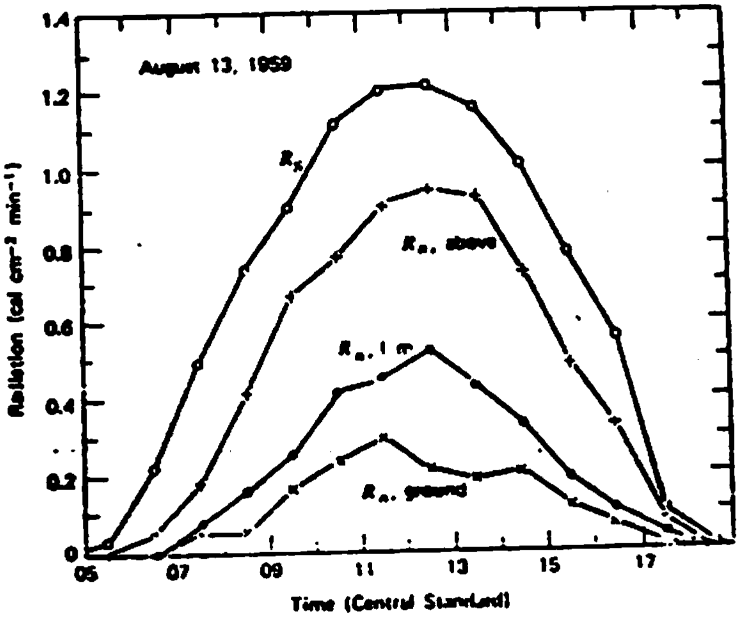


Figure 1.20. Average hourly solar radiation above, and net radiation at various heights within, a corn canopy (after Denmead et al., 1962).

LAMBERT'S LAW

$$I = I_0 \cos \theta$$

where

I = incident irradiance
I_0 = irradiance incident on a plane perpendicular to the source

LAMBERT - BEER EQUATION

$$I = I_0 \; e^{-\delta x}$$

where

δ= extinction coefficient
x = path length

MONSI - SAEKI EQUATION

$$I = I_0 \; e^{-\delta(\mathrm{LAI})}$$

(9)

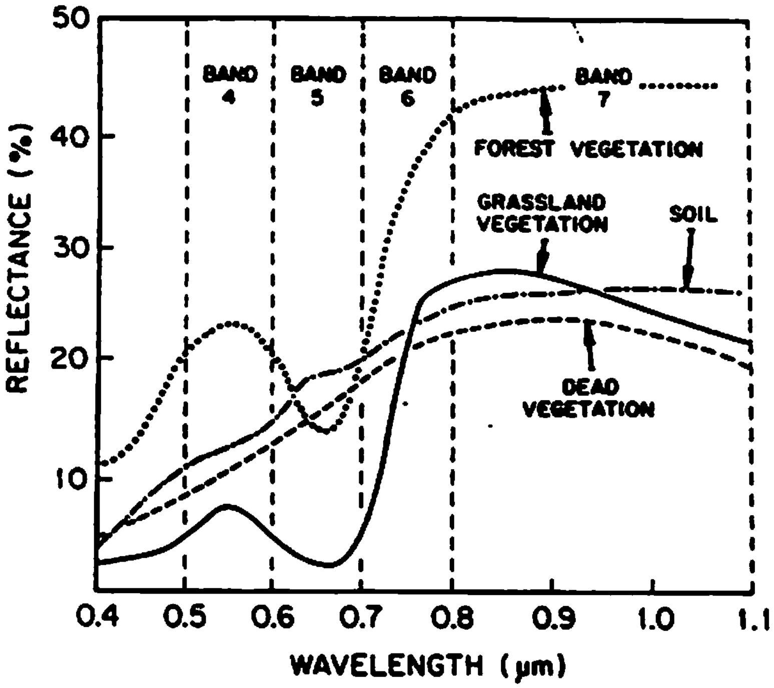
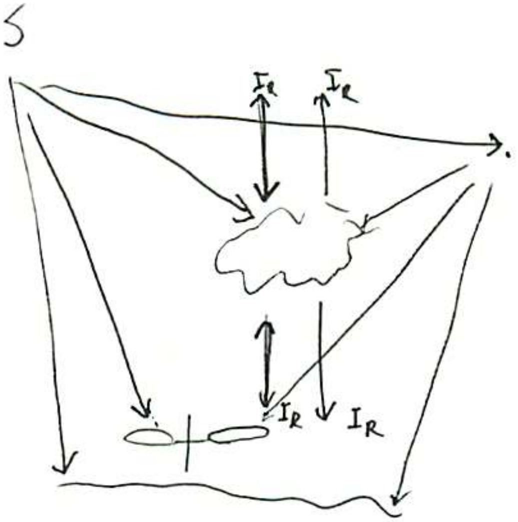


Figure 2 Reflectance of soil, grassland vegetation, forest vegetation and dead or dormant vegetation in the visible and near-infrared portions of the spectrum covered by the LANDSAT MSS. Note the large change in reflectivity in band 5 (visible red) between healthy forest vegetation and bare soil (after McDaniel and Haas, 1982 and Lillesand and Kiefer, 1979).



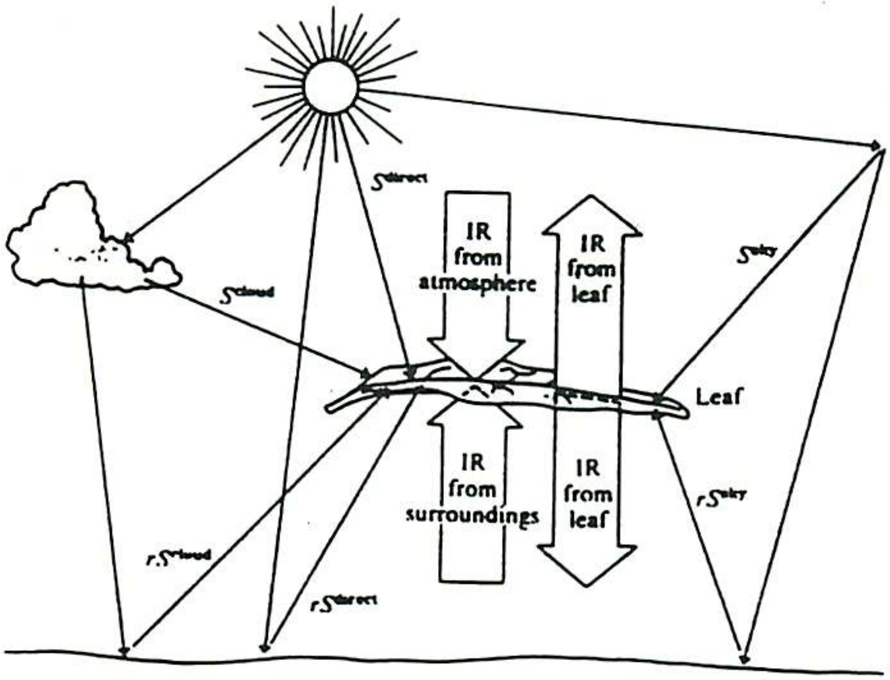


Figure 7.1

Schematic illustration of eight forms of radiant energy incident on an exposed leaf and the infrared radiation emitted from its two surfaces

solar vs thermal radiation

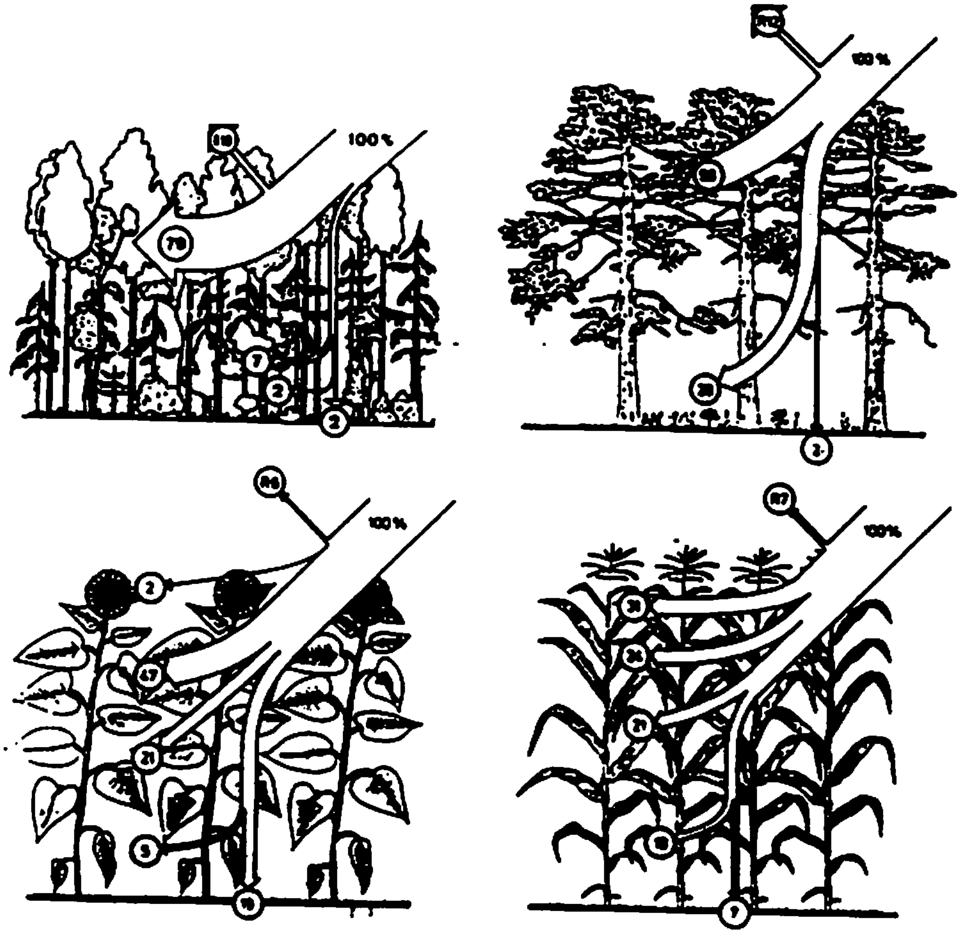


Fig. 2.2. Attenuation of radiation in various stands of plants: a boreal birch-spruce mixed forest (Kairiukštis, 1967), a pine forest (Cernusca, 1977), and fields of sunflowers (Hiroi and Monsi, 1966) and maize (Allen et al., 1964). Of the incident photosynthetically active radiation 6%—12% is reflected (R) at the surface of the stand; most of the radiation is absorbed in the stratum where the foliage is most dense, and the remainder reaches the surface of the ground. Depending on density, arrangement, and inclination of the leaves, quite characteristic differences arise in the distribution of radiation within the stand. Further examples: tropical rain forest (Odum and Pigeon, 1970; Allen et al., 1972), cocoa plantation (Alvim, 1977), Mediterranean sclerophyll stands (Eckardt et al., 1977), dwarf-shrub heaths (Cernusca, 1976), wheat (Baldy, 1973), rice (Udagawa et al., 1974), reeds (Dykyová and Hradečká, 1976), sweet potatoes (Bonhomme, 1969)

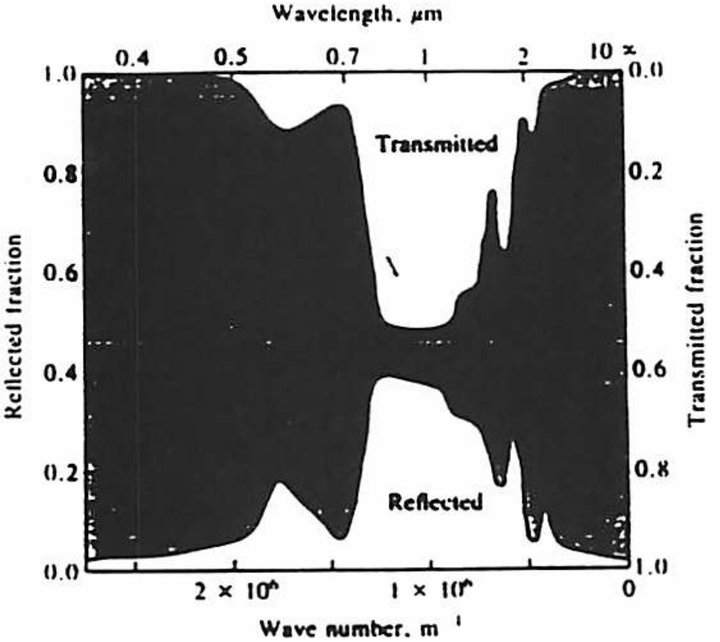


Figure 7.4
Representative fractions of irradiation absorbed, transmitted, and reflected by a leaf, as a function of wave number and wavelength. The sum $a_\nu + r_\nu + t_\nu$ is unity. (See Gates 1965, Gates 1970, and Woolley.)

13

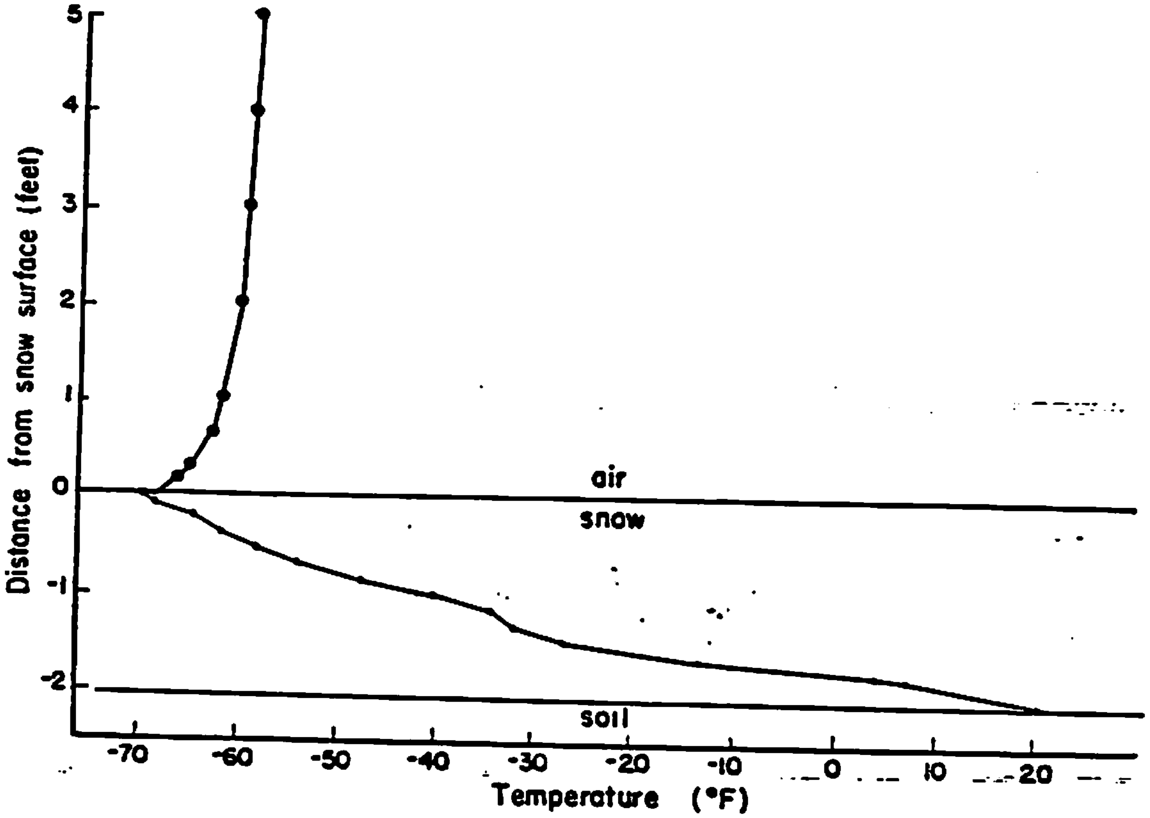


Figure 39. Vertical temperature gradient during a cold snap in central Alaska, an extreme case of microclimatic differences above and below the snow. Measurements were made simultaneously by the use of small copper-constantan thermocouples so arranged that conduction and radiation errors were minimized and the snow cover was undisturbed. (Data of H. McClure Johnson obtained during contract research between Cornell University and Alaskan Air Command Arctic Aero Medical Laboratory, Ladd AFB, Alaska.)

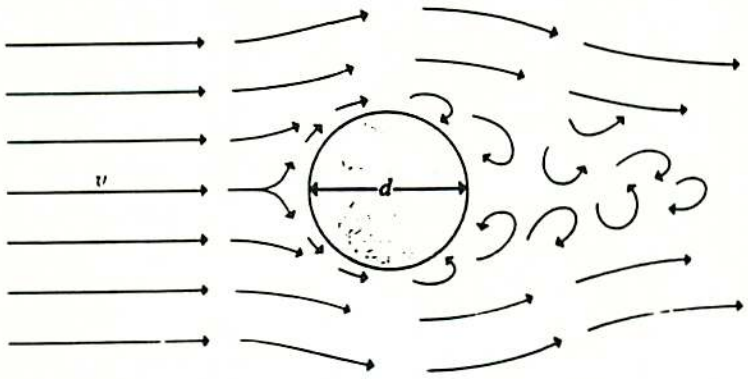


Figure 7.6
Schematic illustration of air flow around a cylinder. Flow can be laminar on the upwind half, but turbulence develops on the downwind side.

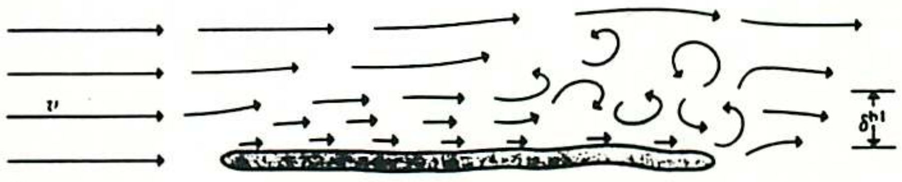


Figure 7.5
Schematic illustration of originally nonturbulent air flowing over a flat leaf, indicating the laminar sublayer (shorter straight arrows), the turbulent region, and the effective boundary layer thickness δ^{bl}. The arrows indicate the relative speed and direction of the air movement.

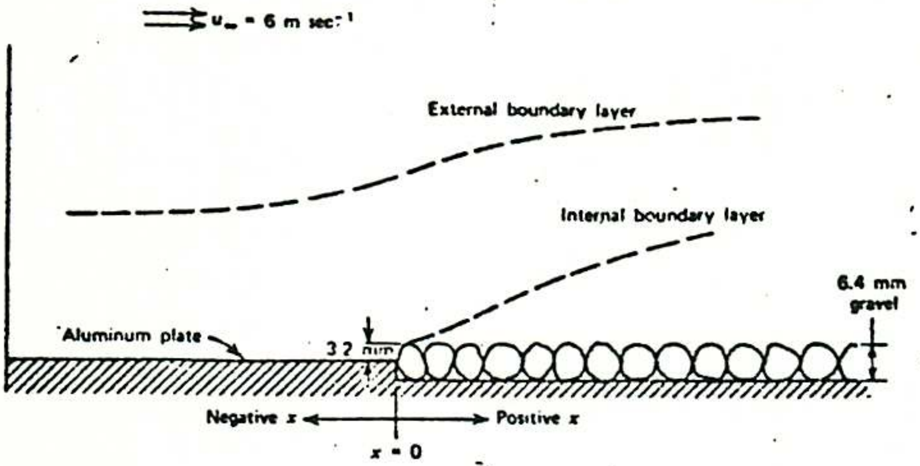


Figure 4.1. Internal and external boundary layers resulting from roughness changes in a wind tunnel (after Yeh and Nickerson, 1970).

internal boundary layer which develops after transition from a smooth to a rough surface.

The thickness of the external boundary varies from perhaps 10 to 100 m, depending primarily upon terrain and location with respect to major earth features such as mountains, oceans, plains, etc.

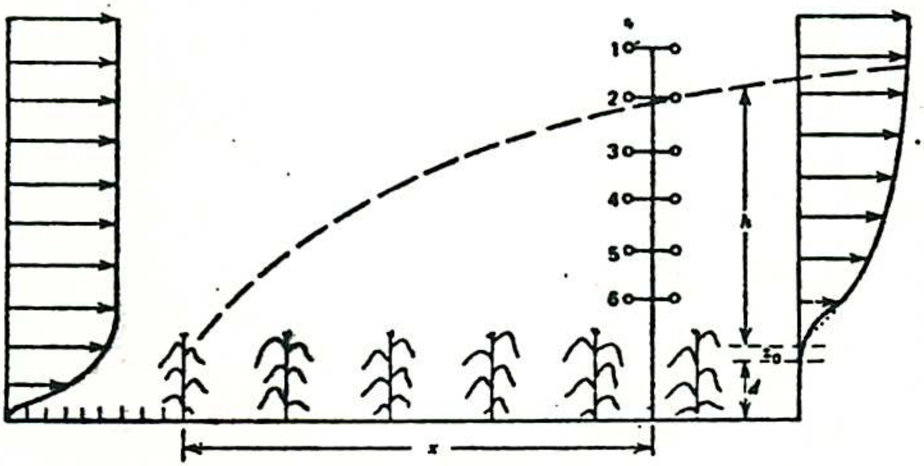
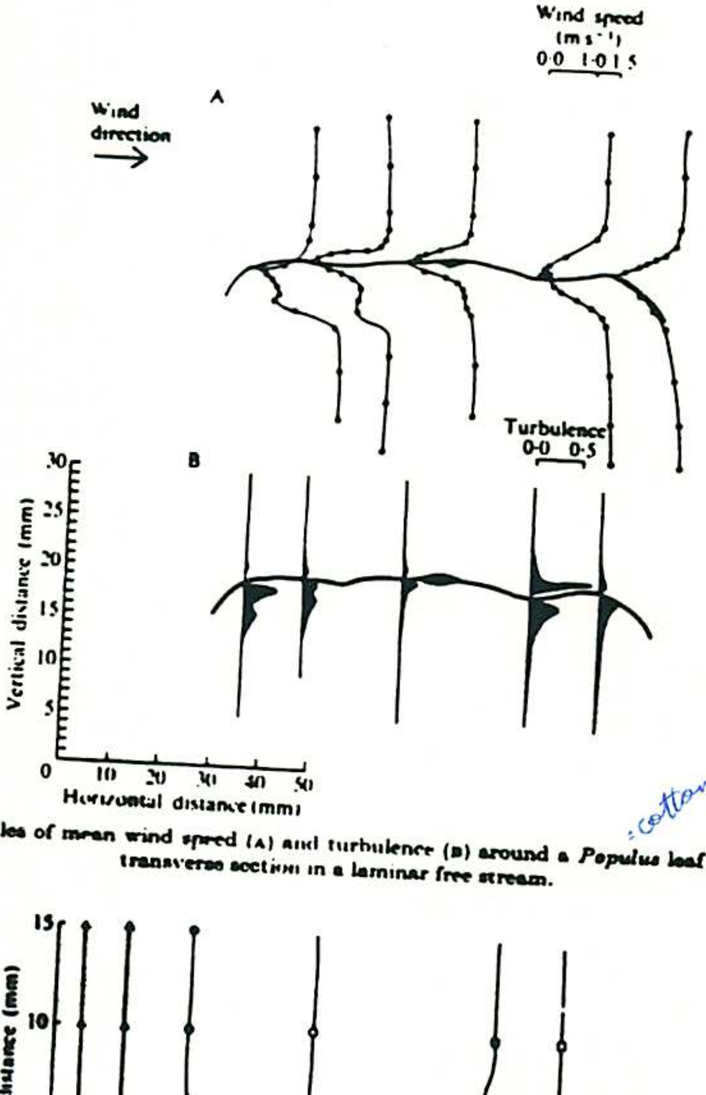


Figure 4.2. Schematic diagram of the growth of the boundary layer over a corn field. Arrows indicate wind direction and relative wind speed in wind profiles (after Lemon, 1960).

(15)

this defines boundary layer



cottonwood

FIG. 1. Profiles of mean wind speed (A) and turbulence (B) around a *Populus* leaf shown in transverse section in a laminar free stream.

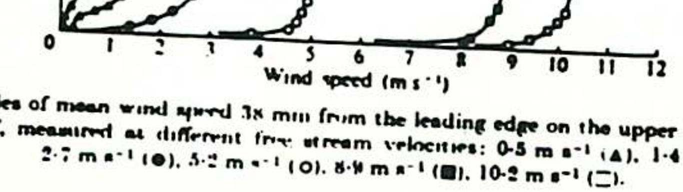


FIG. 2. Profiles of mean wind speed 38 mm from the leading edge on the upper surface of a *Populus* leaf, measured at different free stream velocities: 0·5 m s⁻¹ (▲), 1·4 m s⁻¹ (▲), 2·7 m s⁻¹ (●), 5·2 m s⁻¹ (○), 8·9 m s⁻¹ (■), 10·2 m s⁻¹ (□).

17

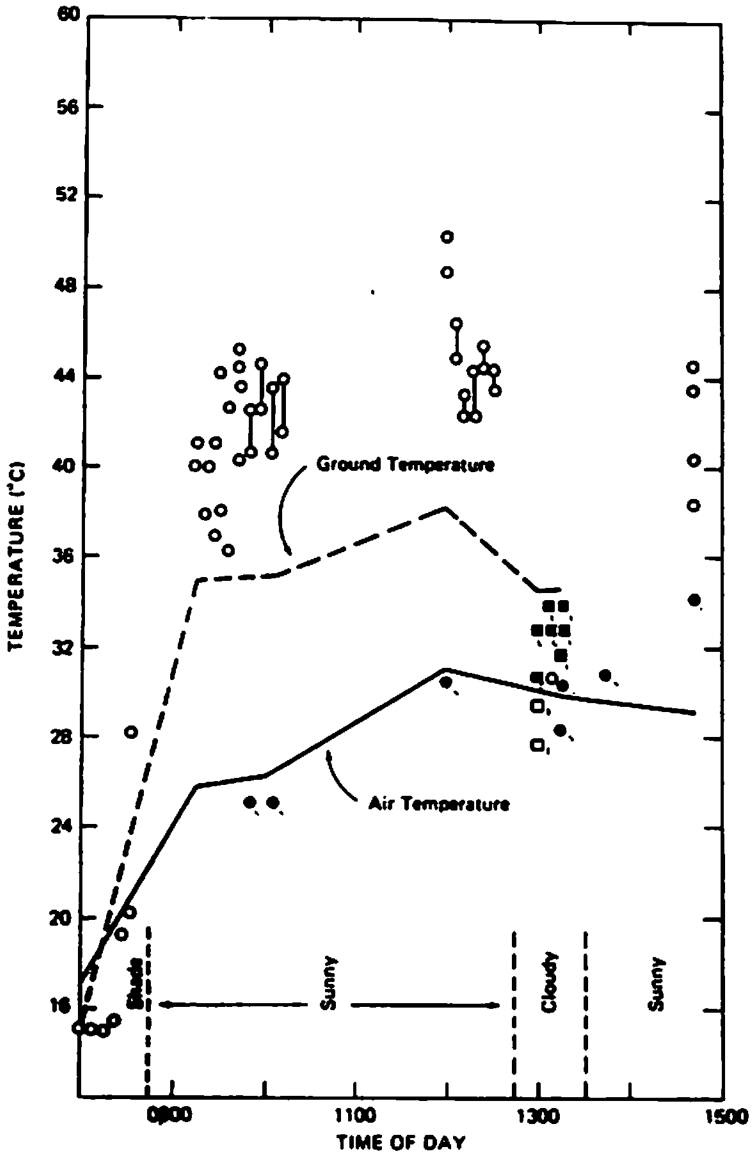


Figure 3.6. Temperatures of *Quercus macrocarpa* leaves as a function of time of day: (○) full sun on leaf; (●) shaded leaf; (□) exposed leaf; (■) cloudy. Connected open circles represent measurements done on upper and lower leaf surfaces. Also shown are (- -) ground and (—) air temperature.

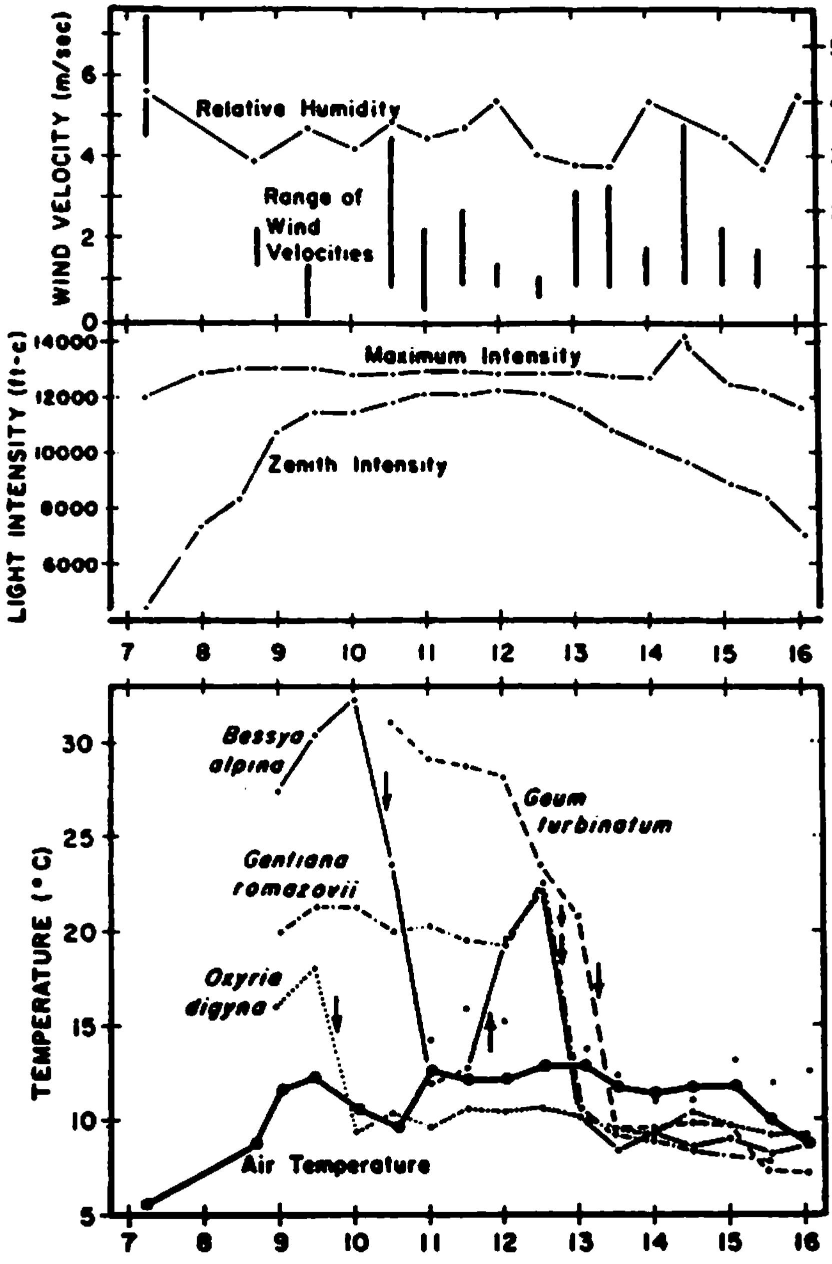


Fig. 1. Temperatures of four alpine plant leaves (Mount Evans, Colorado, 4300 m) during a clear summer day as compared to air temperature, maximum and zenith intensities, range of wind velocities, and relative humidity. Air temperatures connected by heavy lines were measured with a shaded, mercury thermometer. Measurements with a shaded thermocouple were sometimes higher; at other times essentially the same (heavy points unconnected with lines). Arrows pointing down indicate approximate times that the shadow of a rock moved over the plant in question. Measurements were made on an east-facing slope, and so in most cases after a plant went into the shade it was never again exposed to the sun, but the one arrow pointing up indicates the approximate time when *Bessya alpina* was exposed to the sun for the second time. The first slight trace of a cloud appeared at 13.12 h., but clouds became heavy enough to influence light readings at about 14.30 h. Light intensity readings in the shade were about 700 ft-c while the sky was clear but went above 800 ft-c with clouds in the sky (much higher during the few moments while the sun's rays pass close to a cloud). Note the drop in temperature of *Geum turbinatum* beginning about an hour before the plant was covered by shadow. Such a drop might be ascribed to the position of the part of the leaf being measured in relation to the sun's rays

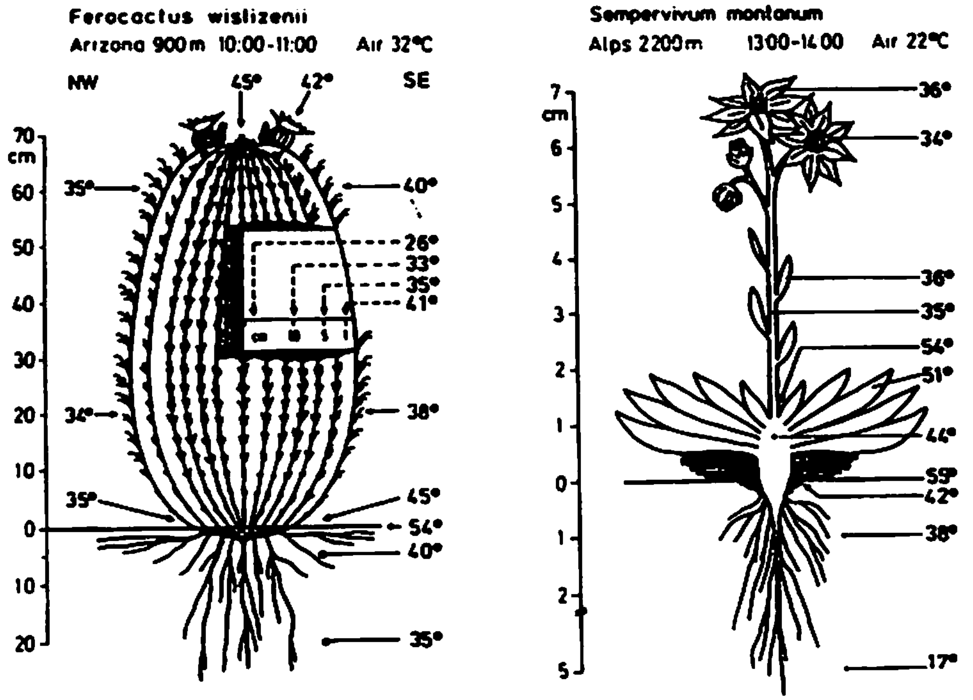


Fig. 2.10. The degrees to which succulent plants are warmed above air temperature under steeply incident radiation. The temperature in the center of the rosette of *Sempervivum montanum* can exceed that of the air by 32° C (unpublished measurements by W. Larcher). The barrel cactus *Ferocactus wislizenii* becomes warmest near the apex; when the sun is high the incident radiation tends to be tangential to the sides of the plant, which thus exceed the surrounding temperature by no more than 10° C (Monzigo and Comanor, 1975; K. Burian, pers. comm.). Further measurements of cactus temperatures are given by Lewis and Nobel (1977) and by Mooney et al. (1977)

21

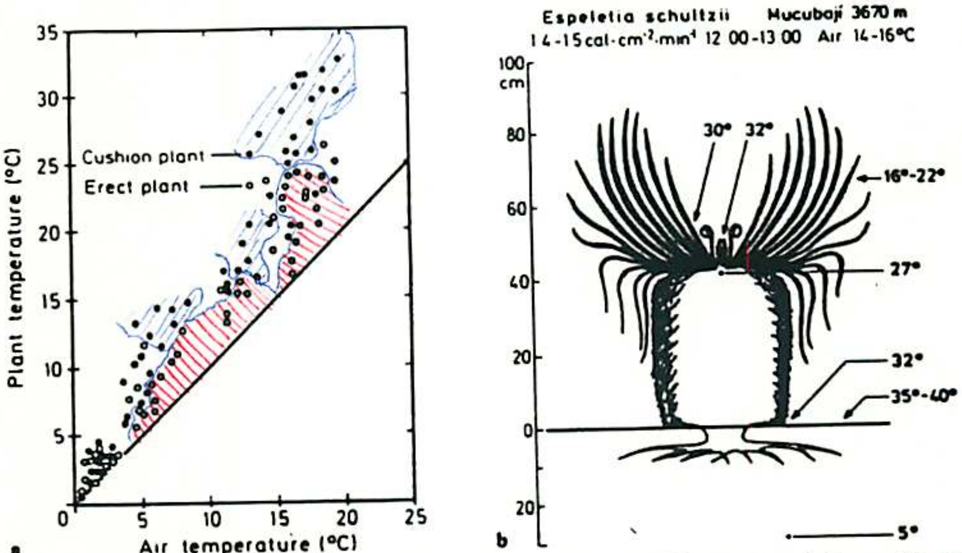
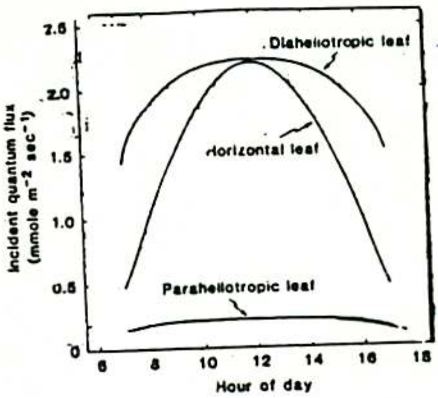


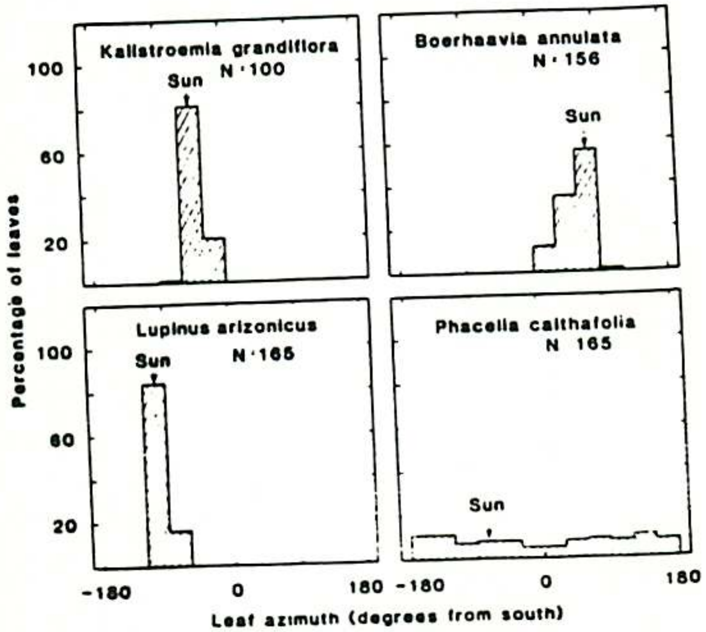
Fig. 2.14. a Leaf temperatures, in sunshine, of alpine plants of different growth forms. Plants growing close to the ground (*filled circles*) become distinctly warmer than those growing upright (*open circles*). From Salisbury and Spomer (1964). b The shoot apex of the giant rosette plant *Espeletia schultzii* in the Páramo level of the Venezuelan Andes becomes warmer than the air under full illumination by the zenith sun. Data of Pannier, Smith and Larcher as cited by Larcher (1975)



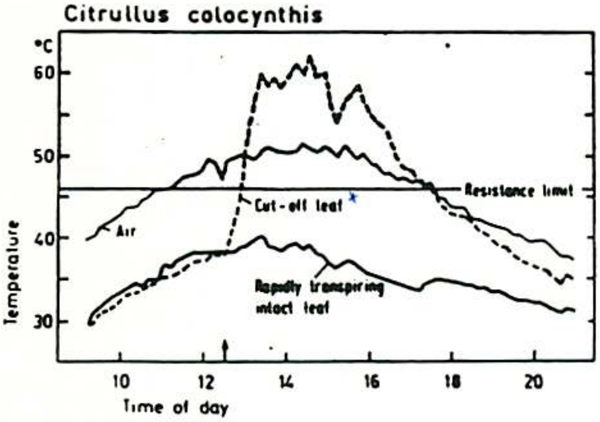
- tracks the sun

- stays away from sun

Fig. 4. Photosynthetically useful solar radiation between 400 and 700 nm incident on three leaf types over the course of the day (19): a diaheliotropic leaf (cosine of incidence = 1.0); a fixed leaf angle of 0°, the horizontal leaf; and a paraheliotropic leaf (cosine of incidence = 0.1).



LE - transpiration



* cut off leaf
∴ no H_2O source

Fig. 2.15. Cooling effect of transpiration upon the leaves of a watered *Citrullus* plant under desert conditions. During rapid transpiration the leaves, despite intense insolation, are much cooler than the air. If a leaf is cut off (*arrow*) so as to make vigorous transpiration impossible, the leaf temperature rapidly rises above that of the air, becoming so high that signs of heat injury appear (the range of temperatures associated with heat injury is shown in gray). Plants like *Citrullus*, which ordinarily maintain a temperature lower than that of the air, can survive in hot habitats only if they are able to transpire at a high rate. After Lange (1959)

19

Figure 9.2
Schematic illustration of small packets or eddies of air swirling about in the turbulent region above vegetation. The eddies, which tend to increase in size with height, carry all molecules they contain more or less as a unit. They are continuously changing size breaking up, or coalescing with other eddies -- making their actual size somewhat hypothetical.

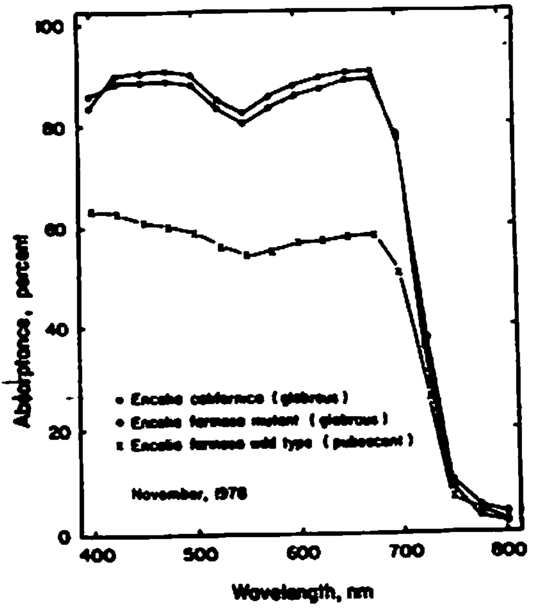


Fig. 3. Leaf absorptance spectra between 400–800 nm for leaves of *Encelia californica*, a glabrous mutant *E. farinosa*, and a normal pubescent *E. farinosa*

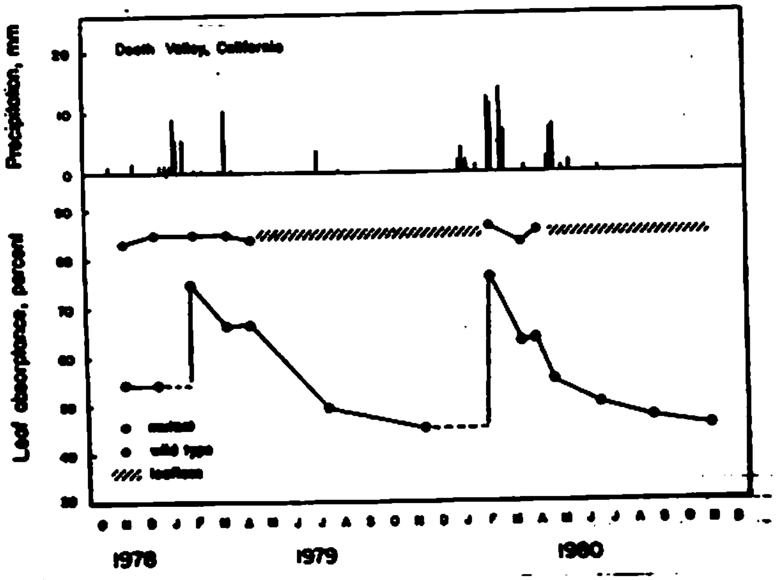


Fig. 5. Top: Time course of precipitation in Death Valley, California. Bottom: Time course of leaf absorptance to solar radiation in the 400–700 nm waveband for the mutant *Encelia farinosa* and the wild type *E. farinosa*. Sample size is 4–5 for the mutant and 10–50 for the wild type.

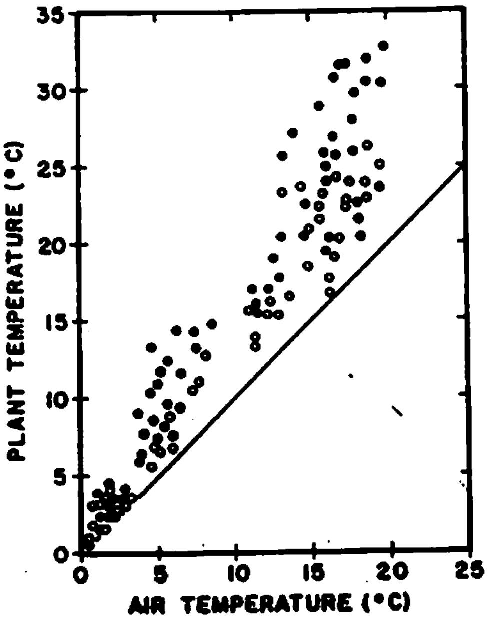


Figure 11.7. Plant temperature data as a function of air temperature obtained at an altitude of 3800 m near Trail Ridge Road in Rocky Mountain National Park, Colo.: (●) cushion plant; (O) erect plant. (After Salisbury and Spomer, 1964.)

㉗

Cambridge
Ann. Bot.

this is bogus
because it doesn't
show to L or R.

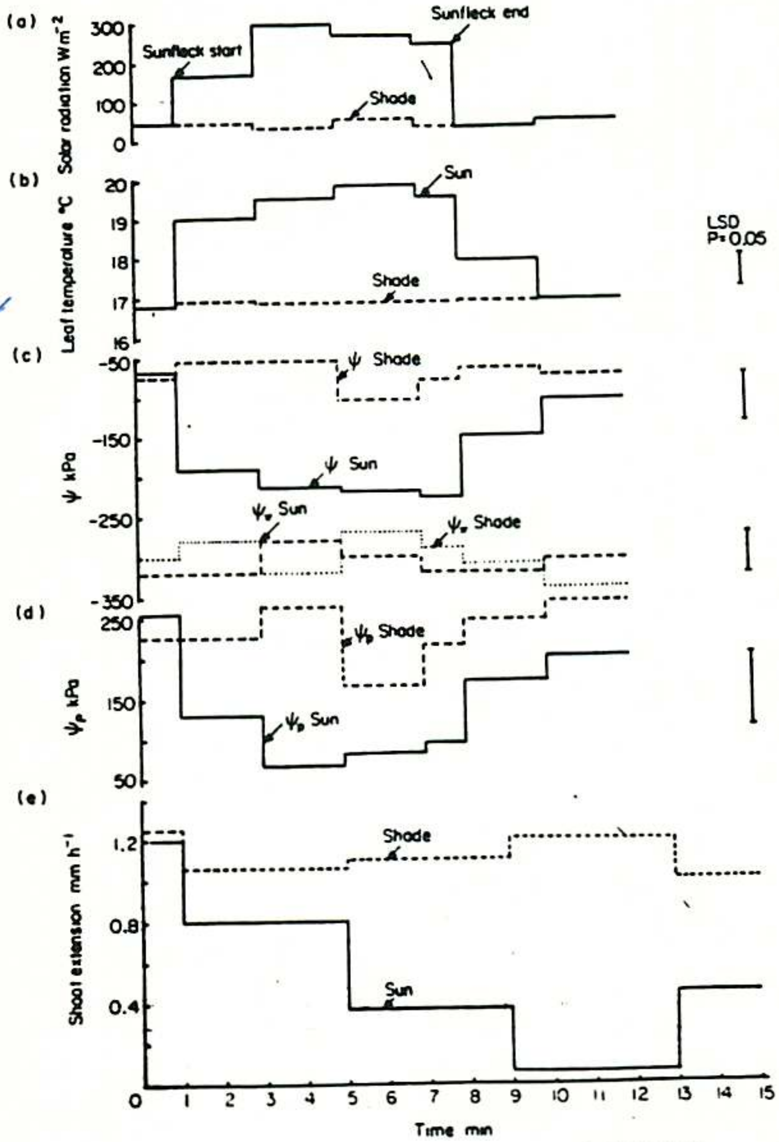


FIG. 5.3. Plant responses to a sunfleck: (a) solar radiation input; (b) leaf temperature; (c) leaf water potential (ψ_L) and osmotic potential (ψ_π); (d) leaf pressure potential (ψ_p); (e) shoot extension. Least significant differences shown at $P = 0{\cdot}05$.

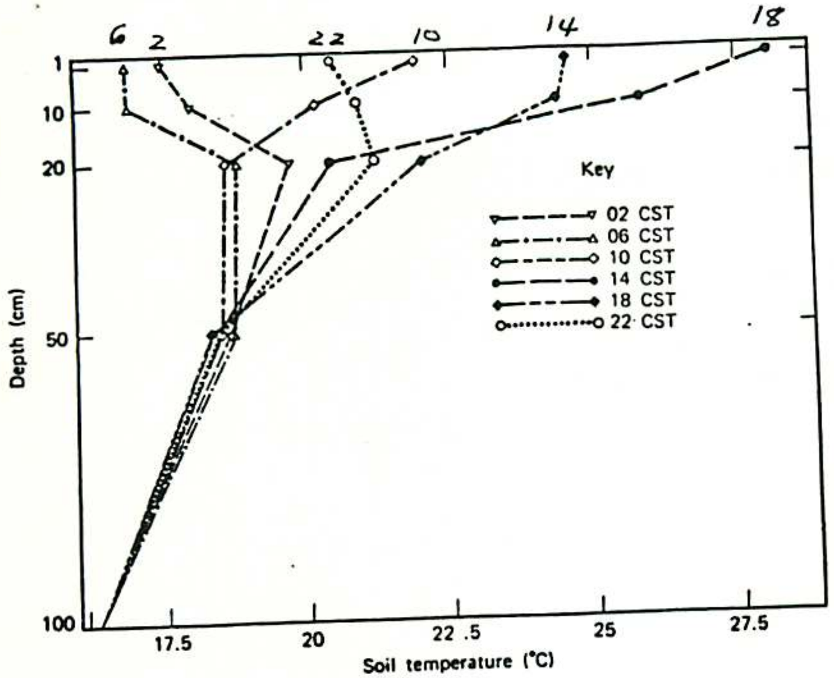


Figure 2.3. Vertical temperature profiles in soil during the course of a typical summer day at Argonne, Illinois, July 27, 1955 (after Carson and Moses, 1963).

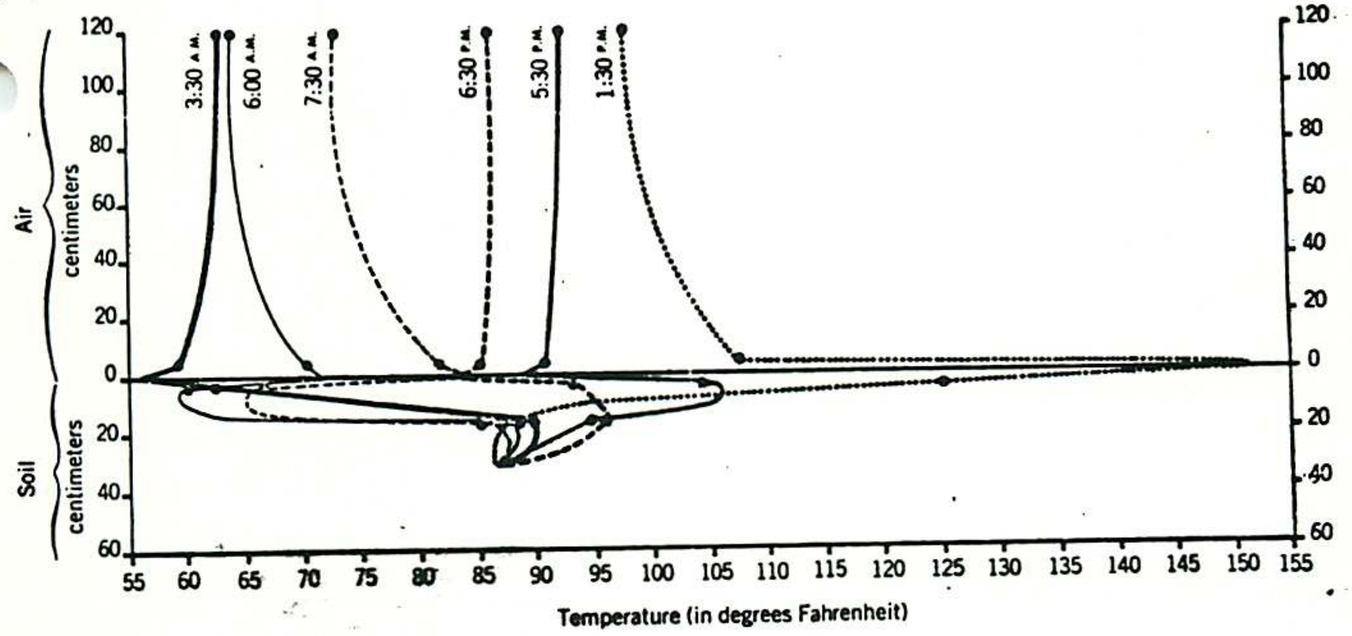


Figure 2-2. The daily cycle of lower air and soil temperatures as shown by temperature profiles at selected times of the day. Note the severity of the soil surface environment as indicated by its low and high extremes as compared with the relative lack of daily variation at minus 20 centimeters. Below 30 or 40 centimeters, only an annual cycle exists. Data from a vegetated sandy area in the Nevada desert (31 July 1953) with clear weather.

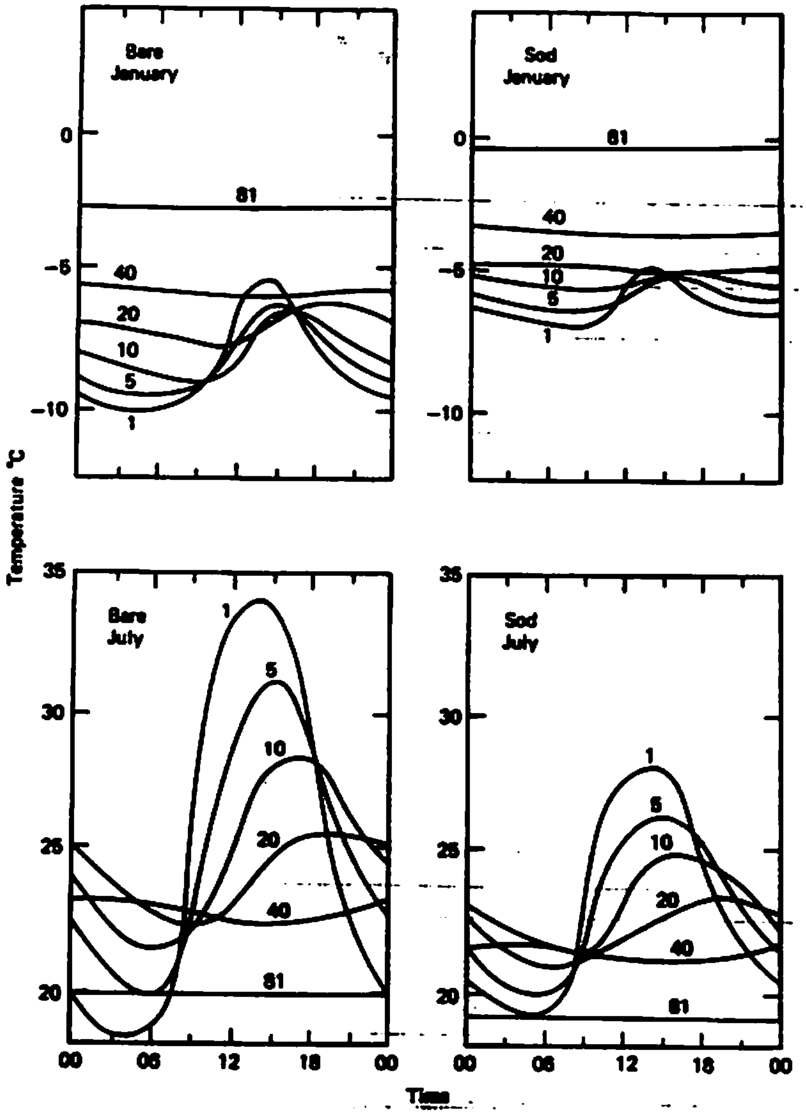


Figure 2.2 Average hourly soil temperature under bare and sod-covered soil at St. Paul, Minnesota in January (top) and July (bottom) 1961. Soil depth is shown in cm (after Baker, 1965).

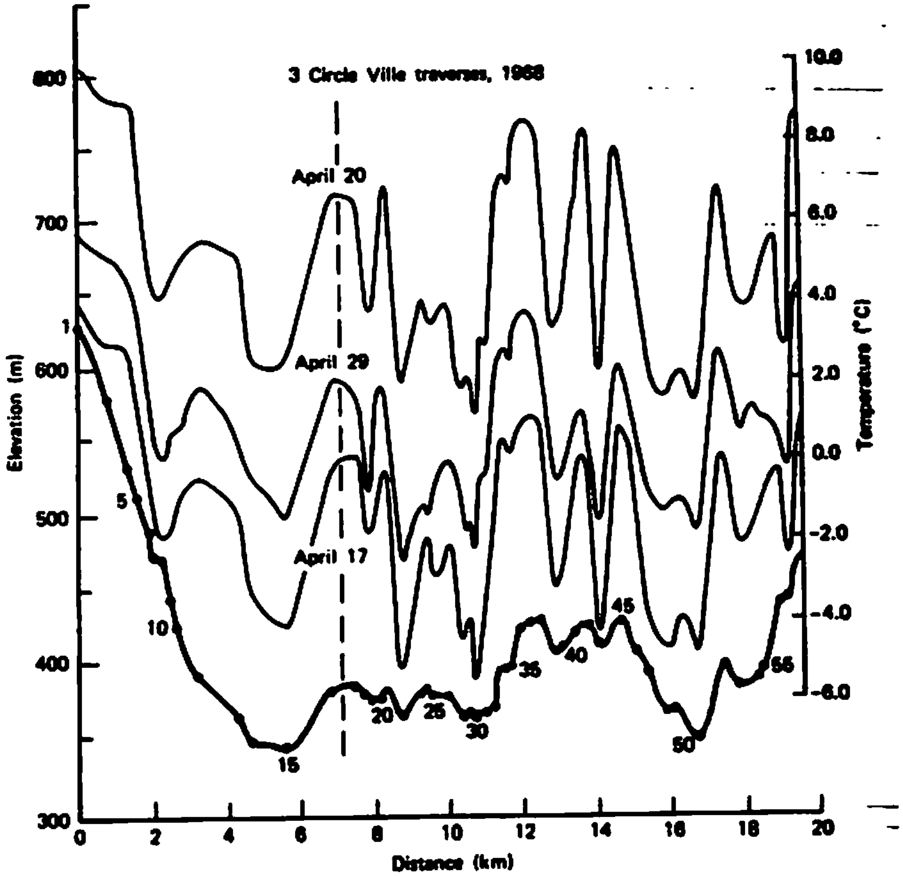
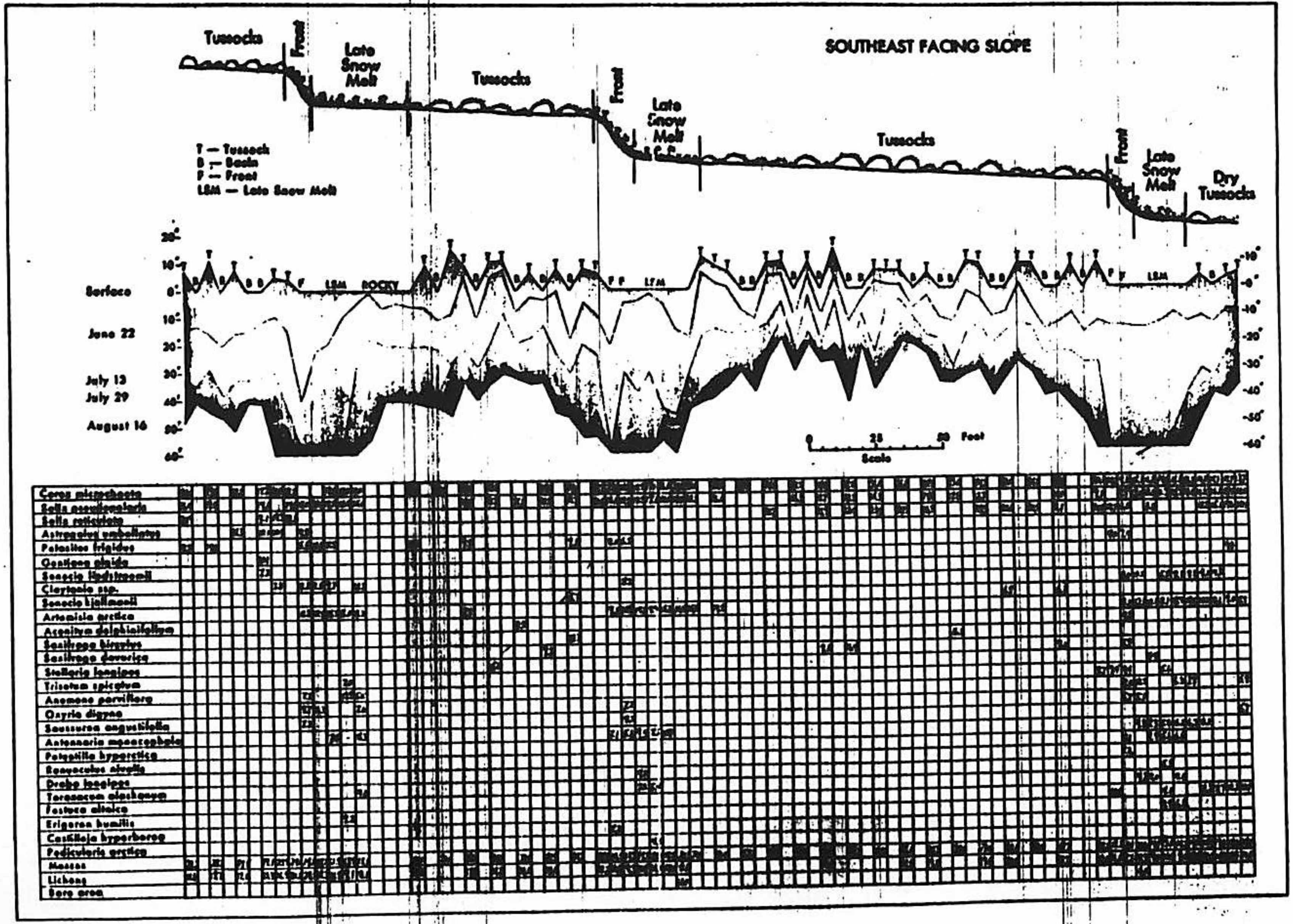


Figure 11.3. Variation of temperature for three mornings in relation to the relief along the Circle Ville traverse with the dots on the relief indicating the observation points (after Hocevar and Martsolf, 1971).


SOUTHEAST FACING SLOPE
Tussocks
Front
Late Snow Melt
Tussocks
Front
Late Snow Melt
Tussocks
Front
Late Snow Melt
Dry Tussocks
T — Tussock
B — Basin
F — Front
LSM — Late Snow Melt
ROCKY
LTM
Surface
June 22
July 13
July 29
August 16
20°
10°
0°
10°
20°
30°
40°
50°
60°
-10°
-0°
-10°
-20°
-30°
-40°
-50°
-60°
0
25
50 Feet
Scale
Carex microchaeta
Salix pseudopolaris
Salix reticulata
Astragalus umbellatus
Petasites frigidus
Gentiana algida
Senecio lindstroemii
Claytonia spp.
Senecio kjellmanii
Artemisia arctica
Aconitum delphinifolium
Saxifraga hirculus
Saxifraga davurica
Stellaria longipes
Trisetum spicatum
Anemone parviflora
Oxyria digyna
Saussurea angustifolia
Antennaria monocephala
Potentilla hyparctica
Ranunculus nivalis
Draba longipes
Taraxacum alaskanum
Festuca altaica
Erigeron humilis
Castilleja hyperborea
Pedicularis arctica
Mosses
Lichens
Bare area

RADIATION BALANCE

		CAL
NET RADIATION	NORTH SLOPE (N)	11900
	SOUTH SLOPE (S)	17200
EVAPORATION	N	2060
	S	2460
TRANSPIRATION	N	3980
	S	4260
SENSIBLE HEAT TO AIR	N	5000
	S	9600

PRODUCTION

		$G \cdot M^{-2}$
ROOT	N	121
	S	94
SHOOT	N	214
	S	228
SEED	N	119
	S	88
TOTAL	N	454
	S	410

NUTRIENT CONTENT OF SHOOTS (%)

	N	P	K	CA
N	1.06	0.16	1.09	0.78
S	1.33	0.20	1.34	0.92

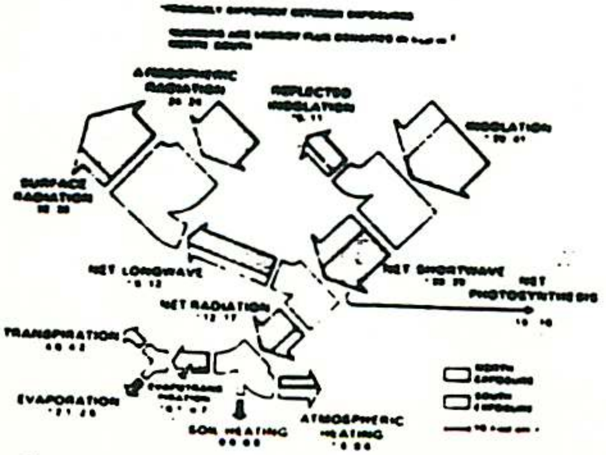


FIG. 11. Flow sheet of energy in the environment on north- and south-facing slopes, spring 1972.

Experimental Plant Ecology (Biology 149) October3, 1989

The response of plants to the radiation environment

Outline for Lectures 5, 6 and 7

1. Seed germination
   Response to Light quality and quantity (Red to Far Red)
   Temperature and rate of germination
   Interaction of dormancy, disturbance and radiation environment (Ambrosia artemisiifolia as a model)

2. Photosynthetic response to radiation
   Leaf structure and function
   Photosynthesis in brief
   Resistance to CO_2 and water exchange
   Biochemical steps in C3, C4 and CAM

   Sun and shade morphology and physiology
   Gas exchange in a rapidly changing radiation environment-
   Sunflecks, induction, tracking and acclimation
   Change in response with changing position in canopy, and age

   Field considerations - whole system photosynthesis

Readings

R.W. Pearcy et al 1987. Carbon Gain by plants in natural environments.Bioscience 37:21-29

K. Loach 1967. Shade Tolerance in trees. I. Leaf photosynthesis and respiration in plants raised under artificial shade. New Phytologist 66:607

C.B. Field 1988. On the role of Photosynthetic responses in constaining the habitat distribution of rainforest plants. Australian Journal of Plant Physiology 1988 15:343-58.

M.G. Barbour, J.H. Burk and W.D. Pitts 1980. Chapter 13, Light and photosynthesis 300-328 in Terrestrial Plant Ecology.

14:10 vs 28:20
- clones of plants

↑ - temperature dependence of germination ① percentage of max. ② rate
 ① depends on location of species
 ② variation in range of responses

 ③ variation in thresholds
 ④ " " " rate

⑥ Dormancy, etc.
- inability of seed to germinate when environment is "good" is dormancy

enforced dormancy

① dormant by nature - "after ripening germination"
② winter dormancy "innate dormancy" "stratification"
 ⓐ - seed coat weathers
 "imbibition : H_2O in"
 ⓑ leeching / washing
 - removal of chemicals that counter giberellic acid effect
 ⓒ movement; death; ingestion
 - longevity

what about sensitivity to light patterns

③ induced or secondary dormancy
 - many factors necessary
 - H_2O; $h\nu$; nutrients; T°
 - if one factor is missing may go dormant and stay even if missing part is returned

Disturbance - see Fig 2
- in soil: dark; low T° fluct; high CO_2
- longevity

Why induced dormancy?
- bec. there is a time when can't "do it" no more
  - too late

Must have
- Want to have some germination regardless of conditions.
- longevity - allows . . .

How differ between fall/spring (similar conditions)
① use environmental cues
- in desert = rain
- how sense? - wash out inhibitor
- but problems . . .

ⓐ degree days - "count" # of days above ~~min~~ some T°

ⓑ early spring protections
① resist cold nights

TEMPERATURE RESPONSE
- range differs

Two Parameters - see Fig 3
- response to T° and patterns of dormancy can tell a great deal.

Variation
phenotype; genotype; morphology

Longevity → measured by "viability" length
① predation   Heisenberg Problem
② death

Jon

10/3

How do you measure longevity
-try and match presence of seed vs. presence of plant
-"experiments" all tough

Experiment Ideas
- seed germination *
- L:D rhythm - w/ diff R:far red
- clones of plants

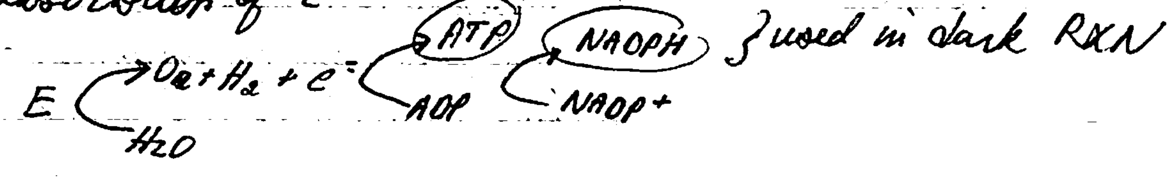
Plants · the Effects of Radiation on ... 10/5

Seed
↓
Respiration
↓
Growth
↓
Photosynthesis

$$CO_2 + H_2\underline{O} \longrightarrow CH_2O + \tfrac{1}{2}\underline{O_2}$$

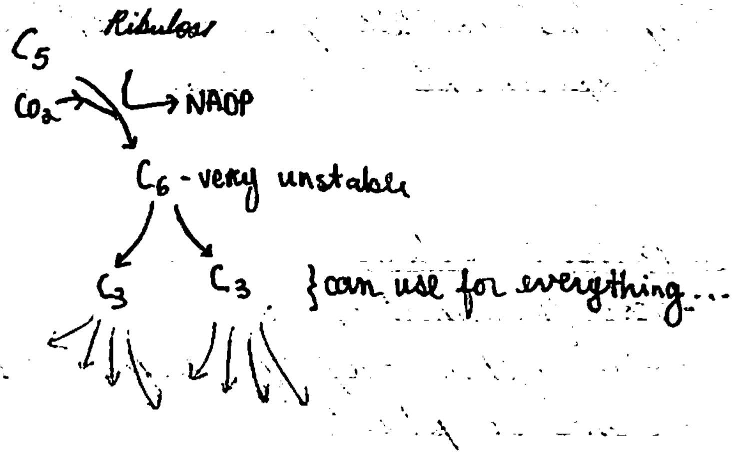
chloroplasts
-grana lamellae - have chlorophyll
-stroma " - where E diffuses into

Light Reactions
·absorbtion of E



} used in dark RXN

Dark Reactions



Photosynthesis Requirements

① Precursors, enzymes, supplies

Resistances

M

Stomata Res R_s
R_m mesophyll

Ⓐ CO₂

air → boundary layer → stomata →
cell walls → cell membranes → chloro
membranes → lamellae

Boundary Layer Resistance R_A
- low but variable
- SA, roughness, wind speed, leaf size,

Stomata Resistance - R_s
- very variable but highly controllable

Mesophyll
~~Boundary~~ Layer Resistance R_m
- high
- relatively constant
- "carboxylation resistance" - which is a problem of enzymes - RUBISCO
- Rubisco activity varies greatly

$1C + 5C \xrightarrow{rubisco} 6C$

$R_A + R_m + R_S$

R_S - variable resistance

What controls stomata opening?

① - Light (closed at night)

② $[CO_2]$ - if low inside then want open

250-300 ppm is good

③ $[H_2O]$ - regardless of $[CO_2]$: $[h\nu]$ - might want to shut down

low H_2O

$\downarrow$

abscissic acid

- If there is low $[H_2O]$ the no $H_2O \rightarrow O_2$ (with e^-)

so would limit ATP & NADPH production

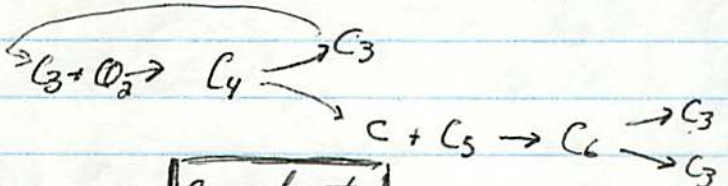
- distinguish betw. $h\nu$ and CO_2 by mutations

Variations in Carbon fixation

① $1C + 5C \rightarrow 6C \rightarrow C_3, C_3$ $\boxed{\therefore C_3 \text{ plants}}$

· the supply here is important

② but can take $CO_2 \rightarrow C_{(A)}$ then break down later



$\boxed{C_4 \text{ plants}}$

see Fig 4

C_4

- sunny open environments
- less efficient
- concentrated in few families

Rubp is both
- carboxylase -
- oxygenase - so went to protect from O_2

C_3
- in high $[O_2]$ → photosyn. decreases
- not problem in ~~C_3~~ C_4

- O_2 is being produced anyway

CAM - Fig 5
- thick leaved ; dry habitat plants
- v. much like C_4
- but separated activity temporally not physically
- but reverse timing

LUNCH!!

~~Day (open stomata~~

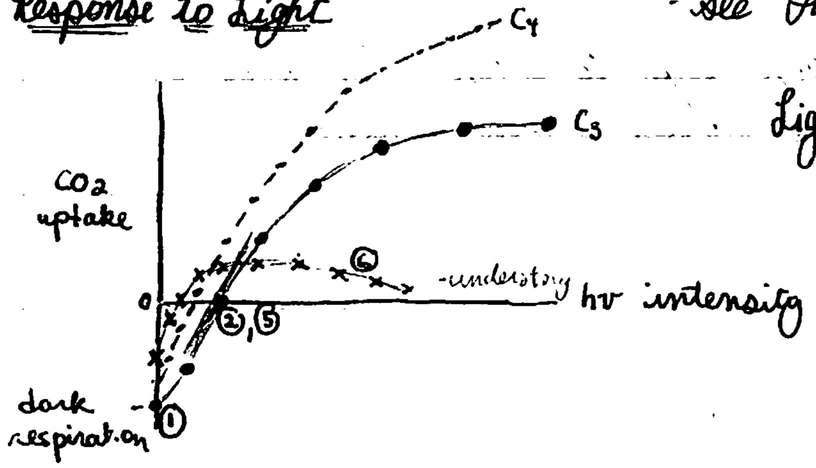
Night
- fix CO_2

Day
- $C_4 + C_5 \longrightarrow C_3 + C_6$

- C_4s are usually acids - accumulate at night

C_3 vs. C_4 - see Fig 6

__Response to Light__ - see Fig 7



Light Response Curve

①rate of dark respiration
②light compensation point $(d[CO_2]/dt = 0)$
③saturation rate
④max photosyn. rate
⑤ __init. slope__ *
- gives idea about "quantum yield" of photosyn.
- should be measure __of__ unit of absorbed light
  __but__ close enough

⑥ destruction of enzymes

can use same species in __diff__ environment
" " diff. leaf in same plant

Sun vs. shade leaves of same ~~plan~~ species
①__Diff morphologies__
high hv = thick, small
low hv : spongy, bigger
} CO_2 & H_2O v. important

__proteins__ (N) found mostly
- Rubisco
- chlorophyll

Thursday

∴ in sun → more N in rubisco
" shade → " " " chlorophyll

Recycling nitrogen up to sun (v. mobile)
cf. *Ecologia* - about value of leaf

10/3

Fig 1

concerned with
① percent
② rate of germination

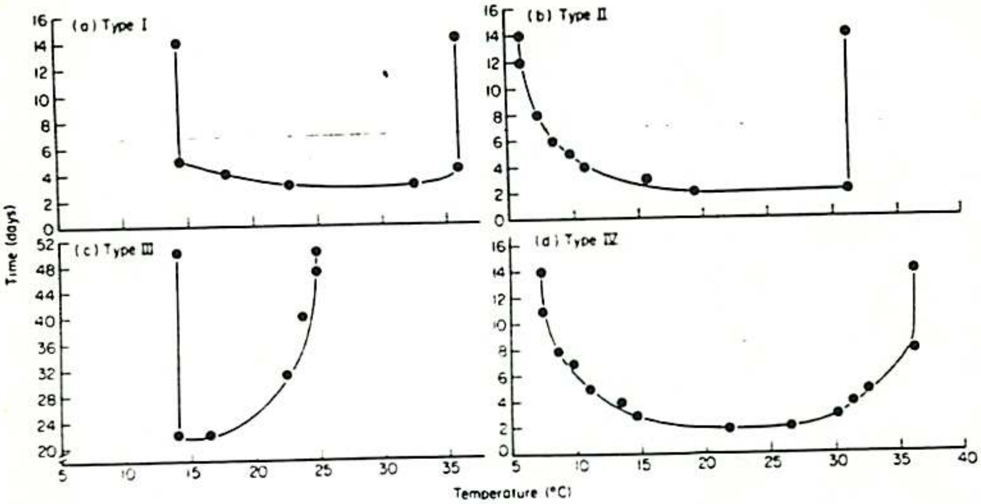


FIG. 1. The main types of germination response to temperature. Each curve has been constructed by plotting for successive days after sowing the maximum and minimum temperatures at which 50% maximum germination is attained. (a) *Ballota nigra* (Type I). (b) *Koeleria cristata* (Type II). (c) *Milium effusum* (Type III). (d) *Senecio squalidus* (Type IV).

variation in r
① range
② thresholds
③ rate

Fig d

10/3

Very many determinants of germination

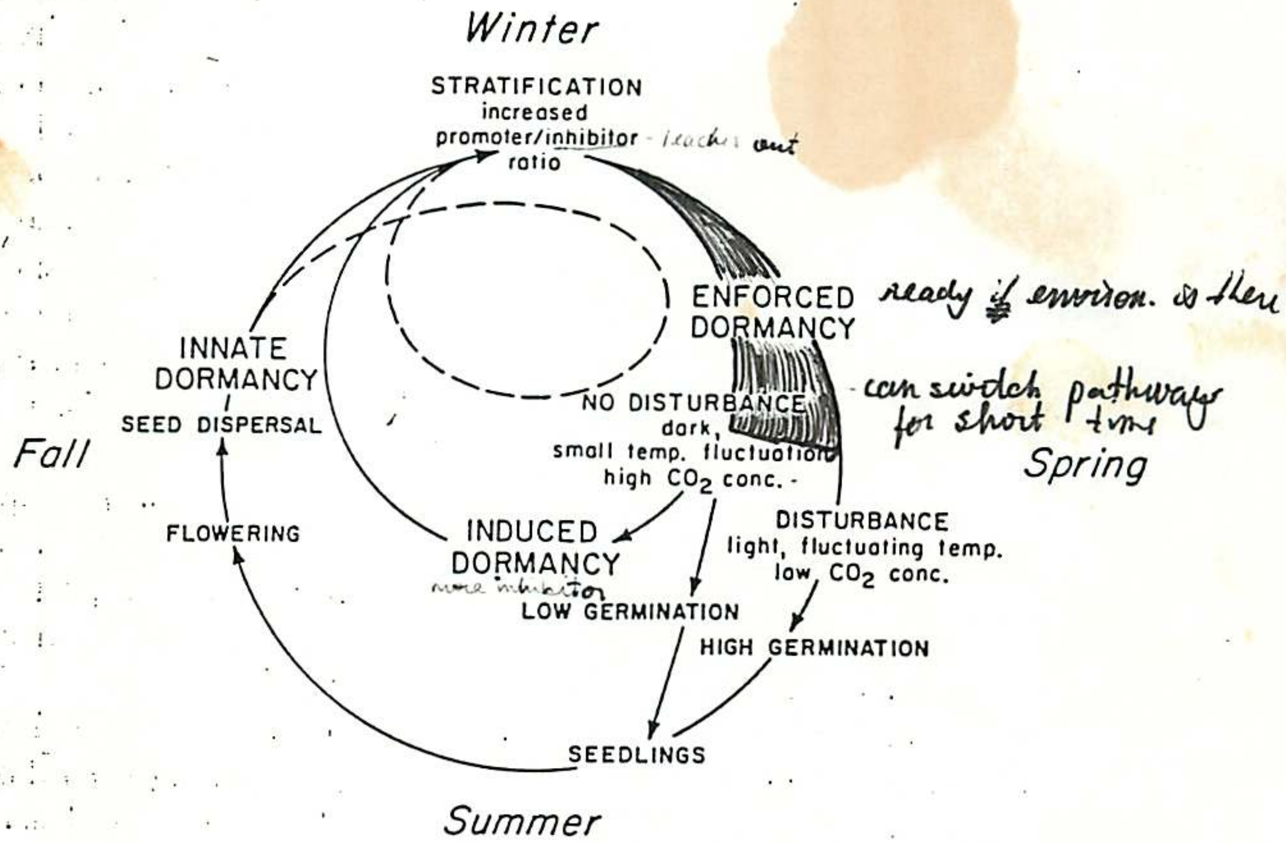


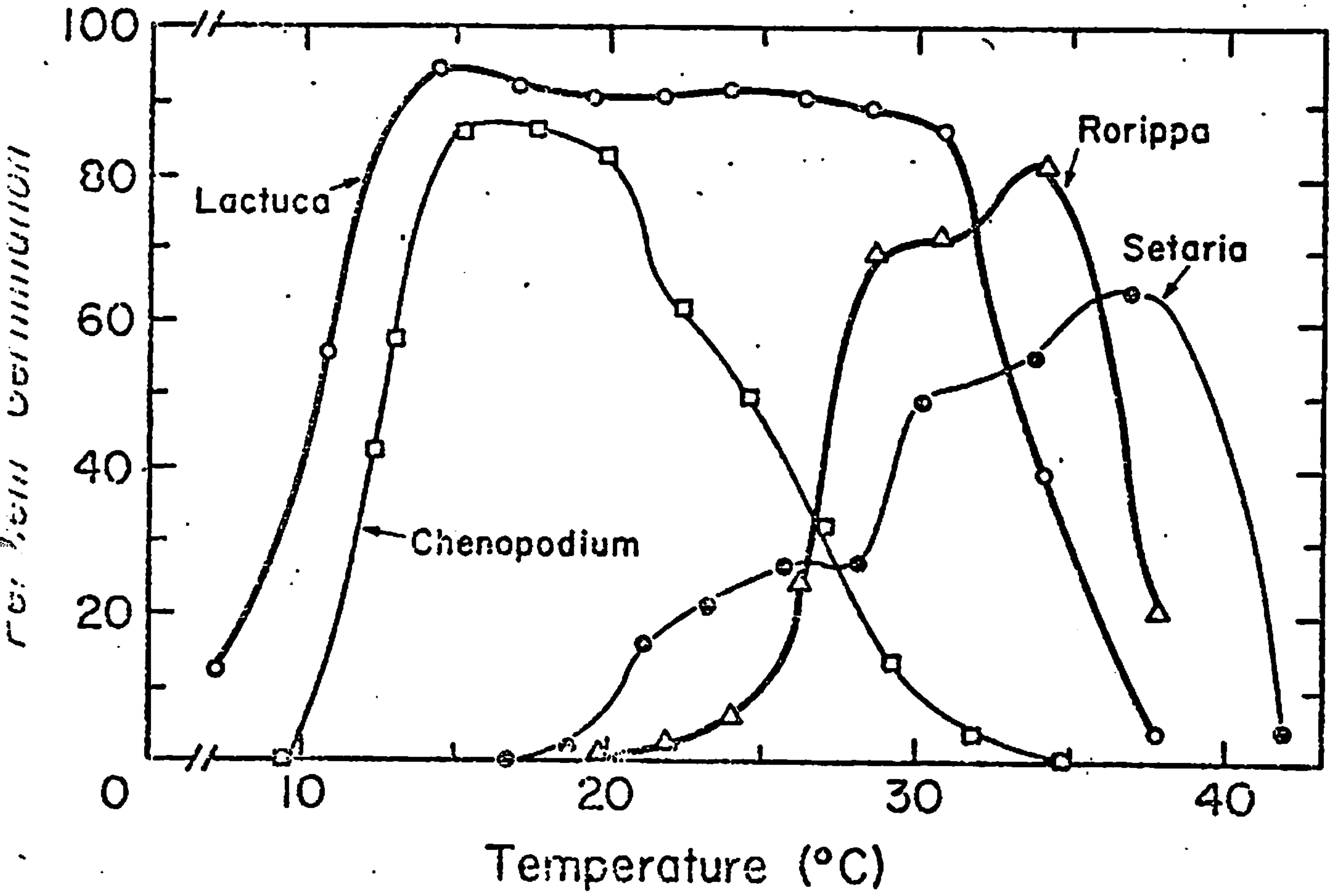
Figure 1 Schematic representation of seed germination in *Ambrosia artemisiifolia* L., a common colonizer in oldfield succession. Dashed line represents seed morphs that require more than one stratification cycle to germinate.

- ragweed
- comes up after disturbance
- seeds last long in soil

Fig 3

10/3

Temperature Response



- these plants are neighbors
- plants in one community coexist <u>because</u> they do this.

<u>Rorippa</u>
-no stratification
(summer)

<u>Setaria</u>
-strat needed

<u>Chenopod</u>
strat. needed
(following spring)

see Fenner, M. <u>Seed Ecology</u>. Chapman

Fig 1

10/5 4

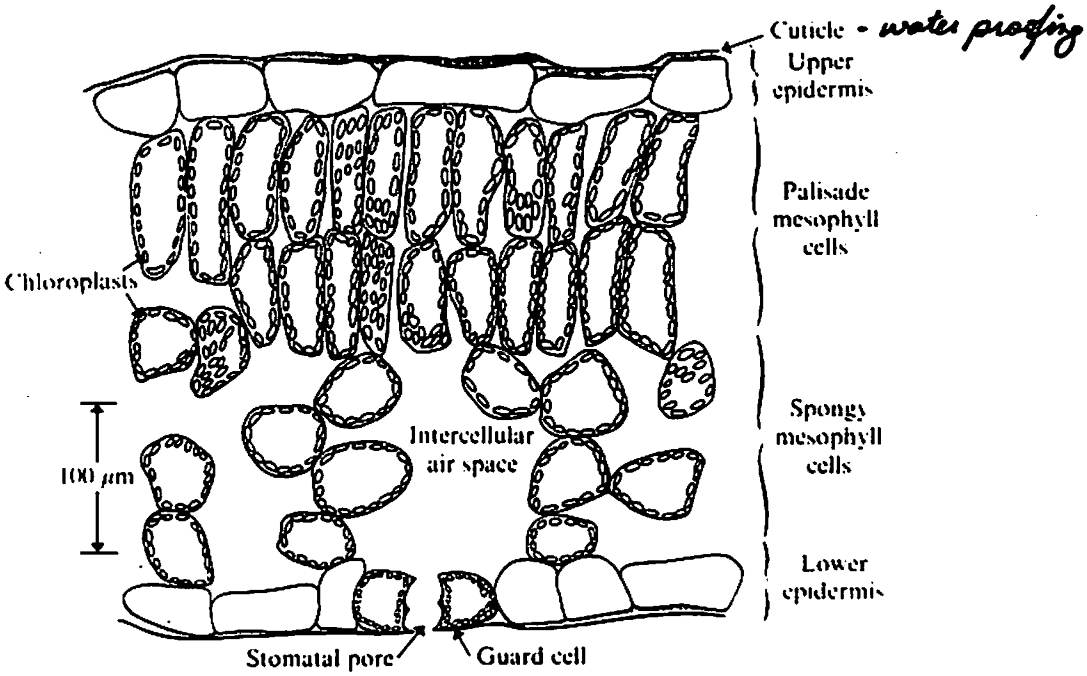


Figure 1.2
Schematic transverse section through a leaf, indicating the arrangement of various cell types. There are often about 30 to 40 mesophyll cells per stoma.

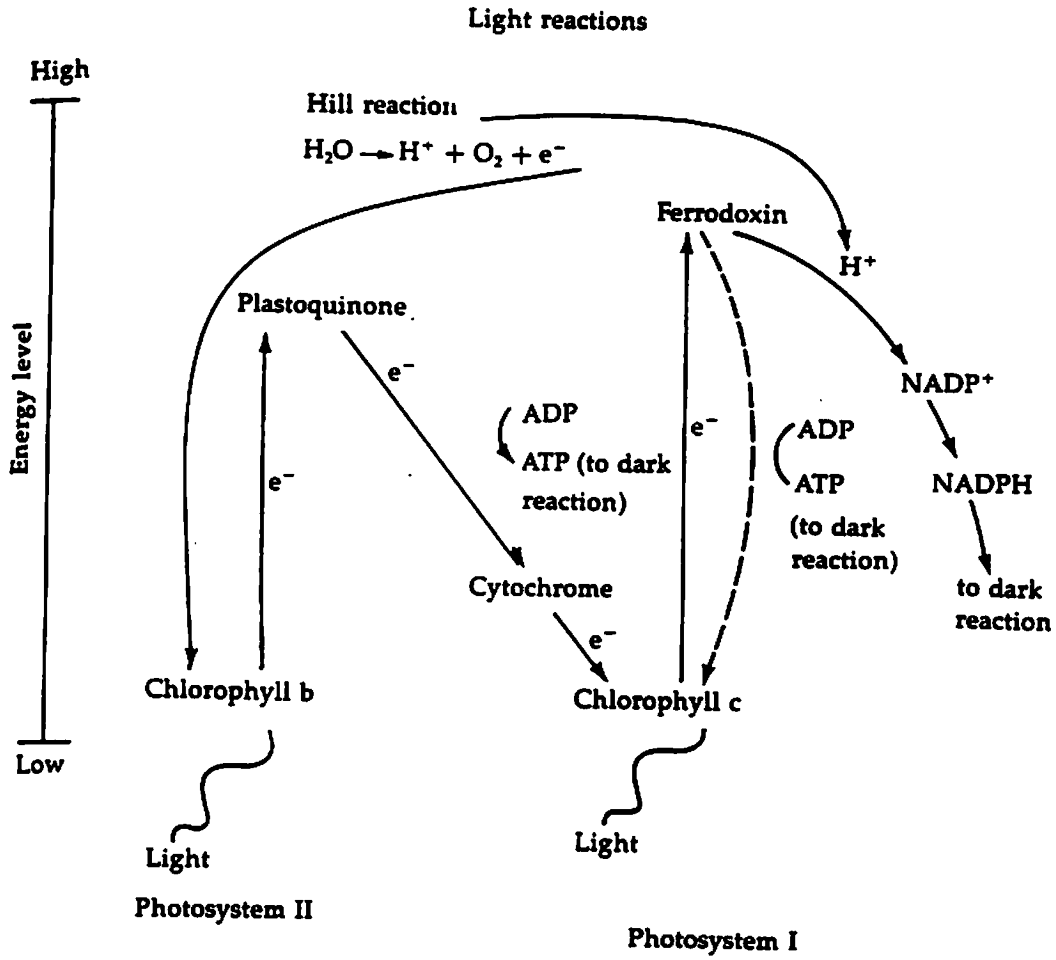


Figure 13-7. Overview of the light reactions of photosynthesis. Note that the chemical expressions are not balanced.

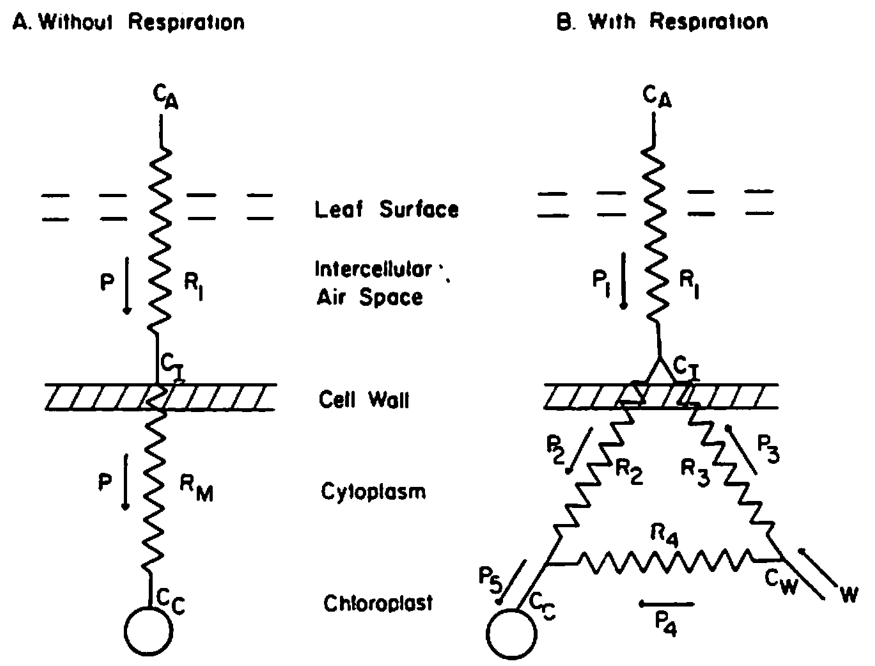


Figure 14.1. Electrical analogs for CO_2 exchange in leaves: (A) simplified resistance network without a respiratory source of CO_2; (B) resistance network with respiration. Fluxes are positive in the direction of the arrows. Symbols: *R*, resistance; *P*, CO_2 flux, *C*, CO_2 concentration; *W*, flux of respiration.

Fig 4

C3

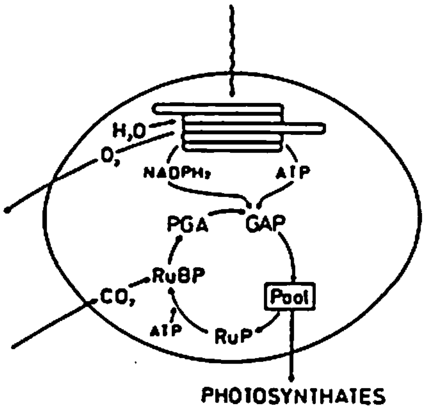


Fig. 3.2. Simplified diagram of CO_2 fixation and assimilation by way of the Calvin-Benson cycle in C_3 plants. *RuBP*, ribulose-1,5-bisphosphate; *PGA*, 3-phosphoglyceric acid; *GAP*, glyceraldehyde-3-phosphate; *Pool*, intermediary C_3 to C_7 compounds; *RuP*, ribulose-5-phosphate. The photosynthates are carbohydrates, carboxylic acids and amino acids. More detailed diagrams can be found in textbooks of plant physiology and biochemistry (see e.g., Bonner and Varner, 1976)

C4
- e.g. - Corn
- two diff types of chloroplasts
- more ~~efficient~~

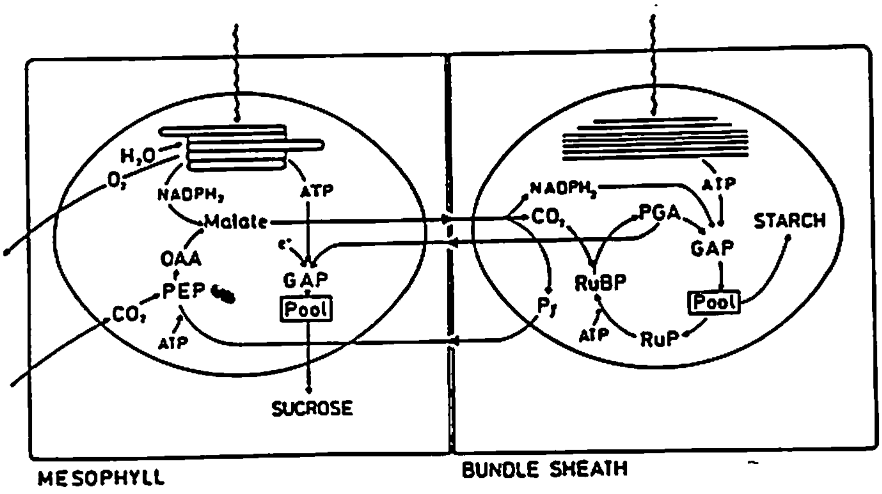


Fig. 3.4. A much simplified diagram of CO_2 fixation via the Hatch-Slack-Kortschak pathway in C_4 plants. *PEP*, phosphoenolpyruvate; *OAA*, oxaloacetate; *PGA*, 3-phosphoglyceric acid; *GAP*, 3-phosphoglyceraldehyde; *RuP*, ribulose-5-phosphate; *RuBP*, ribulose-1,5-bisphosphate; *Pr*, pyruvate. PGA is also produced by carboxylation of C_2 compounds which appear in the pool; the regeneration of PEP from PGA, in which water is given off, is not shown. For detailed diagrams see Hatch and Osmond (1976)

42/8

Fig 7

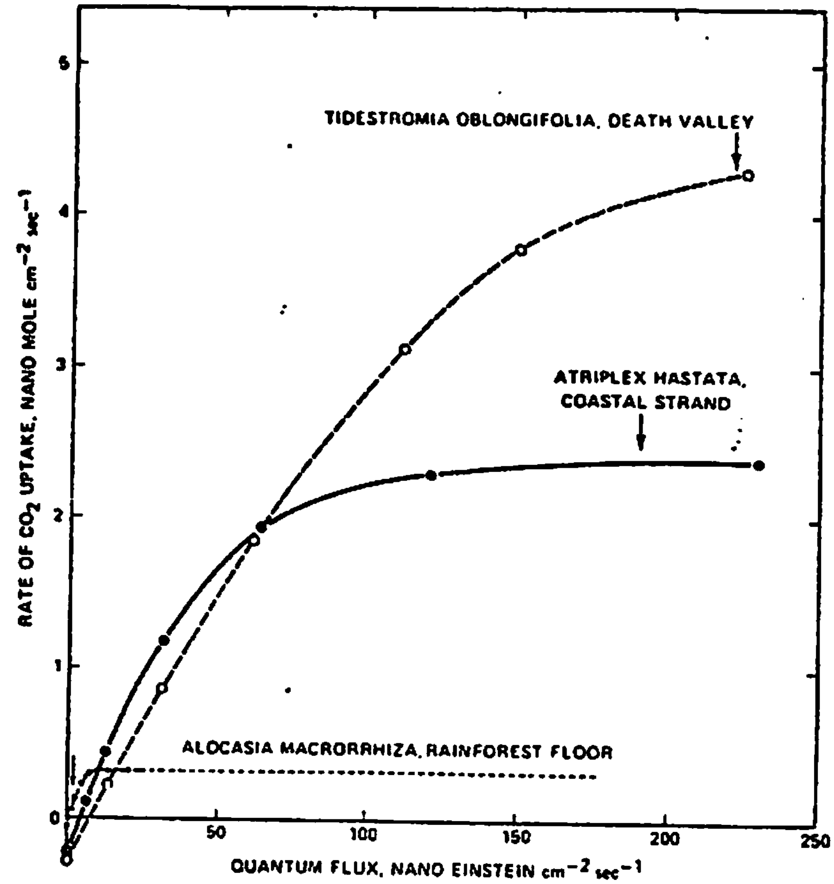


Fig. 1. Light dependence of net CO_2 uptake by single attached leaves, grown under the contrasting light intensity regimes of their natural habitats. Rates were determined at near optimum temperature for each species and at 320 μbar CO_2 and 21% O_2. The arrows indicate the average maximum light intensities to which the plants were exposed during growth (Data from Björkman et al., 1971, 1972; Mooney & Björkman, unpublished).

Fig. 33. Temperature dependence of the activity of RuDP carboxylase from grasses of the temperate zone (C_3 plants) and of PEP carboxylase from tropical grasses (C_4). (After Treharne and Cooper, 1969)

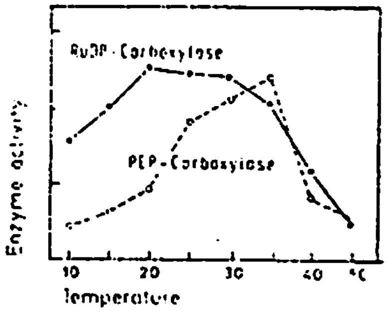


Fig 5

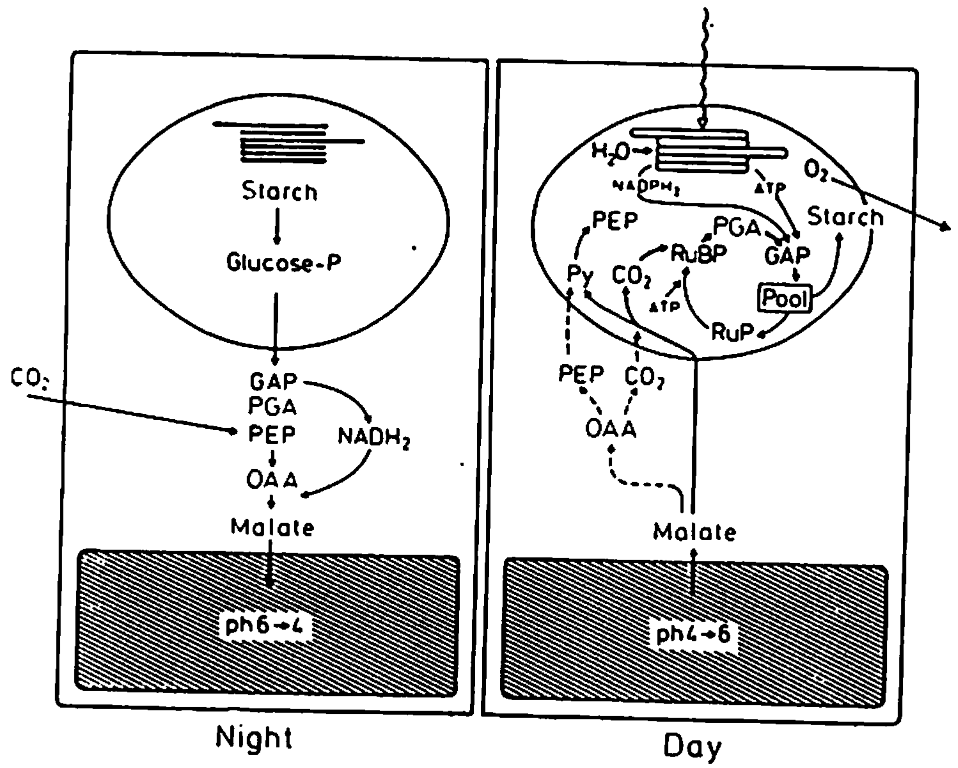


Fig. 3.5. Simplified diagram of the diurnal acid rhythm of CAM plants, and the photosynthetic utilization of the CO_2 released from malate. The way in which CO_2 produced during respiration is utilized is not shown. Labels as in Figures 3.2 and 3.4. Derived from Kluge (1971) and Osmond (1978)

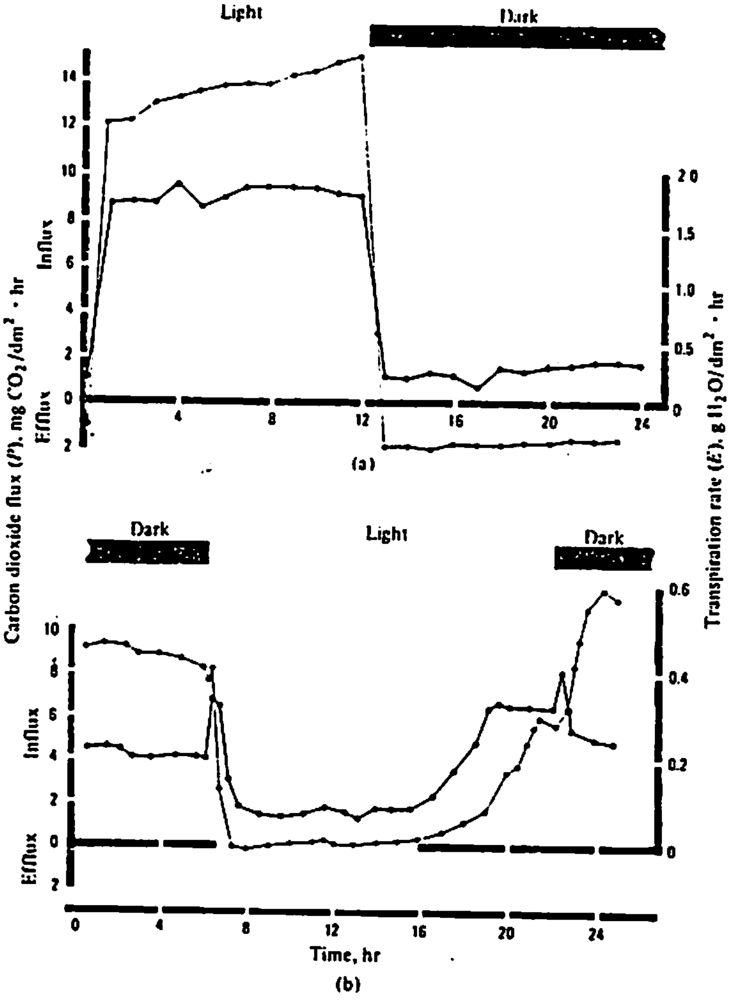


FIGURE 7-2 Diurnal patterns of photosynthesis (light line) and transpiration (dark line) in (a) a sunflower, a C_3 plant adapted to high-moisture habitats, and (b) a CAM desert succulent. The desert species has an inverted stomatal rhythm, with the stomates open during the dark when evaporative stress is low. [After Neales et al. (1968).]

Fig 6 10/5

11

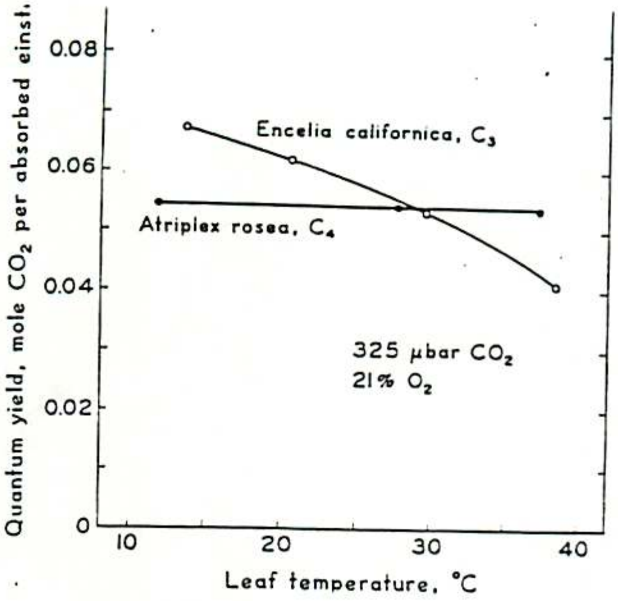
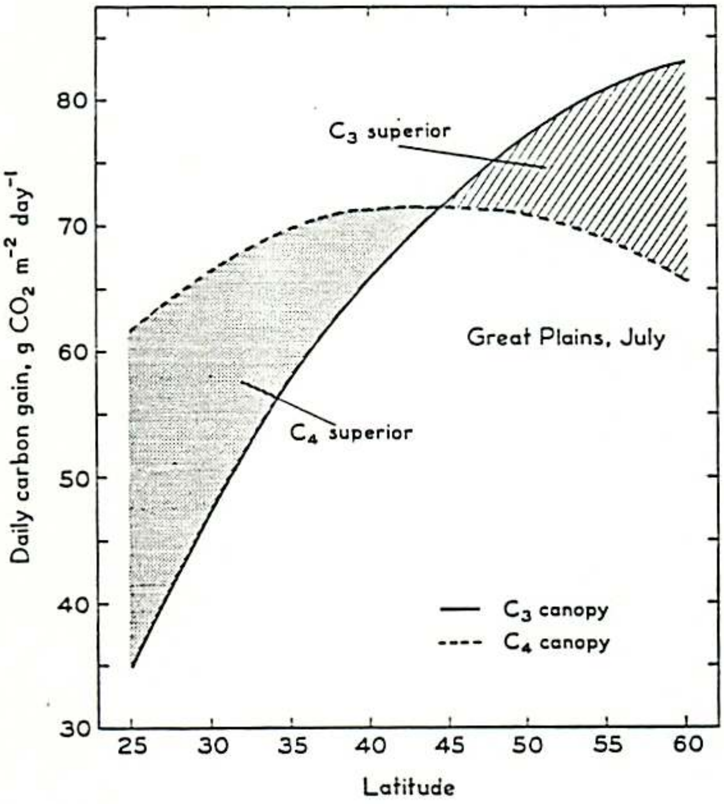


Fig. 1. Quantum yield for CO_2 uptake in C_3 species *Encelia california*, and C_4 species *Atriplex rosea*, as a function of leaf temperature. Quantum yield was measured in normal air of 325 µbar CO_2 and 21% O_2. This figure is based on data from Ehleringer and Björkman (1977)

T° very important
rubisco
vs
pep. carboxylase
- much better at high T°
than rubisco



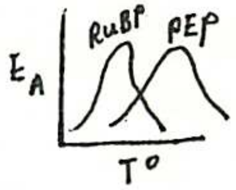
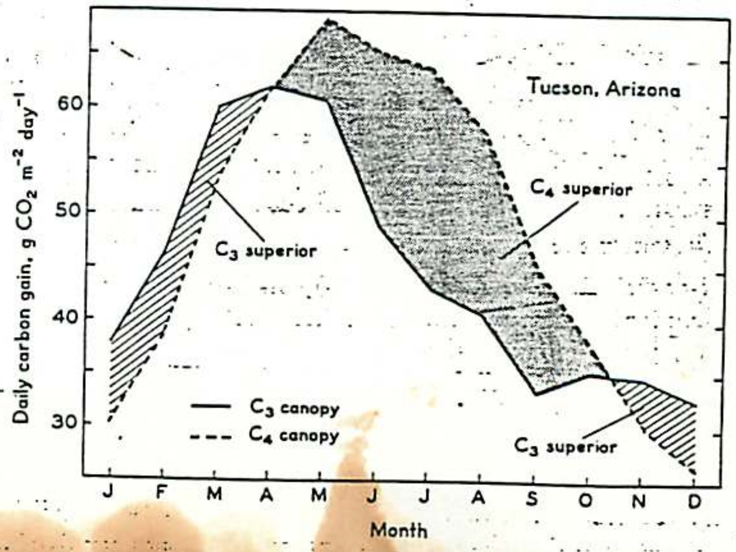


Fig. 4. Simulation of the total daily carbon gain for identical C_3 and C_4 grass canopies (LAI = 4) at different latitudes within the Great Plains of North America during the month of July

Fig. 5. Simulation of total daily carbon gain for identical C_3 and C_4 grass canopies (LAI = 4) at monthly intervals for Tucson, Arizona, within the Sonoran Desert



Characteristics of the Dominant Plants

	CALIFORNIA			CHILE		
	Boulder Creek	Camp Pendleton	San Telmo (Baja)	Fundo Station Laura (Tiltil)	Papudo	Tongoy
Latitude	32 50'	33 15'	31	33 10'	32 30'	30 25'
Estimated Annual Precipitation,mm.	450	200	160	450	350	100
Total % Woody Plant Cover	195.31*	99.50	58.23	59.29	48.42	32.11
Relative % Cover by Leaf Type						
Evergreen	98.58	32.78	12.45	72.61	50.31	31.83
Drought Deciduous	1.41	67.08	62.70	11.55	36.95	41.76
Stem Chlorophyllous	0.00	0.00	0.00	14.54	0.00	0.37
Succulent	0.00	0.06	24.85	0.46	11.36	22.33
Unclassified	0.01	0.08	0.00	0.84	1.39	3.71
Relative % Cover by Photosynthetic Type						
C_3	99.31	99.55	75.17	97.28	86.12	70.60
C_4	0.00	0.00	0.00	0.00	0.00	0.00
CAM	0.39	0.37	24.85	0.17	11.36	22.33
Unclassified	0.30	0.08	0.00	2.55	2.53	7.07

*Figure over 100% due to canopy overlap

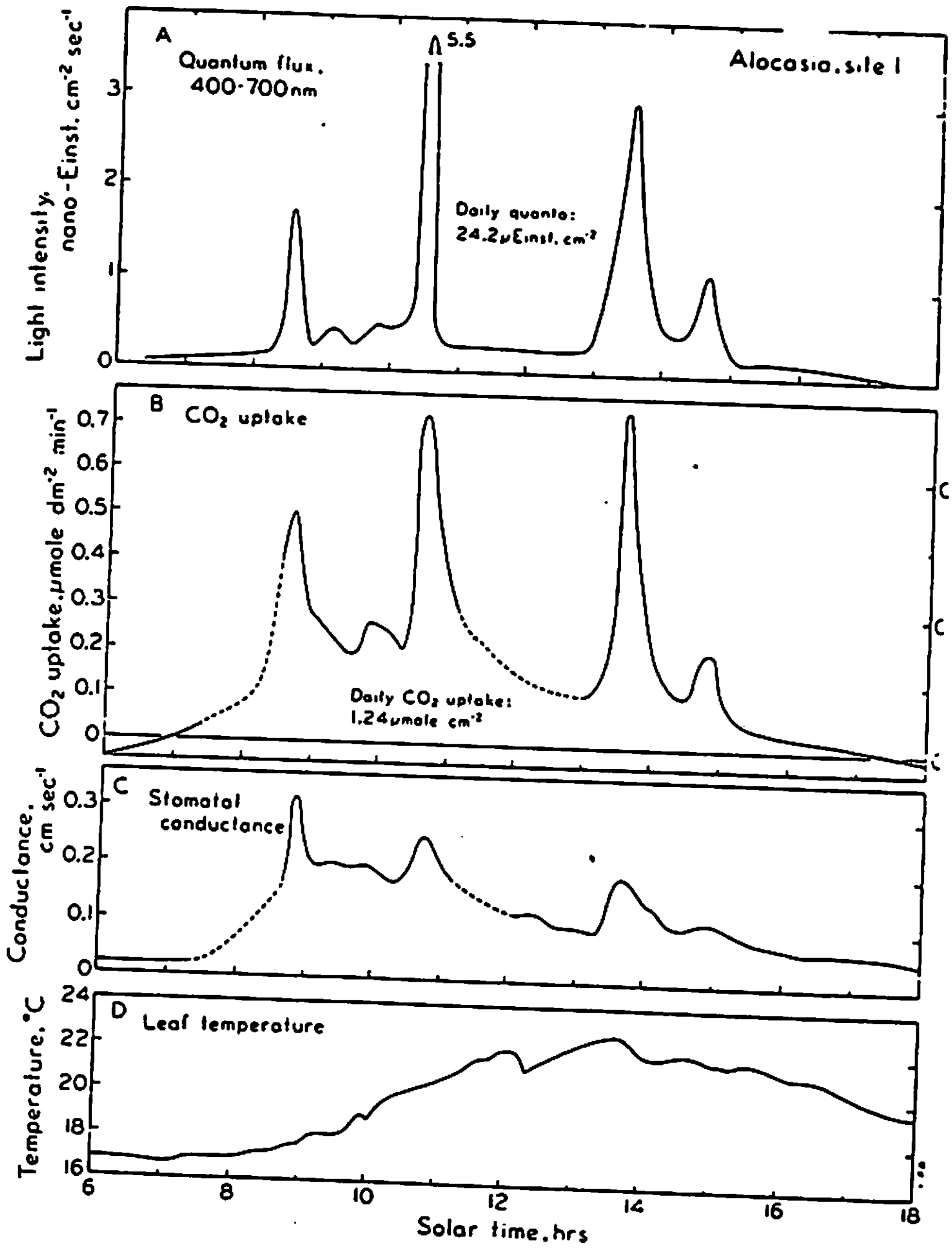


Fig. 7. Daily course of photosynthetic rate and stomatal conductance of an *Alocasia* l relation to the natural variation in quantum flux and leaf temperature at Site 1 on the floor on a clear day (March 31).

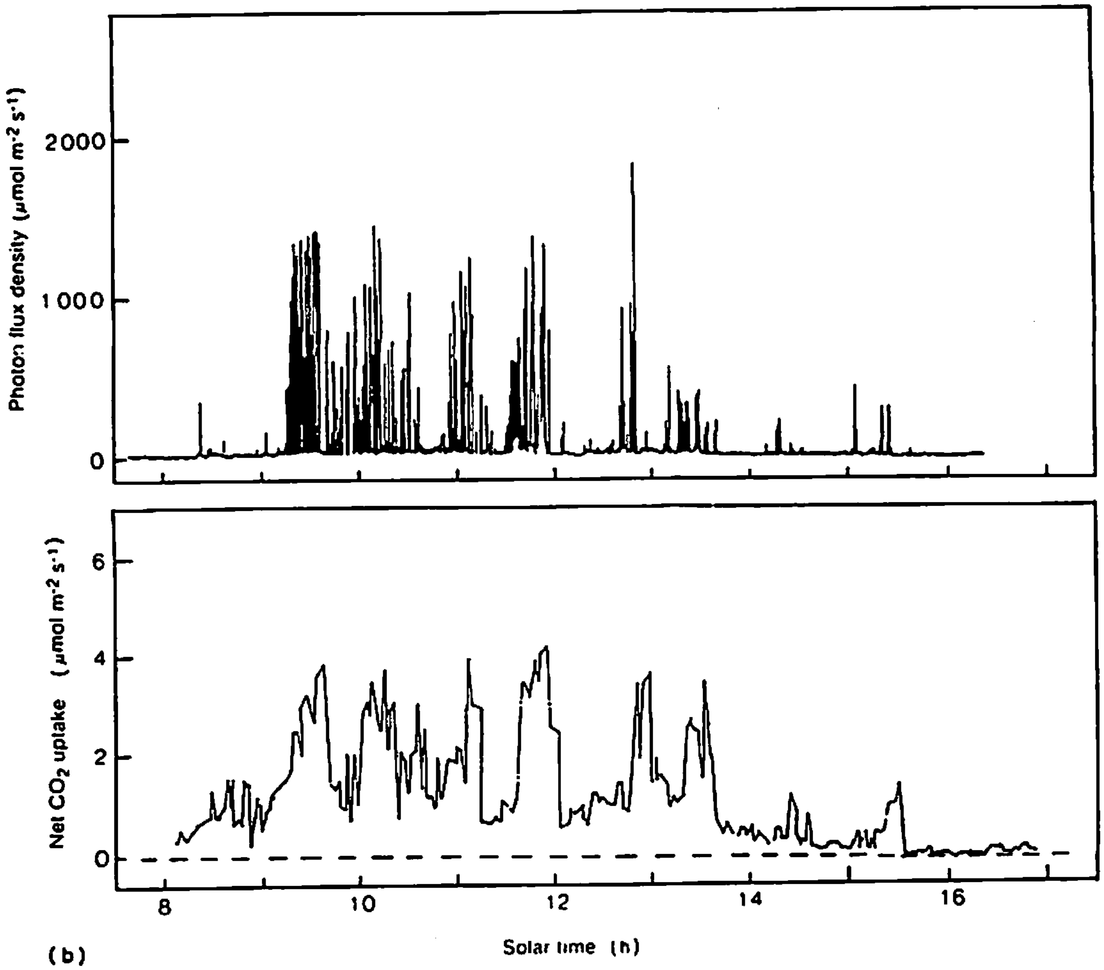


Figure 13.6 Diurnal courses of incident photon flux density, net photosynthetic CO_2 uptake, leaf conductance, and leaf temperature for *Euphorbia forbesii* on 16 July 1981 (a) and for *Claoxylon sandwicense* on 22 July 1981 (b) in Pahole Gulch, Oahu, Hawaii (Pearcy and Calkin, 1983).

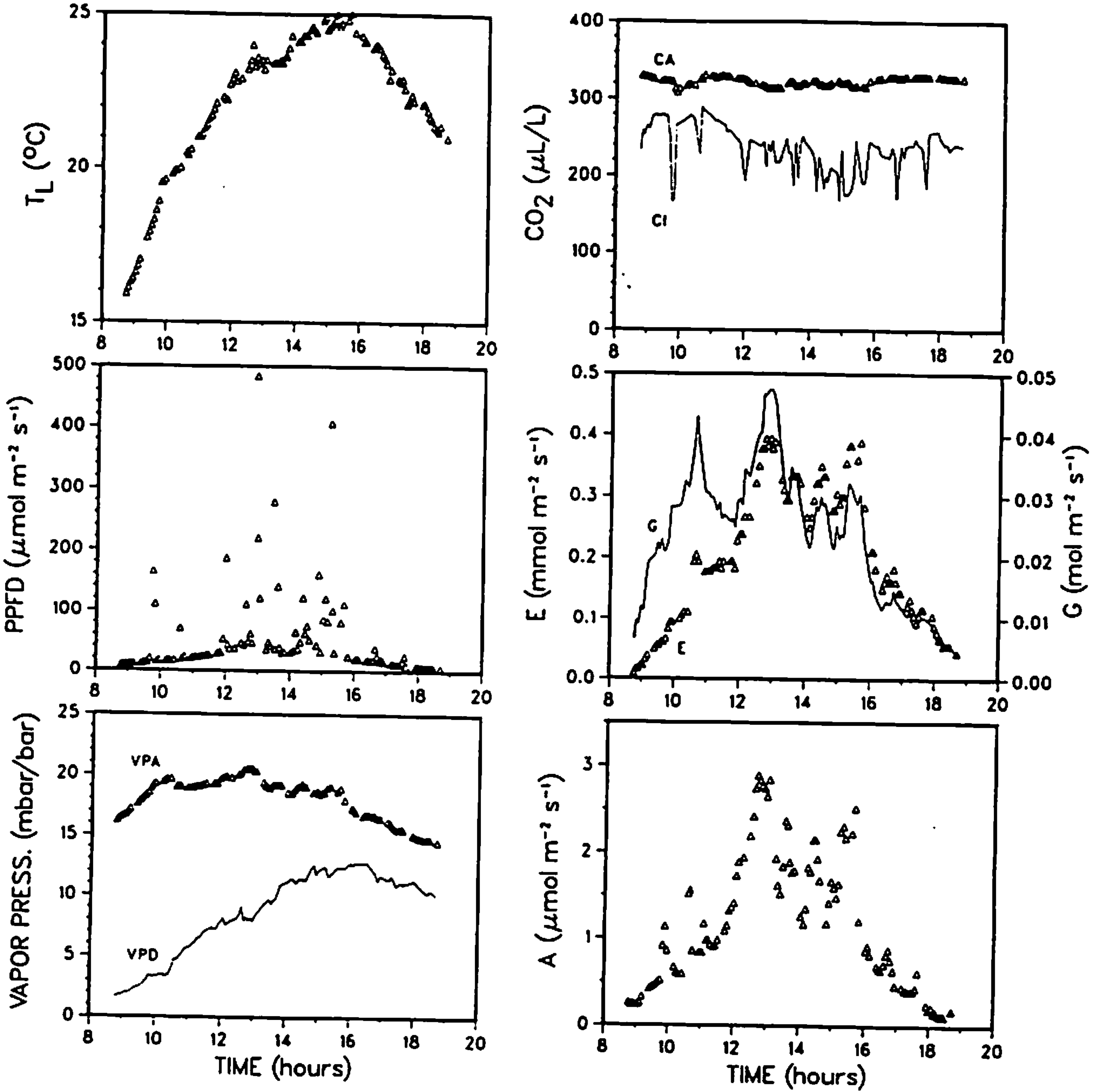


Fig. 5. Diurnal course of photosynthesis *A*, transpiration *E*, leaf conductance to water vapor *G*, and environmental factors for 13 Sept 1981

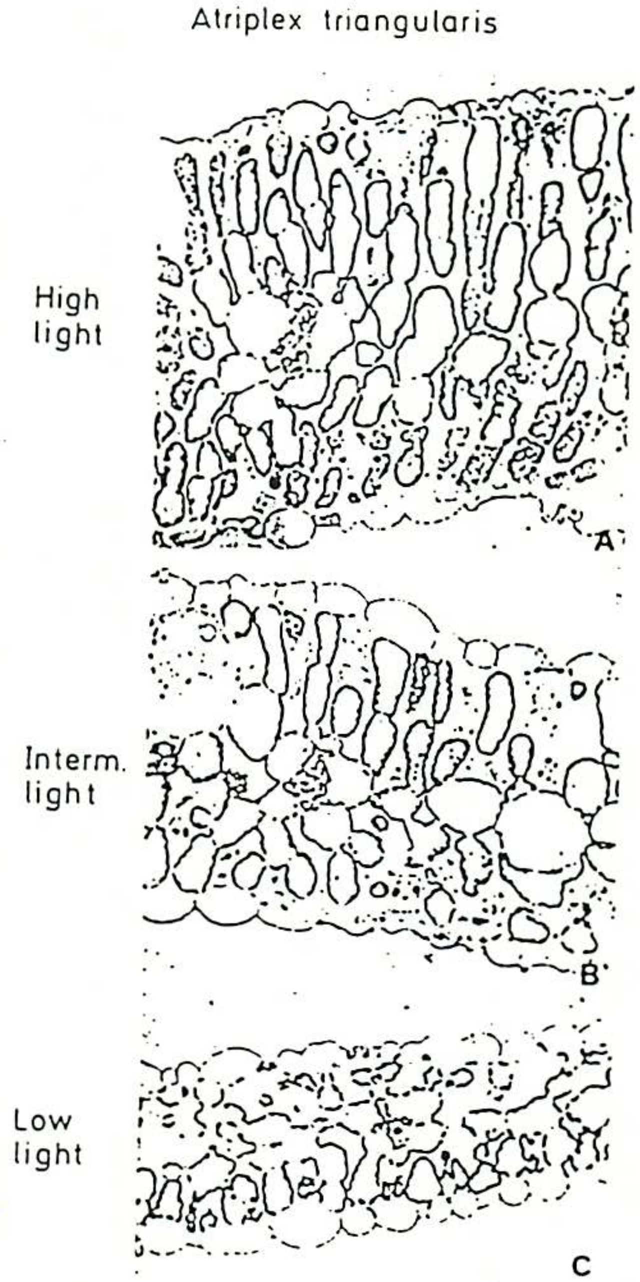


Fig. 9.9. Phase contrast light micrographs of leaf sections from *A. triangularis* plants, grown under three light regimes. (From Björkman et al., 1972a)

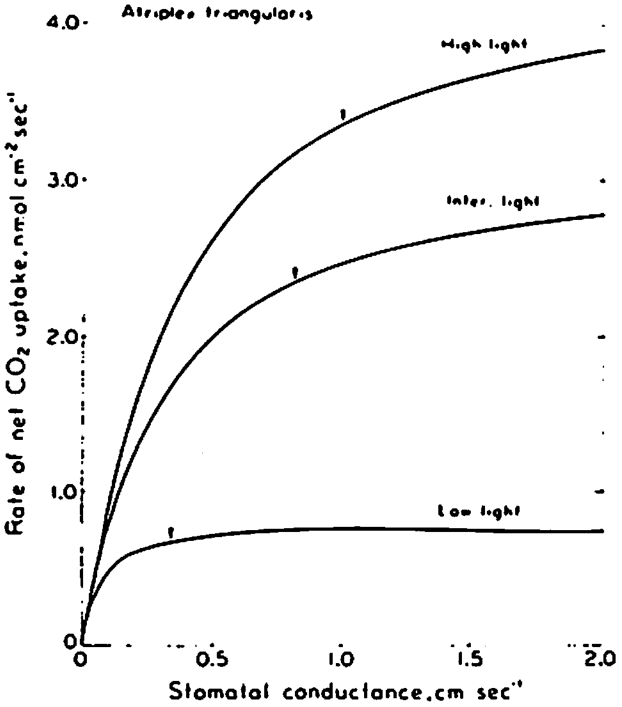


Fig. 9.11. Rate of light-saturated CO_2 uptake as a function of stomatal conductance, calculated from the experimentally determined relationship between CO_2 uptake and intercellular CO_2 pressure. *Arrows* indicate the actual stomatal conductances of the different leaves at light saturation and 320 μbar ambient CO_2 pressure. (From Björkman et al., 1972a)

Table 9.2. Photosynthetic activities and composition of the photosynthetic apparatus in leaves of *Atriplex triangularis*, grown under three different regimes. The numbers in parenthesis indicate the relative values compared with the low-light-grown plants. (Data from Björkman, unpublished)

Characteristic	High light-grown	Intermediate light-grown	Low light-grown
Photosynthetic rate in normal air, nmol cm^{-2} s^{-1} [a]	13.33 (4.85)	9.58 (3.48)	2.75 (1.0)
Leaf specific weight, mg dry wt. cm^{-2}	4.45 (2.51)	3.54 (1.99)	1.77 (1.0)
Leaf soluble protein, μg cm^{-2}	703 (2.40)	608 (2.07)	293 (1.0)
Cytochrome f content, n mol cm^{-2}	0.172 (2.53)	0.112 (1.65)	0.068 (1.0)
Cytochrome b_6 content, n mol cm^{-2}	0.253 (1.85)	0.227 (1.66)	0.136 (1.0)
Cytochrome b_{559} content, n mol cm^{-2}	0.241 (1.76)	0.218 (1.60)	0.136 (1.0)
Chlorophyll (a + b), n mol cm^{-2}	56.9 (1.21)	56.8 (1.21)	46.7 (1.0)
Leaf absorptance (400–700 nm)	0.83 (1.04)	0.83 (1.04)	0.80 (1.0)
P_{700} content, n mol cm^{-2}	0.132 (1.32)	0.131 (1.31)	0.100 (1.0)
Q content, n mol cm^{-2}	1.2 (1.2)	1.2 (1.2)	1.0 (1.0)
Quantum yield of PS II activity, rel. units cm^{-2} [a]	1.2 (1.2)	1.2 (1.2)	1.2 (1.0)
Ratio, mol chlorophyll (a + b) per mol P_{700}	430 (0.93)	433 (0.93)	468 (1.0)
PSI-driven electron transport, nEq. cm^{-2} s^{-1} [b]	20.8 (2.9)	14.5 (2.0)	7.3 (1.0)
PSII-driven electron transport, nEq. cm^{-2} s^{-1} [b]	19.3 (3.8)	11.7 (2.3)	5.1 (1.0)
RuP_2 carboxylase activity, nEq. cm^{-2} s^{-1}	26.0 (4.17)	19.24 (3.08)	6.24 (1.0)

[a] Measured at rate-limiting quantum flux densities

[b] Measured at high quantum flux density; 4 n equivalents correspond to 1 n mol CO_2 or O_2

Table 9.3. Stomatal conductance, stomatal frequency, and photosynthetic capacity in leaves of *Atriplex triangularis* grown under three different light regimes. The numbers in parenthesis indicate the relative values in comparison with the low-light-grown plants. (Data from Björkman et al., 1972a)

Characteristic	High light-grown	Intermediate light-grown	Low light-grown
Stomatal conductance, cm^{-2} s^{-1}	1.02 (2.91)	0.82 (2.34)	0.35 (1.0)
Stomatal frequency, number mm^2	407 (2.18)	335 (1.80)	186 (1.0)
Photosynthetic rate in normal air, nmol cm^{-2} s^{-1}			
a) Actual stomatal conductances	3.33 (4.85)	2.40 (3.48)	0.69 (1.0)
b) Infinite stomatal conductances	3.96 (5.36)	2.77 (3.74)	0.74 (1.0)
Photosynthetic rate in low O_2 and saturating CO_2, nmol cm^{-2} s^{-1}	5.27 (5.48)	3.66 (3.80)	0.96 (1.0)

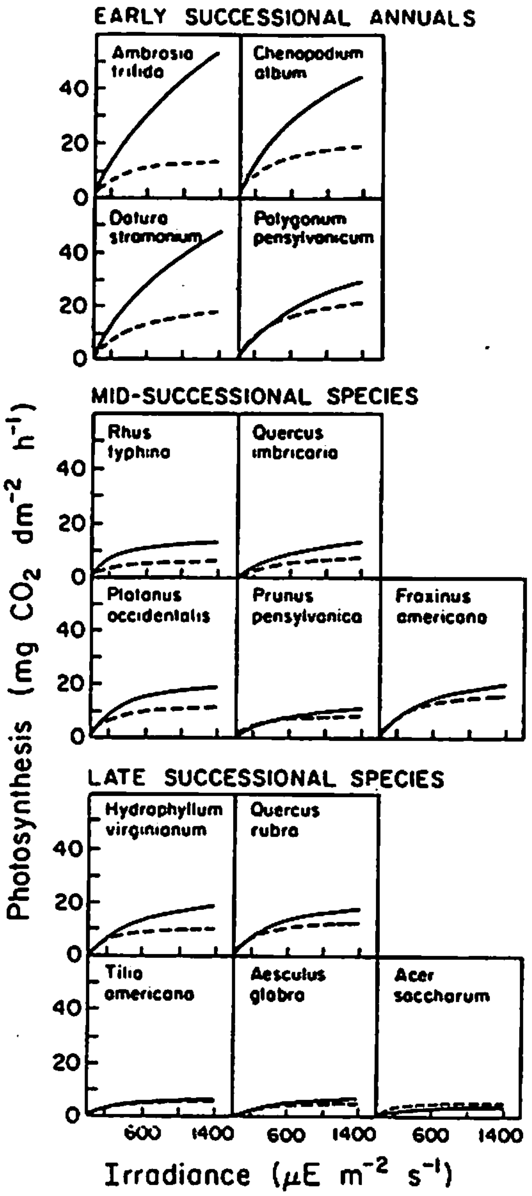


Fig. 1a–c. Photosynthetic response curves to light intensity for early successional annuals (a), mid-successional species (b), and late successional species grown (c) in full sunlight (solid lines) and in deep shade equal to 1% of full sunlight (broken lines)

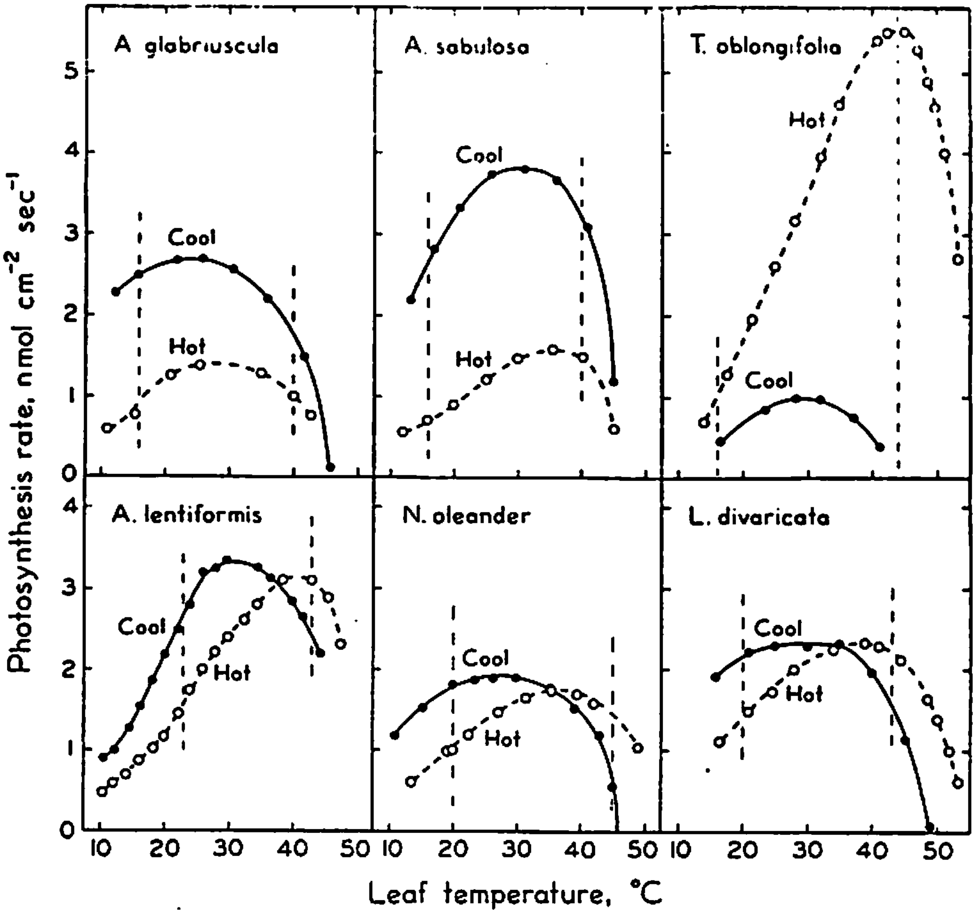


Figure 2 Effect of growth temperature regime on the rate and temperature dependence of light-saturated photosynthesis in normal air for a number of species native to habitats with contrasting thermal regimes. The vertical broken lines indicate the daytime temperatures of the "cool" and "hot" growth regimes for each species. Based on data of (30, 38, 130, 149).

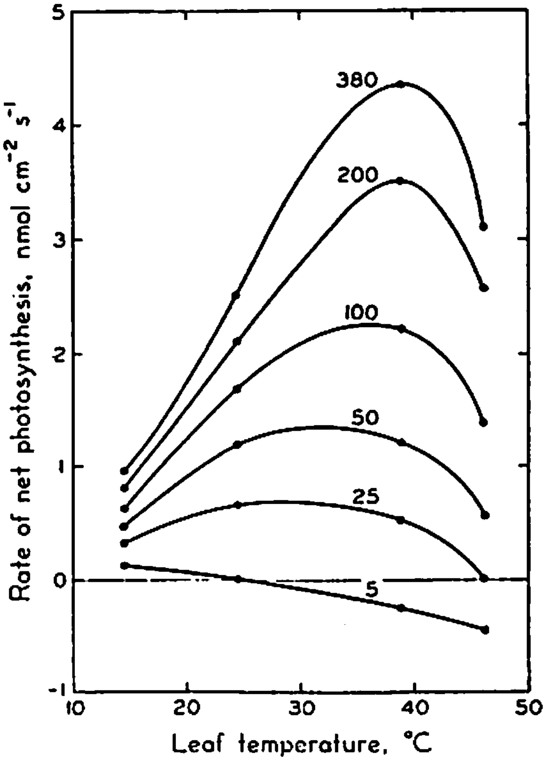
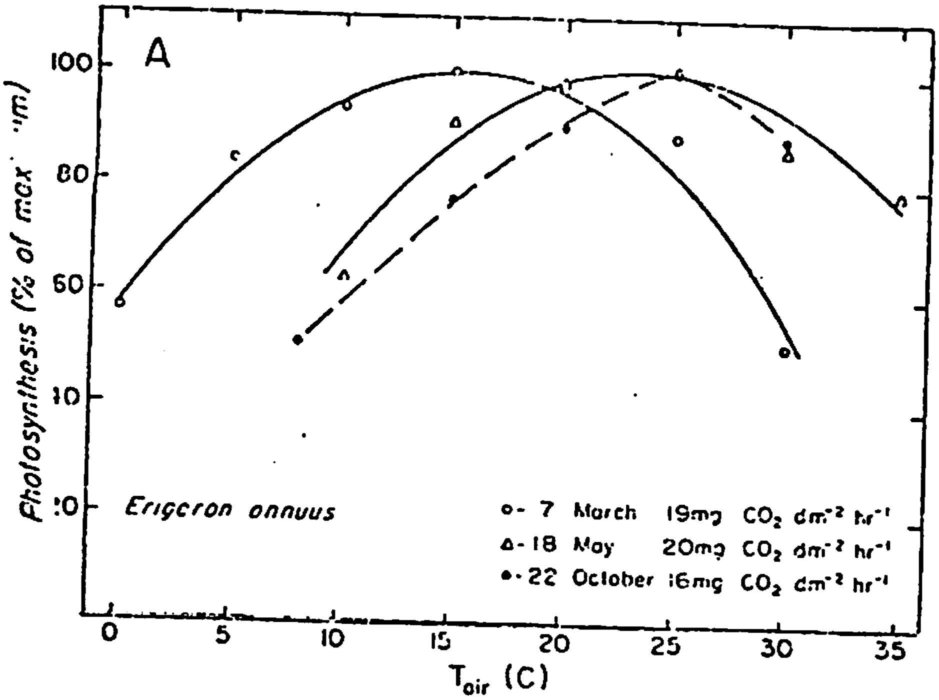


Figure 3 Effect of light intensity on the temperature dependence of net photosynthesis in leaves of *Pennisetum purpureum*. Number near each curve depicts the approximate light intensity (W m^{-2} in the 400–700 nm waveband). Adapted from Ludlow & Wilson (119).



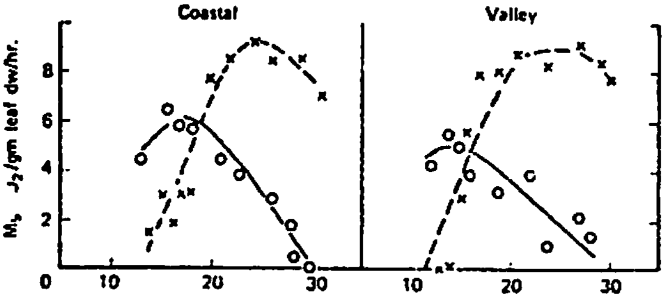
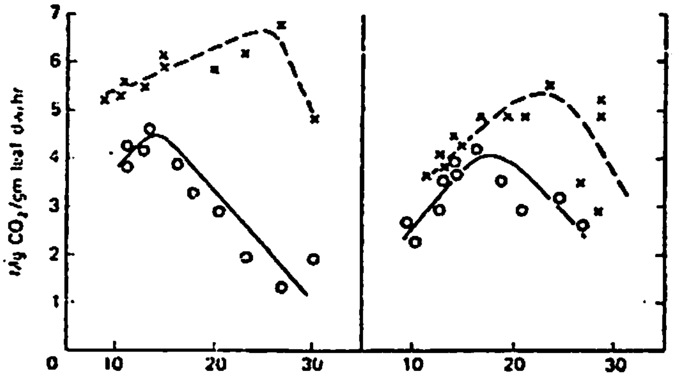


FIGURE 2-11. Temperature curves of photosynthesis of coastal and valley clones of *Encelia californica*. Circles indicate values measured immediately upon removal from 12 days in the cold-acclimation chamber (15°/2°C) and x's, values measured after the plants were maintained 23 hours in the light at 30°C. (From Mooney and Shropshire, 1967.)

FIGURE 2-12. Photosynthetic acclimation to warm temperature of plants of two populations of *Polygonum bistortoides*. In the first column are the results from a coastal population and the second column, a subalpine population. The circles indicate values measured on plants immediately upon removal from 10 days in the cold acclimation chamber; the x's are values measured after plants were kept at 30°C and full light for 25 hours. (From Mooney and Shropshire, 1967.)



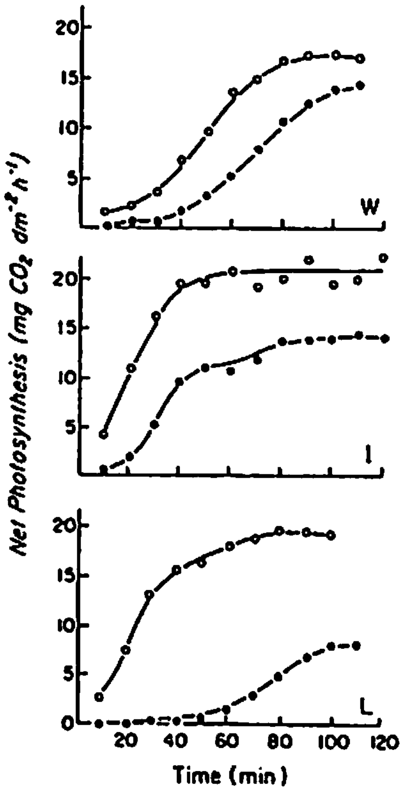


Fig. 3. The change in net photosynthesis following illumination for three populations of *P. deltoides* exposed to 20° C (*open circles*) and 4° C (*closed circles*) nights in April-May. Each point is a mean of two leaves measured on two detached branches

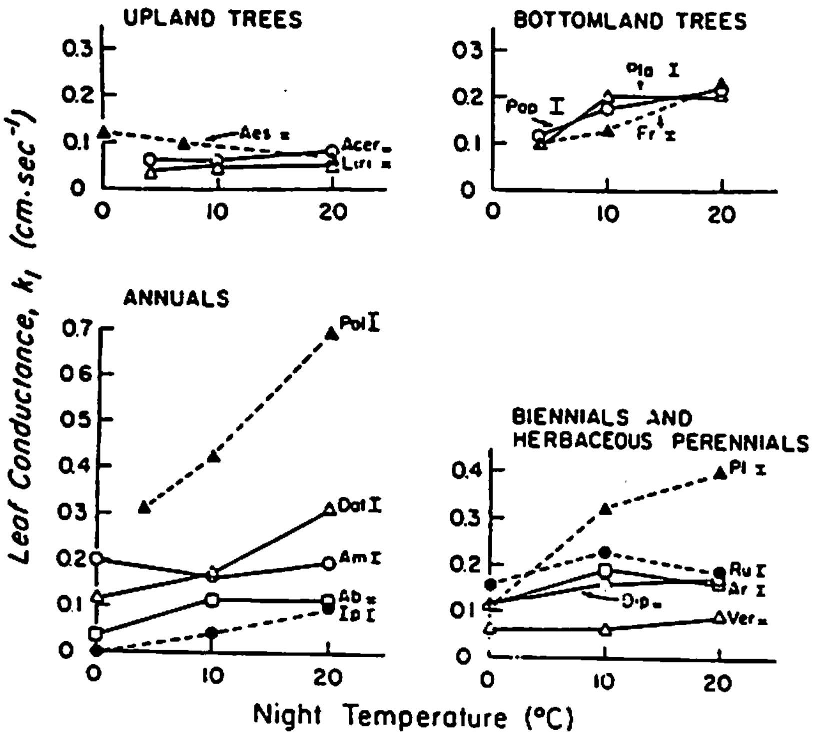


Fig. 1. Response of leaf conductance (cm·sec^{-1}), k_l, to night temperature (0) in 16 early and late successional oldfield species grouped into categories of annuals, biennials and herbaceous perennials, upland, and bottomland trees. Standard errors of control night temperatures are indicated for each species, abbreviated as follows: Ab. *Abutilon*; Acer. *Acer*; Aes. *Aesculus*; Am. *Ambrosia*; Ar. *Arctium*; Dat. *Datura*; Dip. *Dipsacus*. Fr. *Fraxinus*; Ip. *Ipomoea*; Liri. *Liriodendron*; Pol. *Polygonum*; Pop. *Populus*. Pl. *Plantago*; Pla. *Platanus*; Ru. *Rumex*; Ver. *Verbascum*

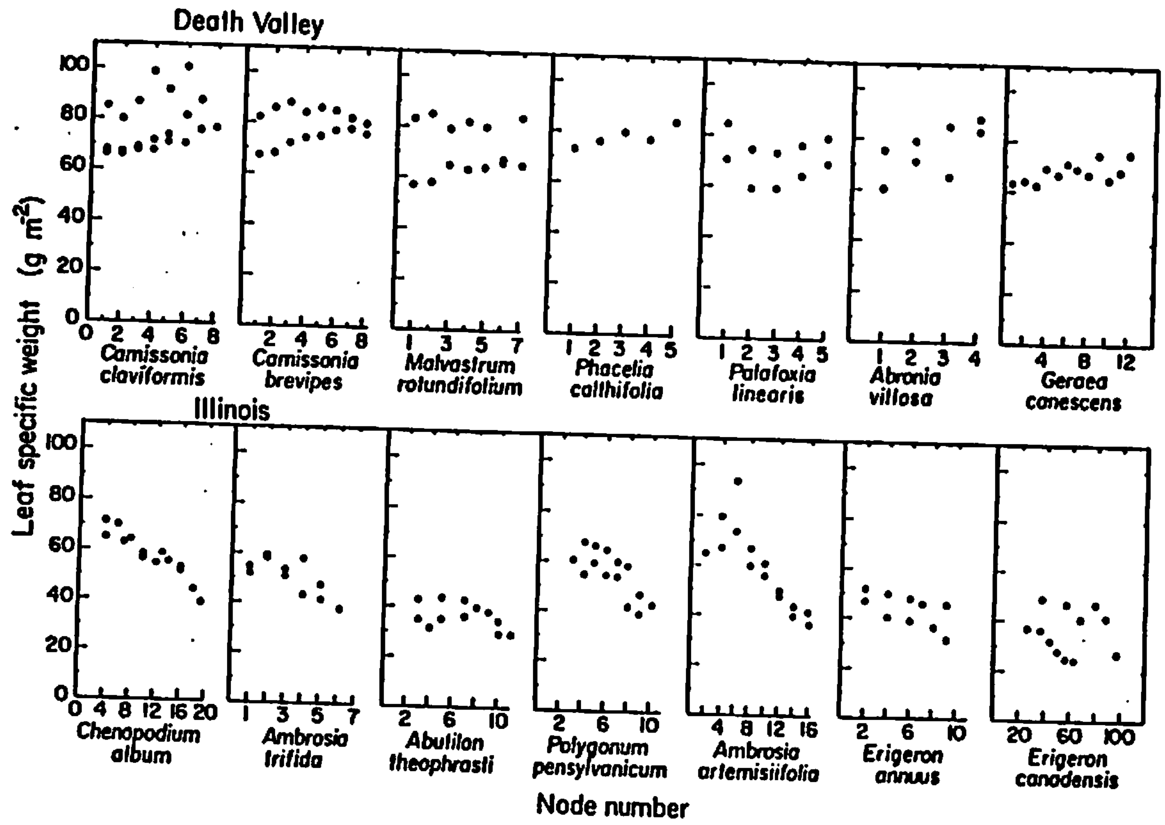


Fig. 1. Leaf specific weight versus nodal position of leaves of desert (Death Valley) and old field (Illinois) annuals. Scales for nodal position were made relative among species by placing the number for the oldest leaves present at the same approximate scale position. Lowest numbers refer to the newest leaves. The data are for two or three individuals per species

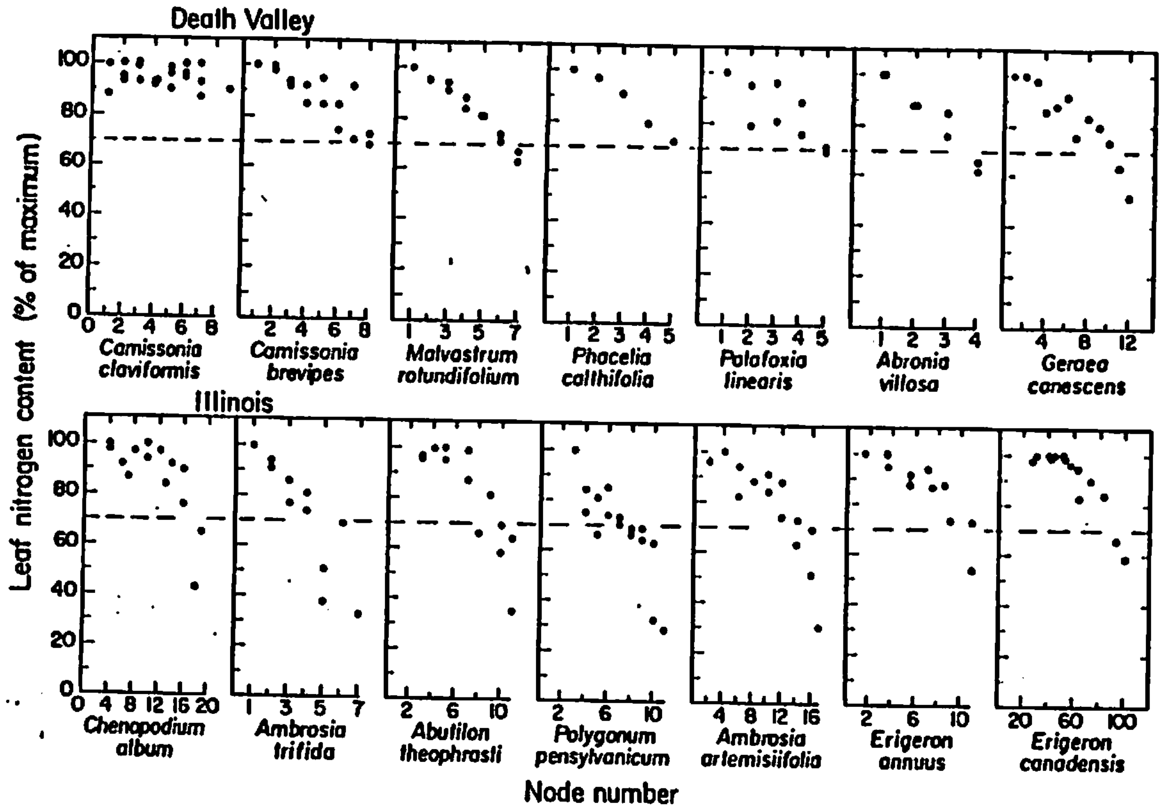


Fig. 2. Leaf nitrogen content versus nodal position of leaves of desert versus old field annuals. Nodal scales relative as in Fig. 1. Dashed line is provided for visual comparison between the responses of the two groups. The data are for two or three individuals per species. A Kruskal-Wallis rank order comparison of the maximum decline in N content of each species indicated a significant difference between the Illinois and Death Valley communities ($p < 0.01$)

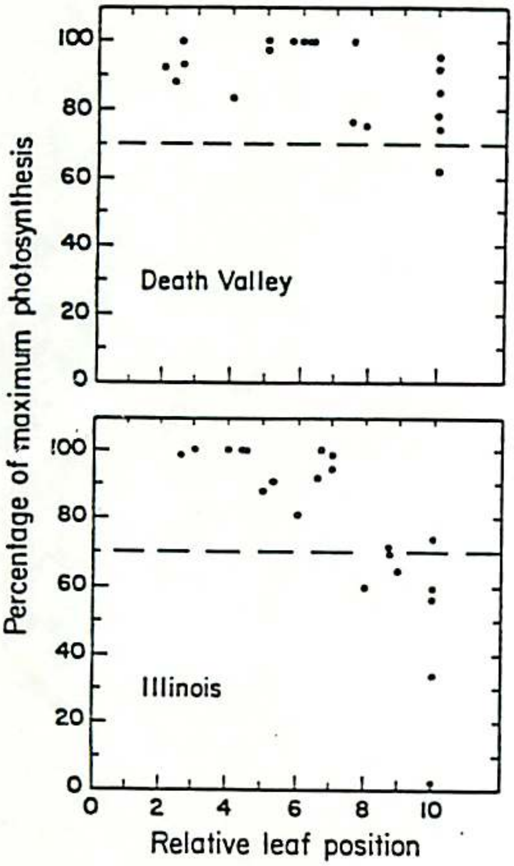
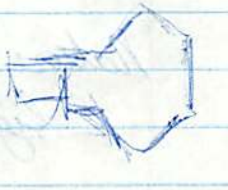


Fig. 4. Percentage of maximum photosynthesis (area basis) in relation to relative leaf position for desert versus old field annuals. Oldest leaves sampled were scaled to 10. Dashed line indicates 70% of maximum photosynthesis and is provided for visual comparison of responses between groups. Using true leaf nodal positions, $r = -0.45$ ($p < 0.05$) for Death Valley and $r = -0.62$ ($p < 0.005$) for Illinois. A Kruskal-Wallis rank order comparison of the maximum decline in photosynthesis of each species (data from Table 1) indicated a significant between the two communities ($p < 0.02$)

J.E.
10/12/87

acclimation to changing temperature

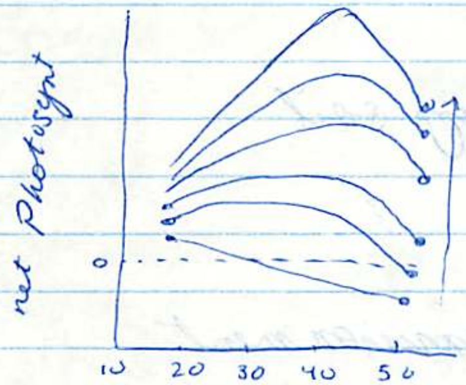


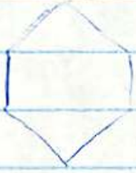
ΔT° ⟶

affect of T° on ...

Photosynthesis

-affect of T° depends on amount of light





-affect of temperature depends on conditions in which plants were grown

~~aff~~

affect of temperature depends on
① light intensity
② growth conditions
③ acclimation time
④ circaannual rhythms (season)
  -in winter; do better in cold

Why does this occur?
① ~~enzy~~ Δ enzymatic activity
② Δ chlorophyll a:b
③ Δ H_2O potential
regeneration of substrates

Nature walk

① light -
- leads to H_2O limitation, so less light may yield same CO_2 gain
-

② temp -

③ CO_2
- highest near respiring soil
- gradients

④ phenology
- may open up envirionment
- maybe diff freeze
  - H_2O
  - light

⑤ architecture

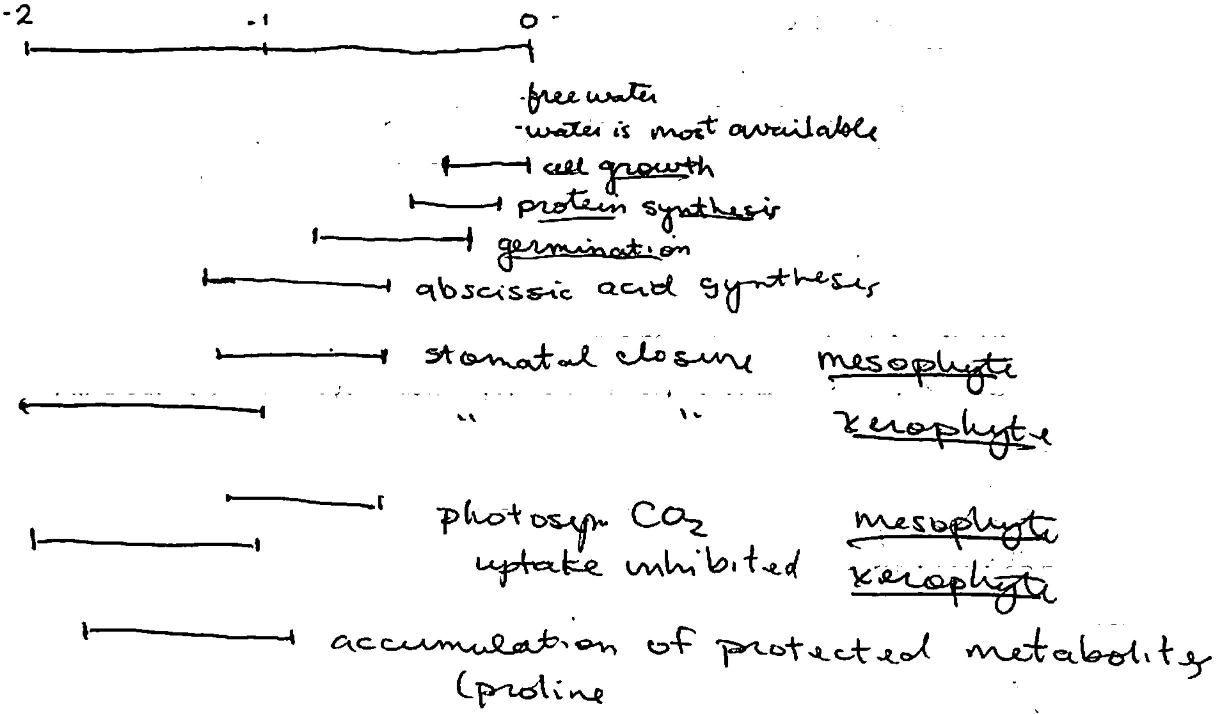
10/17

Water

①universal solvent
②H bonds - v. important for trees

Water Availability

see fig 1



Rainfall - see Fig 3
- quantity
    so places receive NO RAIN
- seasonality

These two characteristics can "predict" ecotype

Fig 4
- amount of H_2O
- distribution of H_2O
- amount of runoff
- amount of evaporation

<u>Trop. Rain Forest</u>

<u>Trop. Seasonal Forest</u>

<u>Mediterranean</u>
- dry, hot summer
- wet, cool winter
- mostly shrubs; trees - can get H_2O from fog, H_2O table, storage in summer - winds w/ fog roll over coast ... H_2O .. H_2O

wheat → H_2O runs out

corn → need H_2O to last in soil during drought

SCALE

Kinds of precipitation

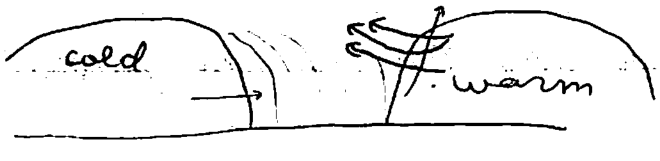
↑ - dust or spores

① Rain - liquid water

dust or spores act as nuclei for condensation

Ⓐ Frontal - collision of air masses of diff T°

air masses $\xrightarrow{\text{wind}}$ collission



cold air pushes (cold front) (same if warm front)
↓
warm air passes over
↓
rain falls

* Diff. in T° (bigger diff. → more rain)

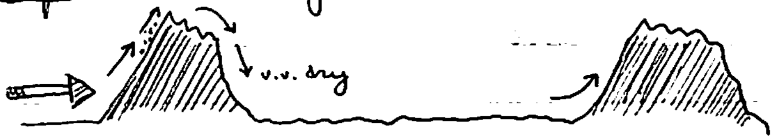
H_2O content

speed

Types of ranfall

B) Orographic

physical barrier

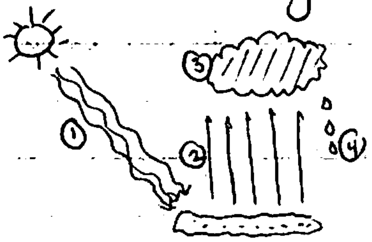


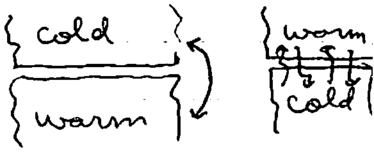
- can be v.v. small physical barriers
  can be due to cities

-

c) Convectional

heating → evap → air rises





can be violent

- local weather
- common in tropics

Can be calm or violent

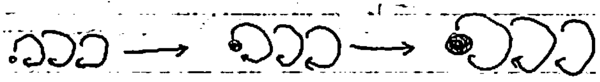
② Snow ~~[illegible]~~ (1:10)

- whereas rainfall drenches ground/plants and can lead to runoff
- snow - accumulates
  may be more gentle release
- excellent insulator
  - survivorship in arctic depends of presence of snow (insulation, predation protection)
- can be "released" at diff times

this area will be uncovered early

- Cons. Law Yound
- Mass-ping

③ Hail



- destructive

④ Sleet ; glaze ...

- can lead to formation of ice around plants

⑤ Dew

- accumulation of moisture on cool surfaces
- common in dry habitats on ~~cool~~ clear nights
- major source of H_2O for plants in dry areas
- channels dew

SO_x & NO_x

Jon Eisen
10/19/89

Plant Water Relations - Suzanne Morse

Water

- constant flux

- Inside Plant

Thermodynamics

- reference - physics & chem. of pure water
- Slatyer - water potential - measure of work ability. Compared to pure water (0).

|

Hydration perspective - how much water could it hold compared to now

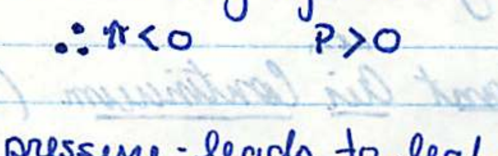
|

see Fig 1 - 10/17

↓

Slatyer - water potential

$$\Psi = \left[\underset{\text{osmotic potential}}{\pi} + \underset{\text{pressure}}{P}\right] + \tau_{\text{matrix}} + g_{\text{gravitational}}$$



water in due to osmosis leads to increase in turgor pressure.

$\Psi = 0$ if fully hydrated

$\therefore \pi < 0 \quad P > 0$

pressure - leads to leaf expansion & other forms of growth. If $P = 0$ then plant cannot grow.

correlations within a species are good but interspecies variation is very high.

HYDRATION

- came from attempts at unifying theory for plants
∴ used plant as reference point

$$\underline{RWC} = \frac{\overset{\text{weight}}{\cancel{\text{amount of } H_2O}} - \text{dry weight}}{\text{saturated wt} - \overset{}{\cancel{\text{relative}}}\ \text{dry weight}}$$

$= 80-100\%$

- **Pressure: Volume Curves**
- **Dehydration Response**

there is a relationship betw. RWC & ψ.

* but - remember it is dynamic *

see Fig 5

Soil Plant $\overset{\text{atm}}{\text{Air}}$ Continuum (SPAC)

night ψ≅0
day ψ<0 due to resistance

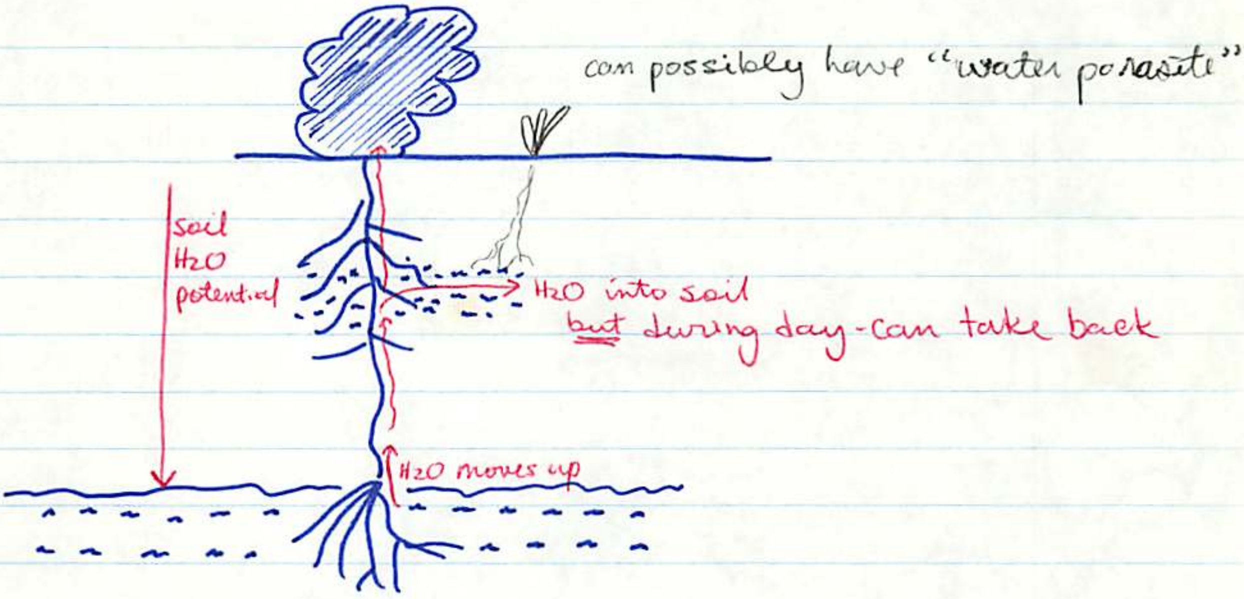
why does ψ change
① resistance to mvmt
② gravity

Plants with higher water potentials than soil:

① **Deserts**

- cacti **are** "higher"
  - lose roots
  - root suberization (waxed)
  - take up water w/ new rain

- hydrolic lift · sagebrush



benefits - resistance partially decreased
- pick up nutrients

Problem, & other

- embolism - air bubbles block xylem
  - when to many air bubbles - better to dump leaves & roto rooter

- see Fig 6

10/17

Fig 1

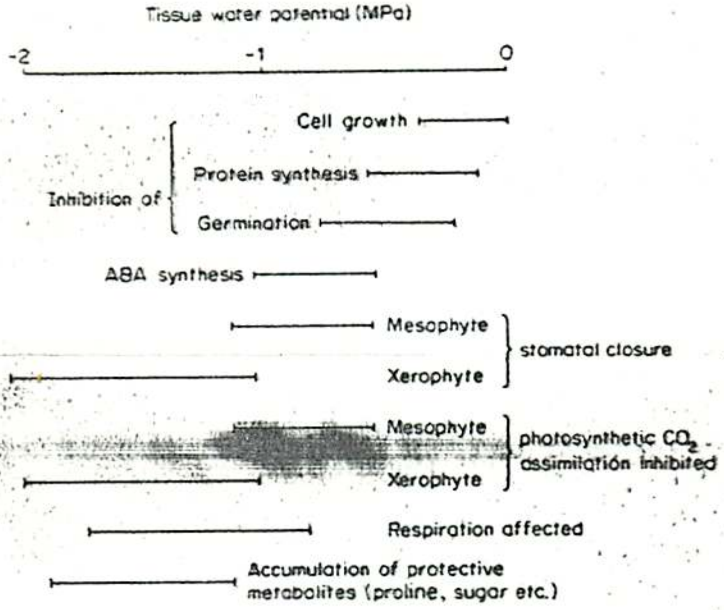


Figure 6.13 The range of tissue water potentials affecting major physiological processes. ABA = abscisic acid. Modified from Hsiao *et al.* (1976) and other authors.

~~all of this is a measure of turgor pressure~~

10/17

Fig 3

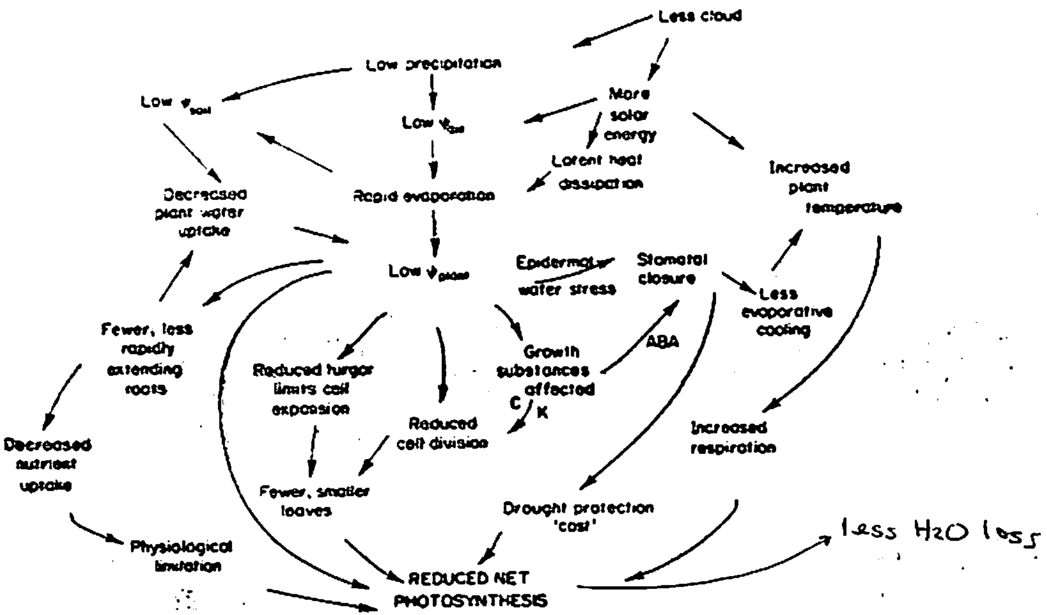


Figure 6.14 Some overall physiological consequences of water stress in plants. ABA = abscisic acid. C = cytokinin. K = kinetin. After an idea of Fritts (1976).

All interrelated

Fig 3

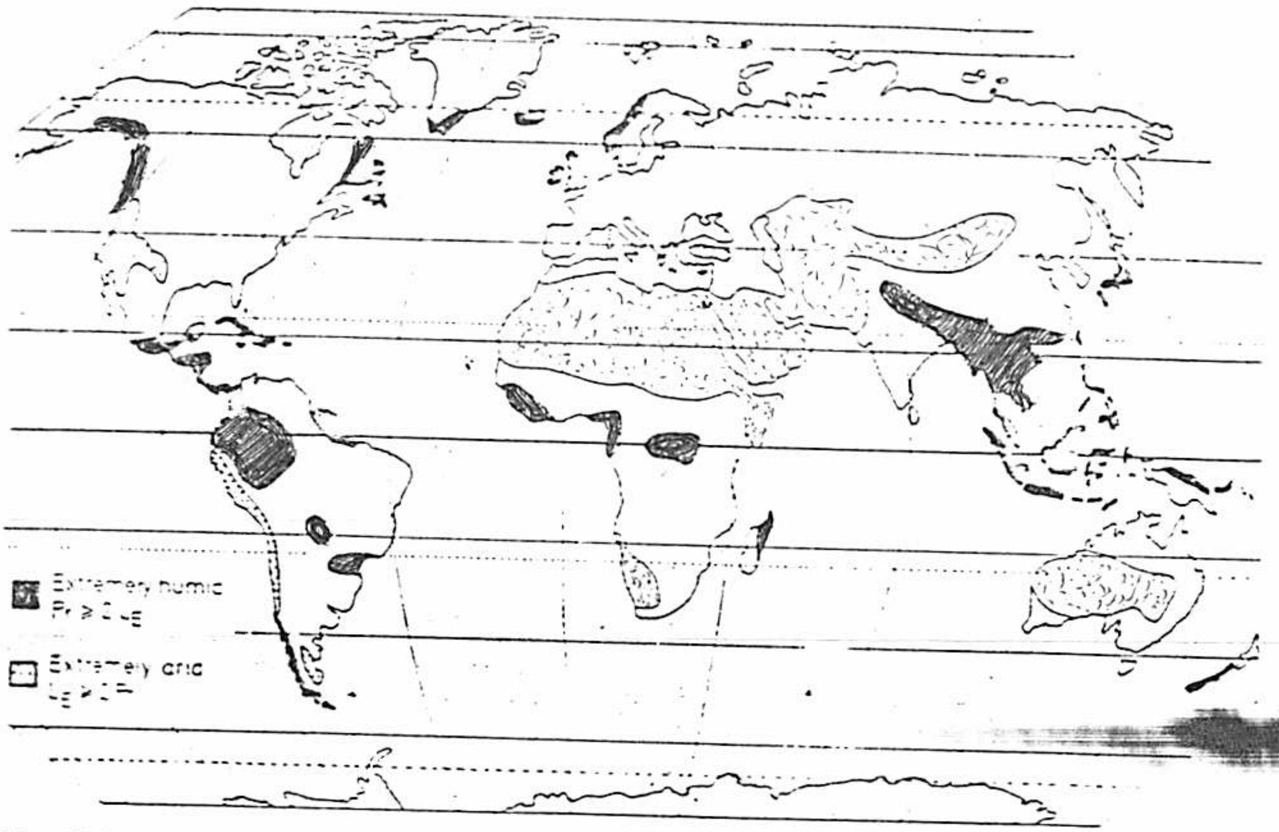


Fig. 5.24. The distribution of extremely humid and extremely arid regions on the earth. Extremely humid: annual precipitation at least twice the amount of water evaporated annually. Extremely arid: annual evaporation at least twice as great as annual precipitation. The demarcation of extremely humid and arid regions is based on the maps of Geiger (1965), giving amount of precipitation and actual evapotranspiration. For precipitation and evaporation maps see Lockwood (1974)

Wet & dry not separated by distance.

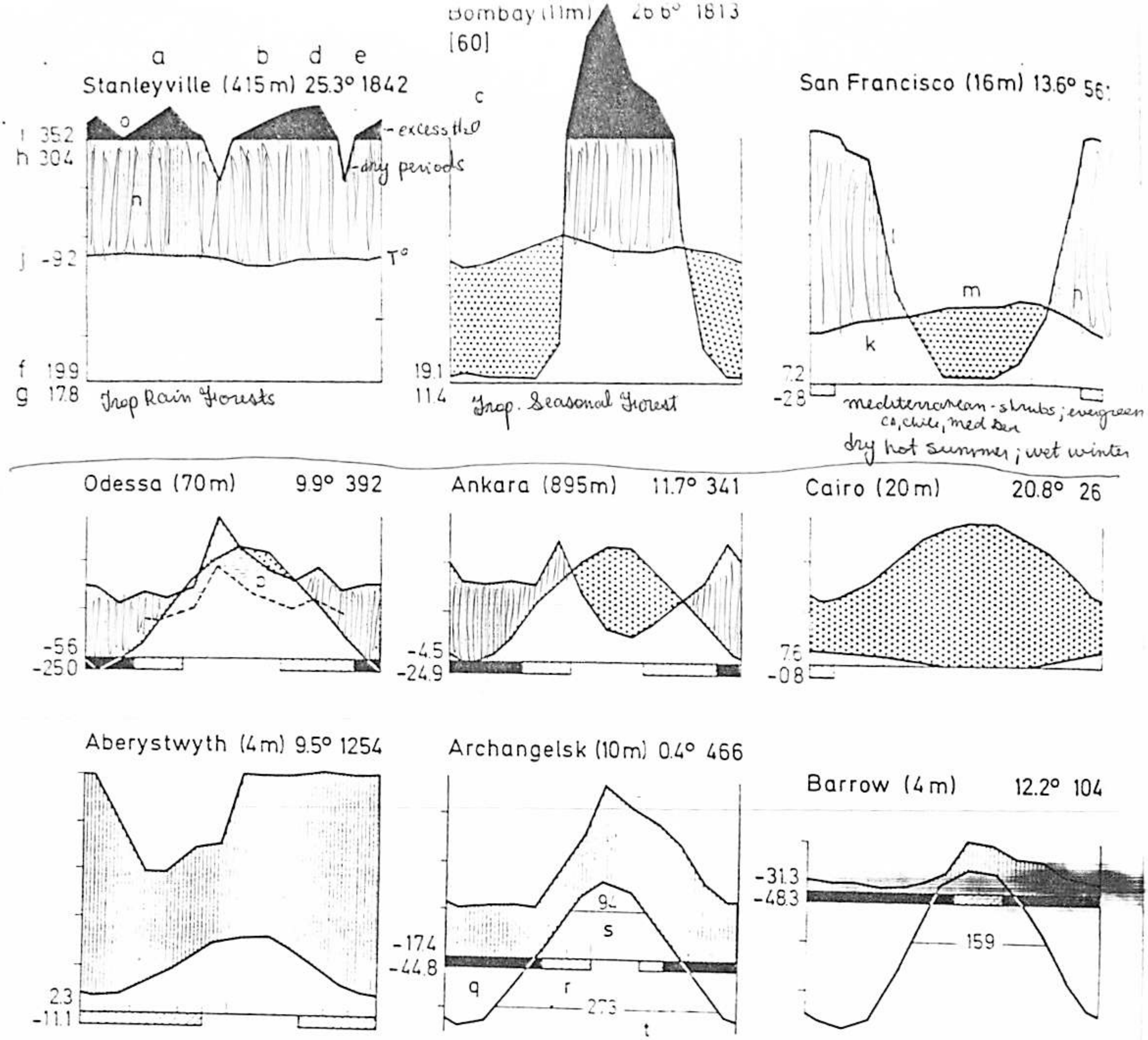
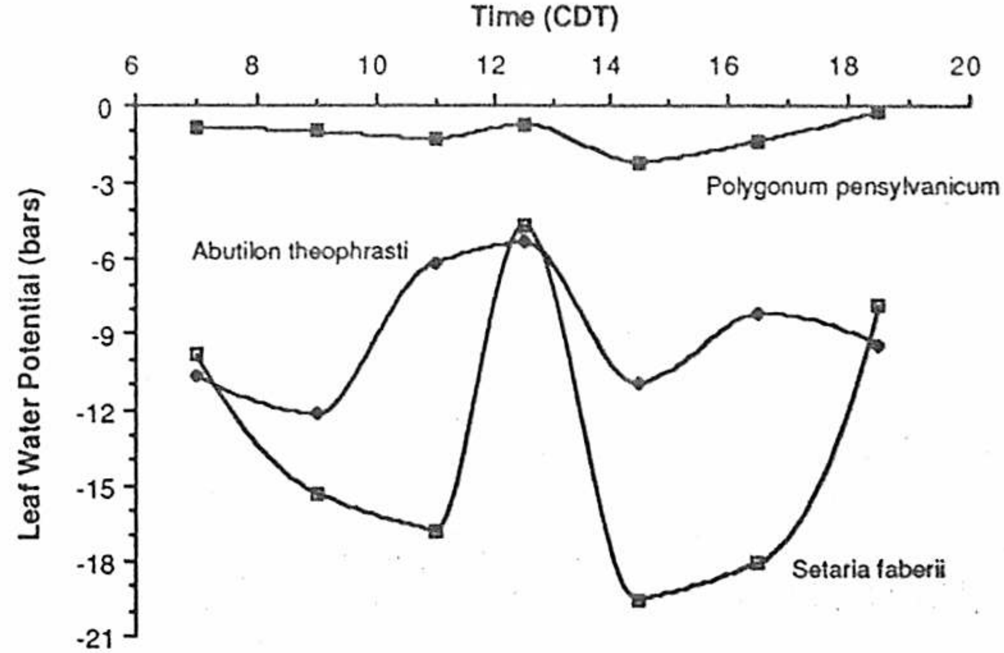


Fig. 5.26. Climate diagrams for *Stanleyville* (Congo, permanently wet equatorial climate); *Bombay* (India, tropical summer-rain climate); *San Francisco* (California, winter-rain region with summer drought); *Odessa* (Black Sea coast, semi-arid steppe climate); *Ankara* (Turkey, Mediterranean climate type with equinoctial rain); *Cairo* (Egypt, subtropical desert climate); *Aberystwyth* (Wales, maritime-temperate climate); *Archangelsk* (taiga zone on the White Sea, cold-temperate climate); *Barrow* (Alaska, arctic tundra climate).
Interpretation of the climate diagrams. *Abscissa*, in the northern hemisphere the months from January to December, in the southern hemisphere from July to June (the warm season is always in the middle of the diagram). *Ordinate*, one subdivision represents 10° C or 20 mm precipitation. *The labels denote*: *a*, station; *b*, altitude above sea level; *c*, number of years of observation; *d*, mean annual temperature; *e*, mean annual precipitation; *f*, mean daily minimum in the coldest month; *g*, absolute temperature minimum; *h*, mean daily maximum in the warmest month; *i*, absolute temperature maximum; *j*, mean daily temperature fluctuation (tropical stations with diurnal rather than seasonal variation); *k*, curve of the mean monthly temperatures; *l*, curve of mean monthly precipitation; *m*, season of relative drought (*stippled*); *n*, relatively humid season (*vertical shading*); *o*, perhumid season, mean monthly precipitation > 100 mm (scale reduced to 1/10, *black area*); *p*, relatively dry season (precipitation curve


Time (CDT)
6
8
10
12
14
16
18
20
0
-3
-6
-9
-12
-15
-18
-21
Leaf Water Potential (bars)
Polygonum pensylvanicum
Abutilon theophrasti
Setaria faberii

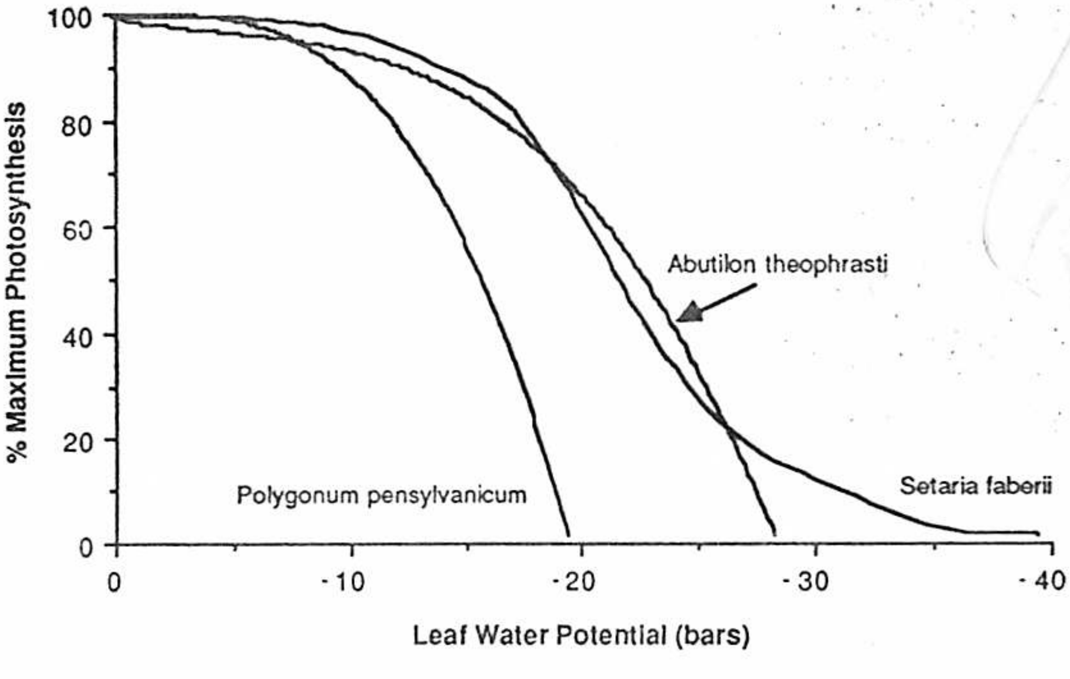

100
80
60
40
20
0
% Maximum Photosynthesis
Abutilon theophrasti
Polygonum pensylvanicum
Setaria faberii
0
-10
-20
-30
-40
Leaf Water Potential (bars)

Fig 5

plant can't get to zero
① still transpiring
② delay

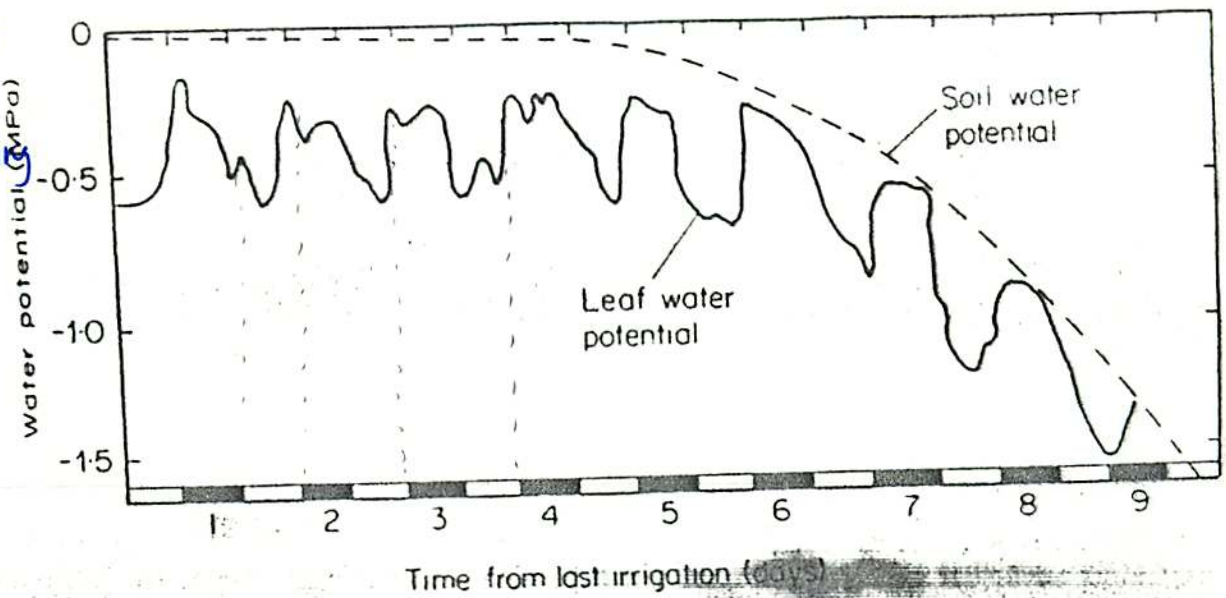


Figure 6.11 Diurnal changes of leaf and soil water potential of a pepper plant rooted in a clay loam soil. Reproduced with permission from W. R. Gardner and R. H. Nieman, *Science*, 143, 1460–1462, Figure 1 (1964). Copyright 1964 by the American Association for the Advancement of Science.

- why does Ψ change if plant is just a tube
  ① resistance to movement
  - leads to gradient betw. leaf & roots
  -

②

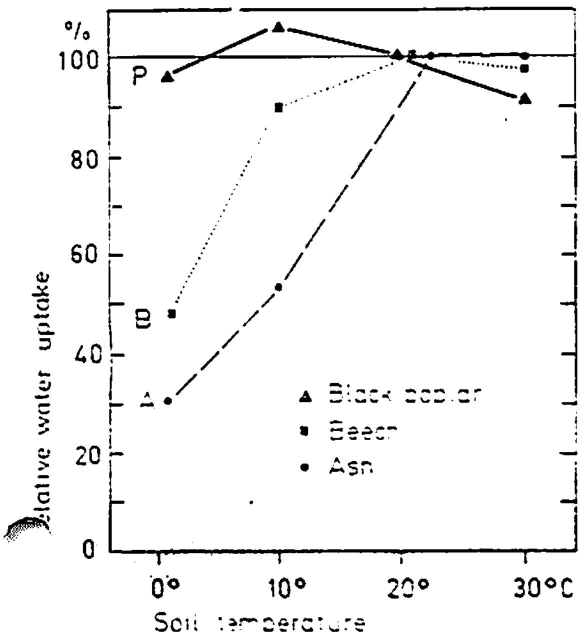


Fig. 5.5

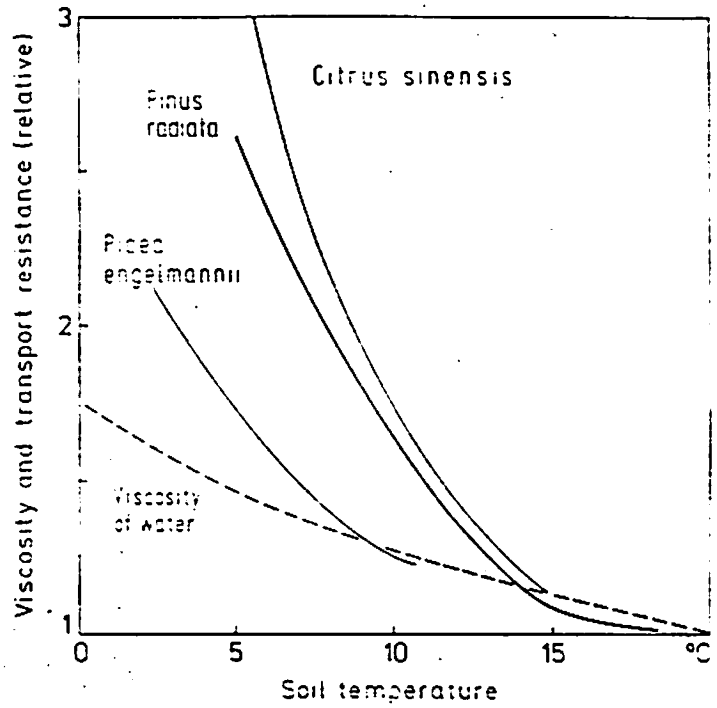


Fig. 5.6

Fig. 5.5. Temperature dependence of water uptake by the roots of *Populus nigra*, *Fagus sylvatica* and *Fraxinus excelsior*. After Döring (1935)

Fig. 5.6. Relative resistance to water transport into and through the plant, and the relative viscosity of the water (as compared with that at 20° C), as soil temperature decreases. In orange trees and Monterey pines reduced root permeability begins to limit water uptake a little below 15° C, whereas in Engelmann spruce from 3000 m above sea level this does not occur until the temperature has fallen to between 5° and 10° C. After Elfving et al. (1972) and Kaufmann (1975, 1977). For classical experiments see Kramer (1940, 1942); low temperature effects on water transfer and uptake are discussed by Dalton and Gardner (1978)

Fig 6

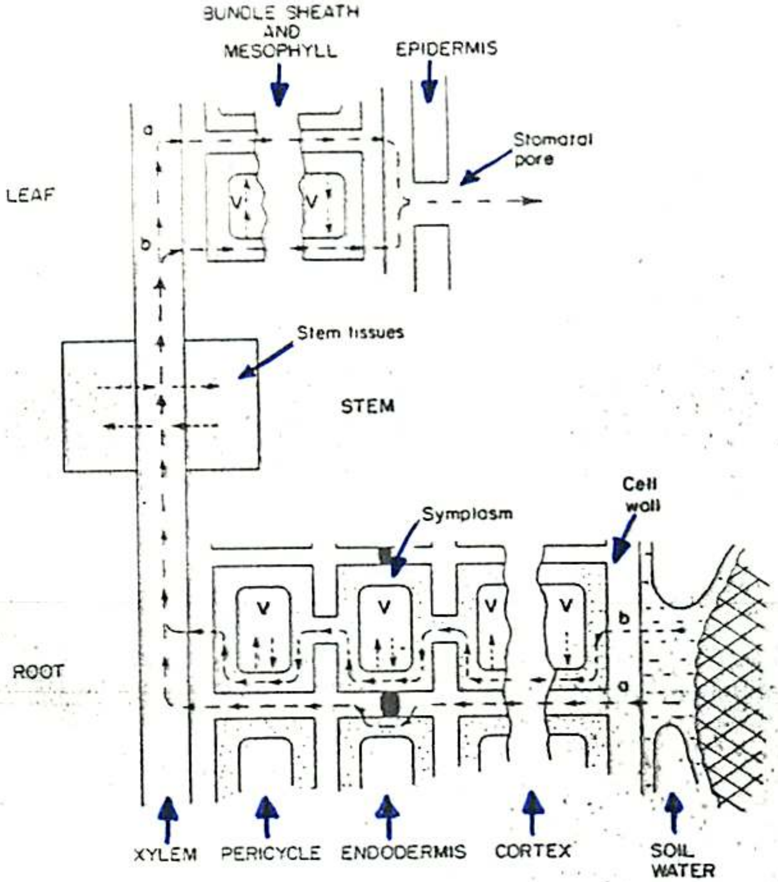


Figure 6.1 Flow paths in the soil–plant–atmosphere continuum (SPAC). Two alternative pathways are shown in parenchymatous tissue, either (a) the cell wall pathway or (b) the symplast pathway. Vacuoles are not involved in the direct mass-flow pathway (→—→—→) but they do slowly equilibrate with local ψ_{wall} or $\psi_{symplast}$ as water status changes (---→). Diffusion in the leaf air space is shown by (–·–·–·→). After Newman (1976) and Weatherley (1969).

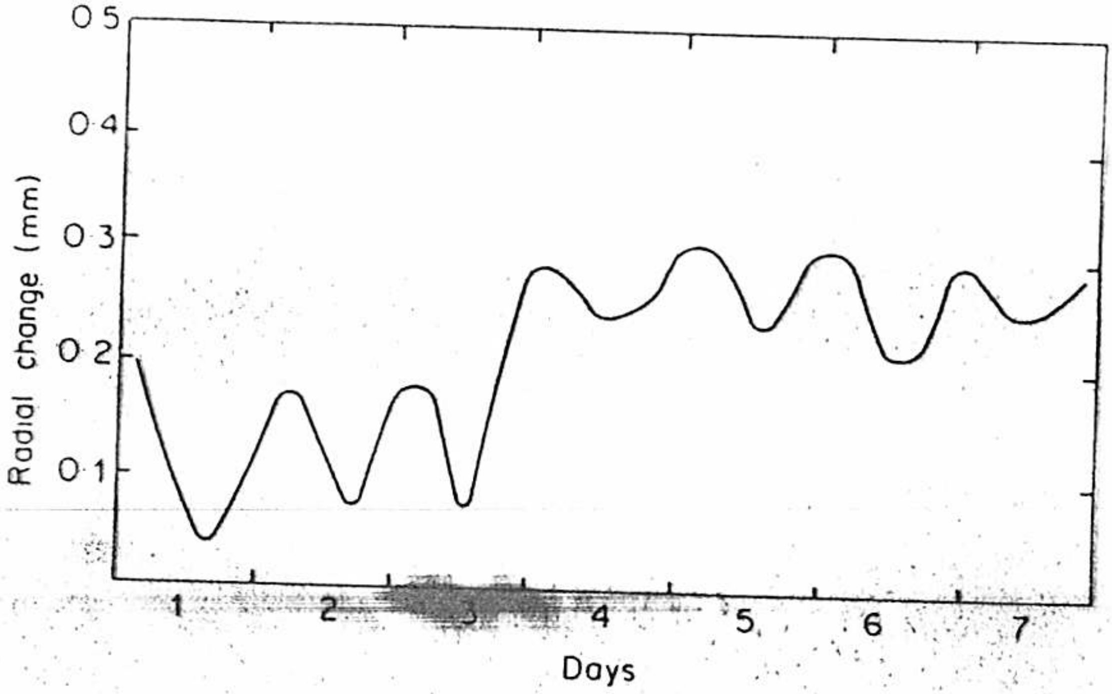


Figure 6.12 Diurnal shrinkage and expansion of the trunk of a *Pinus resinosa* tree in summer conditions. Data of Kozlowski (1964).

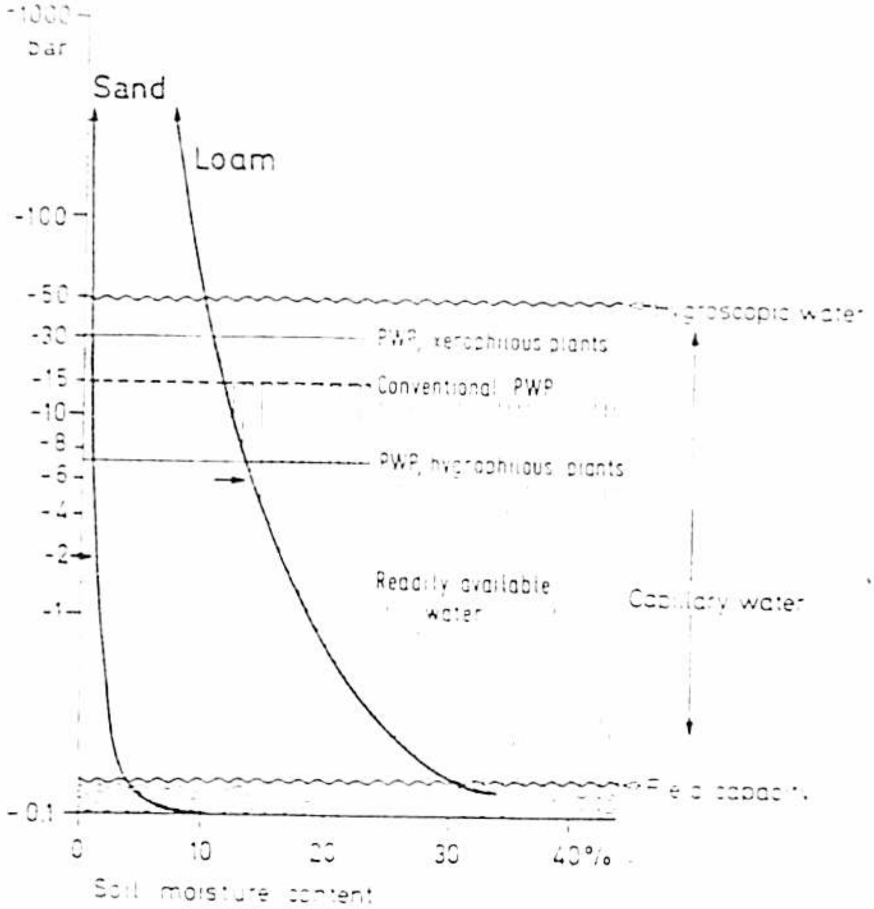
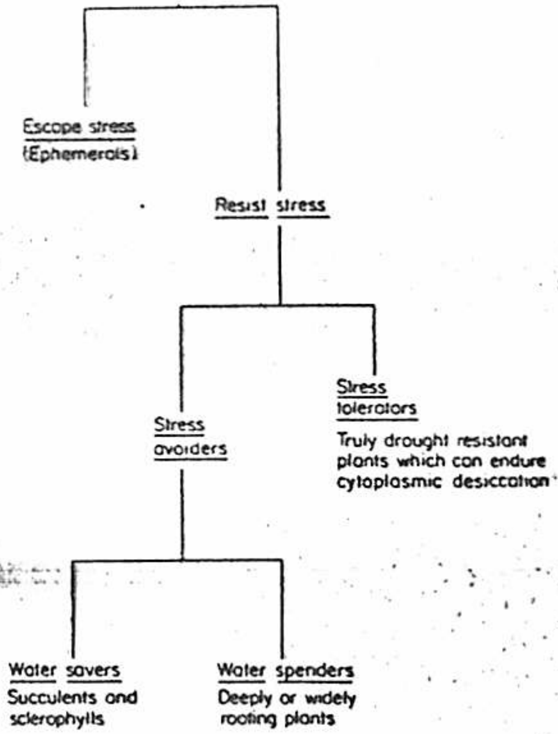


Fig. 5.4. Diagram of the dependence of the water potential of a sandy soil and a loam soil upon the water content of the soil. Depending on pore size. the water potential at field capacity is 0.05 bar (sandy soil) to 0.15 bar (loam). Conventional limiting values: water is exclusively hygroscopically bound at values of Ψ_{soil} of −50 bar and below: water content at field capacity is considered to correspond to $\Psi_{soil} = -0.15$ bar. and the permanent wilting percentage (*PWP*) to correspond to $\Psi_{soil} = -15$ bar. The readily available water depends upon the specific *PWP* of the plants growing on this soil. The *black arrows* are referred to in the text. After Kramer (1949). Laatsch (1954). Slatyer (1967). Rutter (1975). For water uptake and flow in roots see Weatherley (1982)


Escape stress
(Ephemerals)
Resist stress
Stress avoiders
Stress tolerators
Truly drought resistant plants which can endure cytoplasmic desiccation
Water savers
Succulents and sclerophylls
Water spenders
Deeply or widely rooting plants

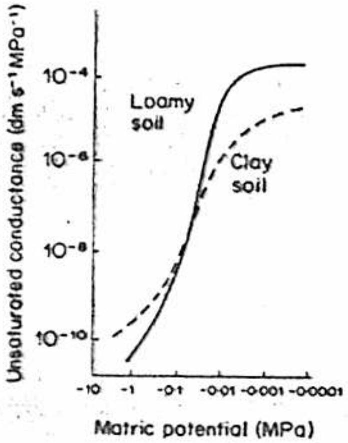


Figure 6.6 The relationship between unsaturated hydraulic conductance and soil water potential in a medium textured loam and in a clay soil.

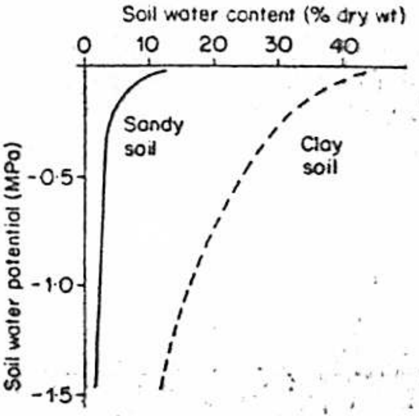


Figure 6.5 Water characteristic curves of a sandy and a clay soil.

Fig 1 10/24

GLOBAL ATMOSPHERIC CO2 LEVELS

350 PPM: CURRENT AMBIENT LEVELS

700 PPM: PROJECTED LEVELS LATE 21ST CENTURY

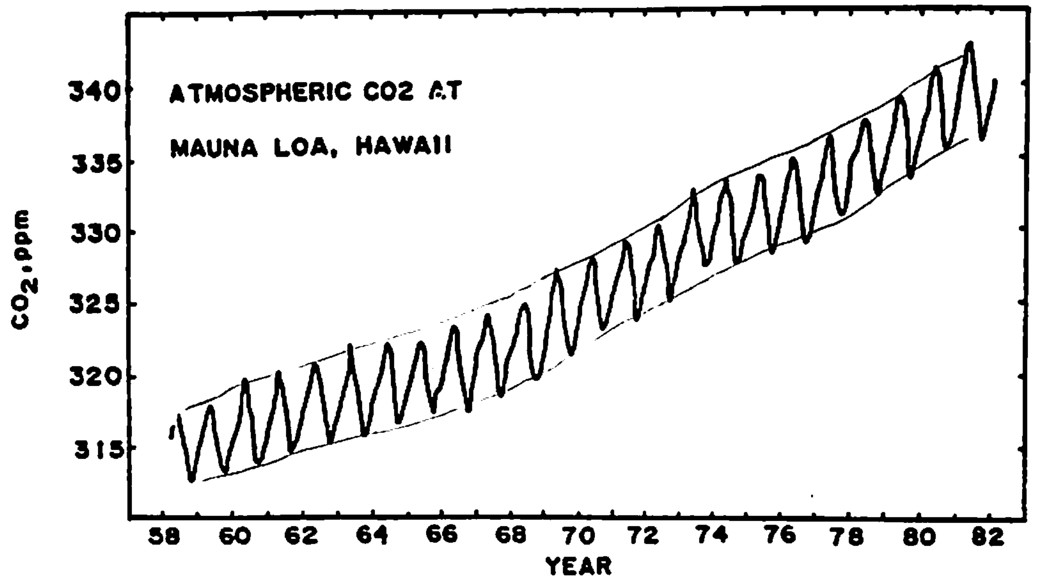
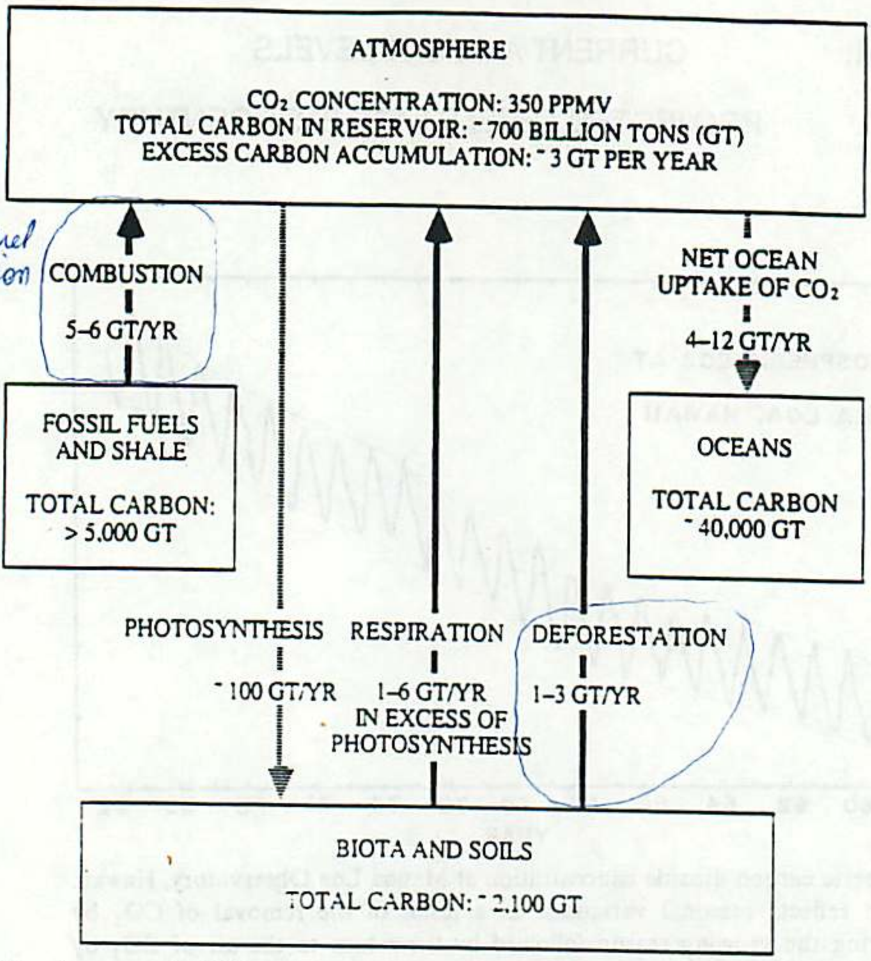


Figure 1 Atmospheric carbon dioxide concentration at Mauna Loa Observatory, Hawaii. The zigzag pattern reflects seasonal variations as a result of the removal of CO_2 by photosynthesis during the growing season followed by the return to the air of CO_2 by oxidation of plant tissues (after Keeling et al 1976a).

Fig 2

FIGURE 5.2
Exchangeable Carbon Reservoirs and Fluxes

②



Fossil Fuel consumption

③

9

6

oceans

The fluxes are in billions of metric tons of carbon per year. The size of the carbon reservoirs is in billions of metric tons of carbon. Carbon transferred to the atmosphere by respiration exceeds the carbon being fixed by photosynthesis because global warming increases the rate of respiration more than it increases the rate of photosynthesis, although the size of the increase is uncertain.

-gigaton = 1 billion metric tons

-Rainforest CO_2 ≅ 20%

③

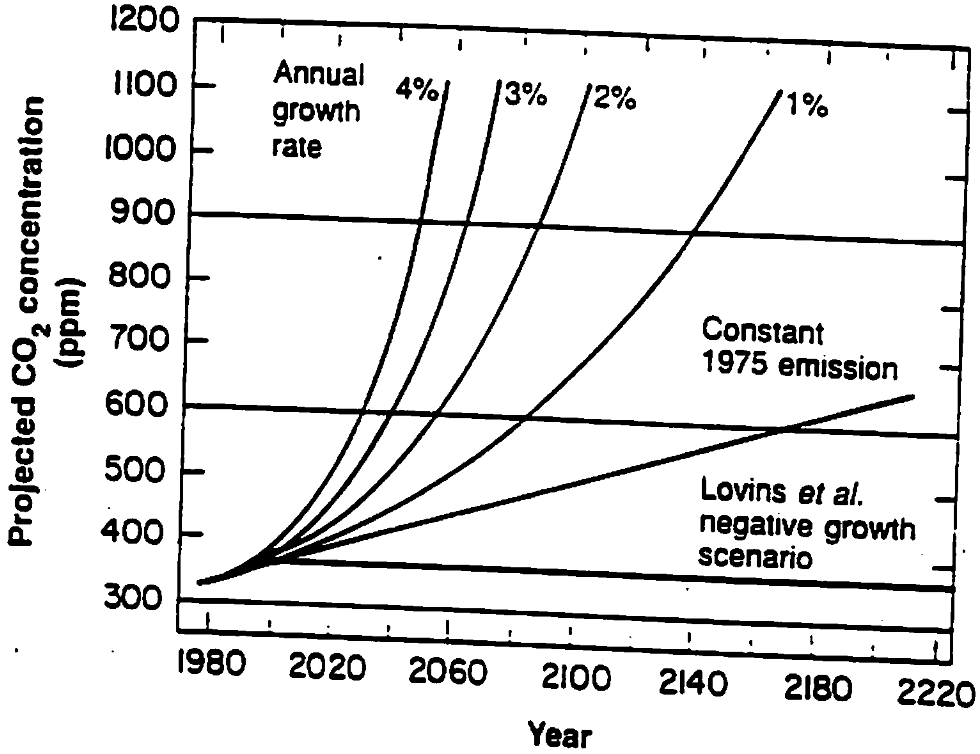


Fig. 3. The extent to which CO_2-induced climatic change will prove significant in the future depends, of course, on the rate of injection of CO_2 into the atmosphere. This depends, in turn, on behavioral assumptions as to how much fossil fuel burning will take place (biospheric effects are neglected in this graph). Since the end of World War II, a world energy growth rate of about 5.3% per year occurred until the mid-1970s, the time of the OPEC price hikes. Rates have come down substantially since then. The figure shows projected CO_2 concentrations for different annual growth rates in fossil energy use, including one for the assumption that no increase in fossil energy use occurs (constant 1975 emission) and even a "negative growth scenario" in which energy growth after 1985 is assumed to be reduced by a fixed amount [0.2 terra watts (TW) per year, which is about 2% of present demand] each year. [Modified from (*11*)]

WHY DO ELEVATED CARBON DIOXIDE ATMOSPHERES AFFECT PLANTS?

1. EFFECT ON PHOTOSYNTHETIC EFFICIENCY (RUBISCO)

A) CALVIN CYCLE - CARBON FIXATION

IN PRESENCE OF
RUBP (C5) + CO_2 ----(RUBISCO ENZYME) -- --2 PGA (C3)

OR....

RUBP (C5) + 02 -(RUBISCO ENZYME)-PGA (C3) + C2 ACID

(RECYCLE C2 ACID --COSTS ATP---PHOTORESPIRATION)

IN ELEVATED CO_2 ENVIRONMENT, SHIFT CO_2/O_2 RATIO SO RUBISCO ENZYME FIXES MORE CO_2 RELATIVE TO O_2, LESS PHOTORESPIRATION, MORE EFFICIENT PHOTOSYNTHESIS (ESPECIALLY FOR C_3 PLANTS)

B. EFFICIENCY ENHANCEMENT LESS IMPORTANT FOR PLANTS WHICH POSSESS C_4 CARBON FIXATION.

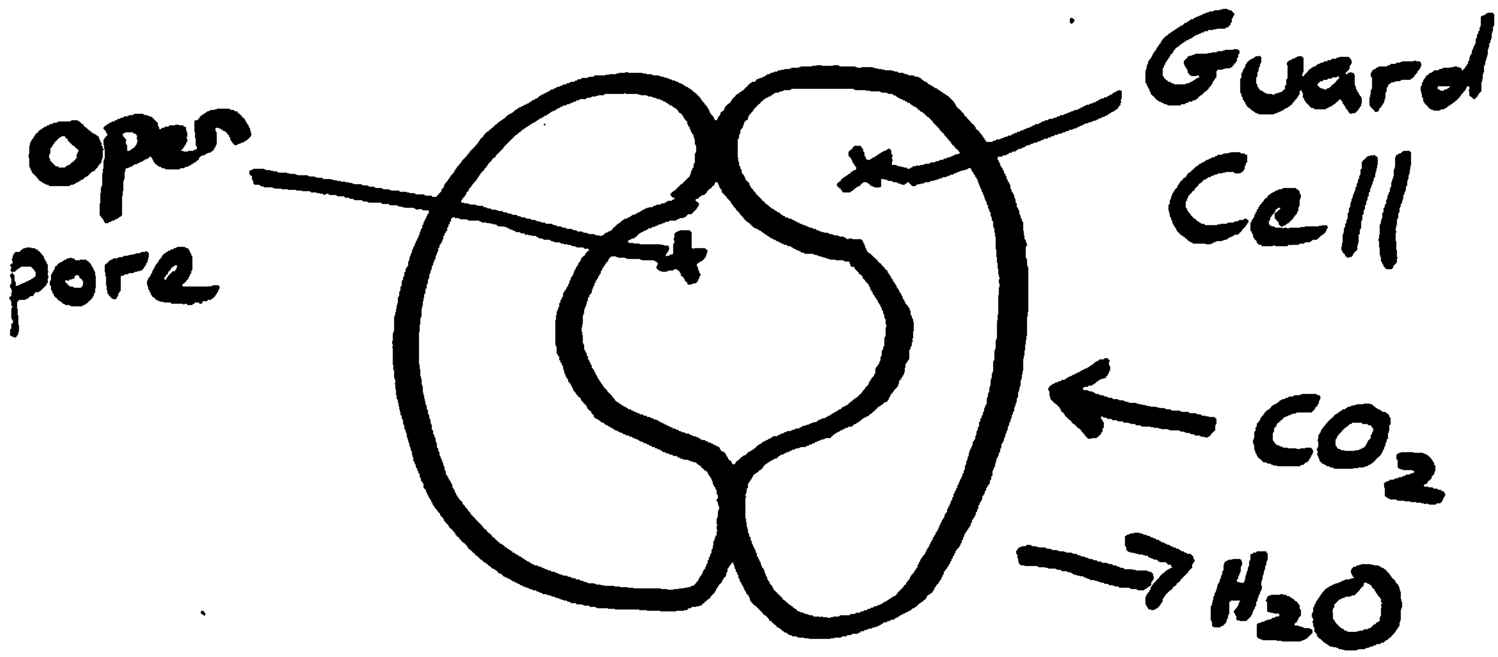
PEP + CO2 ---(PEP CARBOXYLASE ENZYME)--- C4 ACID

C4 ACID SHUNTED FROM BUNDLE SHEATH TO MESOPHYLL.

C4 ACID DECARBOXYLATES (C4---PEP + CO_2) AND CO2 ENTERS CALVIN CYCLE.

PHYSICAL SEPARATION OF INITIAL CARBON FIXATION AND CARBON ENTERING CALVIN CYCLE KEY FOR REDUCING PHOTORESPIRATION (PREVENT O_2 FROM BEING NEAR RUBISCO IN HIGH CONCENTRATIONS).

2. EFFECT ON WATER-USE EFFICIENCY: STOMATAL FUNCTION



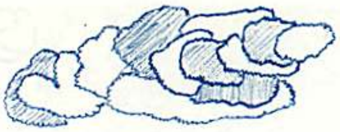
A. JOB OF STOMATA : ALLOW CO_2 INTO LEAF,
PREVENT LOSS OF H_2O FROM LEAF

B. IN ELEVATED CO_2 ATMOSPHERES:

1. CO_2 CONCENTRATION GRADIENT LARGER BETWEEN ATMOSPHERE AND INTERNAL LEAF SPACES
2. THUS, TO FIX SAME AMOUNT OF CARBON (I.E. ALLOW SAME AMOUNT OF CO_2 INTO LEAF), STOMATA CAN BE OPEN FOR SHORTER PERIODS OF TIME.
   LOSE LESS WATER!!

KEY: FOR SAME AMOUNT OF CO_2 ACQUIRED BY LEAF, LESS H_2O IS LOST. THUS, INCREASE WATER-USE EFFICIENCY IN ELEVATED CO2 ENVIRONMENTS.

* Or - reduce stomatal conductance



CO_2 response curve

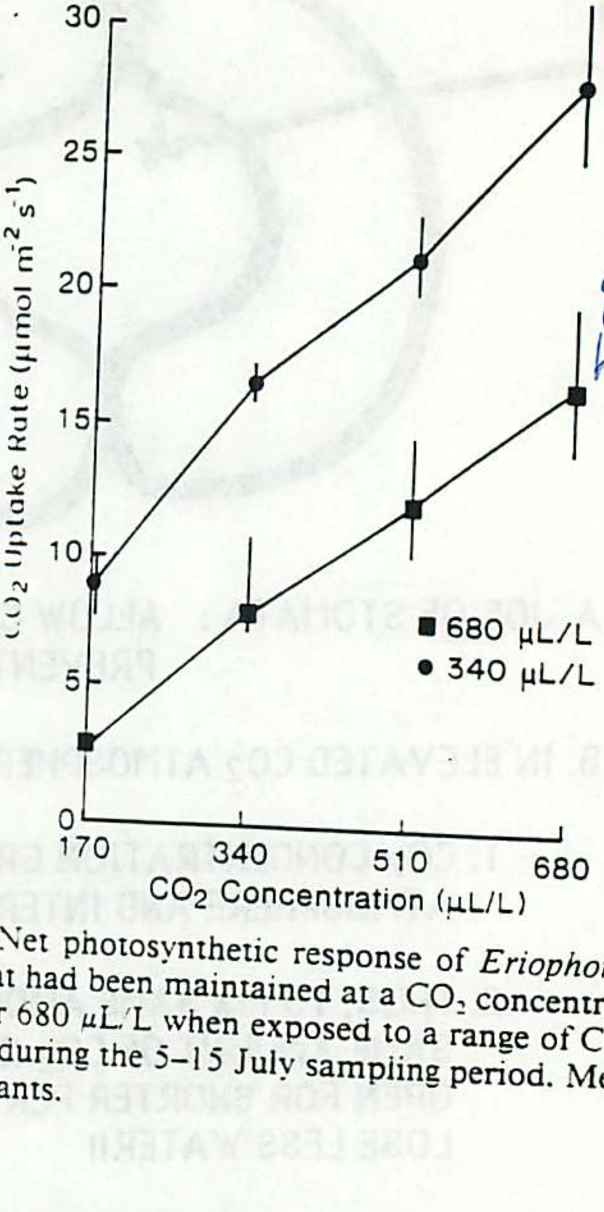
Plants grown in high CO_2 have lower Ps rates.

"Long-term acclimation"

Why

① feedback inhibition
  "too many starches...
  "time lag
  "source-sink
  -run out of substrate
   · triose P → sucrose pathway
  -N dilution effect
«what about T°?

N dilution effect
  -Ps is measured per m^2
  -so- can pull out some N_2 and drop to old Ps rate N



grown in Low CO_2

grown in High CO_2

FIG. 2. Net photosynthetic response of *Eriophorum vaginatum* that had been maintained at a CO_2 concentration of 340 μL/L or 680 μL/L when exposed to a range of CO_2 concentrations during the 5–15 July sampling period. Mean = 1 SE. $n = 6$ plants.

tundra sedge

/7

10/22 #16

⑦

#NE

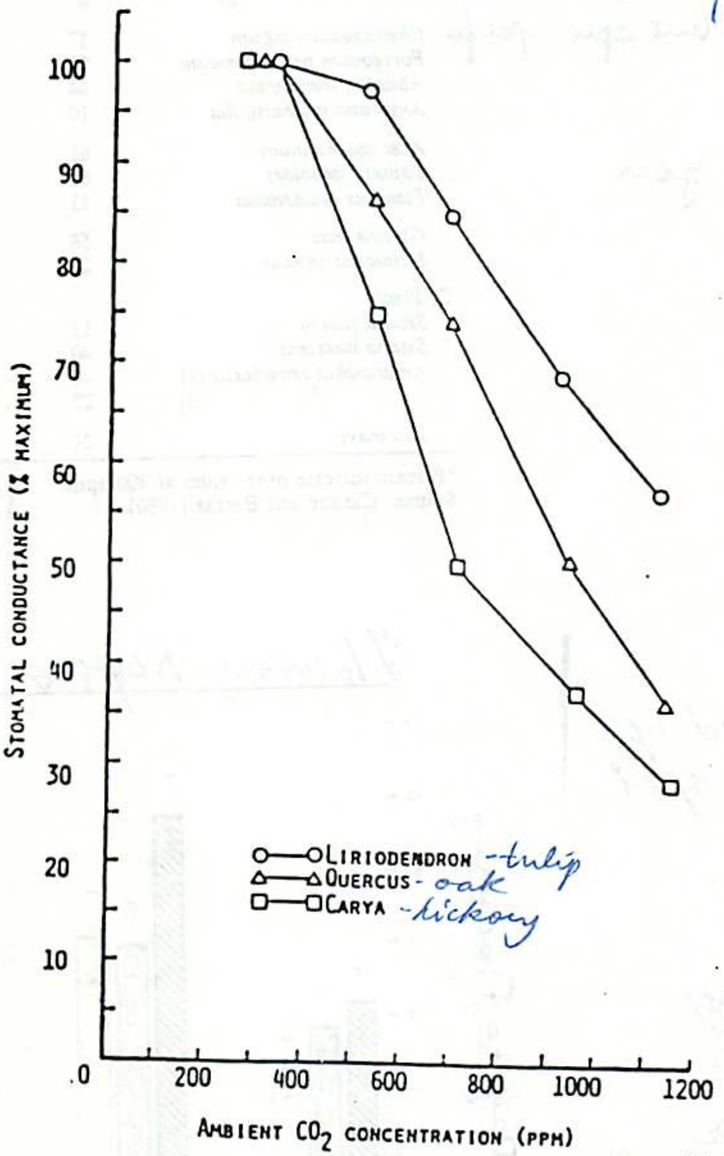


Figure 3B. Stomatal sensitivity to ambient CO_2 concentration in upland trees (seedlings)

Bazzaz et al. 1985

⑧

8

generally higher incr. than C4's but spec. specific.

what would happen if you grew these together.

Table 7.1
Percent Increase in Total Biomass and in Mean Single-Leaf Photosynthesis for Growth 28 Days After Planting at Different CO_2 Concentrations Relative to the Values at 300 ppm

Species	Photosynthesis 600 ppm	Photosynthesis 1200 ppm	Biomass 600 ppm	Biomass 1200 ppm
C_3 Plants				
Datura stramonium(1)	74	96	74	115
(2)	67	83	60	107
Chenopodium album	57	79	76	140
Polygonum pensylvanicum	51	64	48	100
Abutilon theophrasti	44	75	38	65
Ambrosia artemisiifolia	10	24	68	112
Acer saccharinum	61	89	32	63
Populus deltoides	65	74	29	20
Platanus occidentalis	13	30 ↑	33	33
Glycine max	58	75 ↑	47	100
Helianthus annuus	20	38 ↑	40	55
C_4 Plants				
Setaria faberii	13	37 ↑↑↑	42	106
Setaria lutescens	40	20 ↓↓	70	45
Amaranthus retroflexus (1)	41	→ 21 ↓↓	36	59
(2)	27	33	29	48
Zea mays	24	-7	21	10

[a] Percent increase over values at 300 ppm.
Source: Carlson and Bazzaz (1980).

grown in fertile soil so maybe no feedback inhibition.

⑨

Flowering Response

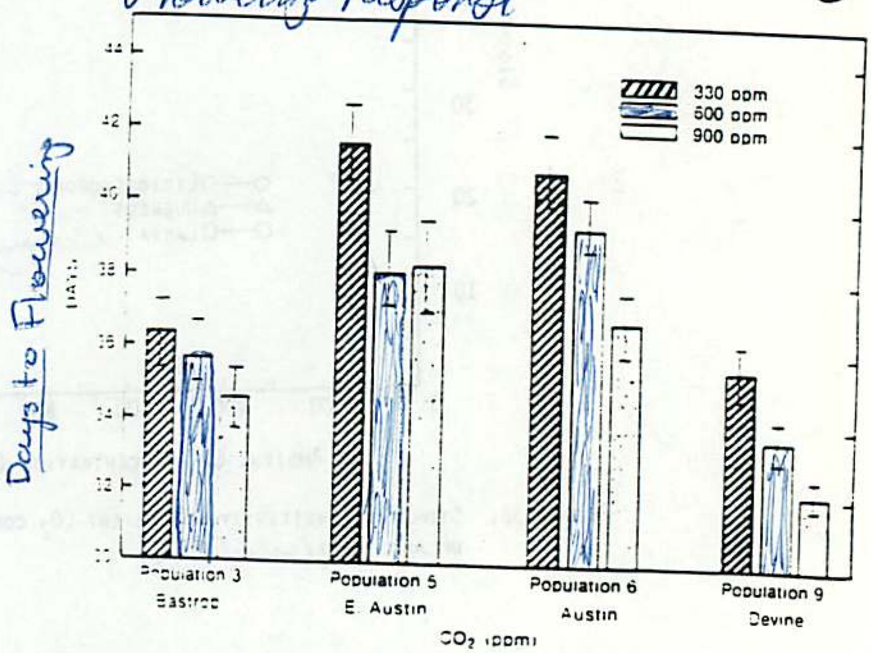


Figure 7.1. The flowering responses of four populations of *Phlox drummondii* to three levels of CO_2. Bars indicate two standard errors. Source: Garbutt and Bazzaz (1984).

Flowering phenology
- in annuals, may speed up growth & lead to sped up phenology.

Gradient of [CO_2] from soil → canopy. may be important.
- seedlings in high CO_2
- get to some pt & then into lower CO_2 - may be trigger.

Plants in low [CO_2] produce more seeds but may be of lower quality.

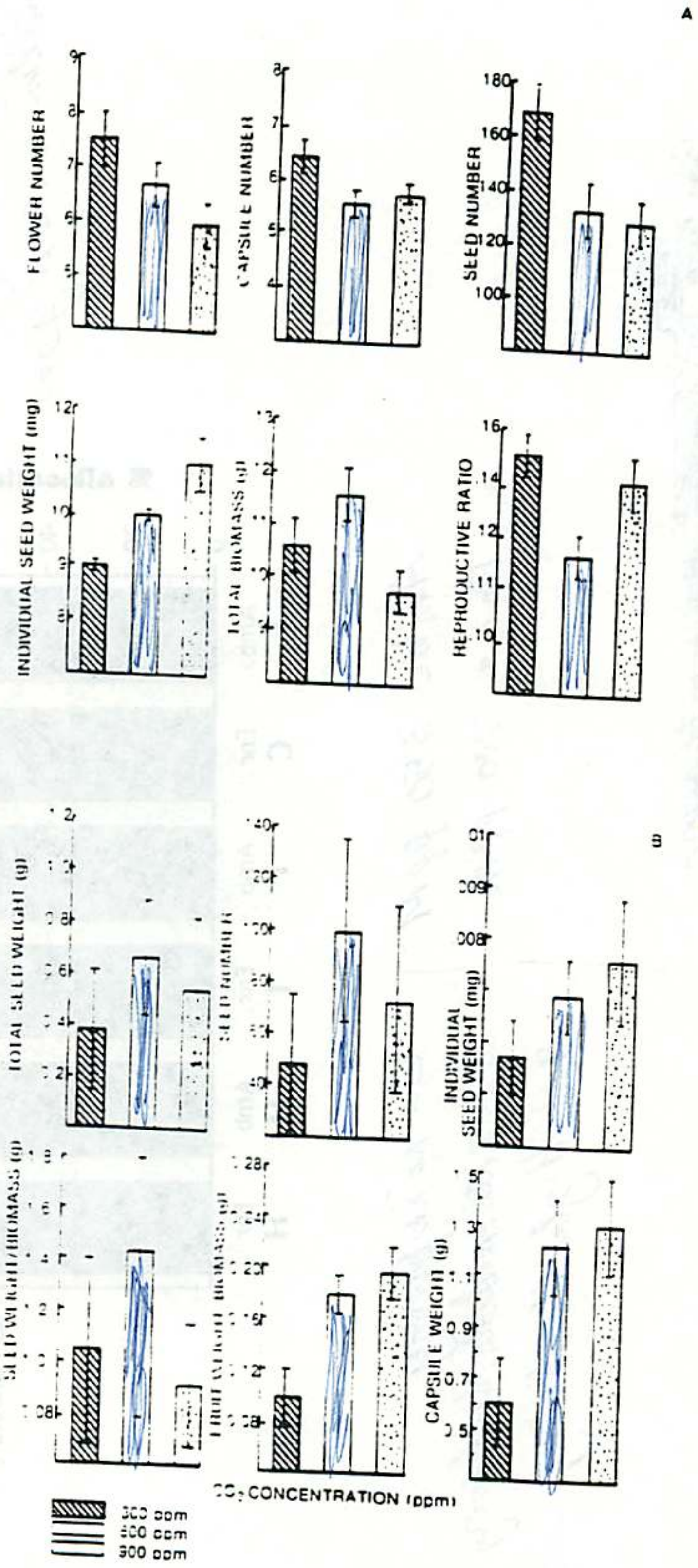
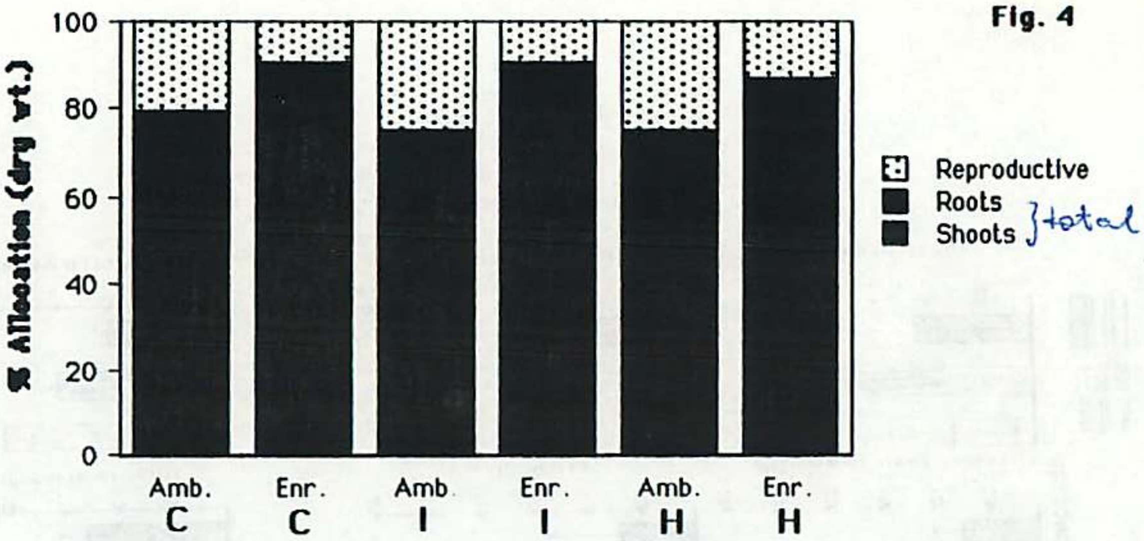


Figure 7.2. The reproductive response of two old-field annuals to concentrations of CO_2. (A) *Abutilon theophrasti*. (B) *Datura stramonium*. All data are on a per plant basis, all weights are grams. Source: Garbutt and Bazzaz (1984).

Plantago lanceolata (short lived perennial weeds)

Fig. 4



}total non repro

more into roots/shoots may lead to higher seedlings next year.

Amb = 350 ppM
Enr = 700 ppM

C = no "herbivory"
I = Intermediate "herbivory"
H = High "Herbivory" = every ½ leaf

~~Enr~~
~~Enr Amb : allocated more into repro~~

Enr - both relative & actual were lower in repro.

Curtis et al 1989 ⑫

C3 community incr. total biomass.

-but diff. environs

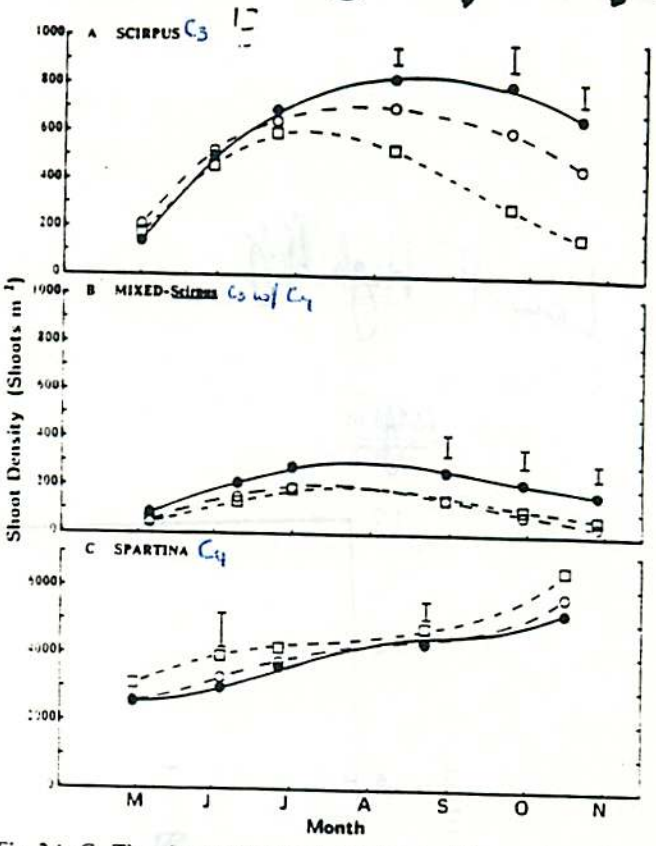


Fig. 2A–C. The change in shoot density in Scirpus (A). Mixed-*Scirpus* (B). and Spartina (C) plots. Treatments were Elevated (●). Ambient (○). and Control (□). Vertical bars are the LSD ($P < 0.05$) and are included where significant differences occur (A and B) or at the second and fourth censuses to indicate variability (C)

Bazzaz et al. ⑬

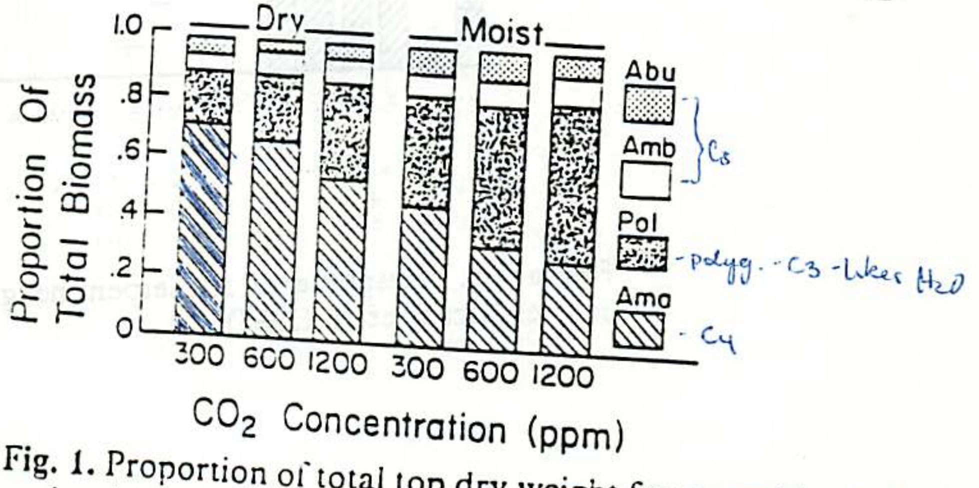
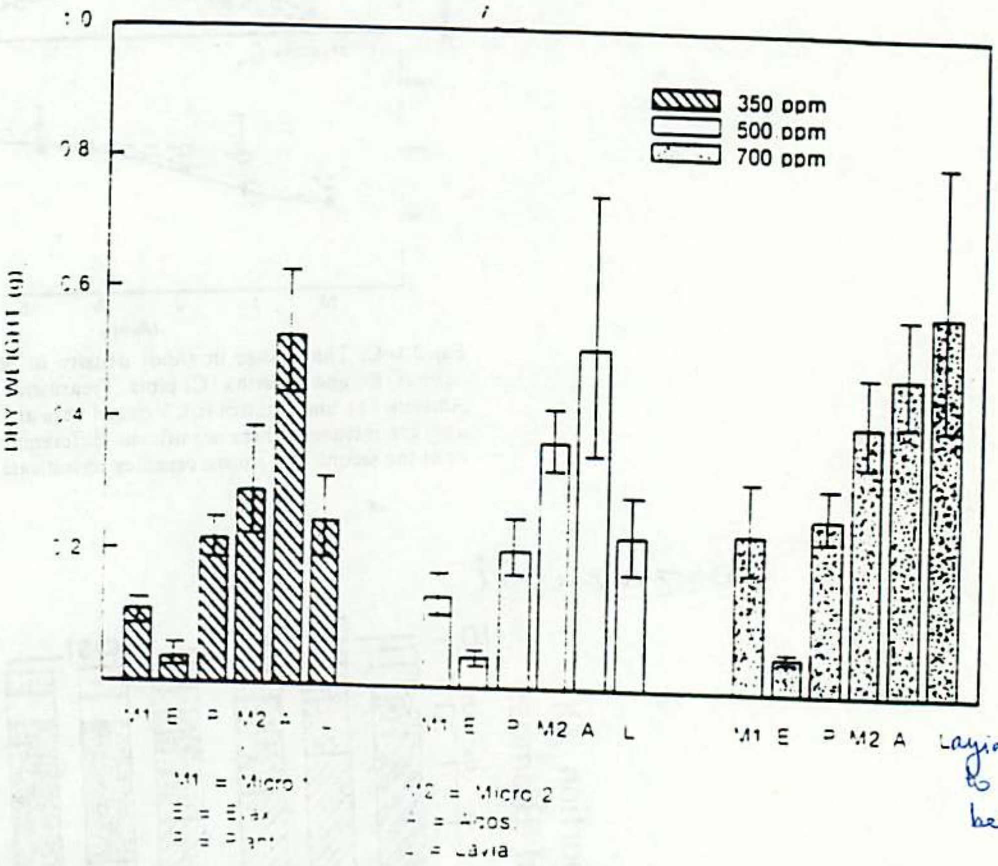


Fig. 1. Proportion of total top dry weight for assemblages of *Amaranthus* (AMA), *Polygonum* (POL), *Ambrosia* (AMB), and *Abutilon* (ABU) grown at 300. 600 and 1.200 ppm carbon dioxide and at either 15 (dry) or 30 (mesic) percent soil moisture

Low P High Mg

Layia



Layia - seems to do a lot better.

Figure 7.8. Response of six serpentine grassland species to CO_2.
Source: Bazzaz et al. (1985).

LIFE AS A LEAF FEEDING INSECT HERBIVORE

1. PERFORMANCE MOSTLY AFFECTED BY LEAF QUALITY:

   A. NITROGEN
   B. WATER,
   C. ALLELOCHEMICALS (I.E. ALKALOIDS, TANNINS, TERPENES, IRIDOID GLYCOSIDES)

CONCENTRATIONS OF THESE FACTORS IN FOOD MATERIAL OF PRIMARY IMPORTANCE FOR DETERMINING INSECT GROWTH RATE, CONSUMPTION RATE, FINAL SIZE

2. "GOALS" OF INSECT HERBIVORE: GETTING "FIT"

   A. GROW FAST
      1. AVOID PREDATORS, PARASITOIDS
      2. COMPLETE DEVELOPMENT WHILE FOOD STILL READILY AVAILABLE AND NUTRITIOUS

   B. GROW TO LARGE SIZE
      1. COMPETITION FOR MATES
      2. OVERALL VIRILITY/FECUNDITY (SPERMATOPHORE SIZE, # OF EGGS LAID)

   C. SIZE OFTEN CORRELATED WITH LONGEVITY

1b

TABLE 1: PLANT TISSUE QUALITY OF *PLANTAGO LANCEOLATA* LEAVES GROWN IN EITHER LOW (350 PPM) OR HIGH (700 PPM) CO2 ENVIRONMENTS

	LOW CO2			HIGH CO2			SIGNIFICANCE
	$\bar{x}$	(sd)	n	$\bar{x}$	(sd)	n	F value
Water (%)	81.57	(2.52)	18	82.45	(1.21)	13	1.37, NS
Nitrogen (%)	1.58	(0.18)	18	1.40	(0.13)	13	8.53, p<0.01
Aucubin (%)	3.68	(1.30)	18	3.22	(1.25)	13	0.34, NS
Catalpol (%)	1.93	(0.91)	18	1.70	(0.99)	13	0.51, NS
Total Iridoids (%) (Auc + Cat)	5.61	(1.79)	18	4.92	(1.26)	13	0.26, NS
Acid Detergent Fiber (%) (cellulose, lignin)	21.84	(2.48)	18	21.26	(2.40)	13	0.41, NS
Neutral Detergent Fiber (%) (cellulose,lignin,hemicellulose)	27.74	(2.78)	18	26.99	(2.91)	13	0.45, NS

Buckeye butterfly

Growth of Junonia coenia larvae reared on either high or low CO2 Plantago lanceolata (error bar = 1 SE)

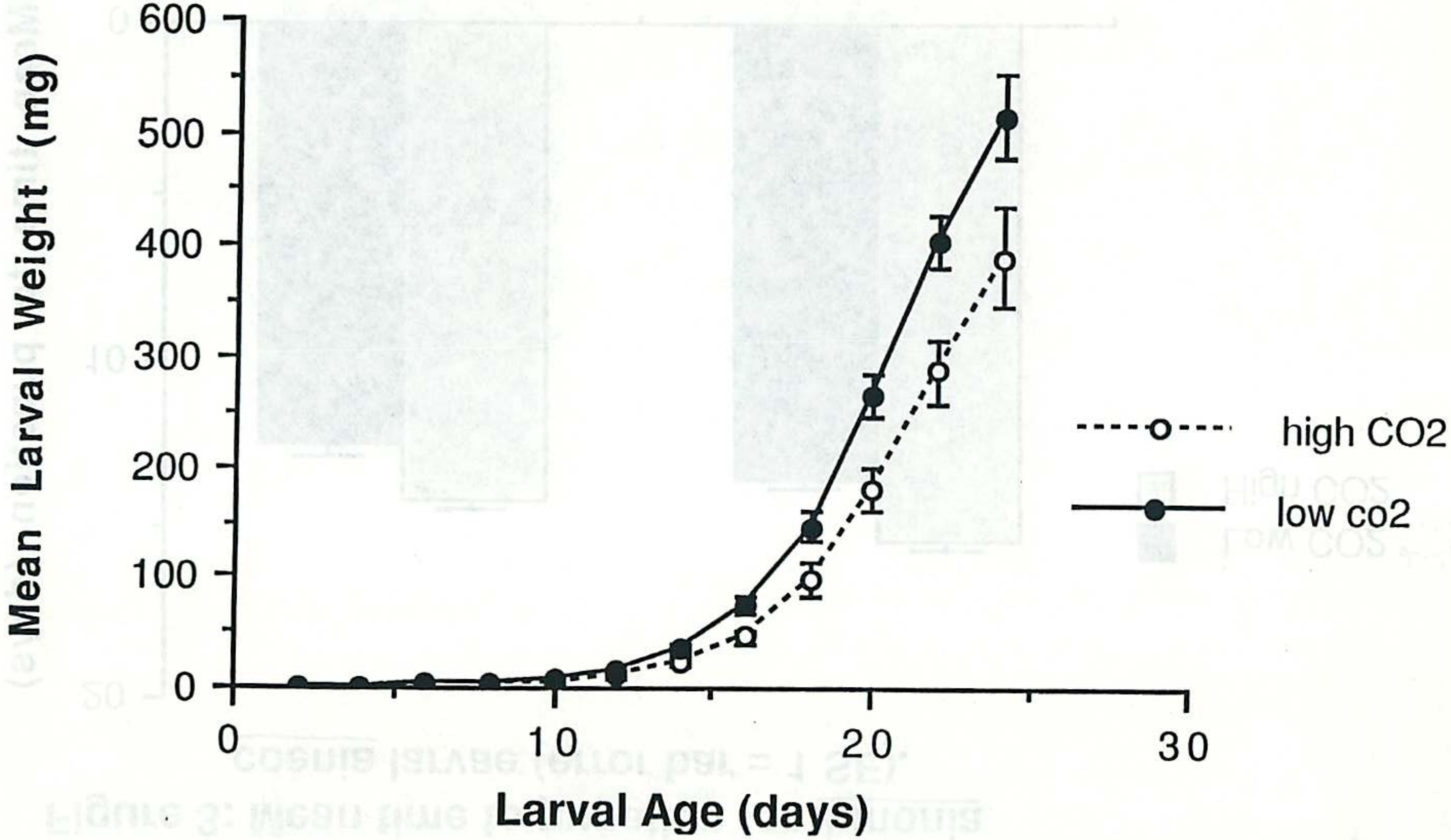
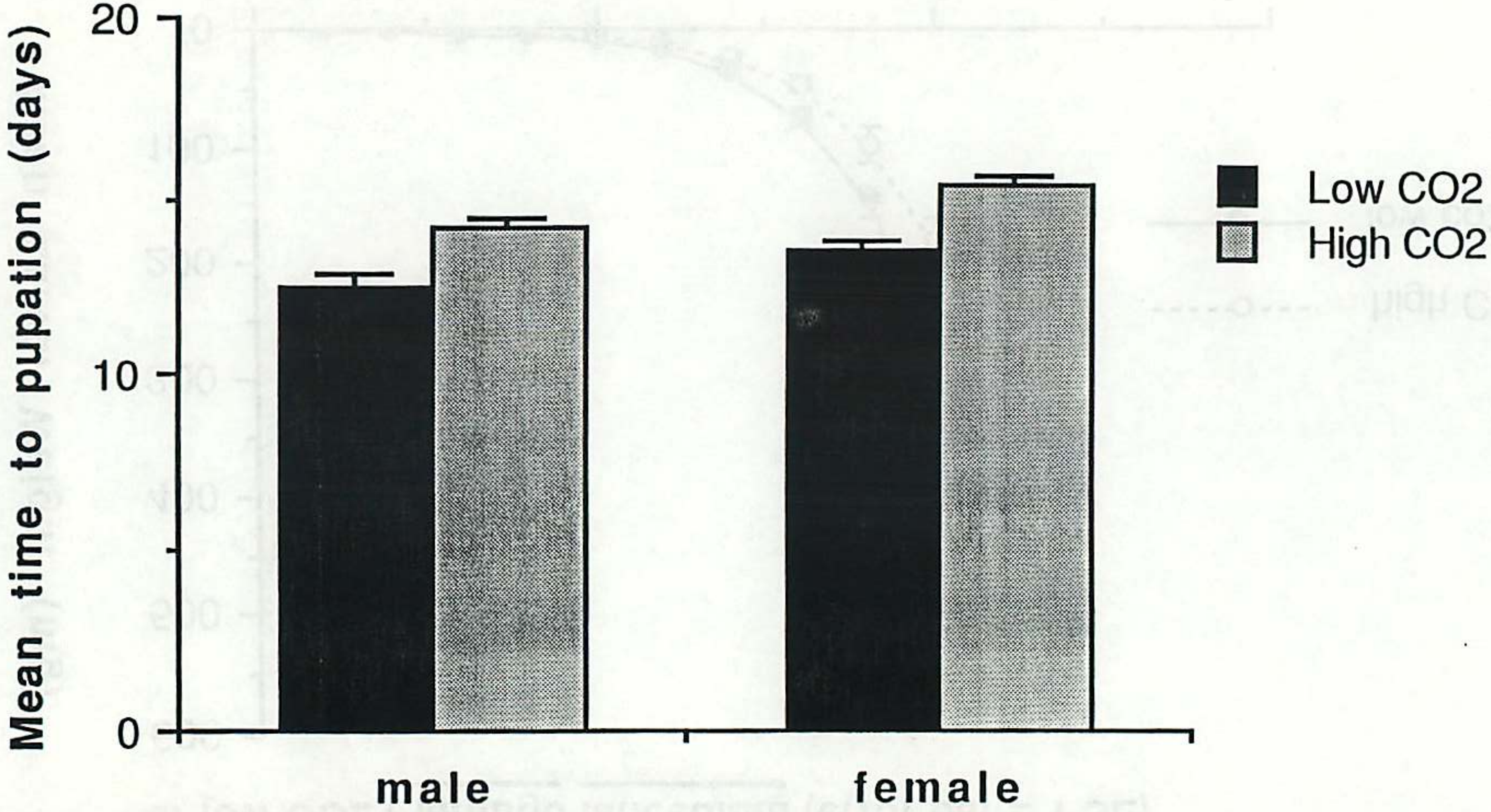
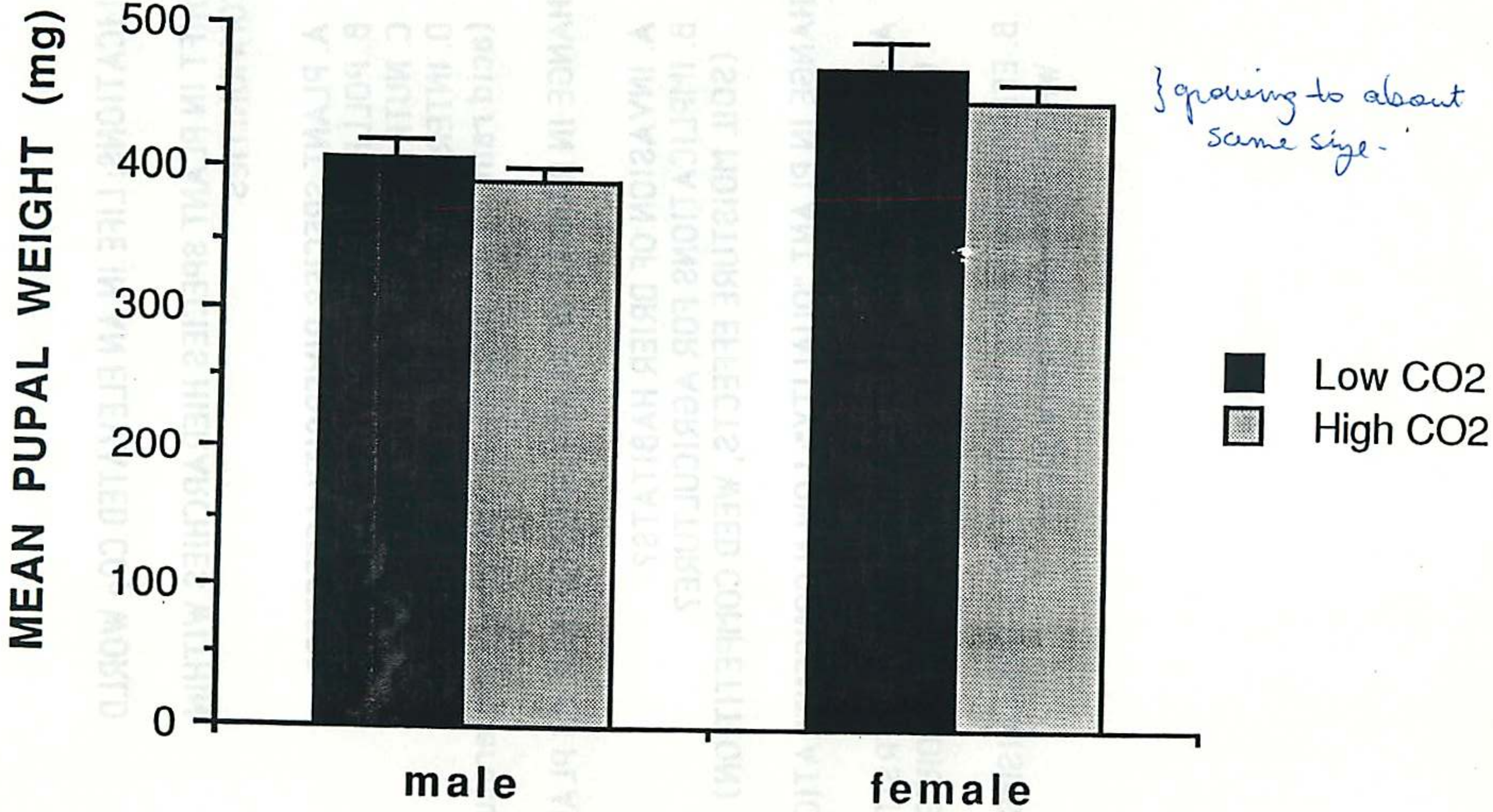


Figure 3: Mean time to pupation for <u>Junonia coenia</u> larvae (error bar = 1 SE).



dvlp. faster

Pupal weights of <u>Junonia</u> <u>coenia</u> reared on either low or high CO2-grown <u>Plantago</u> <u>lanceolata</u>



} growing to about same size.

IMPLICATIONS: LIFE IN AN ELEVATED CO_2 WORLD

1. SHIFT IN PLANT SPECIES HIERARCHIES WITHIN COMMUNITIES

    A. PLANT SPECIES DIVERSITY AFFECTED?
    B. POLLINATORS, HERBIVORES AFFECTED?
    C. NUTRIENT CYCLING AFFECTED?
    D. INTERACTIONS WITH OTHER "STRESSES"
    (acid rain, ozone depletion, elevated temperatures)

2. CHANGE IN RANGES OF PLANT SPECIES (ESP. C3 PLANTS)

    A. INVASION OF DRIER HABITATS?
    B. IMPLICATIONS FOR AGRICULTURE?
    (SOIL MOISTURE EFFECTS, WEED COMPETITION)

3. CHANGE IN PLANT "QUALITY": LOW N CONCENTRATIONS

    A. EFFECTS ON HERBIVORE ABUNDANCE, DIVERSITY?
    (A BLEAK NEW WORLD FOR INSECT HERBIVORES??)

    B. EFFECTS ON UPPER TROPHIC LEVEL ORGANISMS WHICH FEED ON HERBIVORES?

10/24

Bio 149: Experimental Plant Ecology Fall 1989

Lecture Outline for Eric Fajer

Direct and Indirect CO2 Effects on Individual Plants and Communities

1. The Carbon Cycle
   - Anthropogenic alterations: fossil fuels and deforestation
   - Projected future atmospheric CO2 levels

2. Direct Effects of CO2 on Plants
   - Autecological (individual?) responses of plants
     - Photosynthesis: short- and long-term
     - Stomatal Conductance and Water Use Efficiency (WUE)
     - Biomass accumulation: Vegetative and Reproductive
     - Phenology: annuals; flowering responses

3. Implications for Plant Communities
   a. Weeds: C3 vs C4
   b. Trees: Species specific responses

4. Trophic Level Interactions
   - Plant quality changes
   - Herbivores and Food Webs
   - Mycorrhizae
   - Leaf Litter Quality and Nutrient Cycling
   - Pollination Biology

5. Experimentation for the Future

Readings

Fajer, E.D. 1989. How Enriched Carbon Dioxide Environments May Alter Biotic Systems, Even in the Absence of Climatic Changes. Conservation Biology Vol. 3, No. 3. pp 318-320.

Bazzaz, F.A. 1986. Global CO2 Levels and the Response of Plants at the Population and Community Levels. Report OIES-2: 31-6.

Leslie Barbagallo
10/24/89

Eric Trajer

Atmospheric CO_2
Fig 1
Fig 2

Annually
- incr. in E use of 1-2%
- usu. fossil fuels as developing countries try to incr. standard of living

Doubling in $[CO_2]$ possibly by 2040.

Energy use does not necessarily couple with incr. ...

How does $[CO_2]\uparrow$ affect plants

① Photosyn. efficiency ↑

C_3 $RUPB(C_5) + CO_2 \xrightarrow{rubisco} 2\,PGA\ (C_3)$

$RUBP + O_2 \xrightarrow{rubisco} PGA\ \&\ C_2$

recycle C_2 acid $\xrightarrow{ATP}$ photorespiration

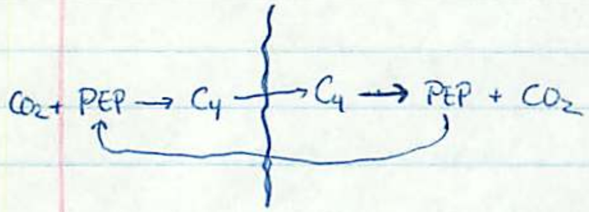
∴ w/ higher CO_2 → reduced photorespiration esp. in C_3 plants.

C_4 - incr. efficiency does not occur

$CO_2 + PEP \xrightarrow[carboxylase]{PEP} C_4$ ↗ O_2 cannot react

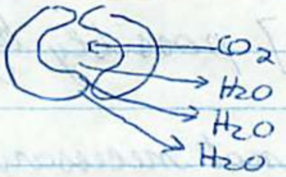
$C_4 \xrightarrow{transport}$ mesophyll

$C_4 \longrightarrow PEP\ \&\ CO_2$



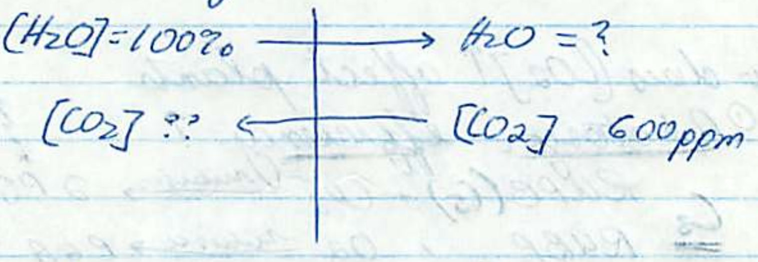
Therefore - differences betw. C_3 + C_4 may lead to competition changes.

② <u>Water-use efficiency</u> <u>Fig 5</u>



How does water go from liquid to gas.

Concentration gradients



plant w/ larger $[CO_2]$ concentration outside - don't have to open as long.

$\frac{\text{Assim}}{\text{Evap}}$

CO_2 ↑ can lead to same Ps rate due to ??..

Fig 7
Higher CO_2 & Stomatal Conductance
[illegible]
① incr. in CO_2 leads to decr. Conductancy

So plant may keep Ps constant and
H_2O efficiency changes. Same trend
f but diff. response in ~~of~~ diff. ~~response~~.
species.

Some plants may be able to colonize
new areas.

W/ Ps rate → some plants may make
new leaves which will incr. overall
Ps but maybe not Ps/m^2

So. Flowering Phenology

Incr. [CO_2] may lead to early flowering which
may screw up coevolution and competition

Incr [CO_2] → decr. allocation to repro.

Community respons
. C3 does better w/ incr. CO_2 (than C4)

Annuals may responde better bec. incr. CO_2
is over ~~first~~ many generations.

What is the concentration of O_2
What about tree rings

Animal - Plant Interactions

Herbivory - what affects
① N concentration in leaves
② H_2O " " "
③ allelochemicals
alkaloids, tannins, terpenes; iridoid glyc.

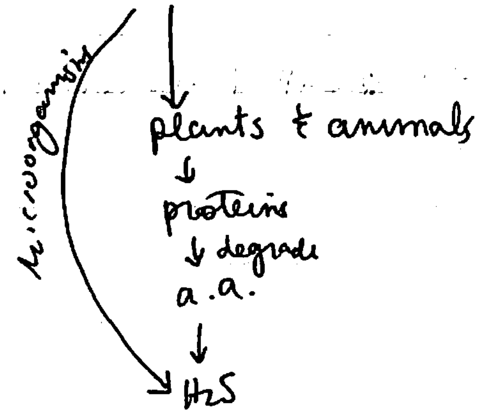
What does insect herbivore want to do?
① Large, fast

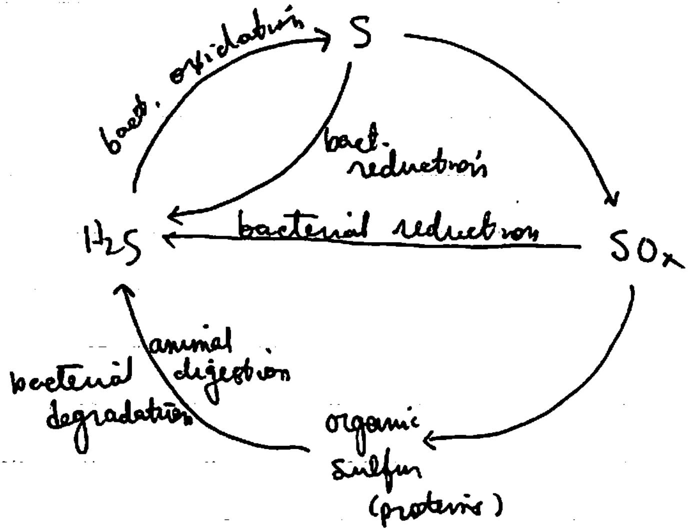
So - what happens to Plant nutritional qualities

SO_4 → .05–1% aa (cys, met → prot & CoA & other enzymes)

NO_3 1-4% aa, prot, nucleotides, NTP's, chloro, coenzymes

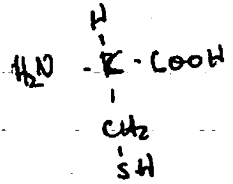
$2S + 2H_2O + 3O_2 \longrightarrow 4H^+ 2SO_4^{2-}$



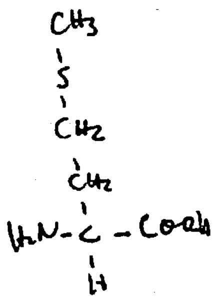


430
~~13,55~~
691
~~243~~
~~281~~
~~450~~
~~532~~
~~570~~

cys



met



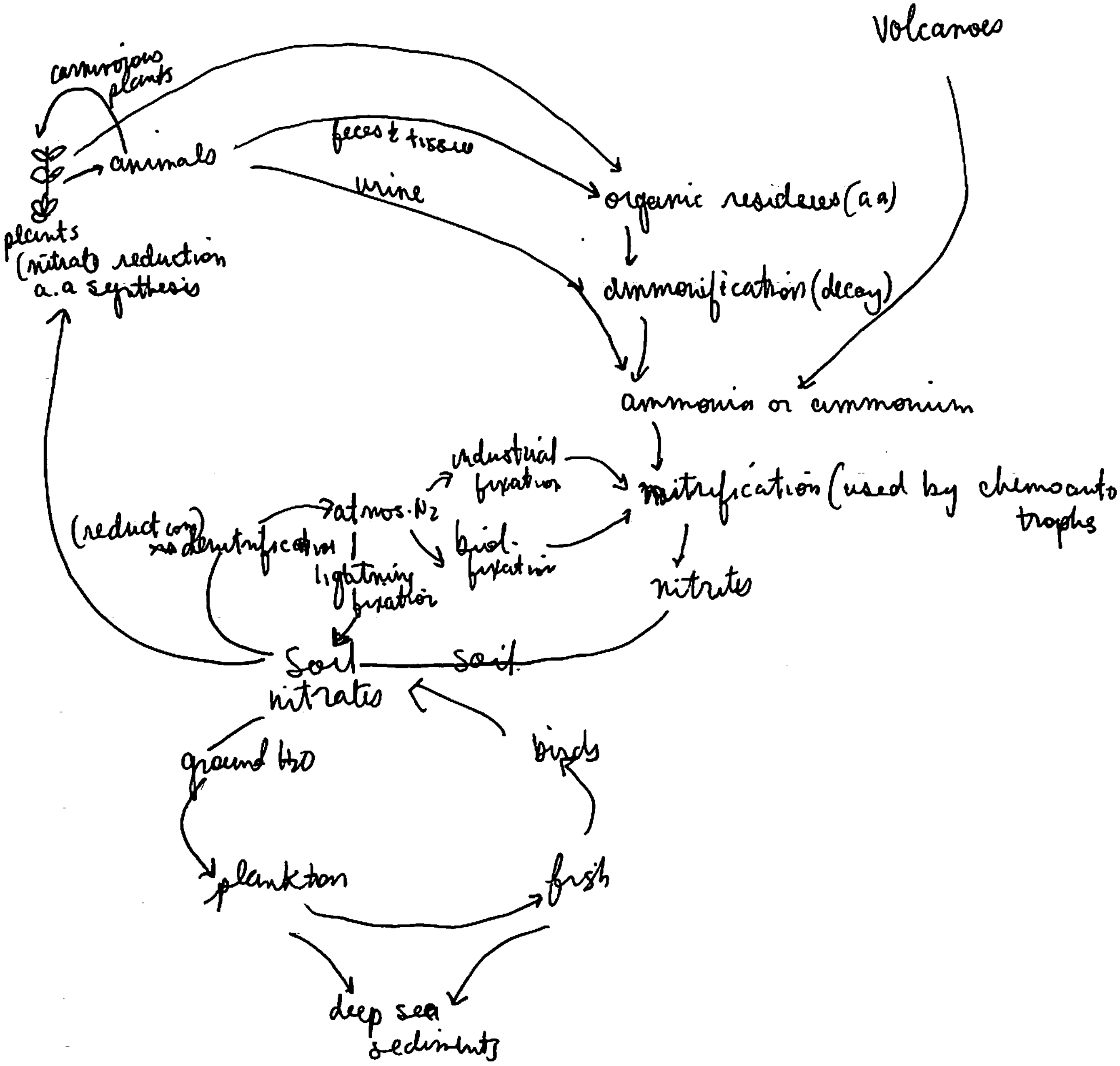
SO_2

- kills lichens, bryophytes
- destroys chlorophyll

ores such as

$CuS + 3O_2 \rightarrow 2CuO + 2SO_2$

affects soil makeup (leaching)



$$2NH_3 + 3O_2 \xrightarrow[\text{synth}]{\text{chemo}} 2NO_2^- + 2H^+ + 2H_2O$$

$$2NO_2^- + O_2 \xrightarrow{\text{nitrobacter}} 2NO_3^-$$

- add NO_2 → nutrient as well as <u>acid</u>!
  algal blooms

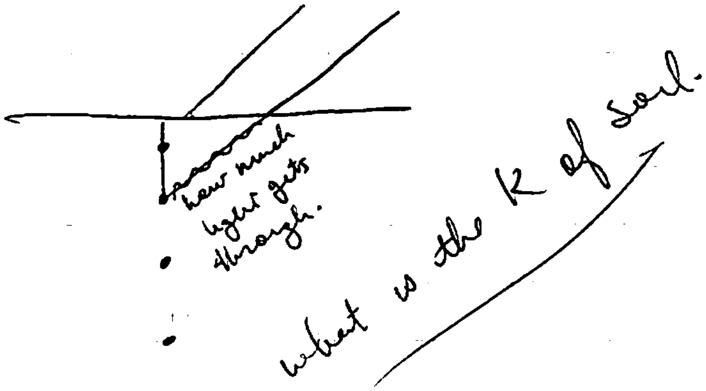
Experimental Plant Ecology

Indeterminate growth: plants will continue to produce new modules until death.

Electromagnetic

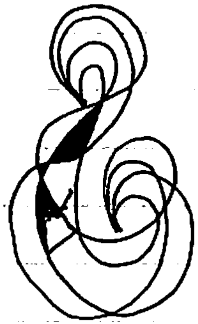
700·800 far red

Remember other plants
- if you wilt to protect self - the plants below may catch up.



Radiation
- pattern
- quantity
- quality

CO_2
↓



Incr CO_2 → less O_2 comp

↘ less N needed

Fig 1
10/26/89

Sources of Ozone Precursors

Emission	Source category	1966	1970	1974	1978
NO_x (as NO_2)	Power plants	650	820	920	940[a]
	Industry	660	690	660	580
	Domestic heating, small trade	100	130	140	140
	Transporation	640	820	990	1,340
Total NO_x		2,050	2,450	2,700	3,000

[a] NO_x emissions (as NO_2) are estimated at 944,000 t a^{-1} for 1980 (VGB 1982)

Table 1.4. Anthropogenic emissions of organic compounds in the Federal Republik of Germany, 1966–1978 in 1,000 t a^{-1}. (Umweltbundesamt 1981)

Emission	Source category	1966	1970	1974	1978
Organic compounds	Power plants	6	8	9	9
	Industry	350	450	480	470
	Domestic heating, small trade	640	720	710	630
	Transportation	400	530	570	650
Total organics		1,400	1,700	1,800	1,750

Fig2

TABLE 4.4
Sum of Economic Surpluses for Corn, Cotton, Soybeans, and Wheat with Alternative Secondary Ozone Standards

(Billions of 1980 dollars)

Ambient standard (ppm)[a]	Expected surplus	Change in expected surplus
0.12	43.726	—
0.10	46.125	2.399
0.08	49.271	5.545
0.14	39.918	−3.808

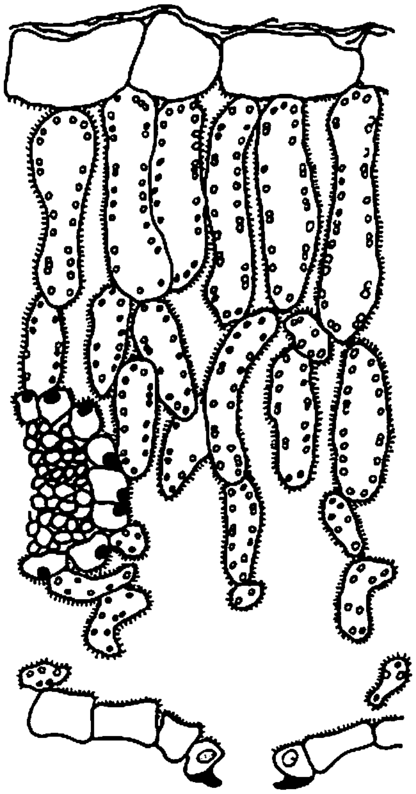
primary standard ← human hazard

NOTE: Calculated from information in Tables 4.1 and 4.3.

[a] 1 ppm O_3 = 41.6 μmol m^{-3}.

DETERMINANTS OF SULFUR DIOXIDE FLUX (J)

$$J_{SO_2} = (C_a - C_l)\cdot(g_a + g_s + g_r)$$



GAS PHASE

PATHWAY CONDUCTANCE

Conductances (g_L)

Boundary layer (g_a)

Stomata (g_s)

Concentration Gradient (ΔC)

Ambient conc. (C_a)

Gas-to-liquid conc. (C_l)

Flux

Leaf surface flux ($J_{Surface}$)

Leaf interior flux ($J_{Internal}$)

$J_{Total} = J_{Internal} + J_{Surface}$

LIQUID PHASE

PATHWAY CONDUCTANCE

Conductance

Residual/Chemical/Mesophyll (g_r)

Chemical Potential Gradient (ΔC)

Gas-to-liquid concentration ($H_m C_l$)

Perturbation site concentration (C_p)

Intermediate concentration (C_s)

Fig 3

Table 3. Changes in net assimilation rate in response to long-term fumigations with sulphur dioxide

Reference	Species	Concentration (ppb)	Duration (d)	Response % control
Murray (1985)	*Medicago sativa* (alfalfa) cv 'CUF101'	75	116	64
Shimizu, Furukawa & Totsuka (1980)	*Helianthus annuus* (sunflower) cv 'Russian Mammoth'	100	35	73
			42	78
Jones & Mansfield (1982a)	*Phleum pratense* (Timothy grass) cv 'Aberystwyth S48'	120	40	85
Jensen (1981)	*Populus deltoides* × *trichocarpa*	250	49	68
Walmsley, Ashmore & Bell (1980)	*Raphanus sativus* (radish) cv 'Cherry Belle'	170	26	66
			36	100
Oshima *et al.* (1979)	*Gossypium hirsutum* (cotton) cv 'Alcala SJ-2'	250	6 × twice weekly	85
Bell, Rutter & Relton (1979)	*Lolium perenne* (ryegrass) cv 'S23'	16	173	65
		25	144	88 NS*
		159	108	69

*NS: not significant.

Fig 4

Table 4. Effects of short-term fumigations (< 1 d) with ozone on photosynthesis

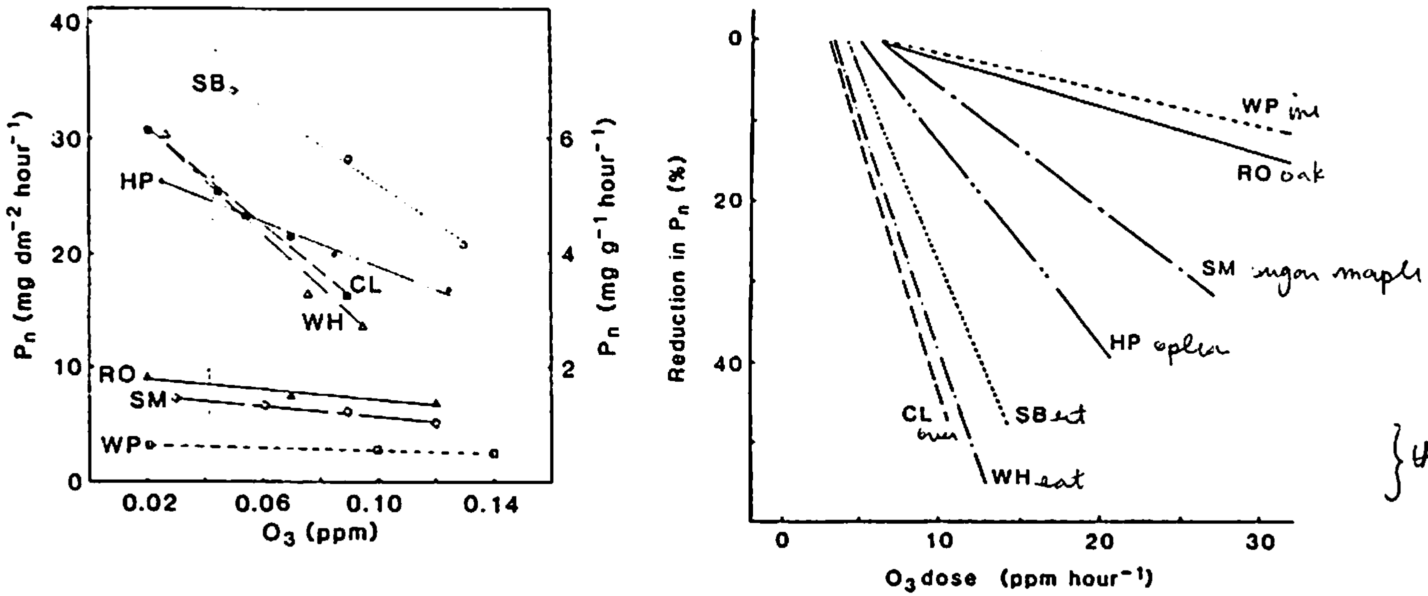
Reference	Species	Concentration (ppb)	Duration (h)	Response % control
Bennett & Hill (1973)	*Medicago sativa* (alfalfa) cv 'Ranger'	100 200	1 1	96 90
Chevone & Yang (1985)	*Glycine max* (soybean) cv 'Essex'	299	2	90
Pell & Brennan (1973)	*Phaseolus vulgaris* (pinto bean) cv 'Pinto'	300	3	78
Hill & Littlefield (1969)	*Avena sativa* (oats) cv 'Park'	400	0.5	67
	Nicotiana tabacum (tobacco) cv 'Bel B'	400	1.5	22
	Lycopersicon esculentum (tomato) cv 'Moscow'	600	1	22
	Phaseolus vulgaris (pinto beans) cv 'Pinto'	450	2	52
	Zea mays (corn) cv 'Golden Bantam'	500	1.5	68
	Phaseolus vulgaris (bush bean) cv 'Tender pod'	500	1.3	65
	Hordeum vulgare (barley)	620	0.5	42
	Triticum aestivum (wheat)	700	1	50
Carlson (1979)	*Quercus velutina*	500	8 on 2 consecutive days	70
	Acer saccharum	500		79
	Fraxinus americana	500		100
Botkin, Smith & Carlson (1972)	*Pinus strobus* (white pine)	500	4	'threshold'
Furukawa & Kadota (1975)	*Populus euamericana*	900	2	61
Furukawa *et al.* (1984a)	*Populus euamericana*	540–720	2	40–58
	Helianthus annuus (sunflower) cv 'Russian Mammoth'			
Furukawa *et al.* (1948b)	*Helianthus annuus* (sunflower) cv 'Russian Mammoth'	200 400	2 2	100 66

Table 5. The effect of long-term fumigations (> 1 day) with ozone on photosynthesis

Reference	Species	Concentration (ppb)	Duration	Response % control
Reich & Amundson (1985)*	*Trifolium repens* (clover) cv 'Arlington'	45 (19)*	180 h 3 wks	70
	Triticum aestivum (wheat) cv 'Vona'	54 (27)	147 h 3 wks	71
	Glycine max (soybean) cv 'Hodgson'	35 (17)	147 h 3 wks	90
	Populus deltoides × *trichocarpa*	55 (25)	214 h 6 wks	65
	Acer saccharum	60 (30)	245 h 7 wks	90
	Quercus rubra	70 (20)	350 h 10 wks	91
	Pinus strobus	100 (60)	252 h 12 wks	92
Reich *et al.* (1986)	*Glycine max* (soybean) cv 'Hodgson'	50 90 130	6.8 h 8 wks	90 89 88
Kress *et al.* (1986) pers. comm.	*Glycine max* (soybean) cv 'Corsoy 79'	<80	Seasonal mean	100
Barnes (1972)	*Pinus strobus* increasing needle age ↓	50 150 150 150	77 d 19 d 36 d 77 d	100 90 100 100
	Pinus taedi *Pinus elliotii* *Pinus serotina*	150	35, 77 and 86 d	100
	Pinus taeda *Pinus elliotti*	50	126 d	88
Taylor *et al.* (1986)	*Picea rubens*	120	4 h × 35 d over 4 months	95

*Numbers in brackets refer to highest concentration at which no effects were detected.

Fig 5



} these a fast growing plants and are affected more.

Fig 7

TABLE 26.1
Influence of Air Pollution on Forest Ecosystems

Response of vegetation	Impact on ecosystem
Class III: High dosage	
1. Acute morbidity	1. Simplification; increased erodibility, nutrient attrition, altered microclimate and hydrology
2. Mortality	2. Reduced stability
Class II: Intermediate dosage	
1. Reduced growth	1. Reduced productivity, lessened biomass
(a) decreased nutrient availability	
(i) depressed litter decomposition	
(ii) acid-rain leaching	
2. Reduced reproduction	2. Altered species composition
(a) pollinator interference	
(b) abnormal pollen, flower, seed, or seedling development	
3. Increased morbidity	3. Increased insect outbreaks, microbial epidemics; reduced vigor
(a) predisposition to entomological or microbial stress	
(b) direct disease induction	
Class I: Low dosage	
1. Act as a sink for contaminants	1. Pollutants shifted from atmospheric to organic or available nutrient compartment
2. No or minimal physiological alteration	2. Undetectable influence, fertilizing effect

Fig 6

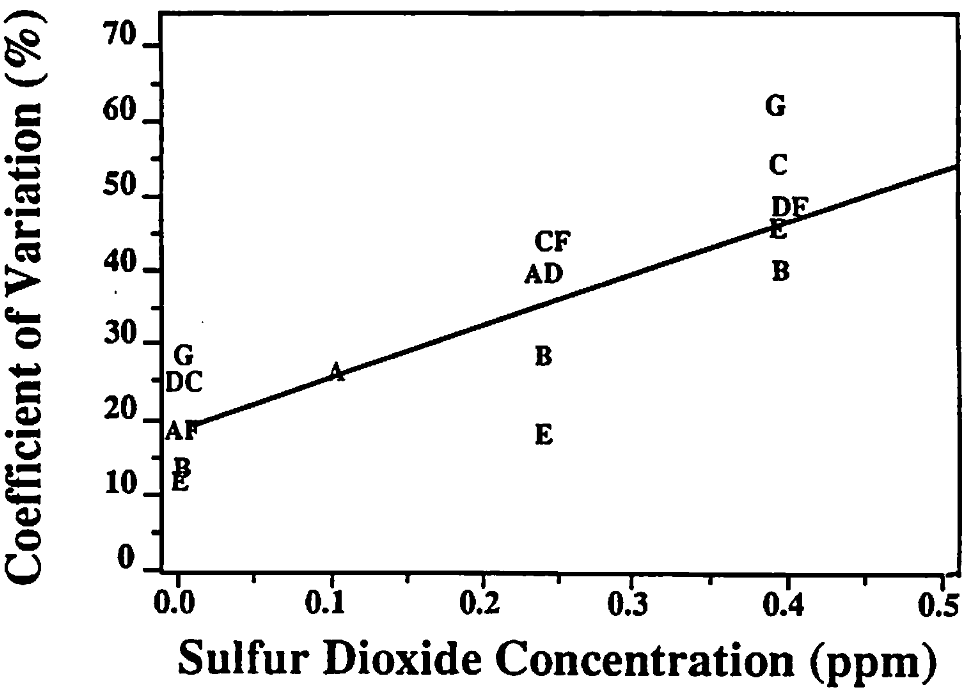
TABLE 15.1
Stomatal Conductance and Visible Foliar Injury in Populations of *Bromus rubens* Collected from a Clean-Air Site and from a Site Exposed to SO_2 for 25 Years in Coastal California

Category	*Bromus rubens* seedlings from: Clean-air population	*Bromus rubens* seedlings from: SO_2-exposed population[a]
Stomatal conductance (mol m^{-2} s^{-1} ± 99% confidence interval):[b]		
Control treatment	0.220 ± 0.093	0.189 ± 0.116
0.5 ppm (20.8 μmol m^{-3}) SO_2	0.166 ± 0.118	0.045 ± 0.011
Blades with tip necrosis (percent):[c]		
Control treatment	0%	0%
0.05 ppm (2.1 μmol m^{-3}) SO_2	15	0
0.2 ppm (8.3 μmol m^{-3}) SO_2	20–25	5–10
0.5 ppm (20.8 μmol m^{-3}) SO_2	40	15

[a] Mean maximum daytime concentration at ground level was 0.09 ± 0.08 ppm (3.7 ± 3.3 μmol m^{-3}), but could, on about 2 or 3 days a year, reach 0.33 ppm (13.7 μmol m^{-3}).

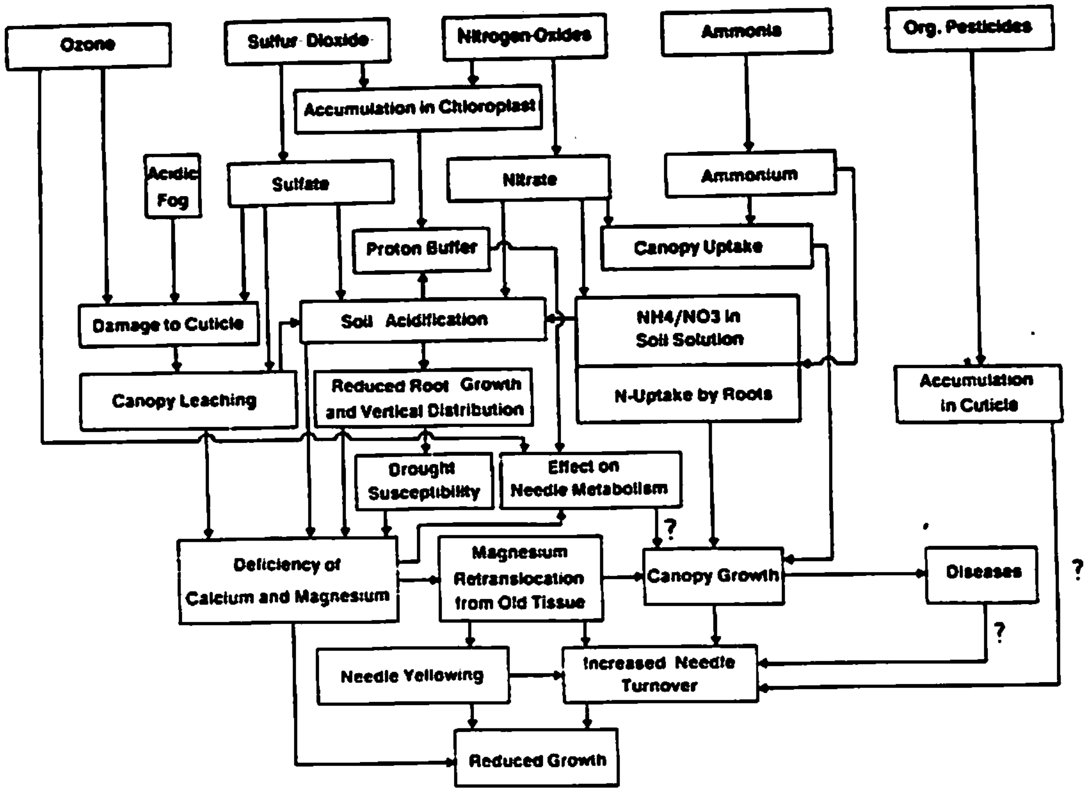
[b] After one week of fumigation, 40 hours per week. Conductance was collected with Li-Cor Li-60 meter, with 1,800 ± 50 μE PAR light impinging on blade of each of 16 plants measured. Chamber temperatures were 28° to 29° C; relative humidity 44 to 47%.

[c] After five weeks of fumigation, 40 hours per week.



- Radishes <u>may</u> have prebuilt ability to adapt due to sulfur metabolism present.

- * mean may not say much.



~~Fig 9~~

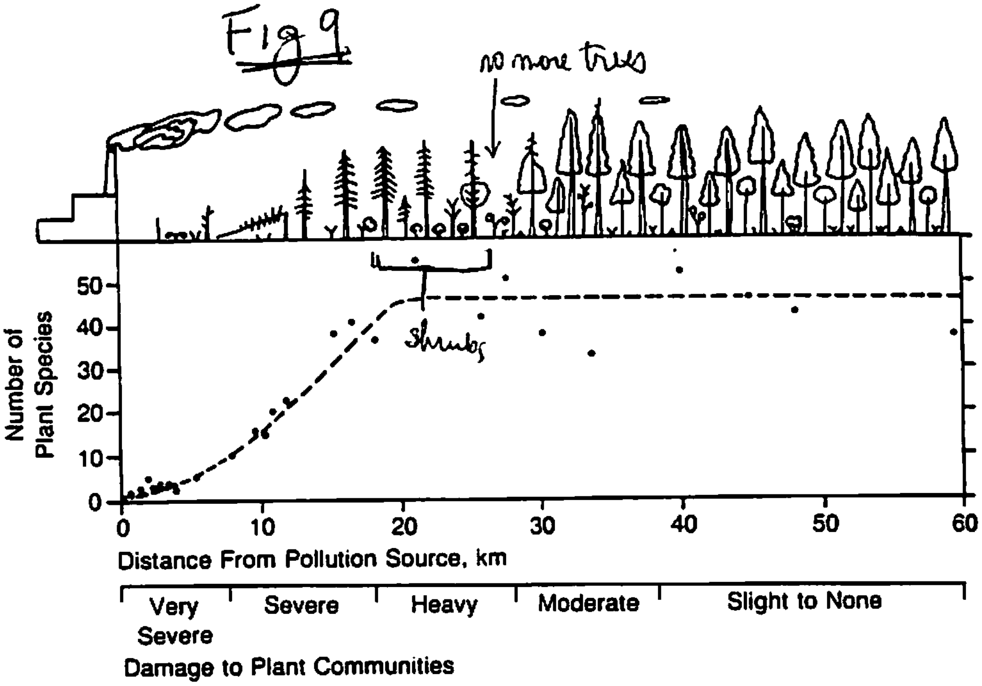


Fig. 26.2. Numbers of plant species at various distances from an SO_2-producing iron-sintering plant near Wawa, Ontario. Reproduced from Whittaker (1975); after Gordon and Gorham (1963).

Fig 8

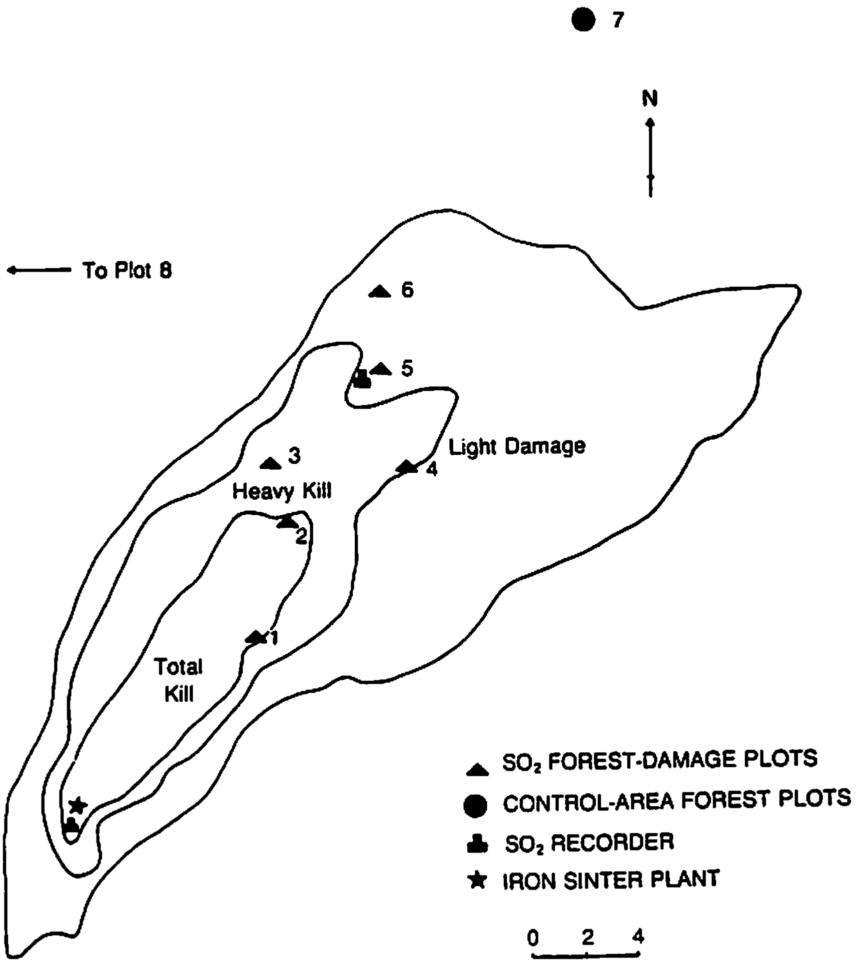
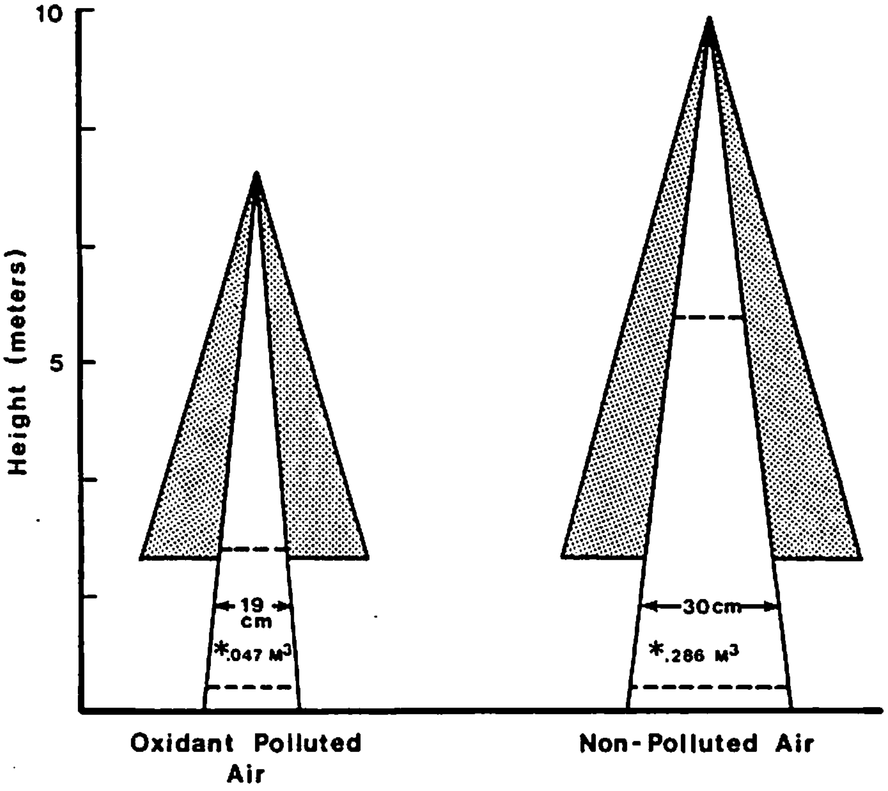


Fig. 26.1. SO_2 injury to a forest ecosystem at various distances from an iron-sintering plant near Wawa, Ontario. Reproduced from Linzon (1978); after Gordon and Gorham (1963).

Fig 16

Ozone and Plant Communities

San Bernardino Mountains



-Decrease Ponderosa Pine

- Increase in White Fir ??

- Increase in Shrub Species

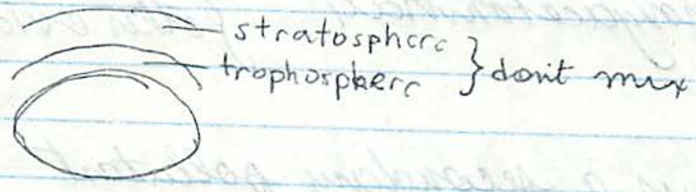
- Decrease in productivity

10/26

Ecological Consequences of Pollution

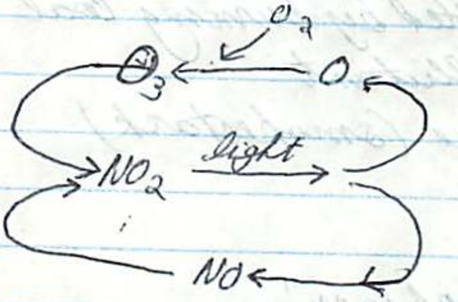
<u>Pollutants</u>

$O_3, SO_2, NO_x, Cl_2, F_2$

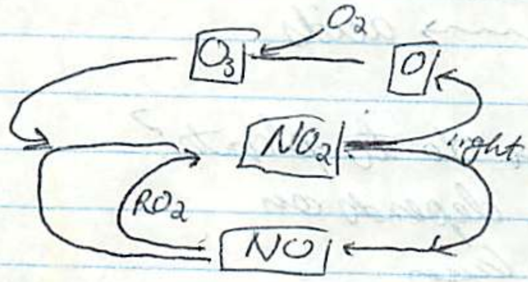


<u>trophosphere</u> -

- O_3 is 10x less than stratosphere



need lots of light for this cycle



w/ pollution NO is oxidized by RO_2 & O_3 increases

- so need light
  NO_2
  hydrocarbons

- when air is still, O_3 incr a great deal
- O_3 highest in afternoon

See Fig 2
- major source of NO_x is from automobiles
- hydrocarbons also from autos

PAN - paroxyacetonitrate } other oxidants
H_2O_2

Ozone is a secondary pollutant

Sulfur Dioxide (SO_2)
- mostly emitted by burning coal rich in S
- primary pollutant
- point source (smokestack)

Acid Rain
"Catch all phrase"
- O_3, NO_x, SO_2 ⇝ acids

What do all these do to plants?
Entrance of SO_2 depends on
① boundary layer
② gradient
③ stomates - this is the major defense plants have

SO_2 & NO_x can affect directly
① acidity
② O_3 → may dissolve coating on spruces and allow inner. pathogens

10/26

Affects of pollution:
- ① enter leaf
- ② cause stomatal closure
- ③ external

Affects inside plant
- ① O_3 dissolves → O_2 radicals → destroys membranes
- ② SO_2 dissolves → H_2SO_3 → S^{2-} → destroys enzymes
  - → O_2 radicals

major difference betw. SO_2 & O_3
- ① plants have sulfur metabolism
  - -but it may overload
  - -& plants store sulfur
- ② O_3 not stored
  - -enzymes that remove radicals help both SO_2 & O_3 reduction but w/ O_3 nothing left over

③ reduce photosynthetic rate
- ⓐ reduce conductance → decr. CO_2
- ⓑ affect pathways

may be a f(x) of amt of conductance - old leaves may be OK

C_3 more susc. bec. have to open more
Cam least susc.

Direct Effects

Acidity

① leaf damage

② reduces P_s & growth

③ change root : shoot ratio
- w/ high SO_2 → more leaves
- ∴ incr. carbon gain slightly

reallocation
- change root:shoot
- " " 2° chem.

C_4
- need lower conductance
- isolate important enzymes

Resistance

Fig 6

- SO_2 - is somewhat natural (volcanoes) so some plants adapted - close stomates -

Affect on Populations

① resistance - how can you predict ability to resist pollutions

look at variance in growth
- bec. ones w/ high growth may put out more seeds.

②different types of damage Fig 7

-SO_2 - bee a point source
creates a gradient Fig 8, Fig 9

O_3 - general pollutant Fig 10

Biology 149
Lecture Outline
2 & 7 November 1989

SOILS

- Definition
- Pedology vs Edaphology

- Soil Composition
  - Primary and Secondary Minerals
  - Weathering Processes
    - Mechanical
    - Chemical
      - Hydration
      - Hydrolysis
      - Carbonation
      - Oxidation

- Parent Material
  - Residual
  - Transported
    - Glaciers
    - Water
    - Wind
    - Gravity

- Soil Forming Processes
  - Parent Material
  - Climate
  - Topography
  - Vegetation
  - Time

- Soil Development and Profile Structure
  - Addition
  - Removal
  - Translocation
  - Transformation

- Processes of Soil Formation

Gleization
Podsolization
Laterization
Calcification

Soil Physical and Chemical Properties
Physical Properties
Texture
Structure
Color
Chemical Properties
Clay Minerals and Lattice Structure
Organic Matter
Cation Exchange Capacity
Base Saturation and pH

shh..-

11/2

Soils

GW motor

Physical weathering
glaciers
freezing
water - erosion
wind - abrasion; sand blasting

Chemical weathering (not distinct of above)
①hydration
$Fe_2O_3 \rightarrow Fe_2O_3\,3H_2O$
hydrolysis
$K_2Al_2Si_6O_{16} \rightarrow Al_2O_3\,2SiO_2\,2H_2O$
oxidation & reduction
$Fe^{2+} \leftrightarrows Fe^{3+}$
carbonation
$CaCO_3 \rightleftarrows Ca(HCO_3)_2$ (soluble)

Two kinds of "parent" material
①residual - formed in place
rock → finer rock → soil

②transported
rock → finer → move → soil
②water (flood plains ...)
③glaciers (can't sep. degradation & transport)
- sorting

2

⑤ wind -

sand dunes } sorting occurs too
locss

— can have all in compination

⑥ gravity

Soil Forming Processes

① parent material -

- v. varied in type & uniformity & quantity
- can get moscaics

② climate

what are indirect? directly - T°, H_2O, sun

high T° → faster decay ← high H_2O → more leaching

high T°, high humid → deep profile
low T°, low humid. → shallow profile

③ topography

- determines drainage

other organisms

biota
+
④ vegetation → soil - reciprocal

diff. turnover rates
productivity
litter quality...

coniferous - acidic needles
deciduous :
grassland - turnover is v. fast root:shoot = ~~02~~ 3-1
depends on H_2O

11/2/89

vegetation cont

- grasslands have other plants
- differ quant & quality of litter
- deep rooted can bring "chemistry" from below
- diff plants grab diff chemicals

⑤ time

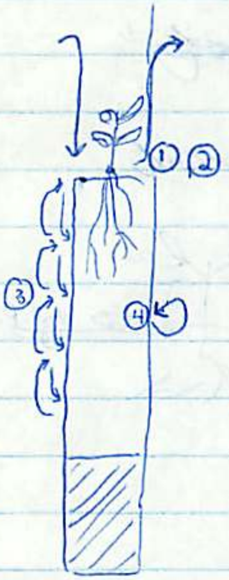
enhances weathering and leaching

Wisconsin glaciation - 20,000 BP
Illinois " "

} can be v. different depends on time

- new soil develops over old soil

Soil Development



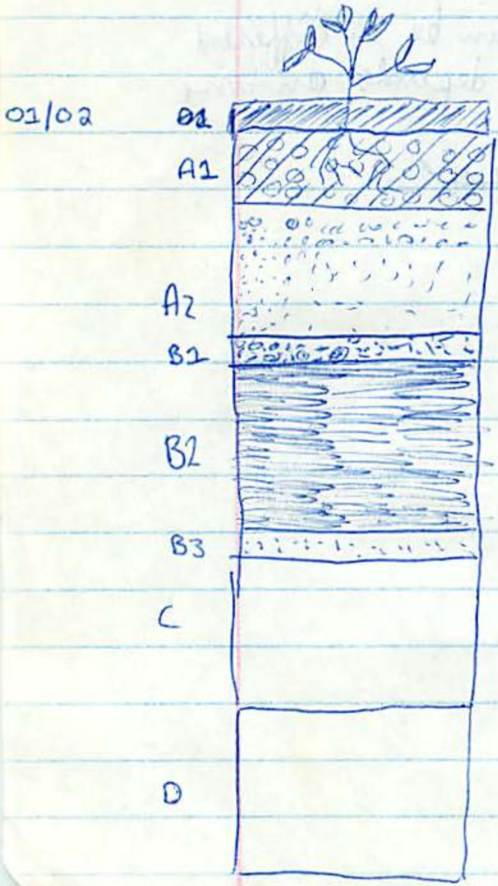
① additions
CHO, N_2, S_2,

② deletions/removals
- minerals, H_2O,
- by plants; animals; evap; leeching

③ translocation
- minerals, CHO
- particles (finer stuff down)

④ transformation
- deyae decay; hydration ...

- Started w/ uniform profile
but w/ changes ∴ get layers



} litter - also in layers - bottom is older, fragmented, decayed
① litter - on top (still recognizable) O1
② humus - on bottom O2

A1 - mixed mineral & organic

A2 - sift from A1 - mineral particles

B2 - maximal deposition of fine grained

C - unaltered parent material

D - bedrock

There is a great variety depending on site
①in grasslands A2 has high organic

②erosion

The boundary lines are not always distinct.

J. Eisen - 11/29

J. Eisen
11/7/89

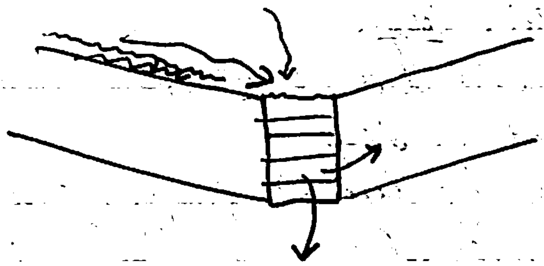
Soils - Boils · Toils · Froils - Coils

Soils & How they are formed · Part II

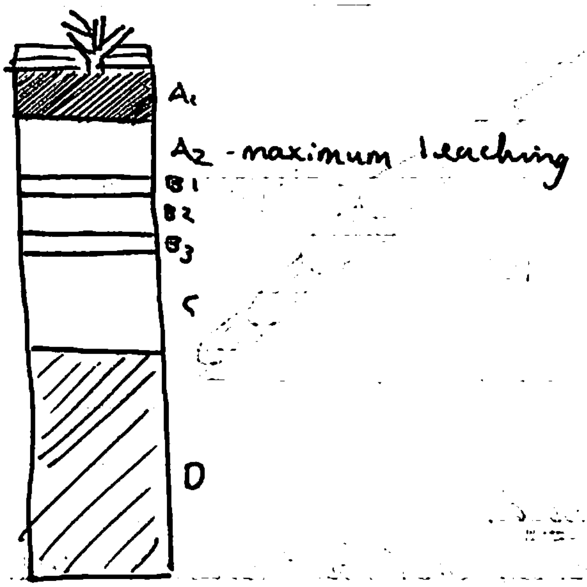
①

Residual · decay of bedrock

In deciduous forest
maple }
oak } oak decays slower ∴ litter depth in ~~oak~~ oak area may be deeper.



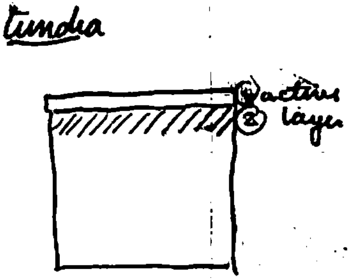
Soil Formation Processes



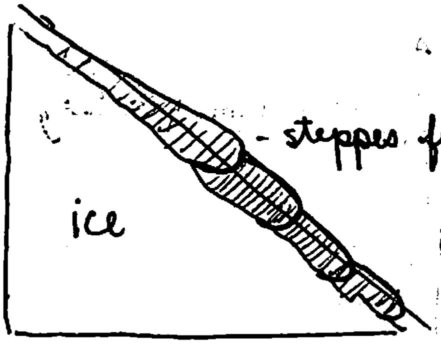
- don't have to have all layers
  - in grasslands A2 is ≅ to A1
- sizes vary greatly

Classification of Soil Formation Processes

① gleization
- occurs in cold, relat. wet climates
- organic H_2O accumulates
- sticky clay layer forms in B
- w/o oxidation - lots of hydrated iron-oxides
  colors: gray, green, blue
- common in tundra, bog



ⓐ active layer -
ⓑ shield due to frozen soil
ⓒ not v. deep
ⓓ churning due to freeze/thaw
ⓔ polygonal -



② podsolization
- occurs in cool (not cold) & lots H_2O (less than gleization)
- acidic litter (gymnosperms)
- over huge areas
  varies greatly - divided into subgroups
- rate of decay isn't very high
- litter/humus layer is v. clear & visible

Si, Al, Fe - 3 Important elements in soil

Podsolization cont.

A_1 -

A_2 - v. heavily leached (H+ replaces Mg, K, ...

-color - ash gray

-mostly silicate (SiO_2); Al, Fe into B_2

B_2 -lots Iron, Al

《FeO_2 = red》

$FeO_2 \cdot H_2O$ = brown *- these are here bec. of H_2O

-so much Fe that forms concretions, like pebbles

If H_2O fluctuates up and down very fast then get "mottled soils"! If H_2O table is predictable & slow get 1 color

Above description is of Northern regions

Loess

uniform in size

·60-70% silt

Ⓐ True podsolization · Northern regions

till from all of these { clay, silt, sand, gravel }

clay, silt } loess from here

till usu. below loess

Ⓑ Gray-Brown Podsolics

-as move S. → warmer

-in deciduous forests

-deeper that true pods

-A_1 thicker; A_2 less highly leached

-B · Al, Fe - w/o much H_2O

lighter in color, brown, yellow, red

Ⓒ Yellow Podsolics

-better drainage

-more O_2 → yellowish/reddish colors

③ Laterization

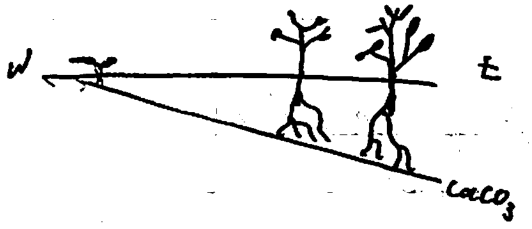
- warm, lots H_2O
- enormous leaching, low nutrients
- profiles v. deep
- Si moves down
- Al, Fe stay up → Reddish soils

- not good for agriculture
  ① low nutrients
  ② wash away

- dominant in tropics but not only type

④ Calcification

- hot, low H_2O
- grasslands, desert
- carbonates leach & deposited in B horizon
- depth of B relates to H_2O
- w/ high H_2O → water deposits solutes deep



Soil Taxonomy - see Fig 3 (79)
- even have Latin names - ...sol

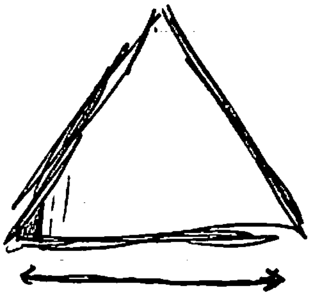
$$\begin{tikzcd}
\text{climate} \arrow[rr, shift left] \arrow[dr, shift left] & & \text{veget} \arrow[ll, shift left] \arrow[dl, shift left] \\
& \text{soils} \arrow[ul, shift left] \arrow[ur, shift left] &
\end{tikzcd}$$

Physical & Chemical Properties of Soil

Physical

① *Texture* - only concerns mineral part
-distrib. of diff. size particles
-

clay - smallest
silt - next
sand - next
gravel - biggest
rocks - not soil



-take soil & separate & do % by weight or vol.

see soil triangle

Clay

-How analyze organic material
① oven - calculate weight diff.
② digestion - uric acid $K(CrO_4)_2$ & -cleaning soln

② Structure
-aggregation of soil particles together

① no connections - Structureless
-sand at beach

② aggregation
-several attached together either through bonding or w/ assistance of organ. glue, roots pushing

PEDS = indiv. aggregate

aggregates · see 84

Ⓐ ·small round PEDS (A1)

·usu. w/ organ. glue

·fluffy, pliable

Ⓑ platy PEDS (A2)

Ⓒ blocks; columns Ⓑ

granular - A1
platy - A2
blocks - B - offers resistance

This determines ① H_2O & O_2 avail
② roots
③ nutrients

③ <u>Soil Color</u>

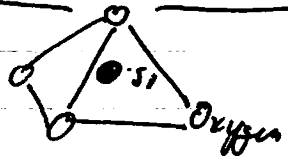
·reflects orgo, H_2O, O_2, & H_2O ↑↓ (fluctuation)

Mg ↑ → dark ← orgo ↑

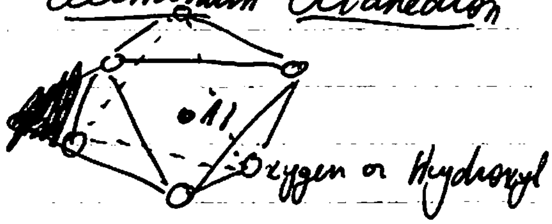
Chemical Properties of Soil

Original (1°) minerals
↓
2° mineral
↓
clay particles

Silica Tetrahedron



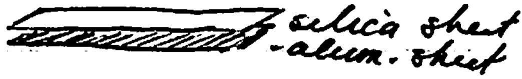
Aluminium Octahedron



Clay means
① 2° mineral w/ spec. lattice structure
or
② particle of given size
or
③ soil texture

Tetrahedrons - Silica

Variations
Lattices



1:1 lattice or 2:1

· Substitution
Si replace Al

What happens to charges
① to attach ions
ⓐ at edges
ⓑ or if unbalanced - esp. in 2:1 $Si^- : Al^+$
ⓒ

Clay Types

Calonite

- 1:1 balanced clay
- non-productive (can't bind nutrients)

Munt Moulonite

- 2:1 unbalanced
- ions stick to clay

4/89

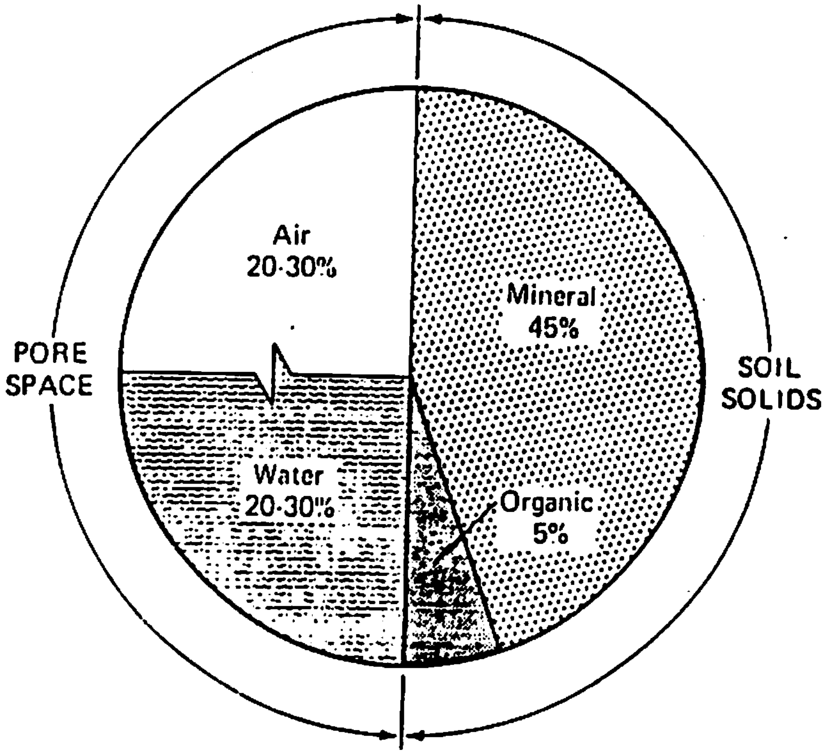


FIGURE 1:4. Volume composition of a silt loam surface soil when in good condition for plant growth. The air and water in a soil are extremely variable, and their proportion determines in large degree its suitability for plant growth.

m Pore space
w/ more H_2O → less O_2 & V.V.

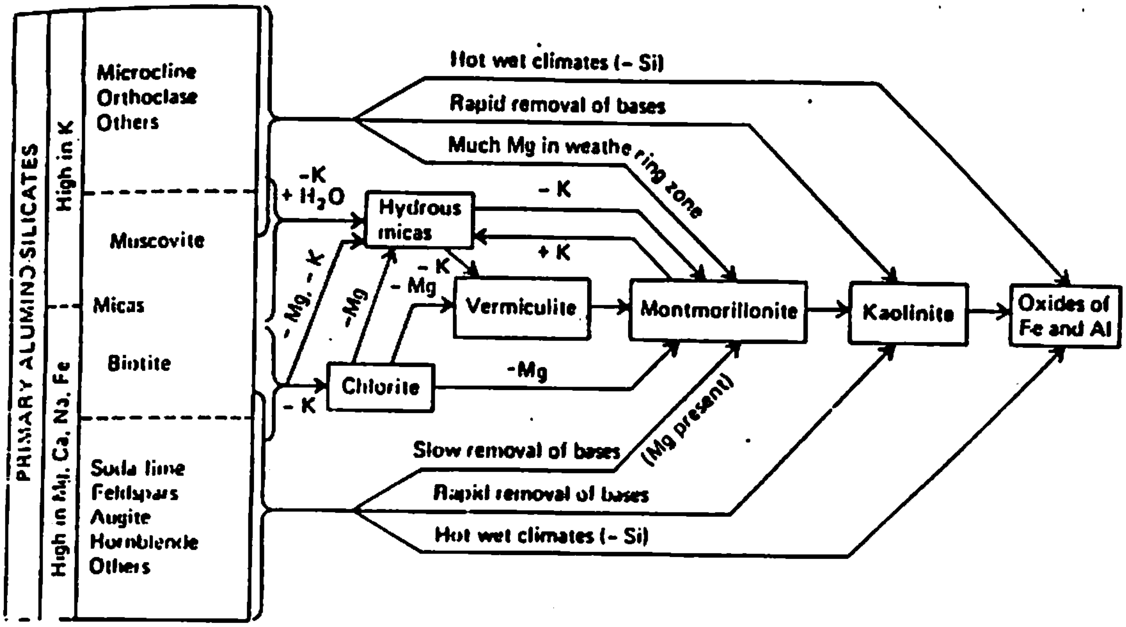


FIGURE 4:9. General conditions for the formation of the various silicate clays and oxides of iron and aluminum. Hydrous micas and chlorite are formed through rather mild weathering of primary alumino-silicate minerals, whereas kaolinite and oxides of iron and aluminum are products of much more intense weathering. Conditions of intermediate weathering intensity encourage the formation of vermiculite and montmorillonite. In each case, silicate clay genesis is accompanied by the removal of soluble elements such as K, Na, Ca, and Mg.

Fig 3

TABLE 12:8. *Classification of Soils into Orders, Suborders, and Great Soil Groups*[a]

Each great soil group is subdivided into numerous soil series and soil types.

Order	Suborder	Great Soil Groups
Zonal soils	1. Soils of the cold zone	Tundra
	2. Light-colored podzolized soils of timbered regions	Podzol soils Brown Podzolic soils Gray-Brown Podzolic soils Red-Yellow Podzolic soils Gray Podzolic or Gray Wooded soils
	3. Soils of forested warm-temperate and tropical regions	A variety of latosols are recognized; they await detailed classification
	4. Soils of the forest-grassland transition	Degraded Chernozem soils Noncalcic brown or Shantung brown soils
	5. Dark-colored soils of semi-arid, subhumid, and humid grasslands	Prairie soils (semipodzolic) Reddish prairie soils Chernozem soils Chestnut soils Reddish chestnut soils
	6. Light-colored soils of arid regions	Brown soils Reddish brown soils Sierozem soils Red Desert soils
Intrazonal soils	1. Hydromorphic soils of marshes, swamps, flats, and seepage areas	Humic-gley soil (includes wiesenboden) Alpine Meadow soils Bog soils Half-bog soils Low-humic Gley soils Planosols Ground-water Podzols Ground-water Latosols
	2. Halomorphic (saline and alkali) soils of imperfectly drained arid regions, littoral deposits	Solonchak soils (saline soils) Solonetz soils (alkali soils) Soloth soils
	3. Calcimorphic soils	Brown forest soils (Braunerde) Rendzina soils
Azonal soils	(No suborders)	Lithosols Regosols (includes dry sands)

Modified from Thorp and Smith (9).

This is the most reasonable one. ★

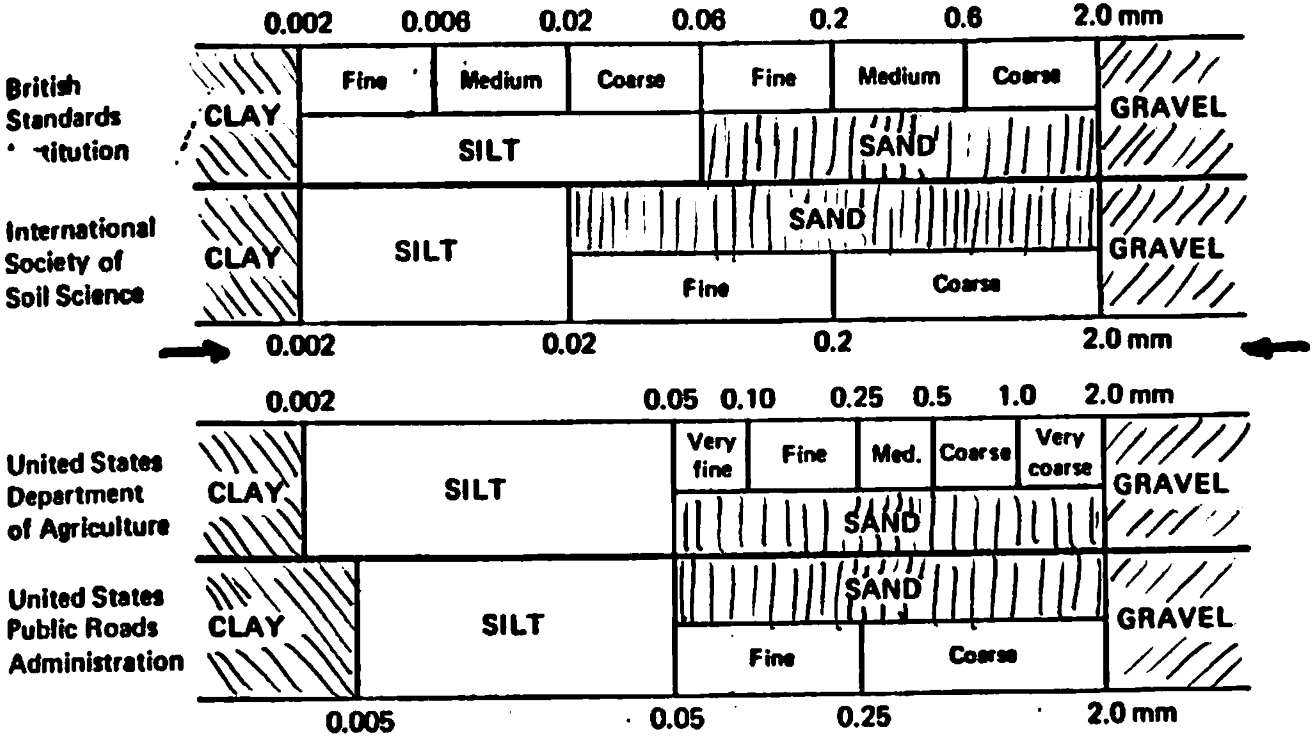
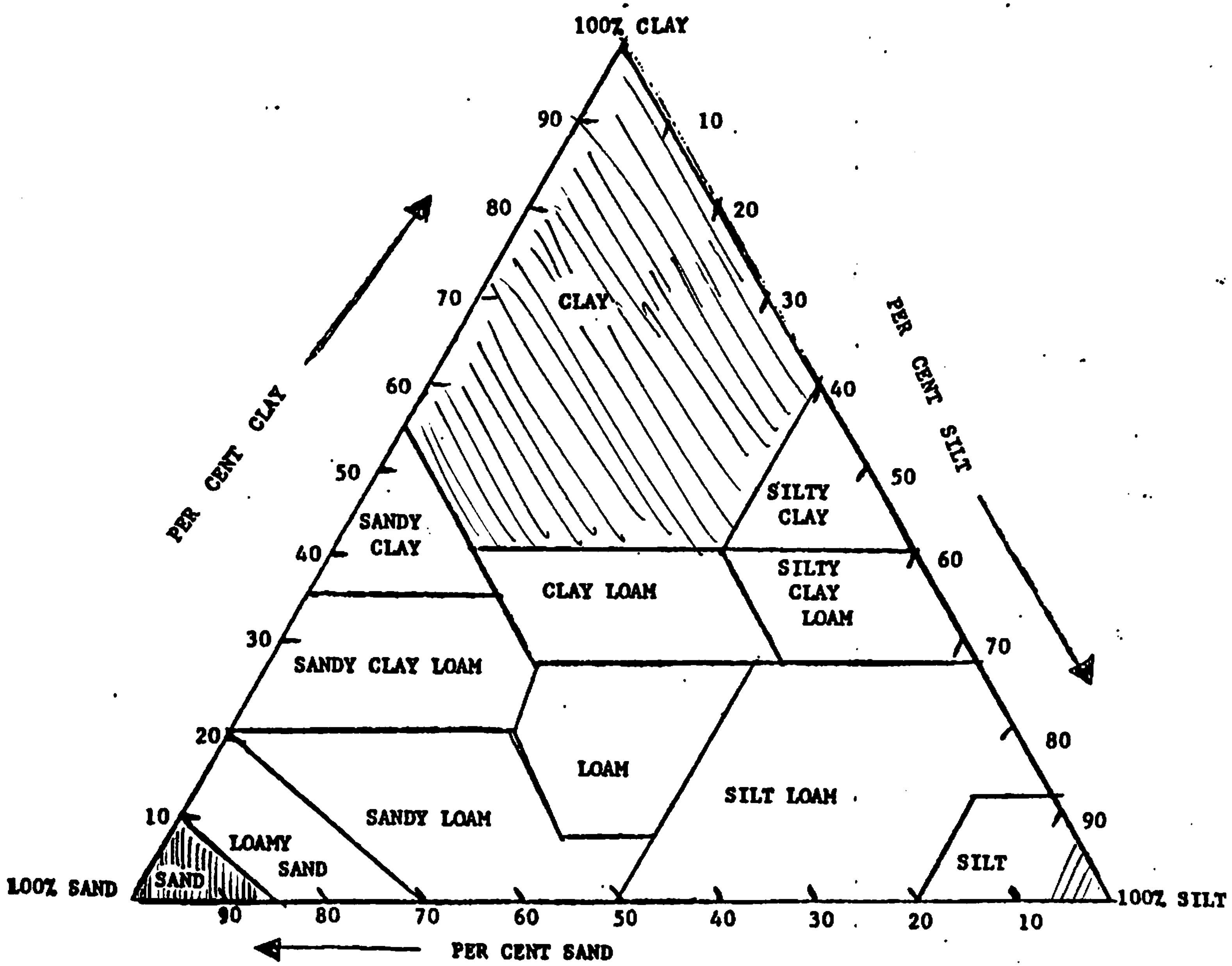


FIGURE 3:1. Classification of soil particles according to size by four systems. The U.S. Department of Agriculture system is used in this text. (Particle diameter in logarithmic scale.)



TEXTURAL CLASSIFICATION OF SOILS

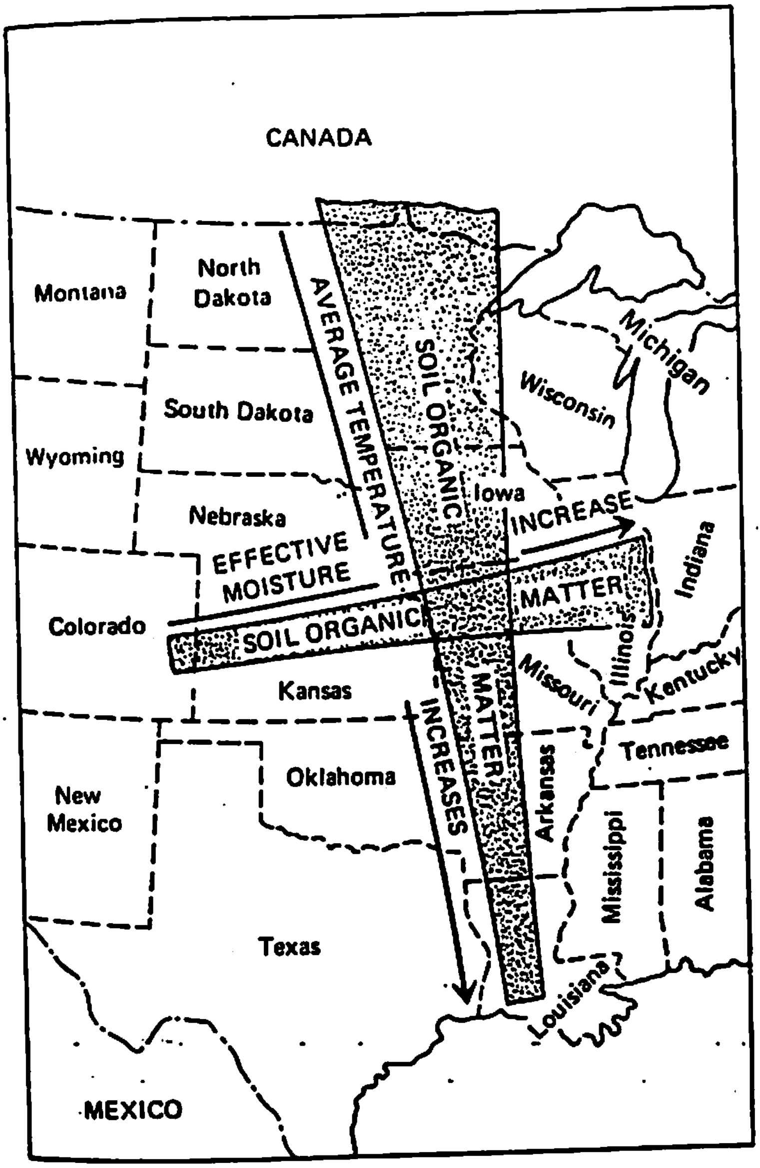
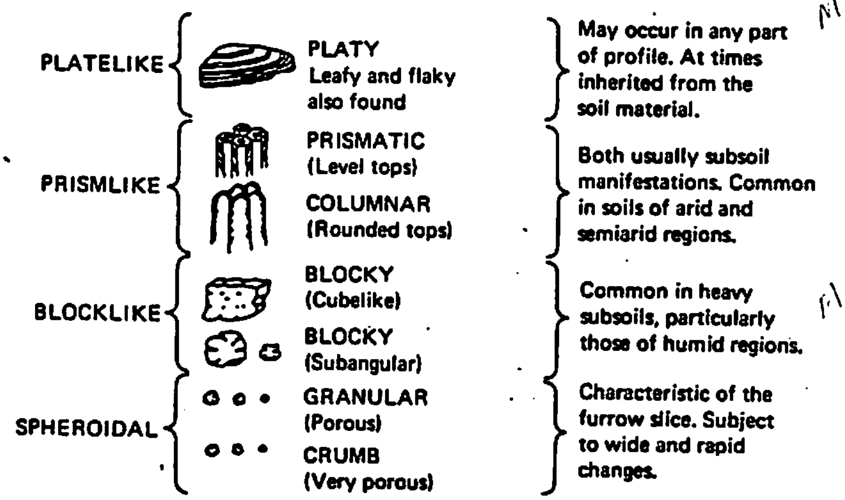


FIGURE 6:8. Influence of the average annual temperature and the effective moisture on the organic matter contents of grassland soils of the Midwest. Of course, the soils must be more or less comparable in all respects except for climatic differences. Note that the higher temperatures yield soils lower in organic matter. The effect of increasing moisture is exactly opposite, favoring a higher level of this constituent. These climatic influences affect forest soils in much the same way.

Mostly in $A_{1,2}$ [illegible] [illegible] cultivation



		Type	
PLATELIKE		PLATY Leafy and flaky also found	May occur in any part of profile. At times inherited from the soil material.
PRISMLIKE		PRISMATIC (Level tops) COLUMNAR (Rounded tops)	Both usually subsoil manifestations. Common in soils of arid and semiarid regions.
BLOCKLIKE		BLOCKY (Cubelike) BLOCKY (Subangular)	Common in heavy subsoils, particularly those of humid regions.
SPHEROIDAL		GRANULAR (Porous) CRUMB (Very porous)	Characteristic of the furrow slice. Subject to wide and rapid changes.

Mostly clays

FIGURE 3:9. Various structural types found in mineral soils. Their location in the profile is suggested. In arable topsoils, a stable granular structure is prized.

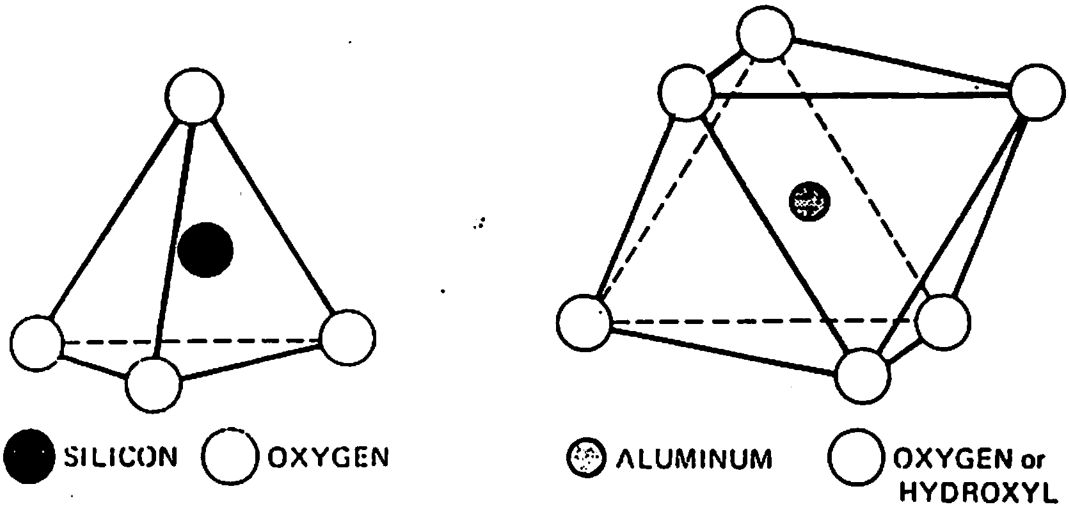


FIGURE 4:3. Diagrammatic sketch of the two basic molecular components of silicate clays. (*Left*) A single *silica tetrahedron*, a four-sided molecular building block with a silicon atom surrounded by four oxygen atoms. When several silica tetrahedra are associated in the same plane, a silica *sheet* is formed. (*Right*) A single *alumina octahedron* showing one aluminum atom surrounded by six hydroxyls or oxygens. An alumina sheet is composed of a large number of these eight-sided molecular units tied together through shared oxygen atoms. (For ease of visualization, the oxygen atoms are shown as being about the same size as the silicon and aluminum. Actually the oxygens are much larger in radius, as shown in Table 4:2.)

TABLE 4:4. *Unit Layer Formulas of Important Clay and Other Minerals Showing the Most Prominent Substitution in the Al and Si Sheets as Well as the Molecules Between Crystal Units*[*]

Readily exchangeable ions shown in brackets.

	Unit Layer Formula				
Clay Mineral	Octahedral (Al Sheet)	Tetrahedral (Si Sheet)	Numbers of Oxygen and Hydroxyl	Between Crystal Units	Unit Layer Charge
Kaolinite	Al_4	Si_4	$O_{10}(OH)_8$		0
Pyrophyllite	Al_4	Si_8	$O_{20}(OH)_4$		0
Montmorillonite	$Al_{3.5}Mg_{0.5}$ $[Na_{0.5}]$	Si_8	$O_{20}(OH)_4$		0.5
Vermiculite	Mg_6	Si_7Al $[Mg_{0.5}]$	$O_{20}(OH)_4$	xH_2O, Mg^{++}	1.0
Chlorite	Mg_6	Si_6Al_2	$O_{20}(OH)_4$	$Mg_6(OH)_{12}$	2.0
Illite	Al_4	Si_7Al $[K_{0.2}]$	$O_{20}(OH)_4$	$K_{0.8}$	1.0
Muscovite	Al_4	Si_6Al_2	$O_{20}(OH)_4$	K_2	2.0

[*] Note that the substitution of Mg for Al or Al for Si is compensated for by either exchangeable or intercrystal unit ions (e.g., Na). (In some vermiculites and chlorites the octahedral layer is filled with four aluminum atoms rather than six magnesium atoms as shown.)

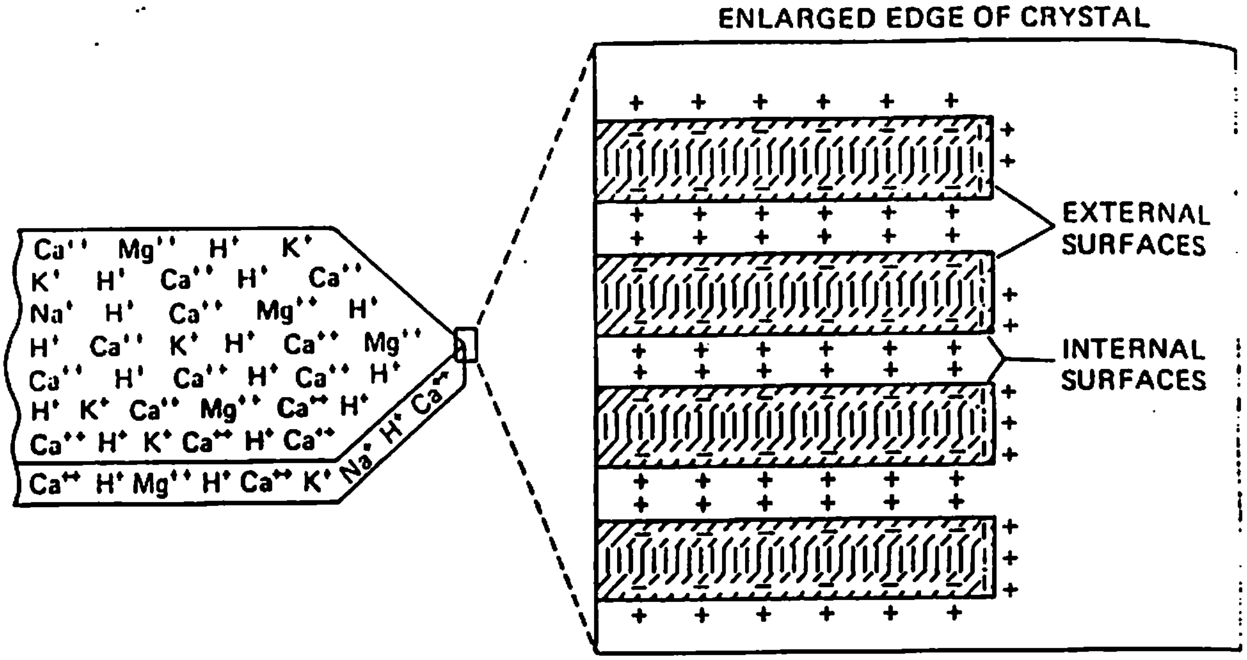


FIGURE 4:2. Diagrammatic representation of a silicate clay crystal (micelle) with its sheetlike structure, its innumerable negative charges, and its swarm of adsorbed cations. An enlarged schematic view of the edge of the crystal illustrates the negatively charged internal surface of this particular particle, to which cations and water are attracted. Note that each crystal unit has definite mineralogical structure.

40

~~27~~

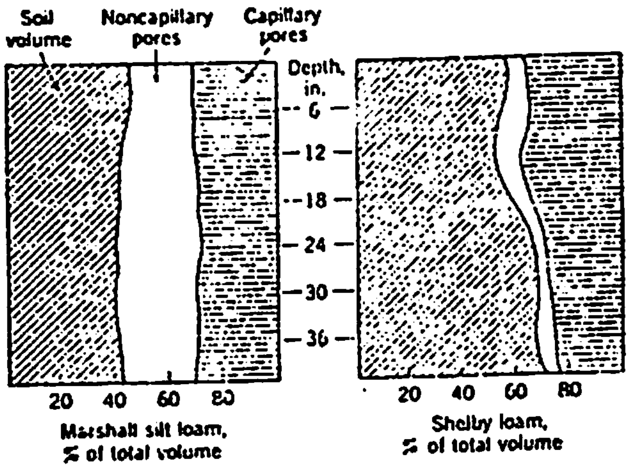


FIG. 2.1 Differences in amount of capillary and noncapillary pore space in two dissimilar soils. A large proportion of noncapillary pore space is desirable because it promotes drainage and improves aeration. (*Reproduced by permission from L. D. Baver, "Soil Physics," 2d ed., John Wiley & Sons, Inc., New York,* 1948.)

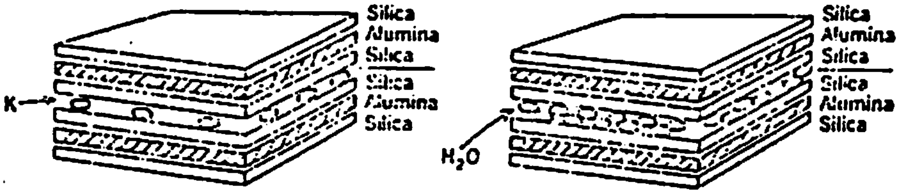


FIG. 2.2 Diagram showing the arrangement of silica and alumina sheets in illite crystals (left) and montmorillonite crystals (right). Entrance of water between silica layers causes the swelling characteristic of soils containing a large proportion of montmorillonite. (*From Thompson,* 1952.)

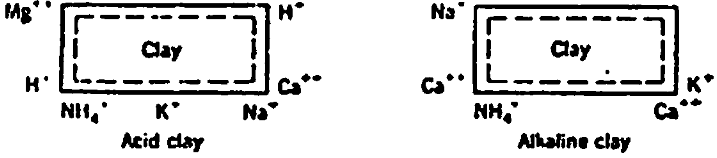


FIG. 2.3 Attraction of cations to the surface of negatively charged clay micelles. If the clay holds a high proportion of hydrogen ions, the soil is acid; if most of the exchange positions are held by basic ions such as Ca^{++}, K^+, and Na^+, it is alkaline. (*From Thompson,* 1952.)

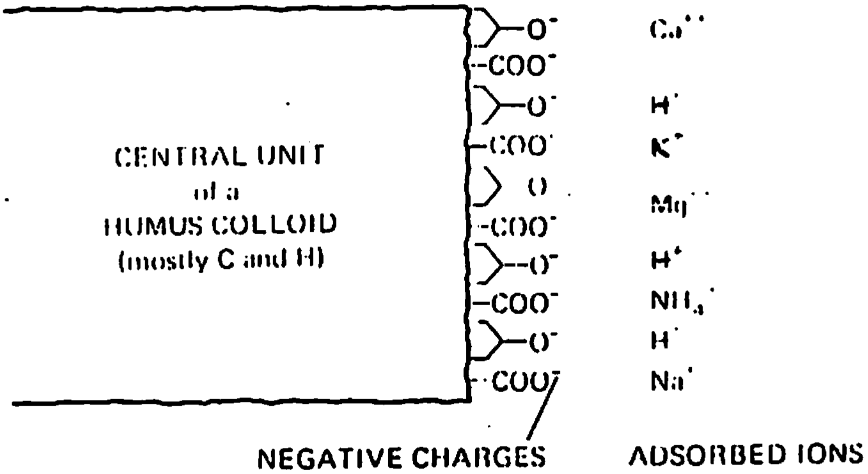


FIGURE 4:10. Adsorption of cations by humus colloids. The phenolic hydroxyl groups (⟩—O^-) are attached to aromatic rings; the carboxyl groups (—COO^-) are bonded to other carbon atoms in the central unit. Note the general similarity to the adsorption situation in silicate clays. In this case only surface adsorption is shown, but adsorption occurs within the micelle as well.

Biology 149 R.C. Crabtree, November 9th 1989

Ecological Aspects of Plant Mineral Nutrition

What mineral nutrients do plants take up?

Mineral nutrients supplies

- Mineral nutrient content of soils
- Plant demands, how nutrients may be supplied (Ion mobilities, cec)

Plant Response to mineral nutrients

- Nutrient reponse curves

Interactions between resources

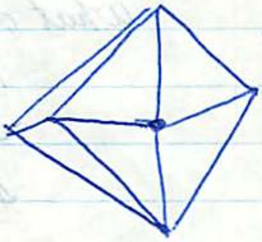
- Balanced nutrition
- Water availability (Consequences for plants of dry areas)
- Nitrogen and photosynthesis

Plant response to low mineral availability

- Morphology (proteiod roots)
- Symbiosis - Mycorrhizae, N fixation
- Chemistry - uptake (siderophores, acid phosphatases)
- Increase nutrient use efficiency - life history implications

Plasticity of response wrt pulses of nutrients (analagous to sunflecks)

Rosie Crabtree



Type of clay
Amt of charge 2:1 usu more '-'

Cation Potential
charge
found on edge
" internally - subst
hydration

Cation Exchange Capacity
① nutrient holding potential

What about neg '-' charged ions
H_2PO_4 NO_3 SO_4^{2-}
What holds them?
① organic matter - is also source

Jona

Jong

Plant Nutrition

What do plants use
- H_2O
- CHO
- macronutrients
  - N - enzymes
  - K - ionic balance; stomates; cofactors
  - P - v. important; ATP, lipids, DNA, enzymes
- micronutrients
  - Mg - cofactor
  - S - proteins, cofactor
  - Fe - cytochromes, cofactors
  - Ca - membranes

What do soils supply?
- P <<< N
- must be in solution; inorganic

Where do nutrients come from?

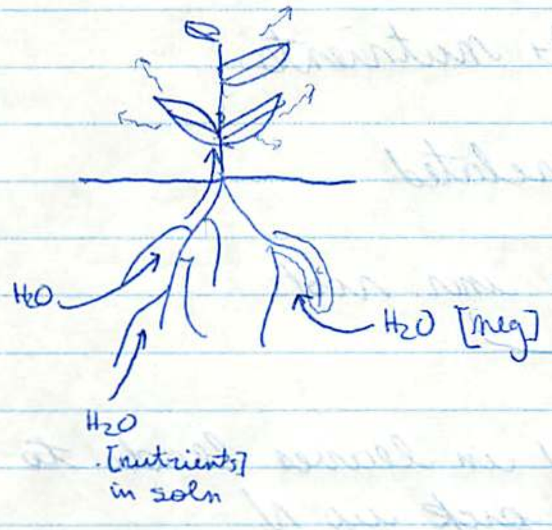
K, P - rocks, sewage
N - atmos; decomposition

- bulk from soil

- rate of mineralization

$\xrightarrow{\text{mineraliz.}} NH_4 \xrightarrow{\text{nitrification}} NO_3$

<< flow cultures >>
- soil solutions are dilute but continuous



when H_2O sucked up, many nutrients come with

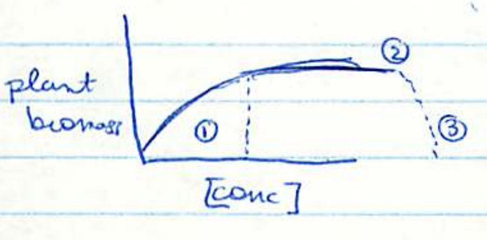
- labile - v. mobile; non-sticky
  - '−' ions rush through

  - '+' ions held tighter
  - tighter things held; worse depletion

- diffusion limited
  PO_4, N

H_2PO_4 ; complexes w/ Fe, Al

<u>Nutrient</u> <u>response</u> <u>curves</u>



① - responsive
② saturated
③ toxicity

levels ↑ ↳ depend on H_2O, $h\nu$

Plants response to 2+ nutrients.

N:P in leaf is correlated

-N ⟶ incr P ⟶ incr. roots ⟶ N

- so investment of N in leaves leads to
  incr. ability to pick up N

- Costs energy to take up N, etc
- Nutrients ↑↓ in xylem / phloem

<u>Retranslocation</u>

-pulling in nutrients from leaves be4 drop

Ca: immobile
Mg: rel immobile
N, K :- v. mobile

<u>Drought</u>

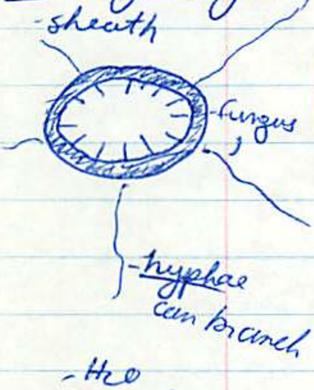
① N_2 & light
② nutrients w/ each other
③ water level
mineralization
mass flow

lateral root formation stimulated by nutrient

crop plants have been bred to work well in high nutrients. Wild plants are used to low nutrients

In nutrient limited plant what do
① more soil reached allocation, branching
- incr SA (root hairs)
- more roots
- wait

<u>ectomycorrhizae</u>



- H_2O
- Mg
- Ca
- N

} into plant

$C_6H_{12}O_6$ out

② hire a partner - symbiosis
some obligate: Dipterocarps

N_2
mycorrhizae
fungi w/ roots

Chemistry
use less → nutrient use efficiency
. exude acids
- " " H_2O

- reuse what you've got

(N2 fixers also need mycorrhizae)

How to improve nutrient

<u>morphol.</u>

root shape

" branching

<u>symbiosis</u>

<u>chem</u>

-<u>siderophores</u> - pick up Fe

efficiency

use less
keep longer
re use
grow slower

} has effects on life history

EXPT. PLANT ECOLOGY
BIO 149 1989 REVIEW

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PLANT MINERAL NUTRITION

Macro and Micronutrients and Their Importance

symbiosis
geochem.

Nitrogen: Proteins/Enzymes
Chlorophyll

NO_3^-, NH_4^+

Most soil-N is organic (i.e. amino-N). However, nitrogen is absorbed by roots as nitrate in aerobic soils and consequently, the nitrogen supplying status of soil depends on the rate of mineralization of organic-N. Ammonium-N is often bound between the lattice layers and is an important source of N in anaerobic waterlogged soils.

geochem

Phosphorous: ATP
Lipids

PO_4^{3-}

Much of soil-P is organic, usually derived from plant litter, animal remains and faeces. Like nitrogen, phosphorous, in organic form, is immobilized and therefore relies on microorganisms for its natural cycling. Inorganic P is also rather insoluble which imposes a rate limitation on biological transfer and prevents significant leaching loss.

Potassium: Ionic Balance
Stomatal Activity
Enzyme Cofactor

K^+

Potassium, in its more simple compounds is a mobile element and very soluble in water. It is often incorporated in alumino-silicate lattice structures preventing leaching loss. Very little K in soil is soluble or exchangeable, however. The remainder is a nonexchangeable component of the soil matrix.

geochem

Sulfur: Some Proteins
Enzyme Cofactor

SO_4^{2-}

Sulfur originates from the mineral matrix in which it may occur as various metal sulfides (FeS_2, ZnS) or as crystalline sulfates. Sulfides generally occur in igneous rocks and sedimentary rocks laid down under anaerobic conditions. Sulfates occur in sedimentary rocks laid down under oxidizing conditions. Plants absorb S as sulfate primarily. However, there is some evidence that S-amino acids may be assimilated as well.

Magnesium: Chlorophyll
Enzyme Cofactor

Mg^{2+}

Mg is derived from alumino-silicate, silicate or sulfate minerals on non-carbonate parent materials or from dolomite and magnesite.

Calcium: Middle Lamella
Membrane Integrity
Membrane Selectivity in Uptake

Ca^{2+}

Calcium is pedogenetically important in that the presence or absence of calcium carbonate may be diagnostic of P/E regime. In soils with a high P/E ratio, the surface layers may be completely leached of free $CaCO_3$ and an advancing front of decalcification passes down the profile at a rate governed by the P/E ratio. If, on the other hand P/E is less than unity, upward movement of capillary water in response to surface evaporation causes $CaCO_3$ enrichment of the A horizon. $CaCO_3$ is also the most common soil constituent responsible for soil alkalinity.

Iron: Cytochromes (electron transport) Fe^{2+}, Fe^{3+}

Iron is considered a micronutrient. However, it has a greater pedogenetic and microbiological significance. Iron availability is dependent on redox conditions and the different forms consequently confer characteristic colors on the soil which act as tell-tails of soil redox status.

Manganese: Micronutrient Mn^{2+}, Mn^{3+}

Manganese deficiency, like iron deficiency, is most commonly associated with high soil pH

Primary Nutrient Sources

N	remineralization
P	rocks-soil solution
K	rocks-soil solution
S	soil solution

Nutrient Availability and Absorption

Plants require a balanced spectrum of nutrients. The amount of nitrogen uptake and assimilation into leaf N (Chlorophyll, RuBisCO) leads to greater photosynthetic rates. In turn, carbon skeletons produced support root respiration necessary for nutrient uptake against concentration gradients.

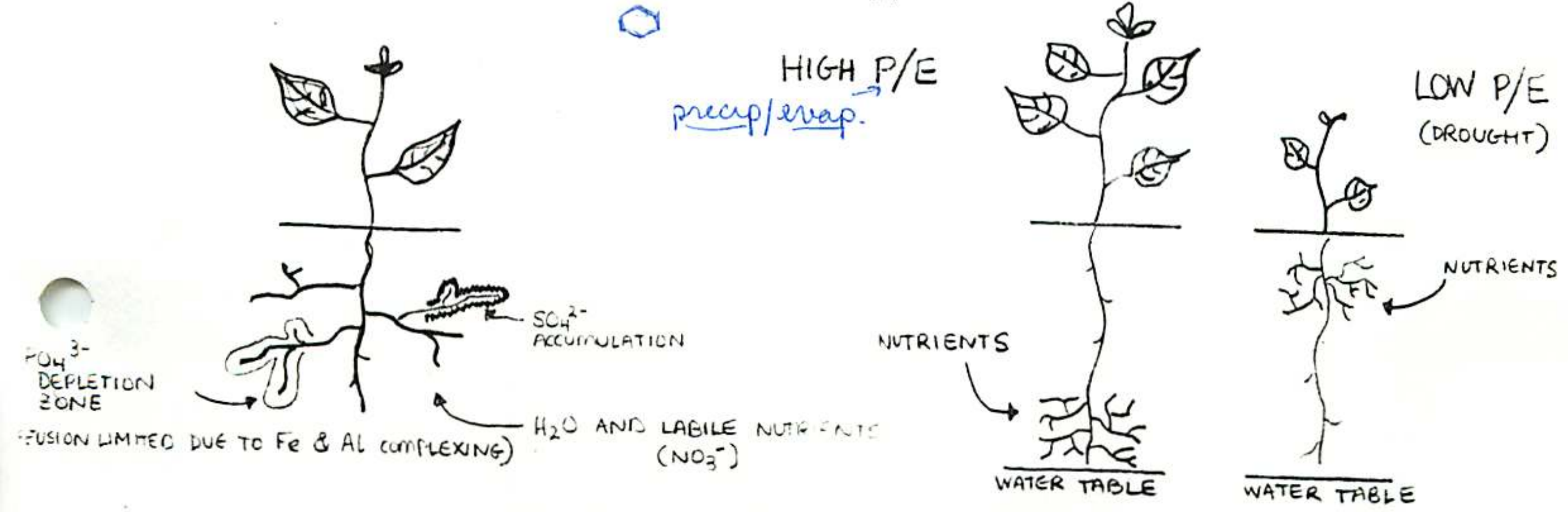
If organic matter is mineralizing fast enough to supply adequate N, it should also be releasing sufficient P for plant growth but, much of PO_4^{3-}-P produced, is precipitated before it can be absorbed. However, mineral concentrations are typically low (dilute) for most nutrients, but they are constantly resupplied by labile (mobile) fractions. In the case of phosphate though, depletion zones may form and P will become diffusion limited, while selectively excluded minerals may accumulate around roots. Establishment of the diffusion gradient, if the rate is slow, will then become the limiting factor of elemental uptake.

Behavior of ions at the absorptive surface generally follow Michaelis-Menten Kinetics:

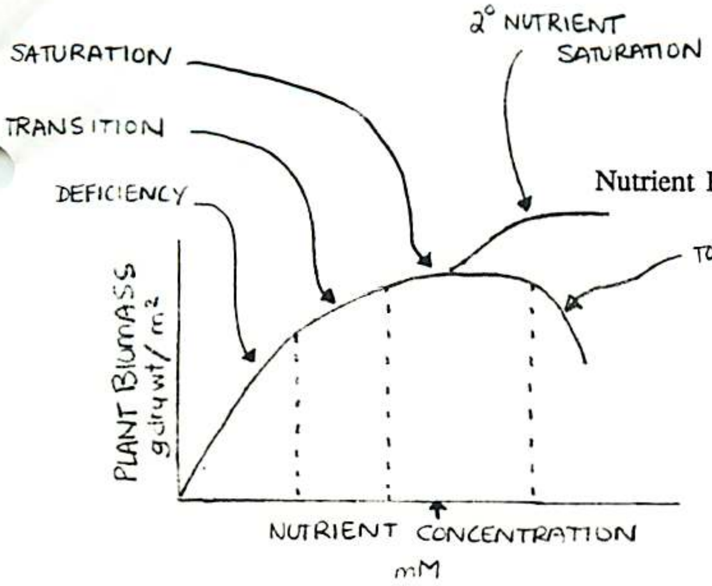
Dilute Solution Mechanism (System I): $V = V_{max}\dfrac{C_{liq}}{K_m + C_{liq}}$

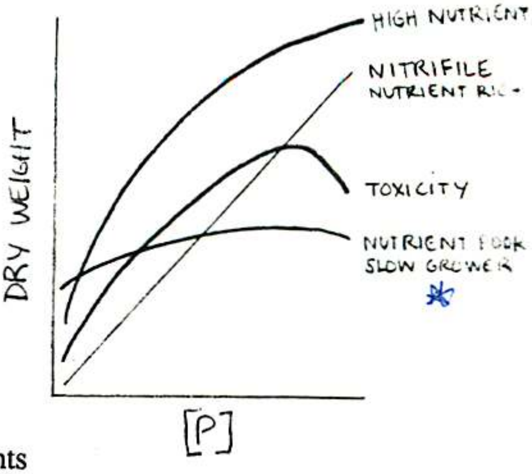
saline = enriched salts

Saline and Enriched Soils (System II): A continued increase with a very shallow slope, often rather irregularly and ultimately reaching a new, ill-defined V_{max}



Nutrient Response Curves





Adaptation to Nutrient Deficient Environments

* is this due to a process like CO_2 in C_4 plants - that they store nutrients so extra doesn't matter?

1. Explore more soil.
    - Increase root allocation
    - Increased surface area
        - Longer root hairs
        - Increased branching
2. Hire a partner.
    - Mycorrhizae (P): May be involved in S and Zn absorption as well.
        - Endo and ecto-mycorrhizae store P as inorganic polyphosphate.
        - Ecto-mycorrhizae may also assist in H_2O uptake.
    - Bacterial Nitrogen Fixers (N)

SYMBIOSIS or parasitism or pos-neutral...

recycling

3. Chemistry.
    - Alter nutrient use efficiency:
        - Life history (perennial, slow growing)
        - Insectivory
    - Alter soil chemistry
        - Siderophores (Iron carriers)
        - Release of photosynthate from roots to encourage microorganism growth.

Soil Toxicity

Colonization relies on selection of tolerant seedlings from the surrounding normal population followed by continuous selection for the tolerance characteristics in the face of the diluting effect of gene flow from surrounding populations and a high rate of turnover.

Endemics to toxic soils persist as a result of a normal gene pool permitting occasional appearance of tolerant recombinants and the tolerant individuals are only present at low frequency in normal habitats as they have less competitive vigour than their normal counterparts. Finally, where tolerant ecotypes are less competitive than normal plants, the toxic habitat may be interpreted as a refugium.

Halophytism

Halophytes cope with osmotic stress, cation nutrition and salt toxicity by a series of mechanisms summarized below:

1. Limitation of uptake or transport coupled with synthesis of organic osmotica (i.e. proline, glycine betaine)
2. Unlimited uptake combined with compartmentation or tolerance of high internal salt concentration.
3. Control of internal concentration and ion balance by excretion.
4. Control of Na and K selectivity at root or organelle surfaces.

11/10/89 ①

Fig 1

Table 5-1 Elemental Analysis of Whole Maize Shoot System and a Selected Maize Leaf. The shoot system included leaves, stem, cob, and grains.

macronutrients

Element	Maize Shoot[a] (% of dry weight)	Maize Leaf[b] (% of dry weight)
Oxygen	44.4	—
Carbon	43.6	—
Hydrogen	6.2	—
Nitrogen	1.5	3.2
Potassium	0.92	2.1
Phosphorus	0.20	0.31
Sulfur	0.17	0.17
Calcium	0.23	0.52
Magnesium	0.18	0.32
Chlorine	0.14	—
Silicon	1.2	—
Sodium	—	—
Iron	0.08	0.012
Manganese	0.04	0.009
Copper	—	0.0009
Boron	—	0.0016
Molybdenum	—	—
Zinc	—	0.003
Aluminum	0.89	—
Undetermined	7.8	—

[a] Data of Latshaw and Miller, *J. Agric. Research*, 27:854. 1924.

[b] Unpublished 1982 data of P. Soltanpour and S. Workman, Colo. State Univ. Soil Testing Laboratory.

Factors → size hierarchies

<u>Size Hierarchies</u>

a) Log nature of plant growth

b) genetic variation

- cloning
- monocultures & pathogens
  - <u>so</u> success of genotype depends on environment. 3rd party can greatly effect size distrib

c) maternal effects

- Lamarckian evolution   can be darwini

d) timing of emergence

earlier → ⊕ longer growth time
→ ⊕ pre-emption of resources
↙
⊖ <u>herbivory</u>

time ≅ space (early = further away from neighbors)

e) environmental heterogeneity

- 50-70% of size variability explained
- so is "chance" more important?
- how important is plasticity?

f) resource competition

- dominance & suppression (small don't grow)
- asymmetric vs symetric competition "directional or non-direction)



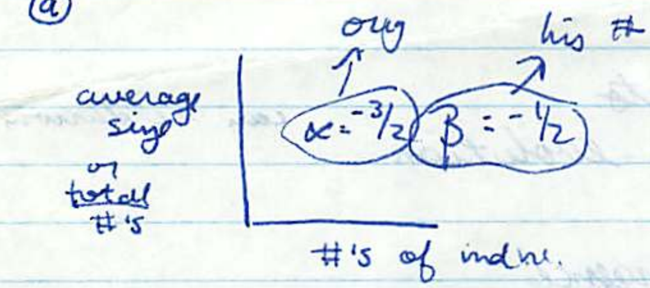
50-70% microenvir.

more variability due to directional resources

Self-thinning 3/2 - across many species
See Silvertön

(Weller) 1987
megamonographs
problems

ⓐ



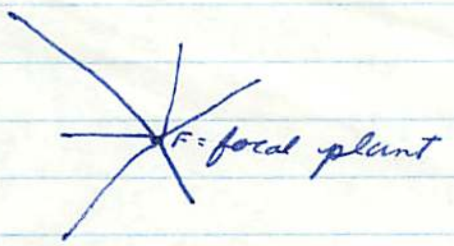
can't have same unit on both axis

ⓑ no independent variable for regressions. So - should use ordination which has no "depend vs. indep)

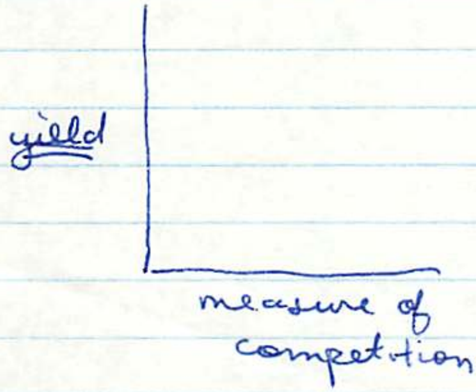
ⓒ how test if objectives

63 sets

Neighborhood Analysis



affect depends on
distance, size of neighbors



fn of density

(

$$w = c\left(\frac{N_1}{d_1^2} + \frac{N_2}{d_2^2} + \frac{N_3}{d_3^2} \cdots\right)$$

w = meas. of comp
c = comp.
d = distance.

Interspecific Interactions : community level

°effect of plant species on community
"keystones"

compet. exclusion

(2)

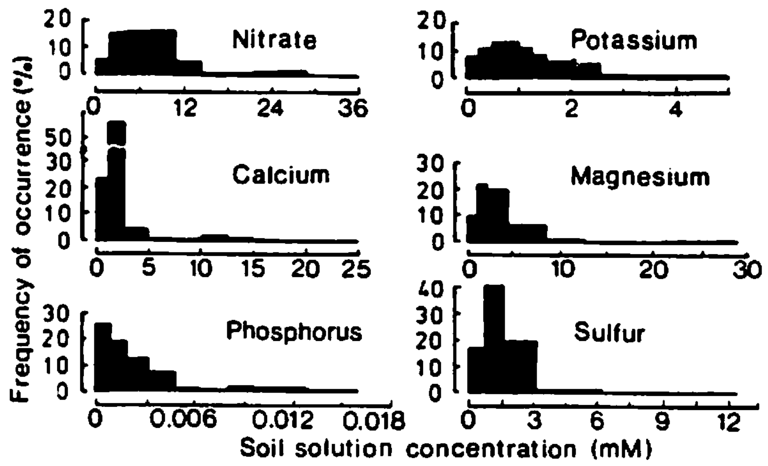


Fig. 13.2 Frequency distribution of the equilibrium concentrations of nutrients in soil solutions from agricultural and horticultural areas. (Redrawn from Asher. 1978: with permission from CRC Press, Inc.)

Table 5-2 Two Nutrient Solutions for Hydroponic Culture.

Hoagland's Solution[a]			Evans' Modified Shive's Solution[b]		
Salt	Molarity	mg/l (ppm)	Salt	Molarity	mg/l (ppm)
KNO_3	0.010		$Ca(NO_3)_2 \cdot 4H_2O$	0.005	
$Ca(NO_3)_2$	0.003		K_2SO_4	0.0025	
$NH_4H_2PO_4$	0.230		KH_2PO_4	0.0005	
$MgSO_4 \cdot 7H_2O$	0.490		$MgSO_4 \cdot 7H_2O$	0.002	
Mixture of 0.5% $FeSO_4$ and 0.4% tartaric acid:			Fe-versenate		0.5 Fe
0.6 ml/l added 3 times/week			KCl		9.0 Cl
$MnCl_2 \cdot 4H_2O$		0.5 Mn; 6.5 Cl	$MnSO_4$		0.25 Mn
H_3BO_3		0.5 B	H_3BO_3		0.25 B
$ZnSO_4 \cdot 7H_2O$		0.05 Zn	$ZnSO_4$		0.25 Zn
$CuSO_4 \cdot 5H_2O$		0.02 Cu	$CuSO_4$		0.02 Cu
$H_2MoO_4 \cdot H_2O$		0.01 Mo	Na_2MoO_4		0.02 Mo

[a] From D. R. Hoagland and D. I. Arnon (1938). University of California Agricultural Experimental Station Circular # 347.

[b] From H. J. Evans and A. Nason (1953). Plant Physiology 28:233–254.

Table 13.2

Estimated Amounts of Mineral Nutrients Supplied to Maize Roots in a Fertile Silt Loam Soil by Root Interception, Mass Flow, and Diffusion[a]

Nutrient	Amount "available" in the topsoil[b] (kg/ha)	Total uptake by crops (kg/ha)	Supply (kg/ha) by		
			Interception	Mass flow	Diffusion
Calcium	4000	45	40	90	—
Magnesium	800	35	8	75	—
Potassium	300	110	3	12	95
Phosphorus	100	30	1	0·12	28·9

[a] Estimated root volume equal to 1% of the soil volume. From Barber (1974).

[b] According to soil testing.

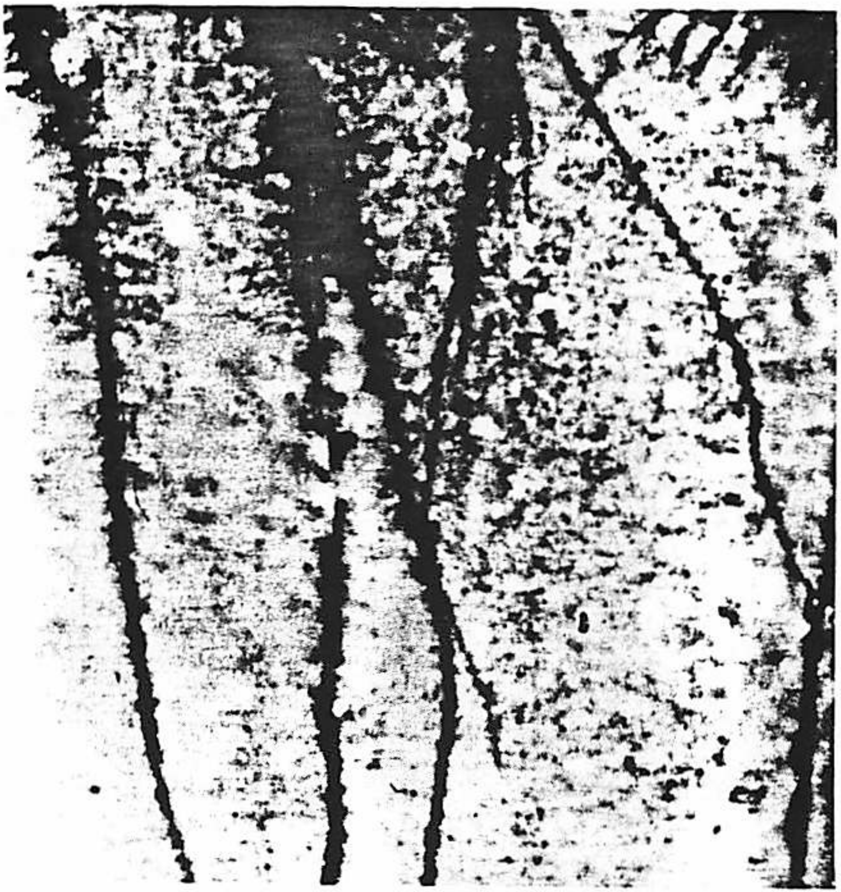


Fig. 13.5 Autoradiograph of maize roots in a soil labeled with ^{32}P showing zones of phosphorus depletion around the roots (removal of ^{32}P indicated by black zones).

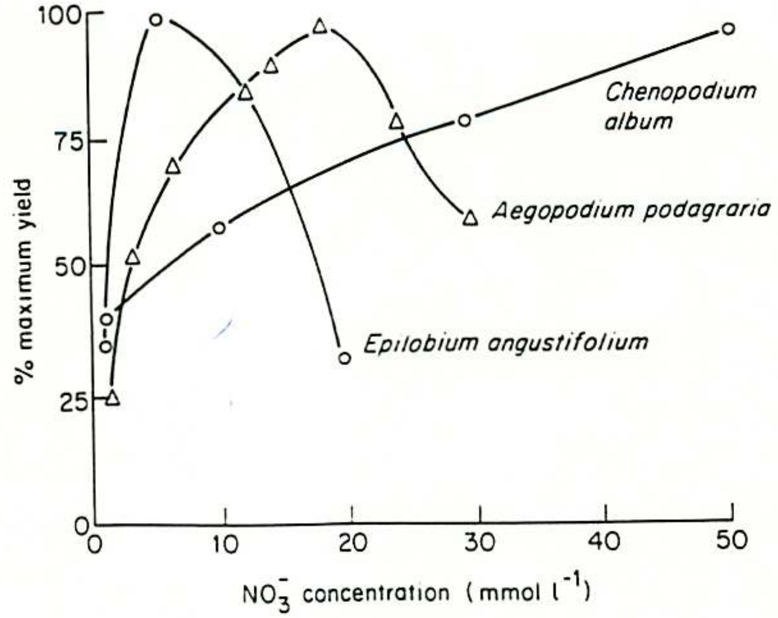
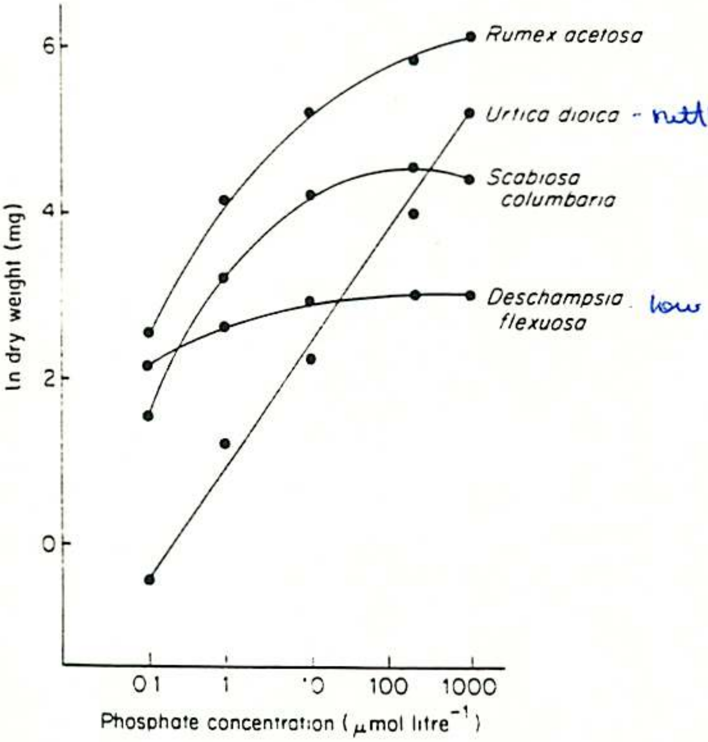


FIG. 3.1. Response of three contrasting plant species to nitrate concentration in solution culture (redrawn from Kinzel, H. (1982). "*Pflanzenökologie und Mineralstoffwechsel.*" Ulmer, Stuttgart).



- nettle

low nutrient

FIG. 3.2. Response of four ecologically contrasted species to phosphate concentration in solution culture, after 6 weeks (from Rorison, 1968).

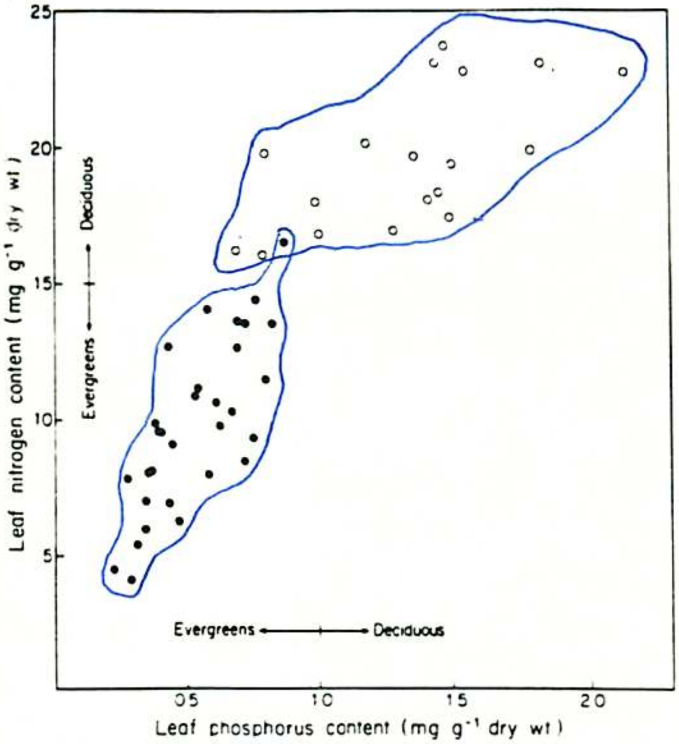


FIGURE 5. Relationship between phosphorus and nitrogen content per unit dry weight in adult leaves of tropical trees from different plant communities (with data from Cuenca 1976; Sobrado, Medina 1980; Marín, Medina 1981). The quadratic equation is: $N = 0.41 + 21.16\,P - 5.22\,P^2$, $r^2 = 0.73$.

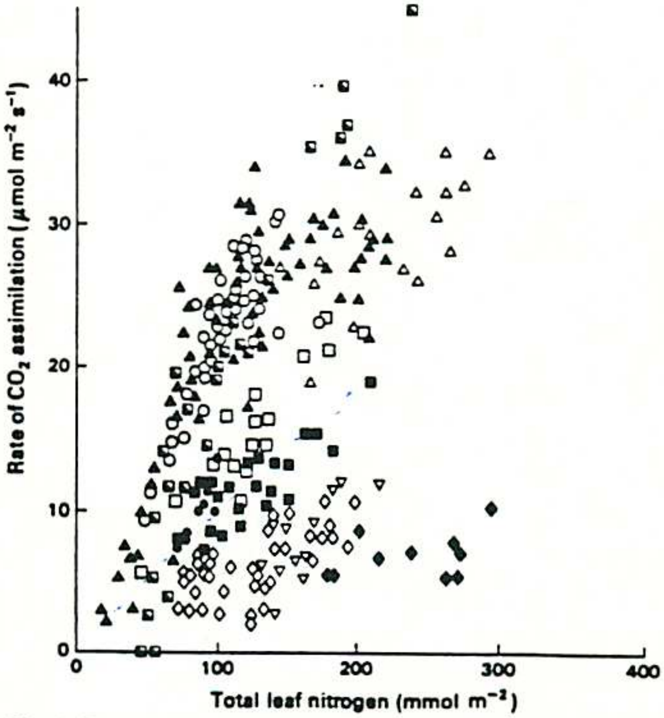


Fig. 1. Rate of CO_2 assimilation at high irradiance versus leaf nitrogen content, both expressed per unit leaf area. ▲ *Triticum aestivum* (Evans 1983, 1985) ○ *Oryza* (Cook and Evans 1983a, b) ▣ *Raphanus raphanistrum* (Küppers et al. 1988) △ Death valley annuals (Mooney et al. 1981) □ Illinois annuals (Mooney et al. 1981). ● *Alocasia macrorrhiza* (Seemann et al. 1987) ■ *Lepechinia calycina* (Field and Mooney 1983) ◇ Californian evergreen trees and shrubs (Field et al. 1983) and rainforest trees (Langenheim et al. 1984) ▽ South African shrubs (Mooney et al. 1983) ◆ *Prunus ilicifolia* (Field et al. 1983)

C

Table 14.8
Effect of Nitrogen Level on Dry Weight, Shoot/Root Ratio, and Total Root Length per Plant[a]

Nitrogen supply (mg/liter)	Dry weight (g/plant)		Shoot/root ratio	Root length (m)
	Shoot	Root		
0	0·24	0·38	0·63	4·7
21	0·75	0·84	0·89	6·2
42	1·34	1·30	1·03	6·8
105	2·40	1·97	1·25	8·1
210	4·49	2·89	1·55	10·2

[a] Experiment was performed on 17-day-old maize plants. Based on Maizlich *et al.* (1980).

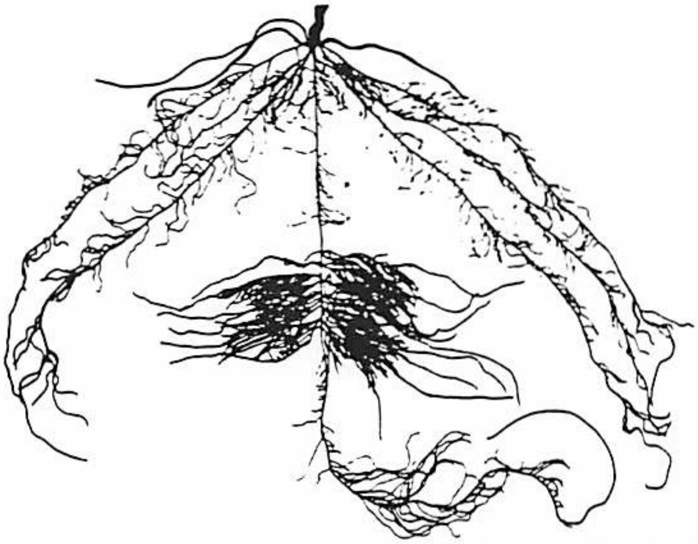


Fig. 14.3 Modification of the root system of barley by providing 1 m*M* nitrate to the midpart of one root axis for 15 days; the remainder of the root system received only 0·01 m*M* nitrate. (From Drew and Saker, 1975.)

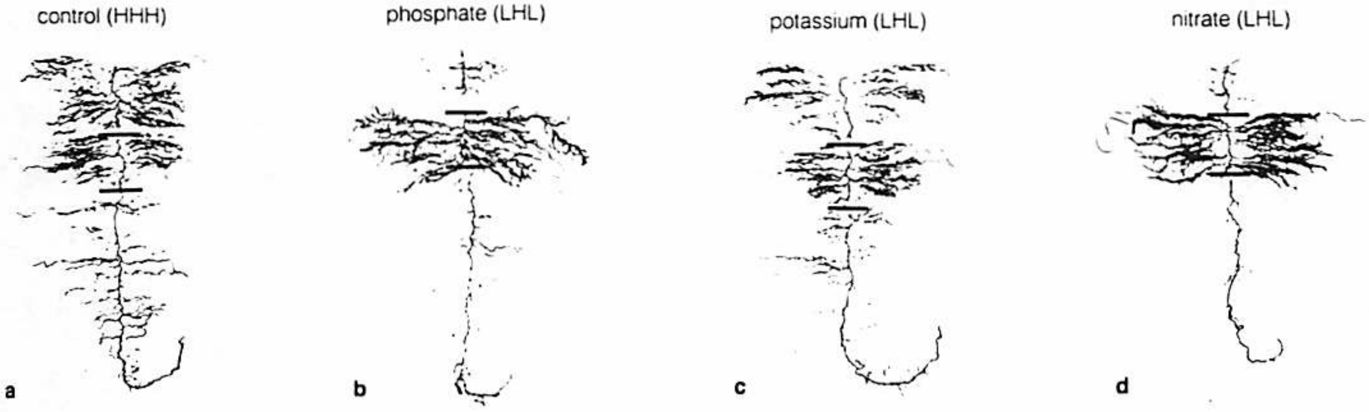


Figure 6-2 Root proliferation of barley in localized zones of sand fertilized with phosphate, potassium, or nitrate. Portions of root systems (shown separated by line-bars) were grown 21 days in sand compartments separated into three layers by wax barriers through which roots could grow but solution did not flow. Layers were fertilized with nutrient solution containing high (H) or low (L) levels of the particular element. Controls (HHH) received high levels of elements in all three layers. Plants exposed to varying potassium showed little proliferation in the well-fertilized central layer, but the acid-washed sand was found to contribute K$^+$. (From M. C. Drew, 1975.)

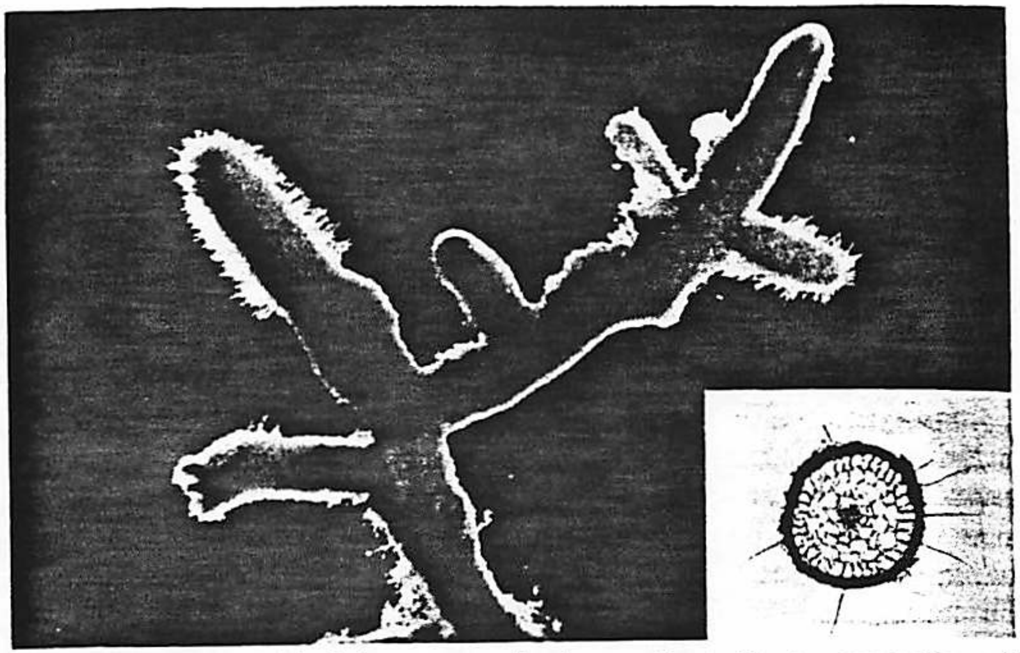


Fig. 15.6 Ectomycorrhizal short roots of oak tree. Inset: Root cross section with hypha mantle and strands of external mycelium. (From Egli, 1983.)

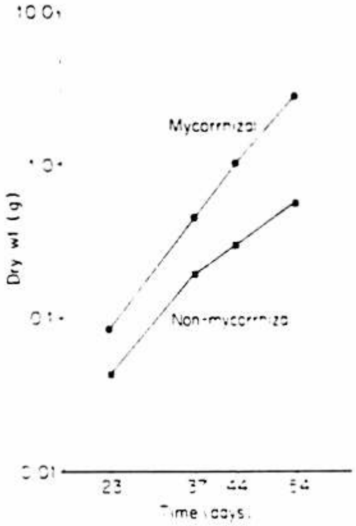


Fig. 3.21. Growth rate of mycorrhizal and non-mycorrhizal onions (data from Sanders and Tinker, 1973).

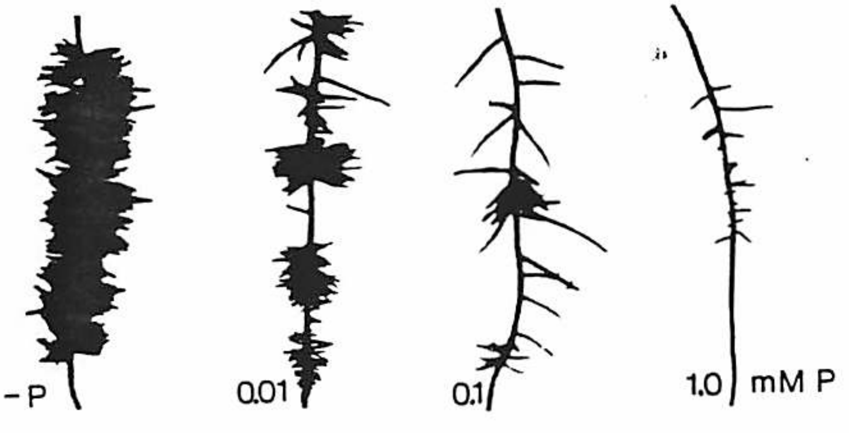


Fig. 15.5 Effect of the phosphorus concentration of the nutrient solution on the root morphology of *Lupinus albus* L. (By courtesy of V. Römheld.)

TABLE 3.12. Responsiveness to phosphate supply, specific root length and root diameter of two arid-zone grasses (Christie and Moorby, 1975).

	Thyridolepis from low P *mitchelliana*	*Cenchrus ciliaris*
Response to P[a]	3·0	29·6
Specific root length (cm mg^{-1})		
3 mg l^{-1}	16·2	13·6
0·003 mg l^{-1}	19·2	27·8
ratio	1·10	2·04
Root diameter (μm)		
Nodal axes		
3 mg l^{-1}	704	968
0·003 mg l^{-1}	552	460

[a] Response to P is the quotient of total dry weight of plants grown at 3 mg P l^{-1} to those grown at 0·003 mg P l^{-1}.

Biology 149

Lecture outline 14 November 1989

Plant Poulations

Definition

Age structure

Size structure (weight , height)

Spatial structure

Genetic structure

Population size

Population growth

Survivorship curves

Fate of individuals

Patterns of fecundity

Patterns of mortality

Population models

Population regulation

Modular demography

11/14/89

Plant Populations

neighbors
① resource modifiers

ambrosia artemesiphol

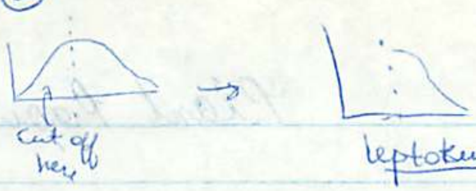
Populations
definitions : more than one individual

size structure
- genetic population - more than one individual that interbreed
- demes - subpopulation that exchange genes frequently
- ecological population - group of indiv. in same place & time. But time & area scale are determined by investigator

Ⓐ Age structure
- scale of cohort varies
- problem if continuous breeding
- differences of minutes can be v. important
- age - mark individuals as emerge
  - age ex post facto

- important to
  ① tell fate of individuals/populations
  ② "episodicity" of recruitment
    repro ⓐ seed timing (masting) beech, dipteros
    phys. ⓑ envir. variation
    biol. ⓒ herbivory
  ③ single events (war, condoms ...)

①


②


Ⓑ Size structure

v. similar patterns to age

- causes of {larger} size

gmes affect everything

① genetic makeup (affects growth
② time of recruitment
③ herbivory
④ environment

- weight, height
v. important bec. of modularity

Ⓒ Spatial structure

① distance to neighbors
② size of "
③ identity of " " (species, genotype)

Patterns
- dispersal of seed & gametes - clumped; spread — depends on disp. agent, fruit, feces; timing
- resources
H₂O; hv; locations (safe site); nutrients

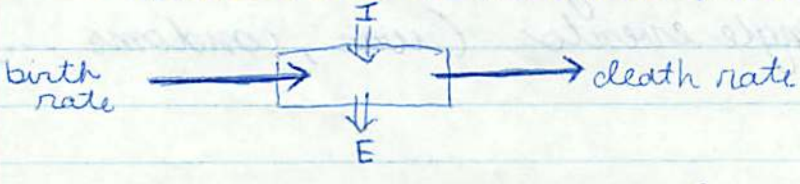
disp. of gametes have nat. selection so that #'s

Ⓓ Genetic structure

Ⓔ Population size

#'s v. important in animals

#'s are hard to determine & not always relevant

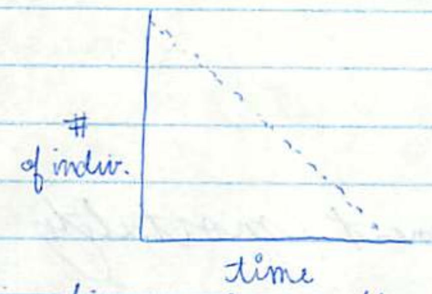


I & E in plants v. limited (clonal propagation)

11/14

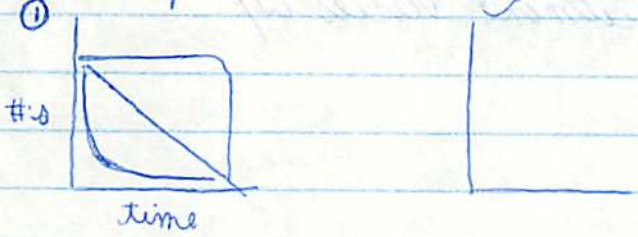
Ⓔ Population ~~rate~~ size (cont)

Birth



Survivorship ~~rate~~ curve

Survivorship curves "in theory"



in Plants must consider

gamete → seed → recruitment → growth → death

Seed output depends on
- age
- environ
- density
- size

Survivorship curves vary w/
- habitat
- year
- starting point
- allocation to repro vs. growth

① more seeds → more competition
② " " → higher cost

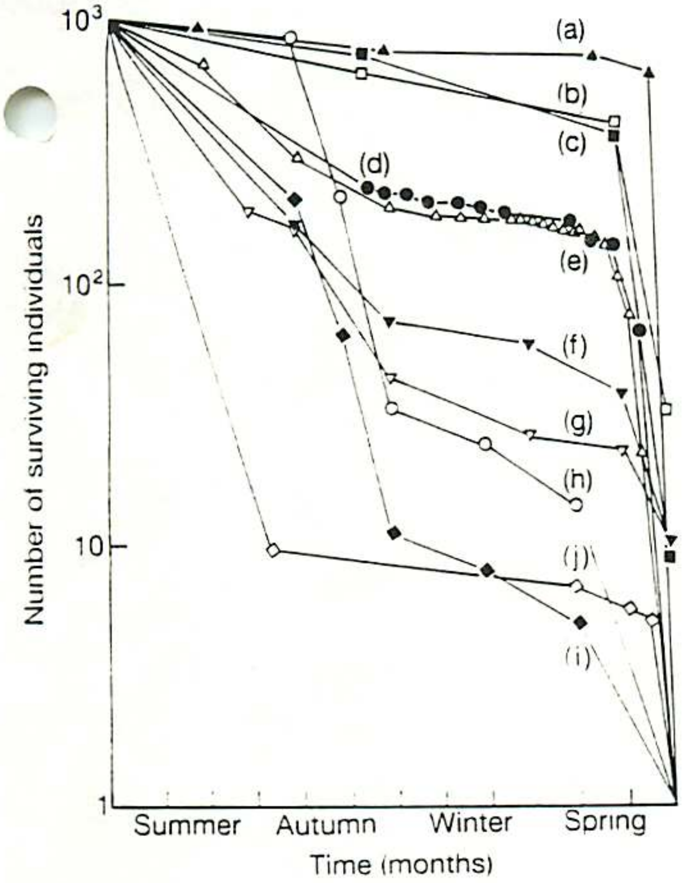
see Fig 3

Macks study
·looked at recruitment / mortality of (Fig 4/106)

mortality & recruitment varies w/
- ① location
- ② density
- ③ timing
- ④ . . . . . .

Population
causes mortality
① seed predation

1 2 3 4 5 6 7 8 9



gonathan

Fig. 5.10. Survivorship curves for natural populations of ten winter annuals from seed production to maturity. The average number of seeds per plant follows the species name. (a) *Vulpia fasciculata*, 2; (b) *Avena barbata*, 4; (c) *Avena fatua*, 4; (d) *Cerastium atrovirens*, 7; (e) *Phlox drummondii*, 23; (f) *Bromus mollis*, 47; (g) *Bromus rubens*, 76; (h) *Sedum smallii*, 114; (i) *Minuartia uniflora*, 305; (j) *Spergula vernalis*, 100–414. References in Watkinson (1981a). Note how the shape of the survivorship curve changes as mean fecundity increases.

Poa annua

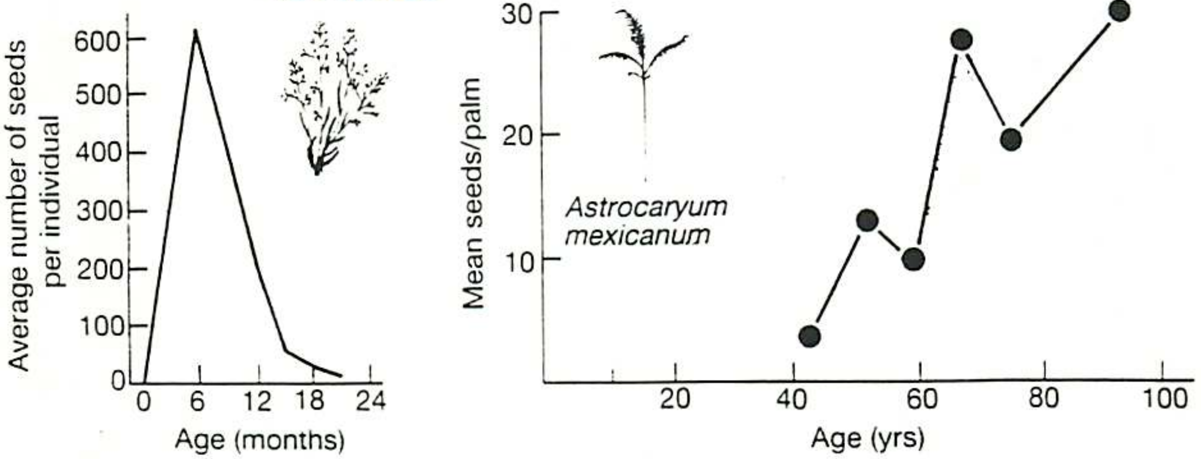


Fig. 5.11. Age-specific fecundity for (a) annual meadow grass, *Poa annua* (from Law, 1975); and (b) the tropical understorey palm, *Astrocaryum mexicanum*. From Sarukhán (1980).

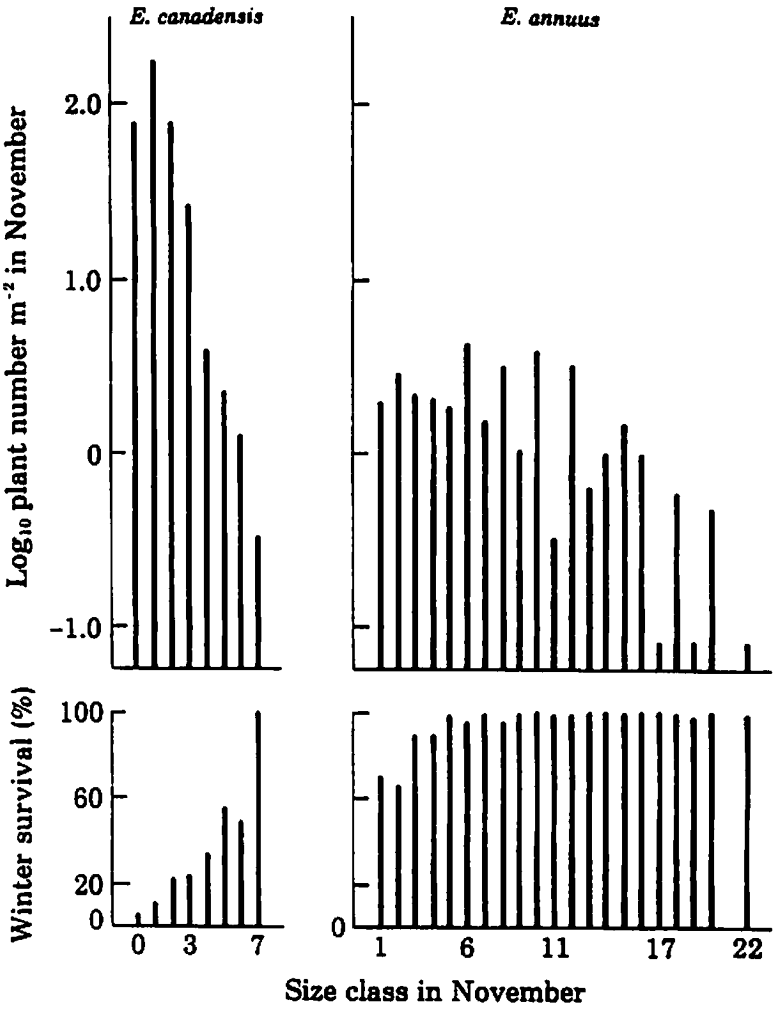


FIGURE 2. Frequency distribution of rosette diameter in November and percentage survival over winter in *E. canadensis* and *E. annuus*.

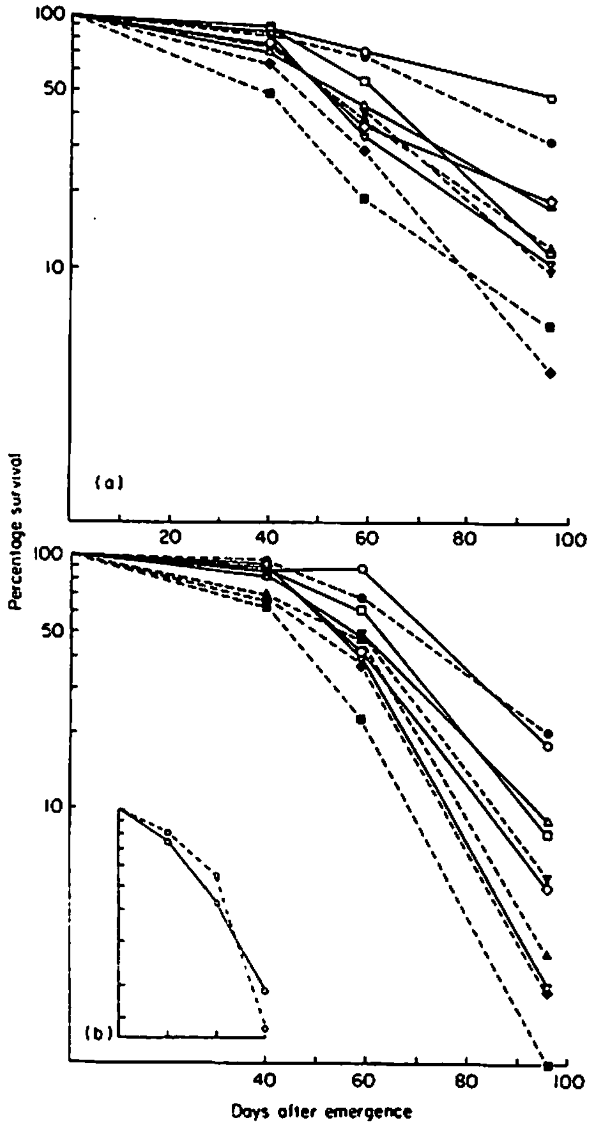


FIG. 3. Genotype-specific survivorship curves for a population of *Phlox drummondii* made up of ten cultivars in low soil fertility (a) and high soil fertility (b) treatments. Inset represents mean survivorship of the population in low fertility (a) and high fertility (b) treatments. The cultivars are: solid lines, Violet (○), Stellata (◇), Coccinea (△), Twinkle (□), Pink Beauty (▽); dashed lines: Atropurpurea (●), Crimson Beauty (▲), Glamour (▼), White Beauty (■), and Blue Beauty (◆).

Fig. 3.8 Population flux in *Ranunculus* species. (From Sarukhan and Harper 1973)

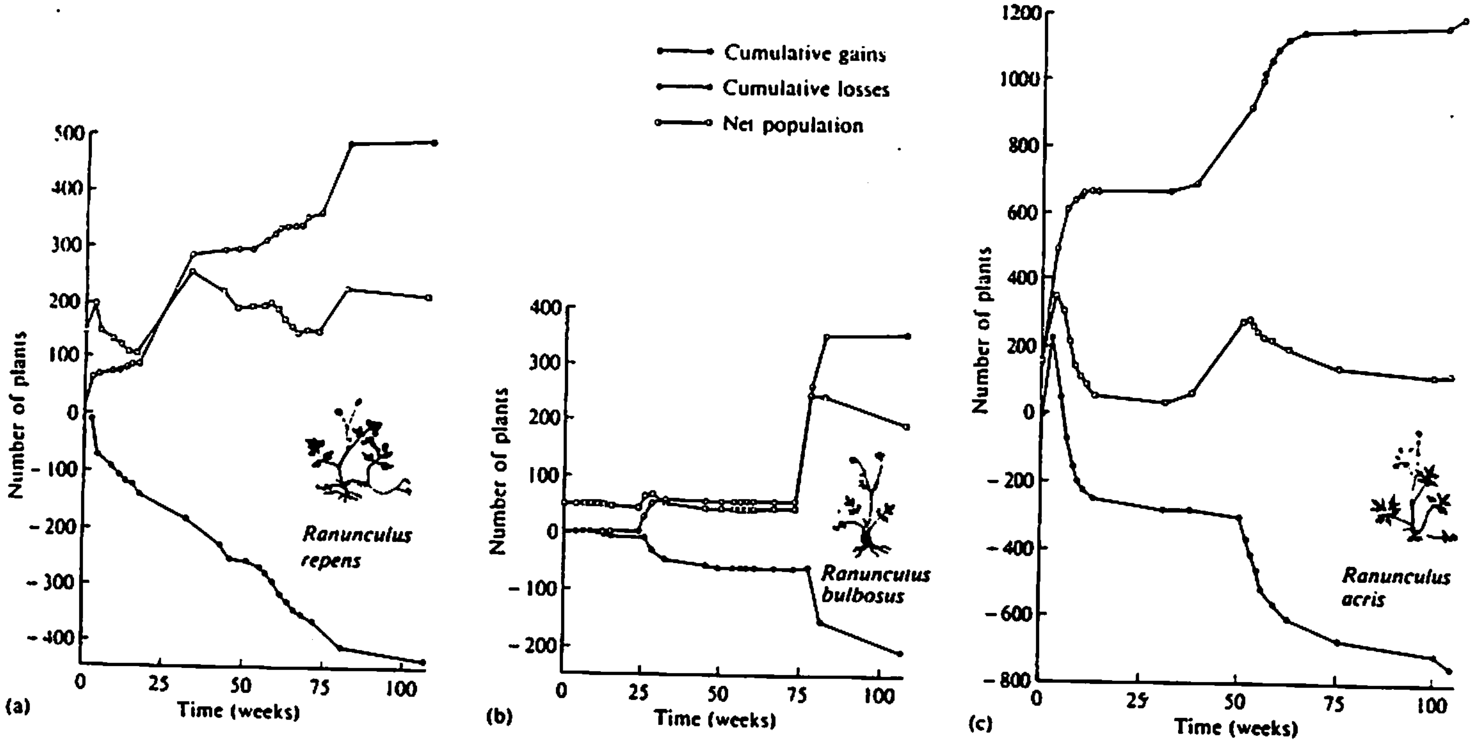


Fig 4

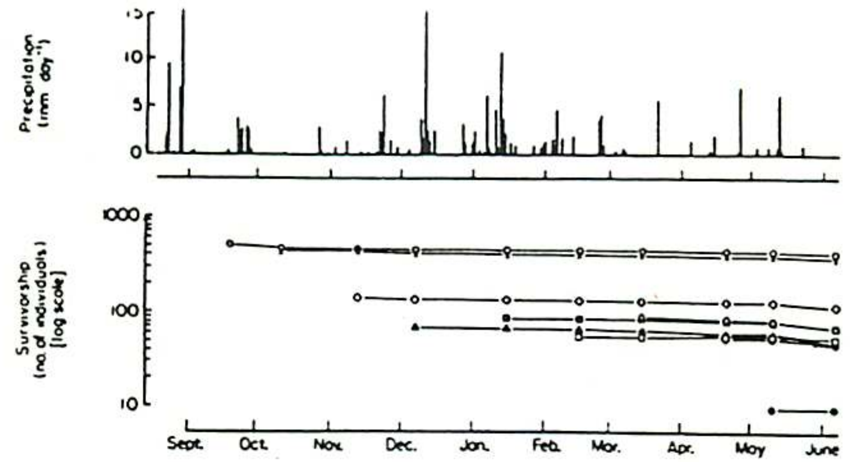


FIG. 7. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the dry site in eastern Washington, U.S.A., during 1977–78. Details as in Fig. 1.

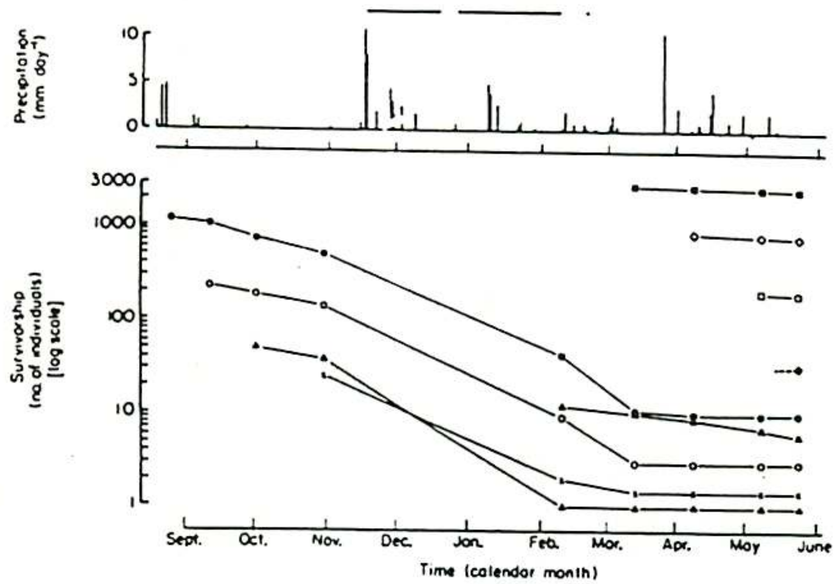


FIG. 8. Composite portrayal of the physical environment and survival of constituent cohorts of the *Bromus tectorum* population at the dry site in eastern Washington, U.S.A., during 1978–79. Details as in Fig. 1.

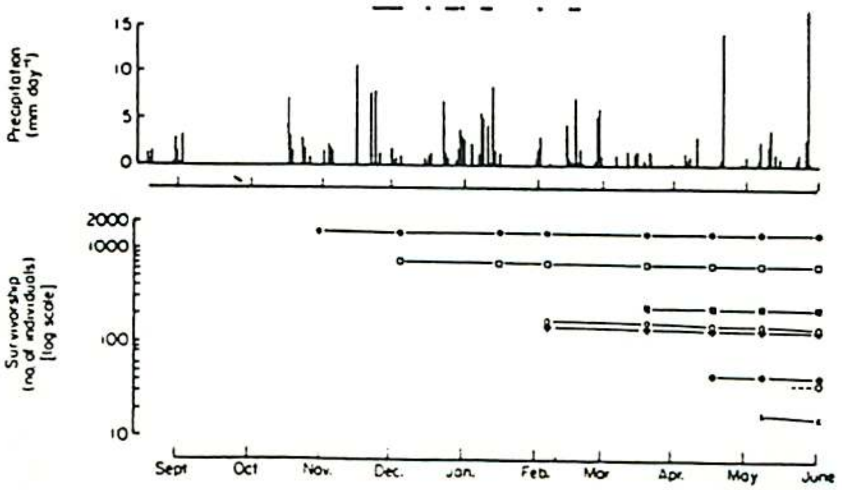


FIG. 9. Composite portrayal of the physical environment and survival of constituent cohorts of the *Bromus tectorum* population at the dry site in eastern Washington, U.S.A., during 1979–80. Details as in Fig. 1.

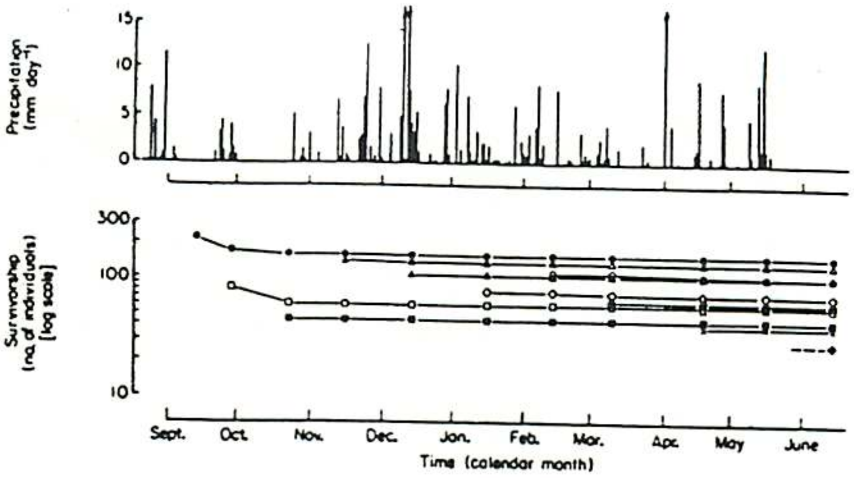


FIG. 4. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the mesic site in eastern Washington, U.S.A., during 1977–78. Details as in Fig. 1.

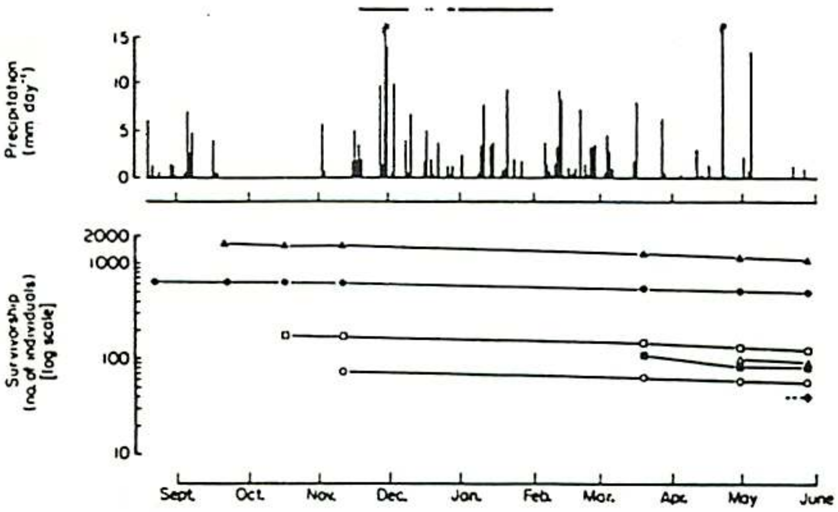


FIG. 5. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the mesic site in eastern Washington, U.S.A., during 1978–79. Details as in Fig. 1.

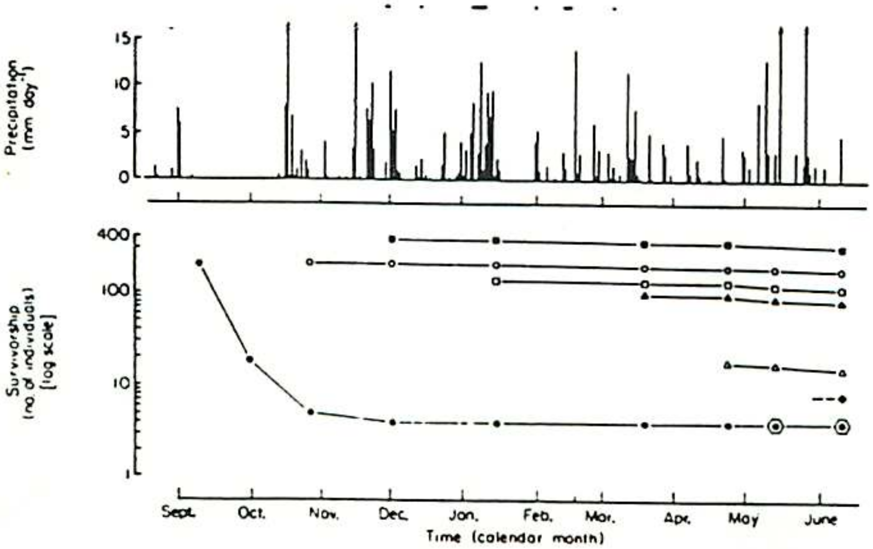
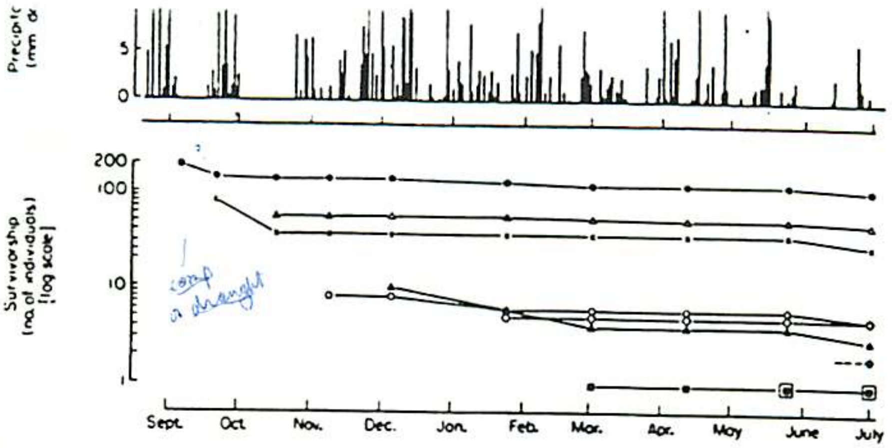


FIG. 6. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the mesic site in eastern Washington, U.S.A., during 1979–80. Details as in Fig. 1.

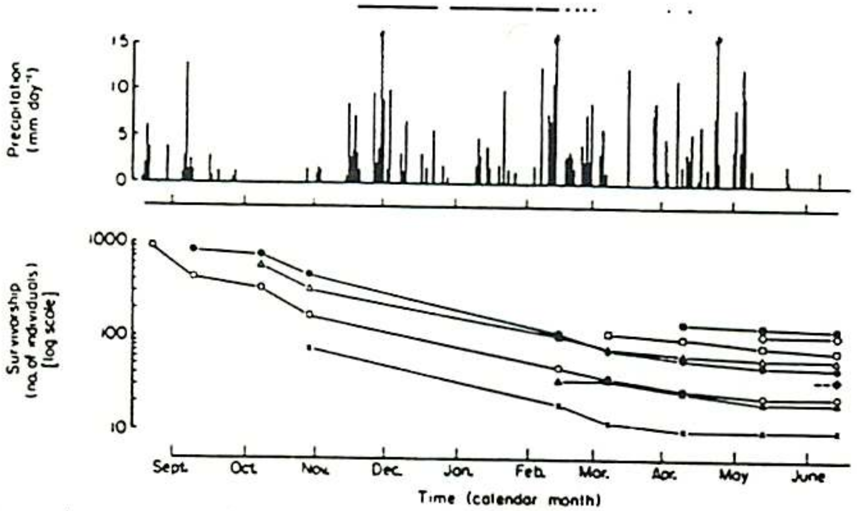
YEAR 1



comp

a drought

FIG. 1. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the moist site in eastern Washington, U.S.A., during 1977–78. (a) Minimum (——) and average (– – –) daily temperatures below 0 °C; (b) estimated daily volume of available moisture per unit volume of soil ($mm^3\ mm^{-3}$) in the 0–10 cm (——) and the 10–60 cm (– – –) soil layers; (c) daily precipitation (mm) and days on which snow was lying are indicated by a horizontal bar across the upper part; (d) survivorship curves for each cohort comprising the population (from Mack & Pyke 1983).



-drier

FIG. 2. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the moist site in eastern Washington, U.S.A. during 1978–79. Details as in Fig. 1.

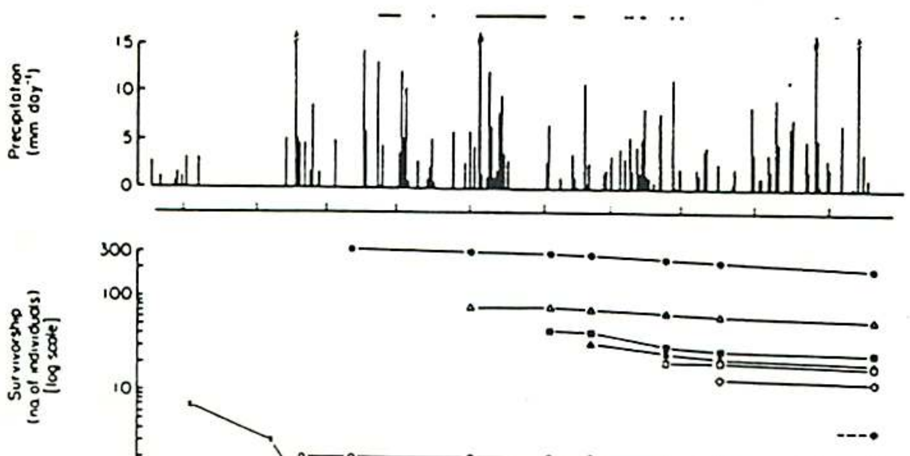


FIG. 3. Composite portrayal of the physical environment and the survival of constituent cohorts of the *Bromus tectorum* population at the moist site in eastern Washington, U.S.A., during 1979–80. Details as in Fig. 1.

Fig. 3.7 Depletion curves for some orchid populations. (Data from Tamm 1972)

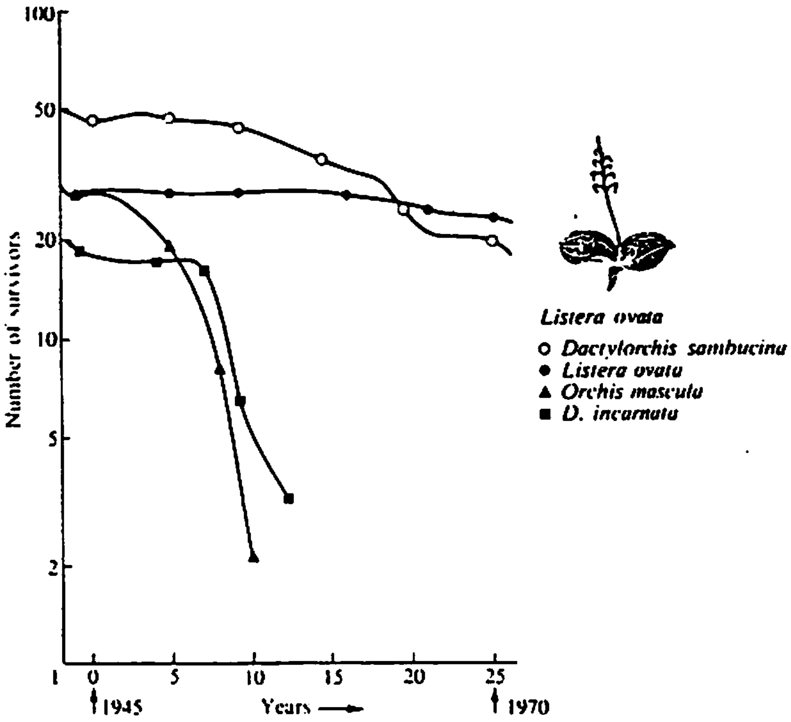
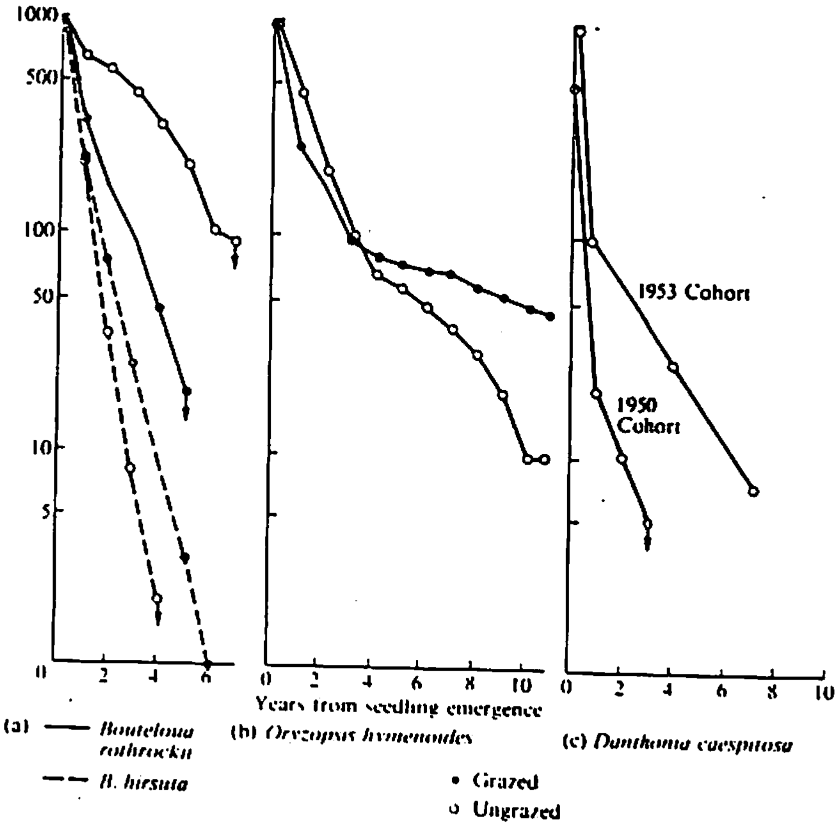


Fig. 3.6 The survivorship of some range grasses in grazed populations and ungrazed populations. Date: *Bouteloua* spp. (Canfield 1957); *Oryzopsis hymenoides* (West, Rea and Harniss 1979); *Danthonia caespitosa* (Williams 1970).



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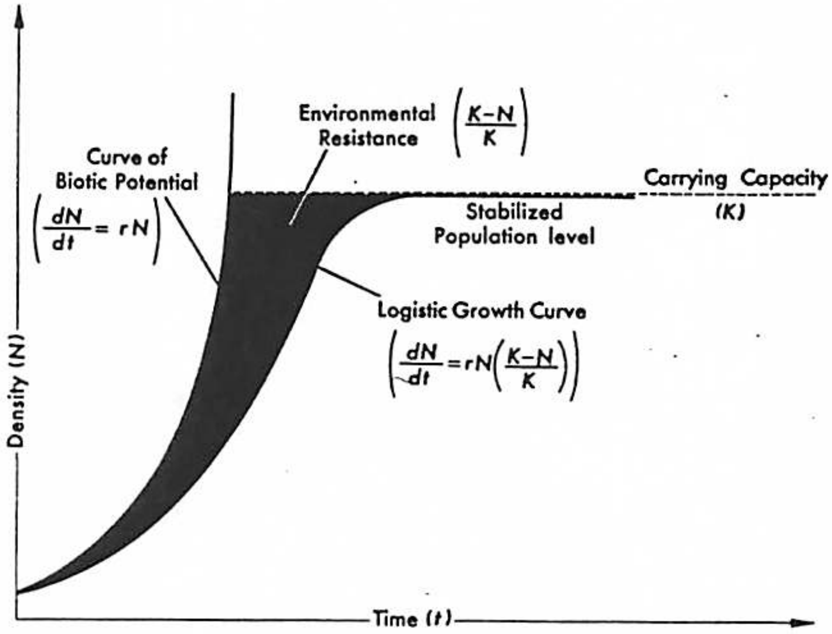


Figure 1-4. Diagram of the theoretical relationships between biotic potential, logistic growth, and environmental resistance.

Table 2.1(a) Life table for *Phlox drummondii* at Nixon, Texas

Age interval (days) $x - x'$	Length of interval (days) D_x	No. surviving to day x N_x	Survivorship l_x	No. dying during interval d_x	Average mortality rate per day q_x
0–63	63	996	1.0000	328	0.0052
63–124	61	668	0.6707	373	0.0092
124–184	60	295	0.2962	105	0.0059
184–215	31	190	0.1908	14	0.0024
215–231	16	176	0.1767	2	0.0007
231–247	16	174	0.1747	1	0.0004
247–264	17	173	0.1737	1	0.0003
264–271	7	172	0.1727	2	0.0017
271–278	7	170	0.1707	3	0.0025
278–285	7	167	0.1677	2	0.0017
285–292	7	165	0.1657	6	0.0052
292–299	7	159	0.1596	1	0.0009
299–306	7	158	0.1586	4	0.0036
306–313	7	154	0.1546	3	0.0028
313–320	7	151	0.1516	4	0.0038
320–327	7	147	0.1476	11	0.0107
327–334	7	136	0.1365	31	0.0325
334–341	7	105	0.1054	31	0.0422
341–348	7	74	0.0743	52	0.1004
348–355	7	22	0.0221	22	0.1428
355–362	7	0	0.0000		

From Leverich and Levin 1979

Table 2.1(b) Fecundity schedule for *Phlox drummondii* at Nixon, Texas

$x - x'$	B_x^{seed}	N_x	b_x^{seed}	l_x	$l_x b_x$
0–299	0.000	996	0.0000	1.0000	0.0000
299–306	52.954	158	0.3394	0.1586	0.0532
306–313	122.630	154	0.7963	0.1546	0.1231
313–320	362.317	151	2.3995	0.1516	0.3638
320–327	457.077	147	3.1904	0.1476	0.4589
327–334	345.594	136	2.5411	0.1365	0.3470
334–341	331.659	105	3.1589	0.1054	0.3330
341–348	641.023	74	8.6625	0.0743	0.6436
348–355	94.760	22	4.3072	0.0221	0.0951
355–362	0.000	0	0.0000	0.0000	0.0000
					$\Sigma = 2.4177$

From Leverich and Levin 1979

LIFE TABLE NOTATION

X = age class or life cycle stage

D_x = duration of life cycle stage

A_x = age of population at each stage

A_x^s = scaled age of population at stage

* l_x = survivorship - # surviving of the original 1000

d_x = mortality - # dying of the original 1000

q_x = mortality rate per 1000 $d_x/l_x \times 1000$

L_x = mean # individuals at life stage (Beginning to end)

T_x = life span of rest of population

* e_x = life expectancy of individual - T_x/l_x

* m_x = age ~~am~~ specific fecundity

$l_x m_x$ = age specific reproductive value

*IMPORTANT

Fig 3

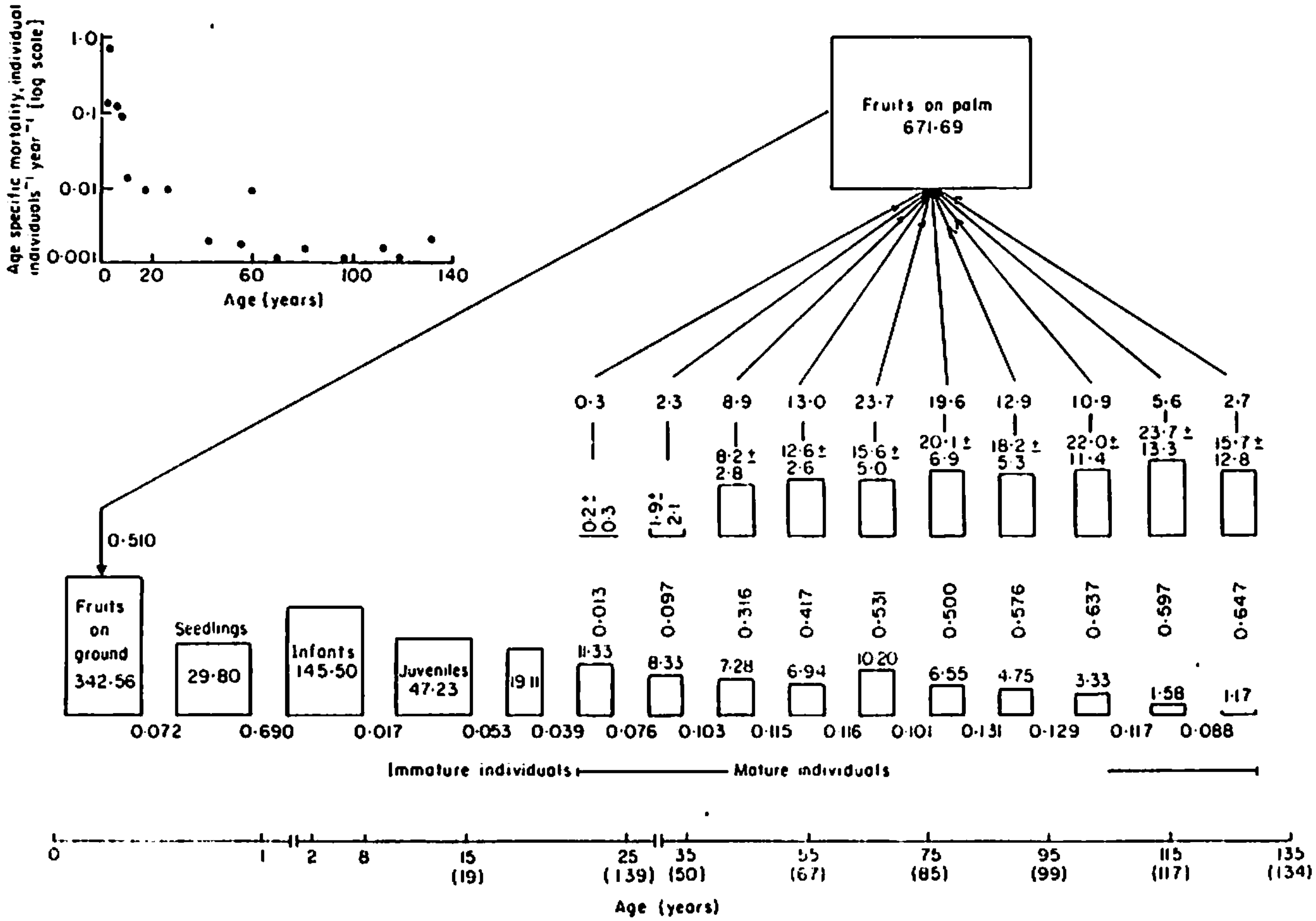
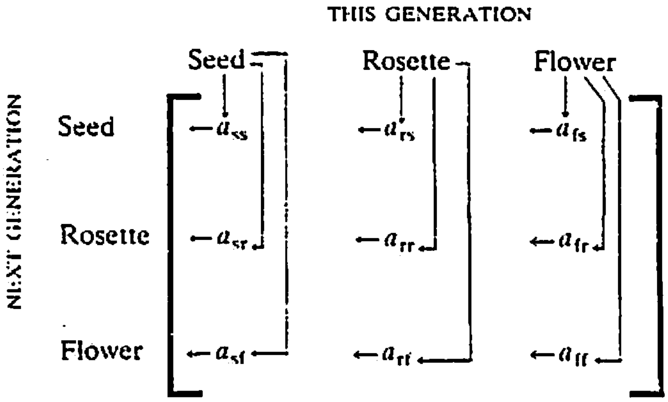


FIG. 1. Population flux model for an average 600 m² plot of *Astrocaryum mexicanum* in 'Los Tuxtlas', Veracruz, Mexico. Box heights represent the density of individuals (on log scale). Numbers between boxes represent the annual probability of moving from one stage to the next. For the mature stages, the probability of reproduction, the mean individual fecundity (± 1 S.D.) and the per cent contribution to the annual fruit production follow each box. Age was estimated from growth rates obtained by measuring directly individual heights in 1975 and 1981 (in parentheses) or from data on leaf production for 30% of the population between 1975 and 1979. The graph (inset) shows the relationship between age and stage mortality.

$$\begin{bmatrix} N_s \\ N_r \\ N_f \end{bmatrix}$$

Matrix 1.
A column matrix of three age classes



Matrix 2.
A transition matrix

$$\begin{bmatrix} a_{ss} & 0 & a_{fs} \\ a_{sr} & 0 & 0 \\ a_{sf} & 0 & a_{ff} \end{bmatrix}$$

Matrix 3.
A transition matrix for an annual

Matrix multiplication

$$\begin{array}{cccc} A & \times\; B_1 & = & B_2 \\ \begin{bmatrix} a_{ss} & 0 & a_{fs} \\ a_{sr} & 0 & 0 \\ a_{sf} & 0 & a_{ff} \end{bmatrix} & \begin{bmatrix} N_s \\ N_r \\ N_f \end{bmatrix} & & \begin{bmatrix} (N_s\, a_{ss}) + (N_f\, a_{fs}) \\ (N_s\, a_{sr}) \\ (N_s\, a_{sf}) + (N_f\, a_{ff}) \end{bmatrix} \end{array}$$

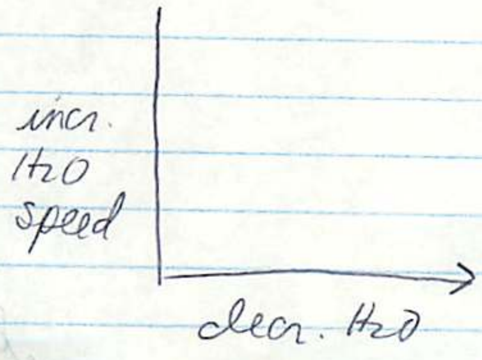
Stuart's tau
11/15/89

Affects of Wind
① Transpiration
Δ Boundary layer
Δ E, G, H,

but boundary layer thickness not as important as other effects of wind

is the effect due to damage such as leaf loss, H_2O loss, or are new leaves put out in certain pattern

incr wind
↙ ↘
decr. bound layer ↓ incr. transp
incr. evap. heat loss ? ↓ decr. transp.



Density-Dependent Regulation and Plant-Plant Interactions
Part I

I. "Regulation": Density Independent vs. Density Dependent

II. Taxonomy of Density Dependent Processes and Plant-Plant Interactions

III. Intraspecific Interactions
a. Agro/Ecosystem Level
-Yield-Density Relationships
-Time=> Growth = Density
-Yield-Density and Resource Levels
-Density: Individuals or Units of Biomass (Plasticity)
-Density-Yield: Responses of Different Organs

b. Population Level
-Density and Survivorship; Environmental Effects
-Density and Survivorship of Genets vs Ramets
-Density and Germination
-Density and Average Individual Size; Envt Effects
-Density and Allocation/Architectural Responses
-Density and Fecundity; Envt Effects

c. Density and Variation in Individual Sizes: Hierarchies
1) -Normal vs Skewed Distributions
-Measures of Size Variability: Skewness, CV, Gini coefficient
-Hierarchy development in a natural Impatiens stand: growth rate of dominant and subordinate individuals
-Density and Hierarchies
2) -Causes of Plant Hierarchies
-Resource Competition: Dominance and Supression
-Asymetric vs Symetric Competition:Light vs Water
-Genetic Variability
-Maternal Effects
-Timing of Emergence
-Environmental Heterogeneity
-Log Nature of Plant Growth
3) -Pathogens and Stand Structure

d. Individal Level
-Neighborhood Models
-Thiessens Polygons

e. *Self Thinning and -3/2 Law??*

Intro to Plant Populations
J. Silverton

11/6/89

PWayne - Plant Populations

only

-create "tables" of survivorship from one stage to next.

-but this doesn't give idea as to causes just #'s.

Plant - Plant Interactions

I) Regulation - processes which affect abund, distrib, dynam
  Density-dependent - neighbors affect resources & controllers

  Density-independent - neighbors aren't important
    e.g. - hurricanes
      - Δ resources & controller

Plant-plant interactions
  Plants living next to each other
  +
  } many of both : symbiosis; shade; H_2O; herbivory
  -

  (occur at every phase of life cycle)
  ① pollen - genetic

  ② timing important

  ③ light quality can be influenced by distant neighbors

  ④ herbivory; architecture; pathogens

Plant-Plant Interactions

Affected by
- ① biotic - plant; comp; commens; every stage
- ② biotic - animal; herb; pollin
- ③ physical - macro & micro
- ④ self - architecture; timing of growth

Studies
- ① agriculture
- ② statisticians

Definitions
- ① what is "competition"; how quantify?
  how affect community

Interspecific } can be v. similar
Intraspecific }

Fig 5

Plant-plant interactions - proximal neighbors influencing resources & controllers

* Density effects affects on search images; pollination herbivory; crypsis; pathogens
- these are reciprocal in that all indiv. in pop. will be affected v. similarly

Interference - neg. P/P interactions
Intercedence - pos P/P "   "

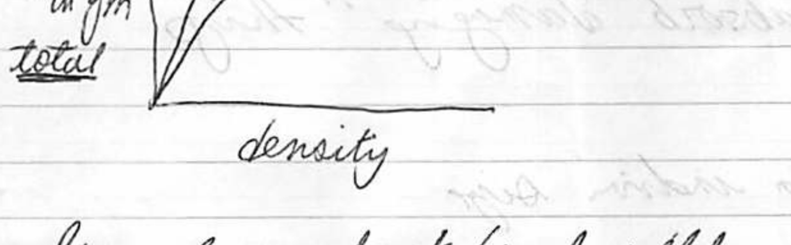
Competition - two indiv. who both want same thing but hard to measure, hard to know what plants need.

Neg P/P interaction (interference)
competion
envir. degrad.
allelopathy, chem interferenc
physical
parasitism
higher order

Pos P/P - v. similar
resource sharing
envir. ameleoration (shading)
chem. interceding
phys " "
higher order

System level

see 6



law of constant final yield

amt of biomass may be more useful than # of plants.

while total biomass has constant yield
<u>but</u>

(7) ① grain amount in maize

dips at end

in agronomic studies there [illegible] is very little variation betw. individuals

* density affect v. dependity on envir. characteristics

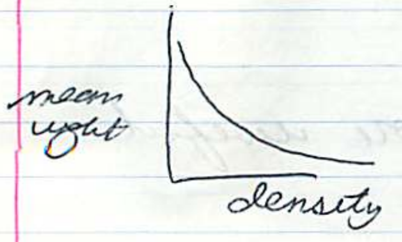
Life Cycle

germ Density and Germination field

Linhart

- - could be that inhibitors released affect others
- - could be things needed for cracking seed
+ - may help push each other up
+ - may absorb "damaging" things

Size * Density & mean indiv. size



affect of density is limited when other "density independent" factors come into play

Density & plasticity - see Clements
- most dramatic affect of repro.

so that was average affect but what about variability w/in pop.

what happen w/ plants on own
- big ones multiply faster bec of more mass.

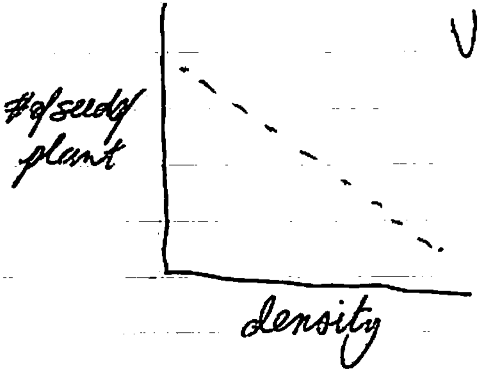
what are causes of skewness

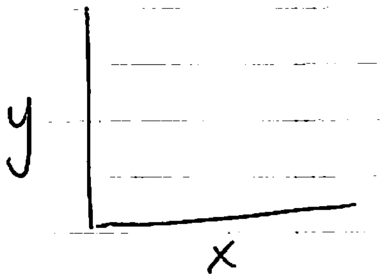
what factors generate hierarcheis
① resource competition
  directional vs. non-directional
  - light vs. CO_2
  - directional resources result in asymmetry (big get bigger)

② genetic variability

③ maternal effects
④ timing
⑤ microenvironmental heterogeneity
⑥ "log" nature of plant growth
⑦ biotic environment

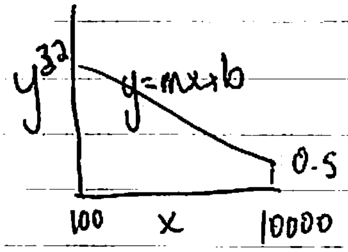
Vulpia

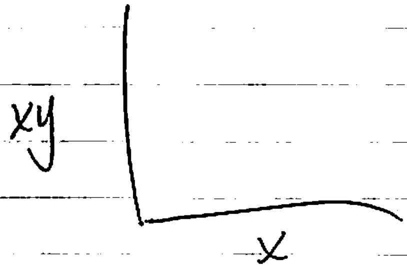


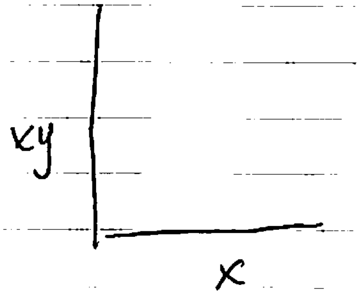


$m = \frac{y-y}{x-x} = \frac{-2.7}{9000}$

$y = mx + b$





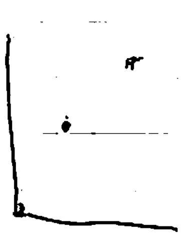


$y = mx + b$

$(xy) = mx^2 + bx$

$z = mx^2 + bx$

$z = \frac{-2.7}{9000}x^2 + bx$



$z = \frac{-2.7}{9000}x^2 + 3.4x$

Bio 149: Experimental Plant Ecology Nov. 21, 1989

Density-Dependent Regulation and Plant-Plant Interactions
Part II

Hierarchies (cont.)

- -Causes of Plant Hierarchies
  - a) Log Nature of Plant Growth
  - b) Genetic Variability
  - c) Maternal Effects
  - d) Timing of Emergence
  - e) Environmental Heterogeneity
  - f) Resource Competition: Dominance and Supression
    - -Asymetric vs. Symetric Competiton: Light vs Nutrients

- -Hierarchies in Heterospecific Populations

Self Thinning and the -3/2 "Law"?

- -General Theory and Widespread Support
- -Thinning in Heterospecific Stands
- -Weller's modification to thinning theory

Response of Individuals to Local Density: A Neighborhood Approach

- -Wiener's Nieghborhood model
- -Potential for extension to multispecies neighborhoods
- -Thiessens Polygons

Interspecific Interactions

a) Community Level

- -Effect of Giant Ragweed on Community Productivity and Diversity
- -Perturbation Analysis and Coastal Plant Community Structure

b) Population Level

- -Interspecific Plant-Plant Interactions in Granite Outcrop Island Communities
- -Heterospecific Thinning and Hierarchies (see above)

c) Average Individual Level

- -Extension of Density Response Models to Two Species
- -Density, Mixed Density, and Response Surfaces
- -Complex PPI through Time in Mixtures of Stellaria and Poa: Density, Frequency, and Nutrient Effects
  - -Species Relative Growth Performances
  - -Species Substitution Rates
  - -Relative Resource Total (RRT)

Substitutive Designs (Replacement Series): No Short Cut

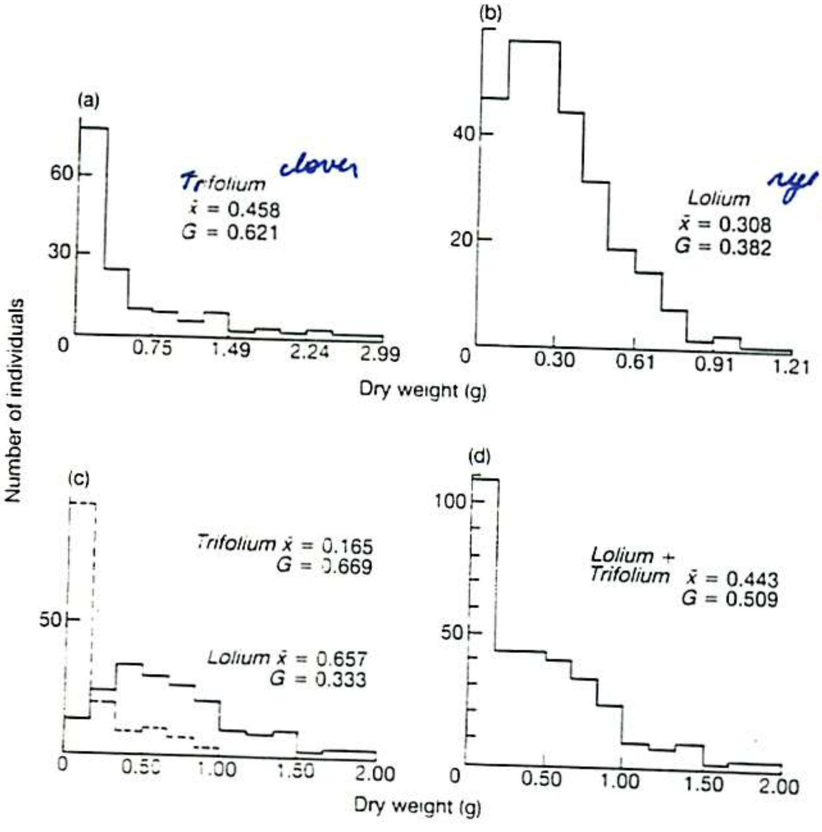


Fig. 4.8. Dry weight distributions for (*a*) monospecific populations of *Trifolium incarnatum*: (*b*) monospecific populations of *Lolium multiflorum*: (*c*) mixtures of *Trifolium* (hatched lines) and *Lolium* (solid lines) with their weight distributions shown separately: (*d*) the mixture as a whole, both species taken together. $\bar{x}$ = mean weight. G = Gini coefficient. From Weiner (1985).

G coefficient doesn't change much when grown together vs. apart.

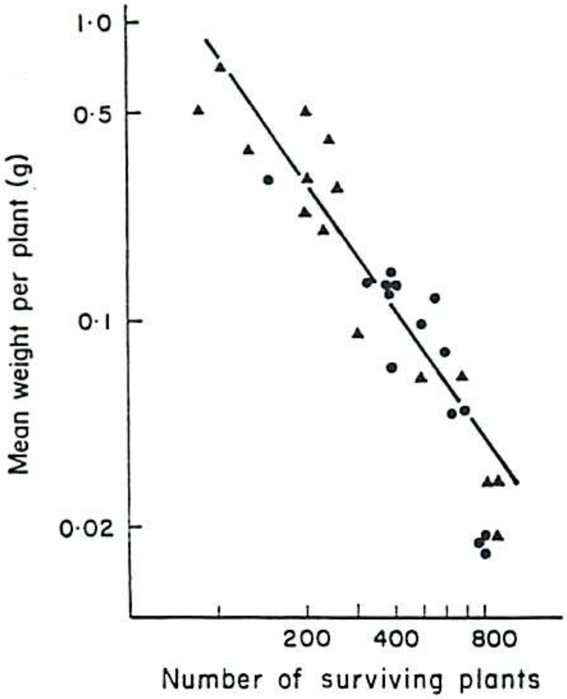


FIG. 1. Relationship between mean dry weight per individual and numbers of surviving plants in mixed populations of *Sinapis alba* and *Lepidium sativum* undergoing thinning in fertile (▲) and non-fertile (●) soils.

both are cultivated mustards

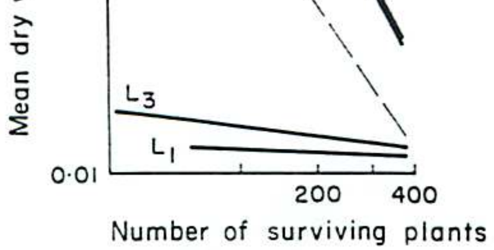


FIG. 2. Regression slopes of mean dry weight per plant on number of surviving plants of *Sinapis alba* and *Lepidium sativum* grown together under two soil fertility levels. (S_1) *Sinapis alba* in the less fertile John Innes No. 1 compost, (S_3) in fertile John Innes No. 3 compost. (L_1) *Lepidium sativum* in John Innes No. 1, (L_3) *L. sativum* in John Innes No. 3 compost. Dashed line illustrates the theoretical $-1{\cdot}5$ slope predicted by the thinning law.

WELLER (1987)

- 448 Data sets !!!
- modifications
  - (a) Density vs. Biomass (vs Avg Wt.) → $\boxed{\gamma = -3/2 \cong \beta = -1/2}$
  - (b) PCA vs Regression (No independent variable)
  - (c) Statistical Tests of Hypotheses.

(*) Of 63 comparable data sets
- 19/63 support -3/2 law
- 20/63 Signif. Diff than -3/2
- Variability of slopes correlated w/ life forms & ecological groups.
- All spp combined = -3/2; thinning <u>Band</u> vs line

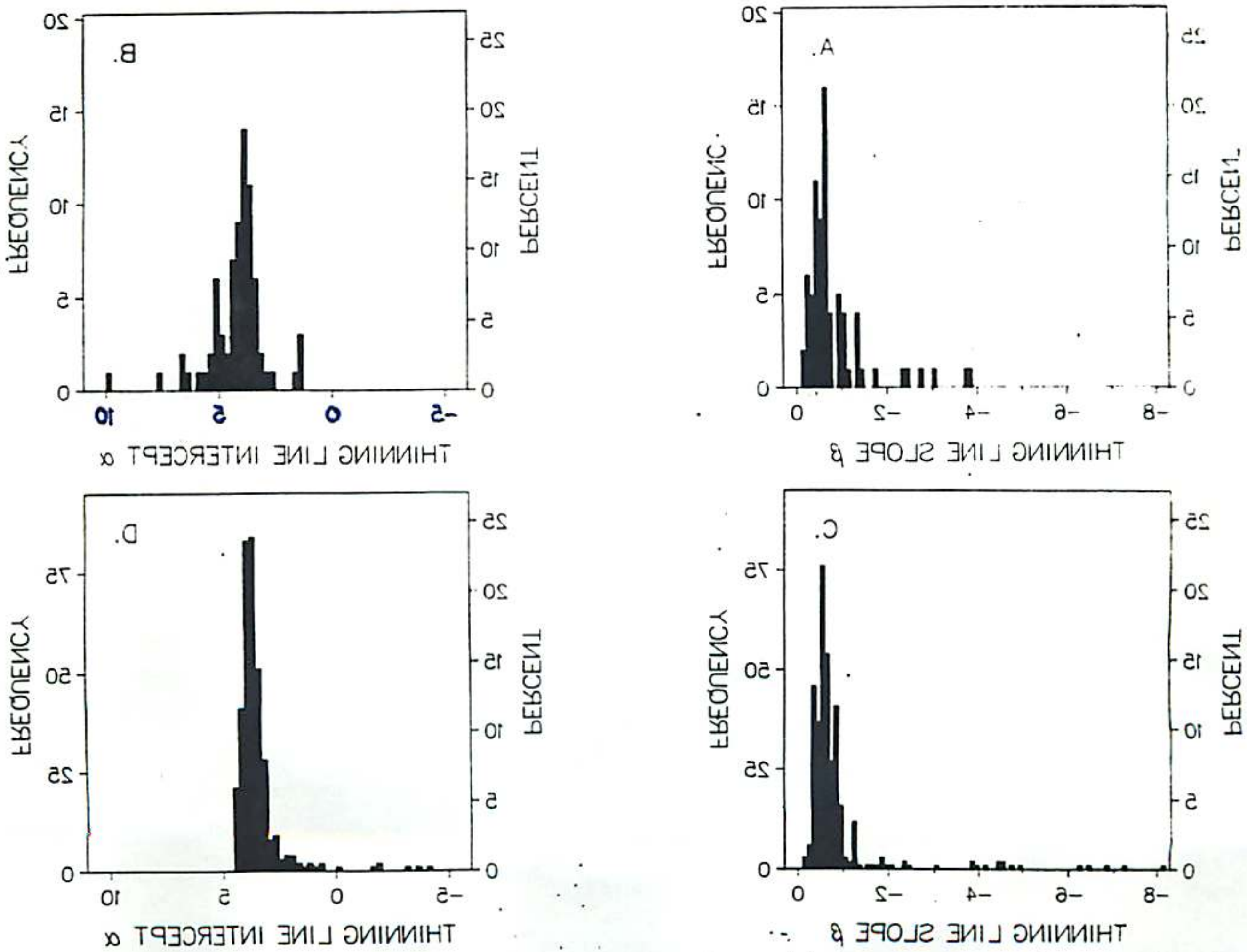


FIG. 5. Histograms for the slopes and intercepts of fitted thinning lines. (A) and (B) show the distributions of slope β and intercept α, respectively, for log B–log N thinning lines in the experimental and field data. (C) and (D) show the same distributions for thinning lines in the forestry yield tables.

TABLE 3. Spearman correlation coefficients of shade tolerance with thinning line slope and intercept, from the forestry yield data.

Thinning parameter	Means for shade tolerance groups*					Spearman correlation	
	1	2	3	4	5	r_s	P
Temperate angiosperms							
Slope β	−0.391 (10)	−0.547 (18)	−0.685 (18)			−0.52 (46)	.0002
Intercept α	3.632 (10)	3.437 (18)	3.517 (18)			−0.19 (46)	.22
Temperate gymnosperms							
Slope β	−0.916 (32)	−0.748 (78)	−0.642 (47)	−1.149 (69)	−0.459 (41)	0.35 (267)	<.0001
Intercept α	3.123 (32)	3.438 (78)	3.732 (47)	3.280 (69)	4.172 (41)	0.57 (267)	<.0001

* Sample sizes are given in parentheses. Shade tolerances are ranked on a scale of 1 (least tolerant of shading) to 5 (most tolerant) as in Appendix Table A2.

angio: as shade tolerance incr. slope incr. } variability may
gymno: as shade tolerance incr. slope decr. } be v. important

TABLE 2. Comparisons of thinning line slope and intercept among plant groups.

Group	n	Slope β		Intercept α	
		Mean	Median	Mean	Median
Experimental and field data (EFD)					
Herbaceous monocots	8	−0.44	−0.39	4.45	4.24
Herbaceous dicots	25	−0.74	−0.65	5.17	5.09
Temperate angiosperm trees	15	−0.65	−0.53	3.78	3.72
Temperate gymnosperm trees	19	−0.87	−0.65	3.79	3.88
Eucalyptus trees	4	−1.26	−1.03	2.87	3.07
Tropical angiosperm trees	4	−2.56	−2.55	2.20	2.21
Kruskal-Wallis tests for differences among six EFD groups			β $H_5 = 17.9$ $P = .0031$ α $H_5 = 41.1$ $P < .0001$		
Forestry yield table data (FYD)					
Temperate angiosperm trees	58	−0.60	−0.63	3.50	3.56
Temperate gymnosperm trees	281	−0.80	−0.61	3.54	3.72
Eucalyptus trees	12	−3.90	−4.39	1.09	1.79
Kruskal-Wallis tests for differences among three FYD groups			β $H_2 = 14.9$ $P = .0006$ α $H_2 = 11.9$ $P < .0027$		
Kruskal-Wallis tests for differences between gymnosperms and angiosperms			β $H_1 = 3.77$ $P = .052$ α $H_1 = 8.30$ $P < .004$		

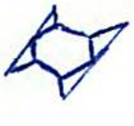
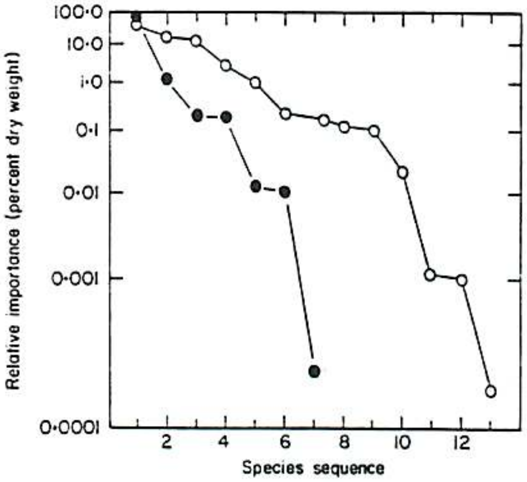


Table 1. *Mean biomass, density and diversity of plants in plots with ('control') and without ('removed')* Ambrosia trifida *on* 1 *August* 1975

	Biomass (g m⁻²)		Number m⁻²	
	Control plot	Removal plot	Control plot	Removal plot
Ambrosia trifida L.	1597	0·0	32·6	0·0
Chenopodium album L.	30	169·5	47·4	119·6
Cannabis sativa L.	7	0·01 *	1·0	0·2
Polygonum pensylvanicum L.	6	372·0	3·6	158·0
Abutilon theophrasti Medic.	0·4	9·5	1·0	19·4
Setaria faberii Herm.	0·2	101·0	0·6	254·6
Ipomoea hederacea Jacq.	0·01	0·7	0·2	4·8
Ambrosia artemisiifolia L.	—	7·2	—	3·6
Bromus japonicus Thunb.	—	2·9	—	21·2
Erigeron annuus (L.) Pers.	—	2·4	—	0·2
Chenopodium hybridum L.	—	1·1	—	1·2
Setaria glauca (L.) Beauv.	—	0·3	—	0·4
Amaranthus hybridus L.	—	0·01	—	0·2
Oxalis dillenii Jacq.	—	0·01	—	0·4
Total ± S.D.	1641 ± 140	666 ± 40	86 ± 7	583 ± 34

$\overline{H}$ (mean species diversity); control plot = 0·21; removal plot = 1·64.

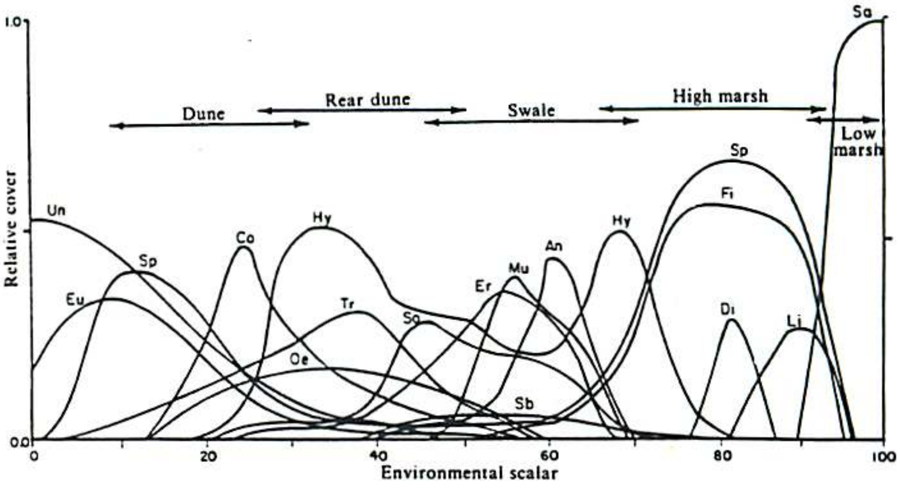
- is the weight of those removed counted.
- can this just be indic. of how much removed.



ambrosia = keystone species

Fig. 1. Dominance-diversity curves for two communities of annual plants, with (●), and without (○) *Ambrosia trifida.*

Fig. 1 Direct gradient ordination for 16 herbaceous species occurring along the Core Banks, North Carolina transects. The environmental scalar is based on a weighted distance from the beach and the inverse of depth to the water table. Species curves were plotted from running averages. Abbreviations for species are as follows: Un, *Uniola paniculata*; Eu, *Euphorbia polygonifolia*; Sp, *Spartina patens*; Co, *Conyza canadensis*; Oe, *Oenothera humifusa*; Hy, *Hydrocotyle bonariensis*; Tr, *Triplasis purpurea*; So, *Solidago sempervirens*; Er, *Eragrostis pilosa*; Mu, *Muhlenbergia capillaris*; Sb, *Sabatia stellaris*; An, *Andropogon scoparius*; Fi, *Fimbristylis spadiceae*; Di, *Distichlis spicata*; Li, *Limonium carolinianum*; Sa, *Spartina alterniflora*.



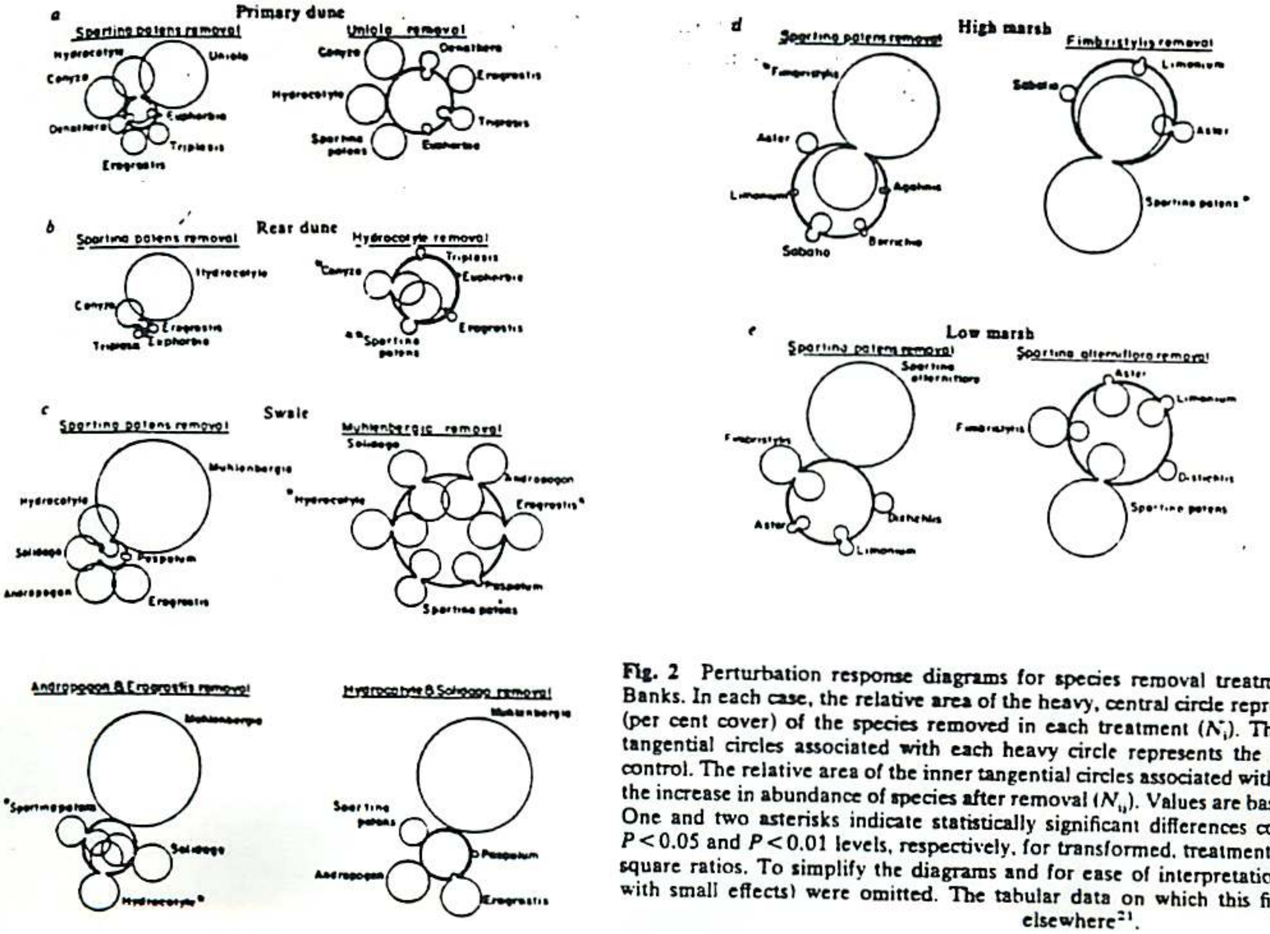
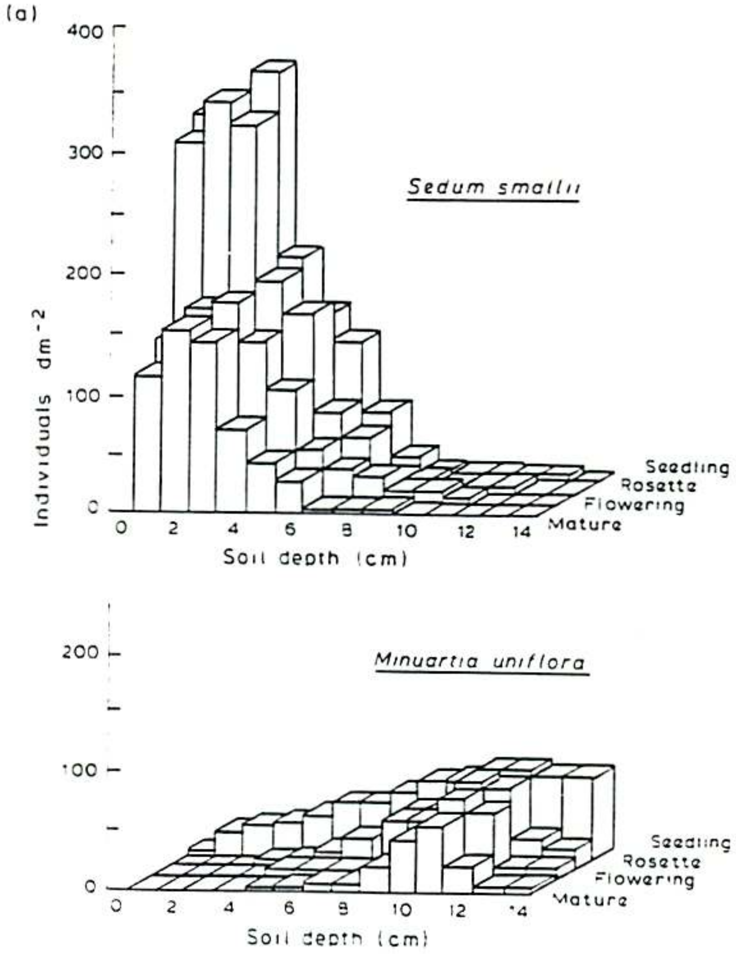
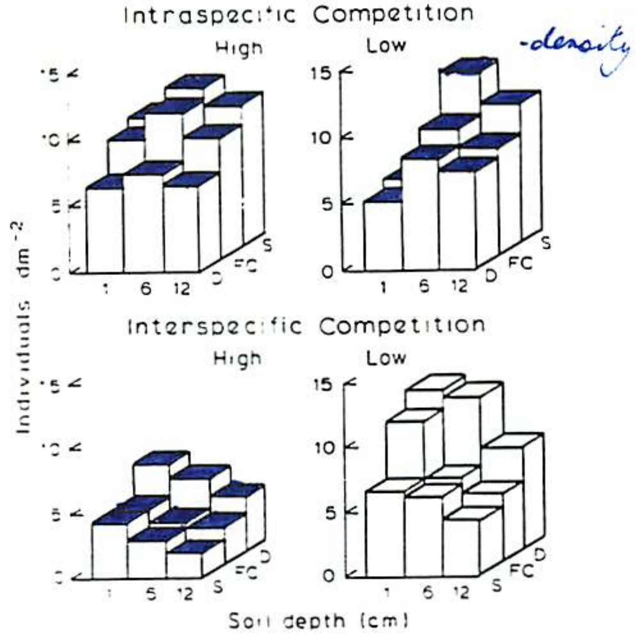


Fig. 2 Perturbation response diagrams for species removal treatments at five sites from C Banks. In each case, the relative area of the heavy, central circle represents the relative abundan (per cent cover) of the species removed in each treatment (N_i). The relative area of the out tangential circles associated with each heavy circle represents the abundance of species in control. The relative area of the inner tangential circles associated with each heavy circle represe the increase in abundance of species after removal (N_{ij}). Values are based on untransformed mea One and two asterisks indicate statistically significant differences compared with the control $P<0.05$ and $P<0.01$ levels, respectively, for transformed, treatment and block × treatment me square ratios. To simplify the diagrams and for ease of interpretation, negative N_{ij} values (m with small effects) were omitted. The tabular data on which this figure is based are present elsewhere[21].

Silander & antem


(a)
400
300
200
100
0
Individuals dm⁻²
Sedum smallii
Seedling
Rosette
Flowering
Mature
0 2 4 6 8 10 12 14
Soil depth (cm)
200
100
0
Minuartia uniflora
Seedling
Rosette
Flowering
Mature
0 2 4 6 8 10 12 14
Soil depth (cm)

(b)

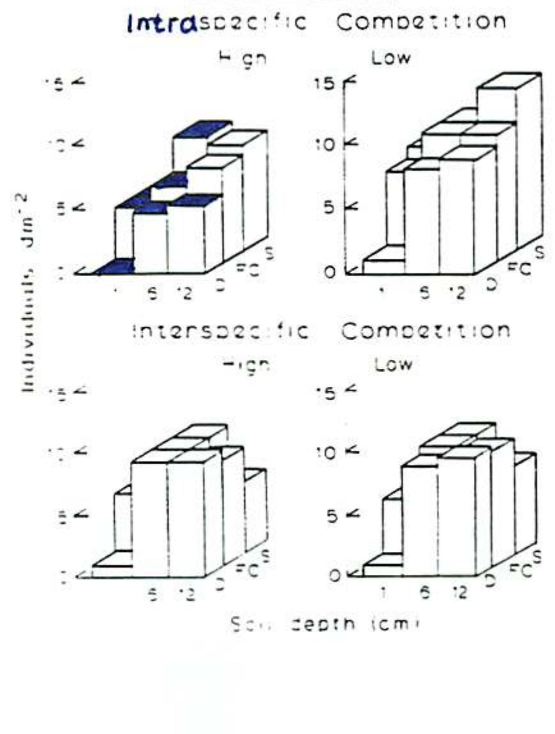


Sedum smallii

Intraspecific Competition -density

Interspecific Competition

(c)

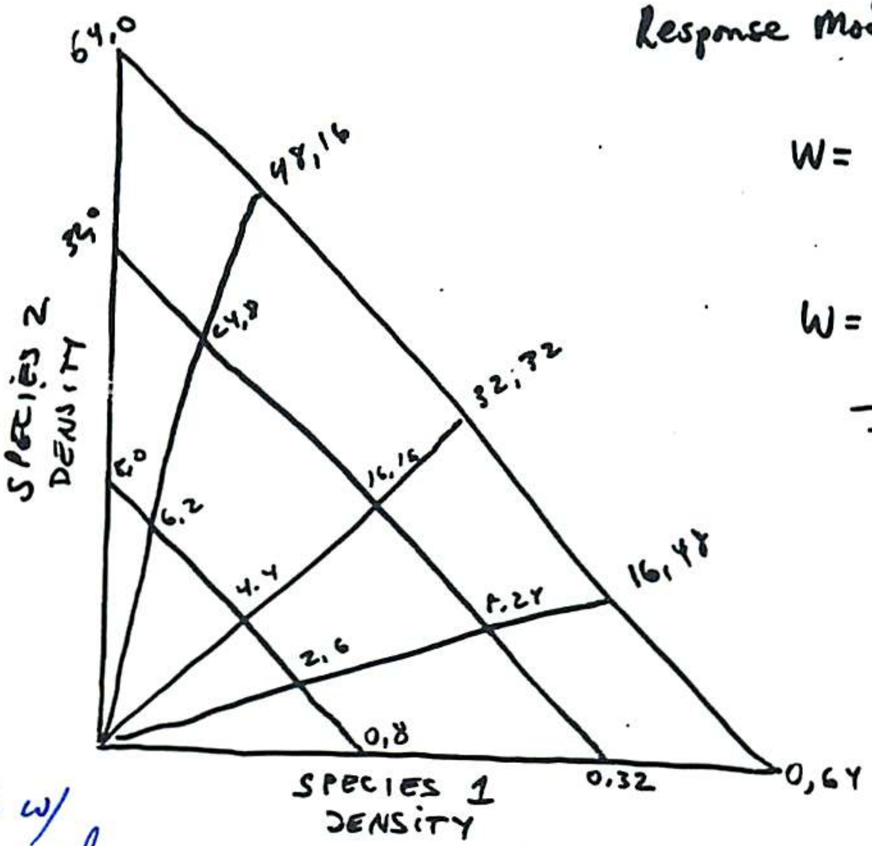


Minuartia glabra

Intraspecific Competition

Interspecific Competition

Extension of Density Response Models → 2spp.



$$W = f(d_i)$$

$$\downarrow$$

$$W = f(d_1, d_2)$$

mixed density
vs
joint density.

take shortcuts w/ two species and pretend 64 of one equals 32 of each.

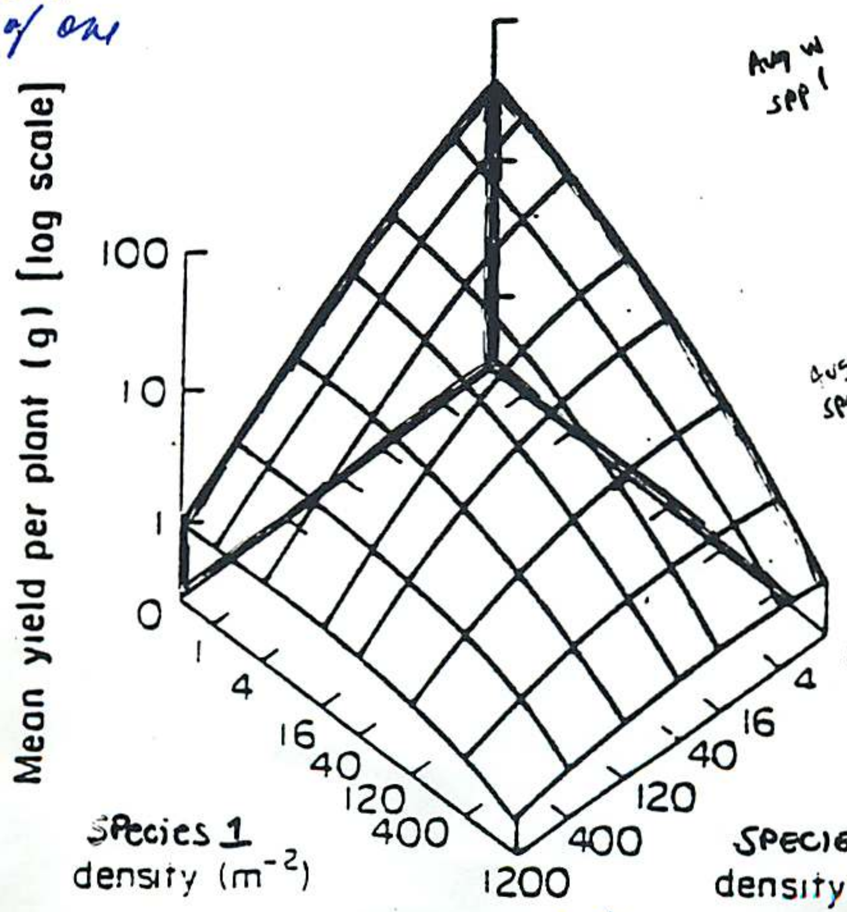
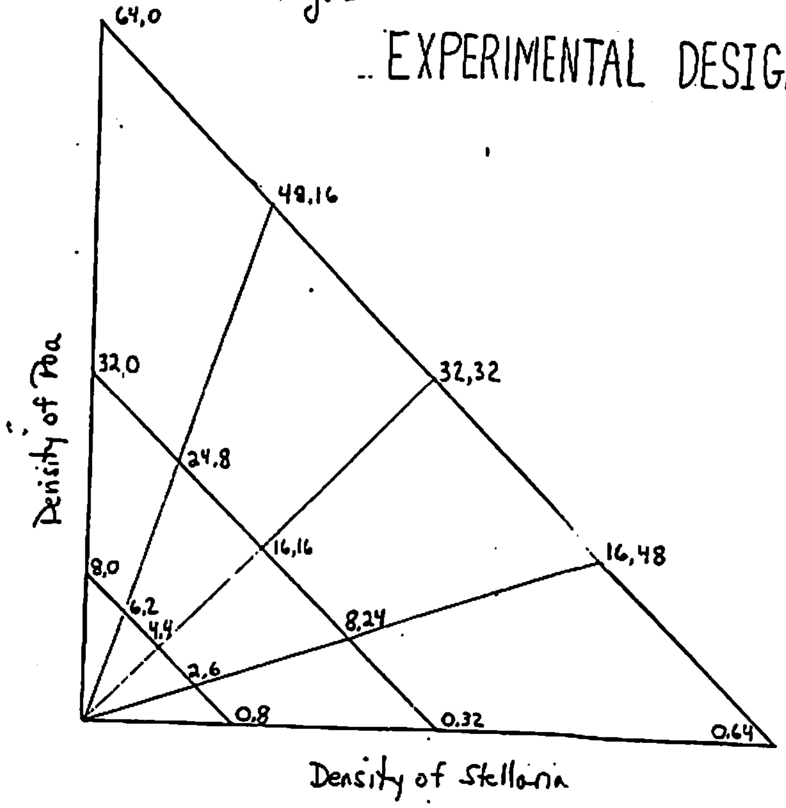


Fig. 1

EXPERIMENTAL DESIGN



15 MIXED DENSITIES X 3 NUTRIENT LEVES X 2 REPS

X 3 HARVEST [$\rightarrow 4 = 2 \times 1 + (2 \times \frac{1}{2}$

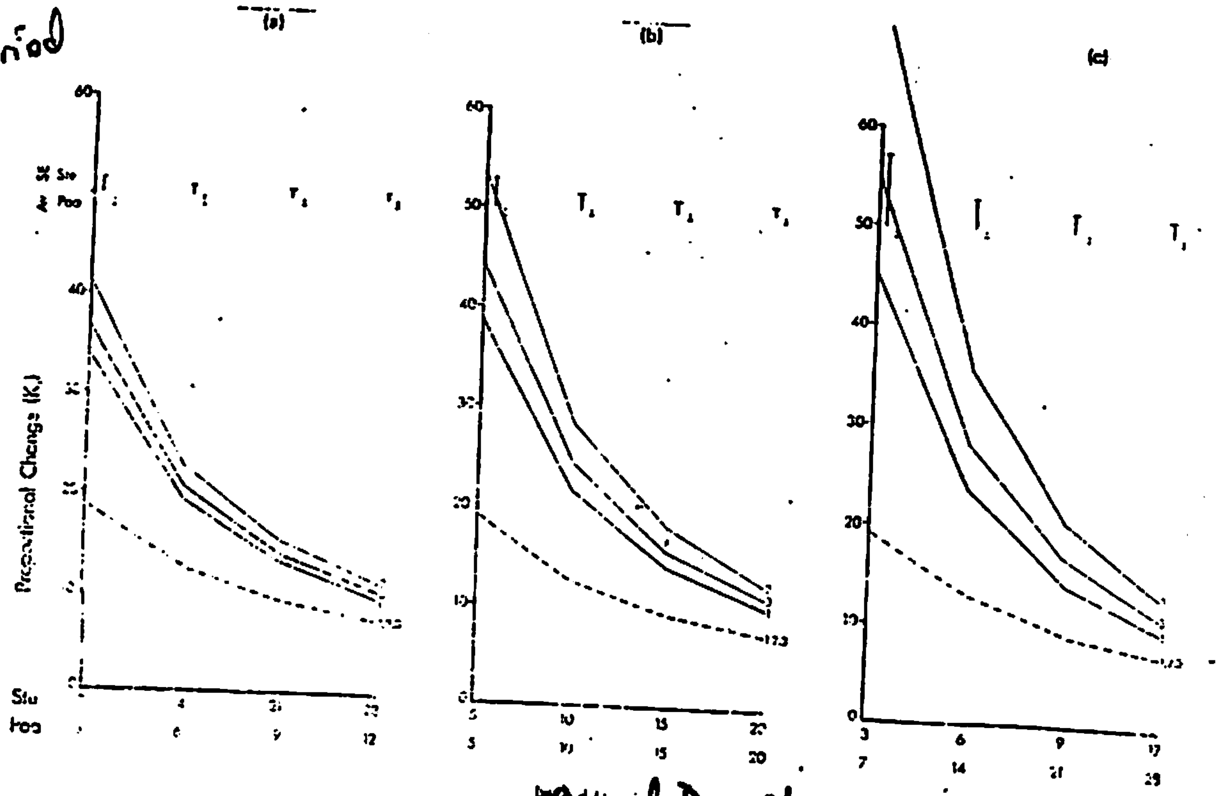
= 270 POTS

Proportional Growth (K_i)

$$K_i = \frac{W_{t2}}{W_{t1}} = \frac{\text{output}}{\text{input}} = \text{"Efficiency"}$$

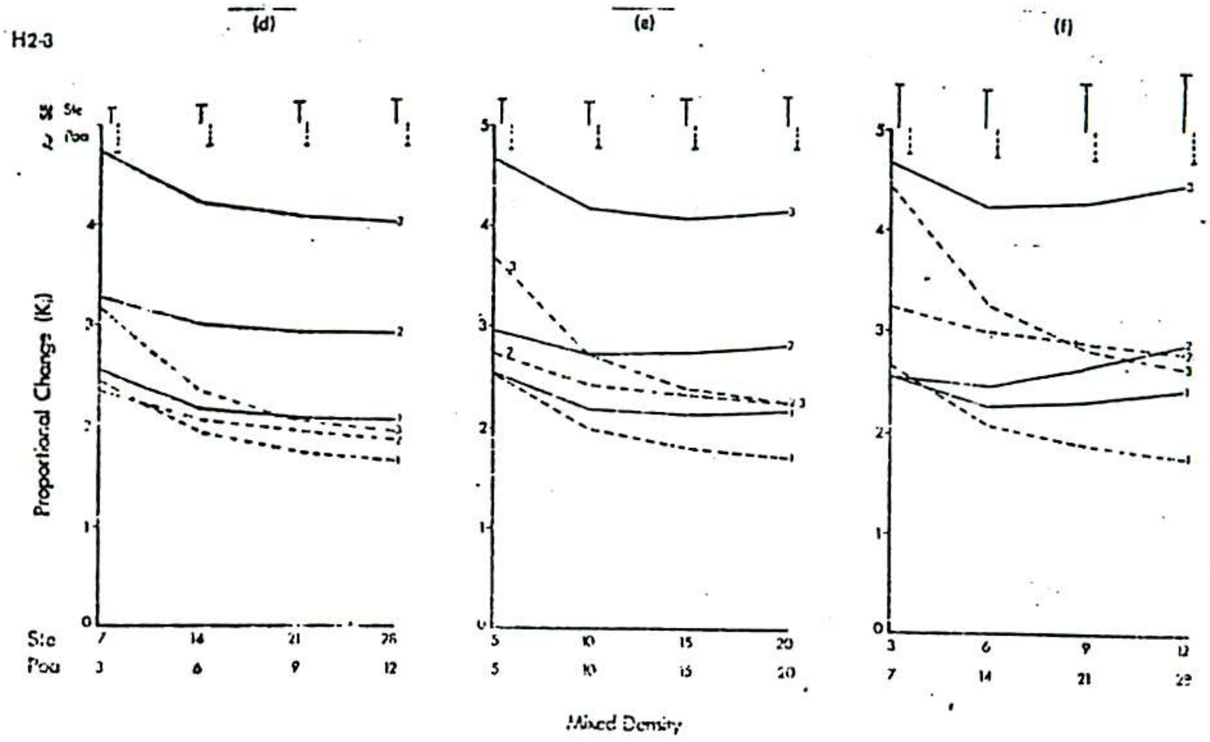
HI-2

Time Period 1

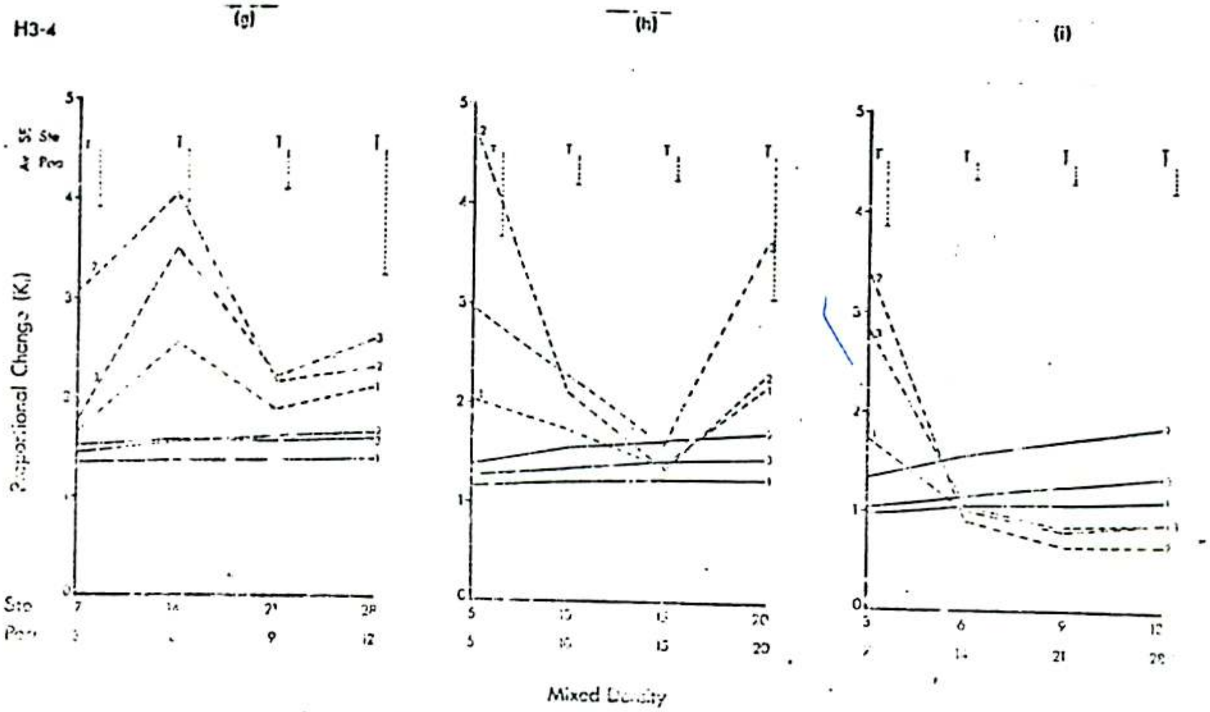


Mixed Density

Pd 2



Pd 3



a) K ↓ rapidly → time for both spp.
b) Δ's w/ mixed density & nutrients
c) Relative performances reverse → time; In Pd3, much smaller Poa growing faster than Stellaria.
(– phenology)

Table 6: Substitution rates for Stellaria and Poa for three harvests and three nutrient levels.

Harvest	Nutrient level	Poa						
		1	5	10	15	20	25	Uniform
Stellaria's view of Poa								
2	1	0.18	0.34	0.55	0.76	0.97	1.18	-
	2	-0.11	0.06	0.27	0.47	0.68	0.89	-
	3	0.05	0.21	0.42	0.63	0.84	1.05	-
3	1	0.47	0.51	0.56	0.61	0.66	0.70	-
	2	0.38	0.44	0.52	0.60	0.67	0.75	-
	3	0.27	0.35	0.45	0.55	0.64	0.74	-
4	1	-	-	-	-	-	-	1.07
	2	-	-	-	-	-	-	0.45
	3	-	-	-	-	-	-	0.91
Poa's view of Stellaria								
2	1	-	-	-	-	-	-	0.80
	2	-	-	-	-	-	-	0.80
	3	-	-	-	-	-	-	0.80
3	1	-	-	-	-	-	-	1.36
	2	-	-	-	-	-	-	4.41
	3	-	-	-	-	-	-	2.60
4	Not calculated							

< 1 even though Stellaria axis bigger.

Architecture!

Substitution rates

- not reciprocal !
- Δ w/ time
- Δ w/ Mixed density
- Δ w/ Nutrient Envt.

Relative Resource Total (RRT)

"A measure of whether species in mixtures are capturing more or less (resources: i.e. growing!) relative to pure stands."

(or, where in pure stands do you find equally, average size individuals?)

RRT > 1 : More Capture in mixtures (or more efficient use/growth)

RRT < 1 : Interference → less efficient growth in mixtures

RRT

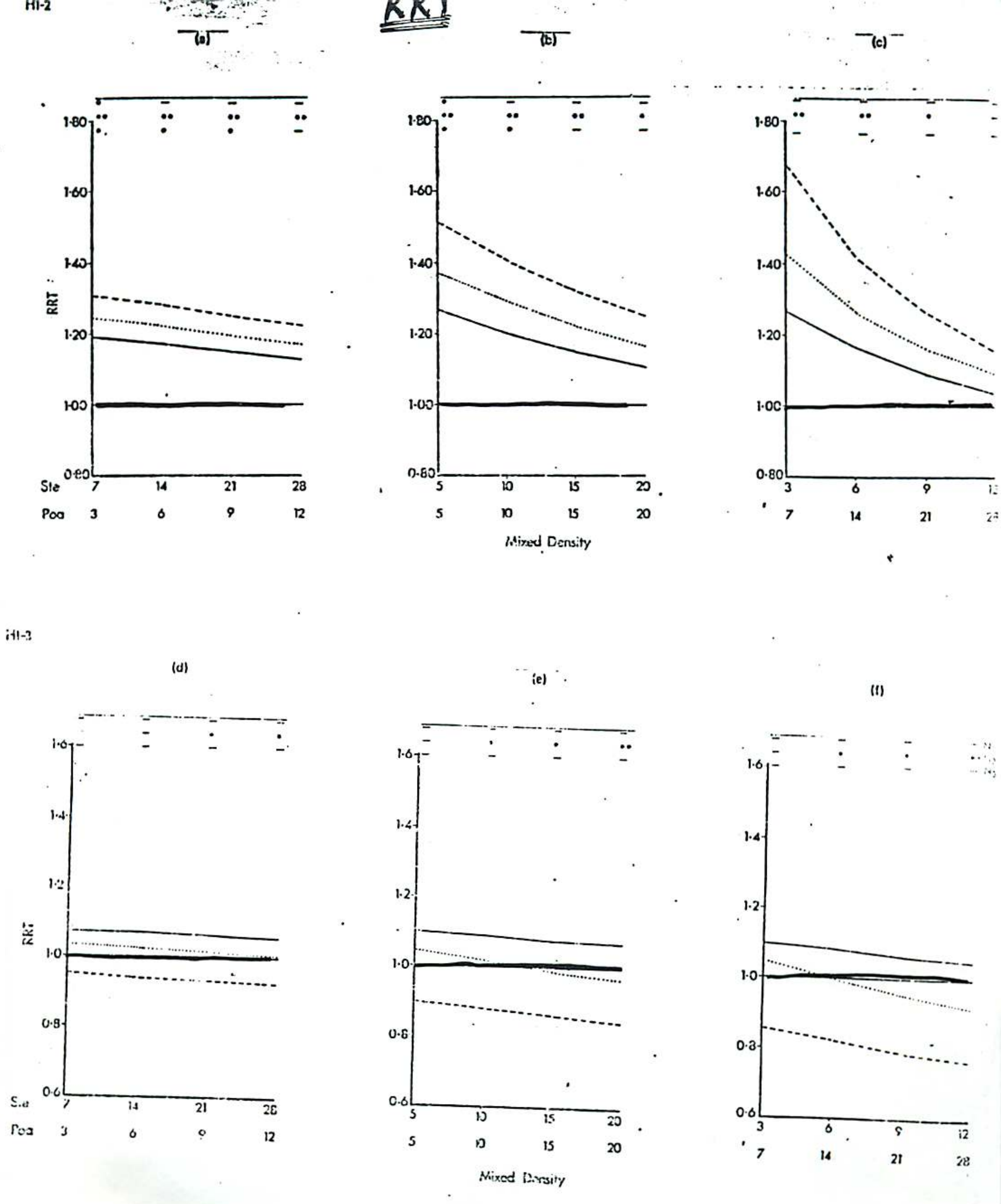


Figure 5: Relative resource total (RRT) for three nutrient levels, (N1 ——, N2 ------ and N3 ·········), three relative frequencies (70:30, 50:50 and 30:70), and a range of mixed densities. Values are presented for periods H1–2 (panels a–c), and H1–3 (panels d–f). The significance of the difference of the RRT value from unity is shown for each nutrient level at each of four mixed densities.

Fig 1

Fig. 1.1 An idealized plant life history. (Adapted from Harper and White 1971)

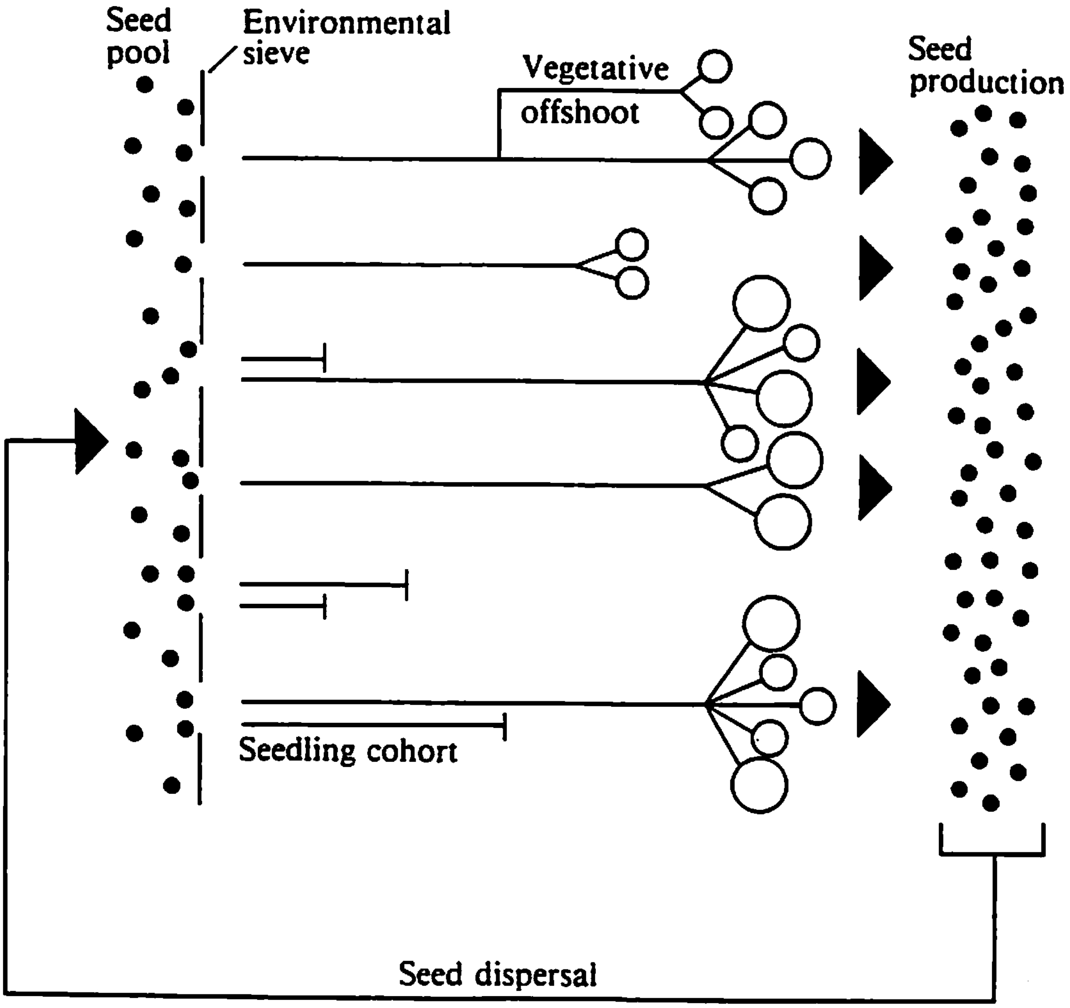
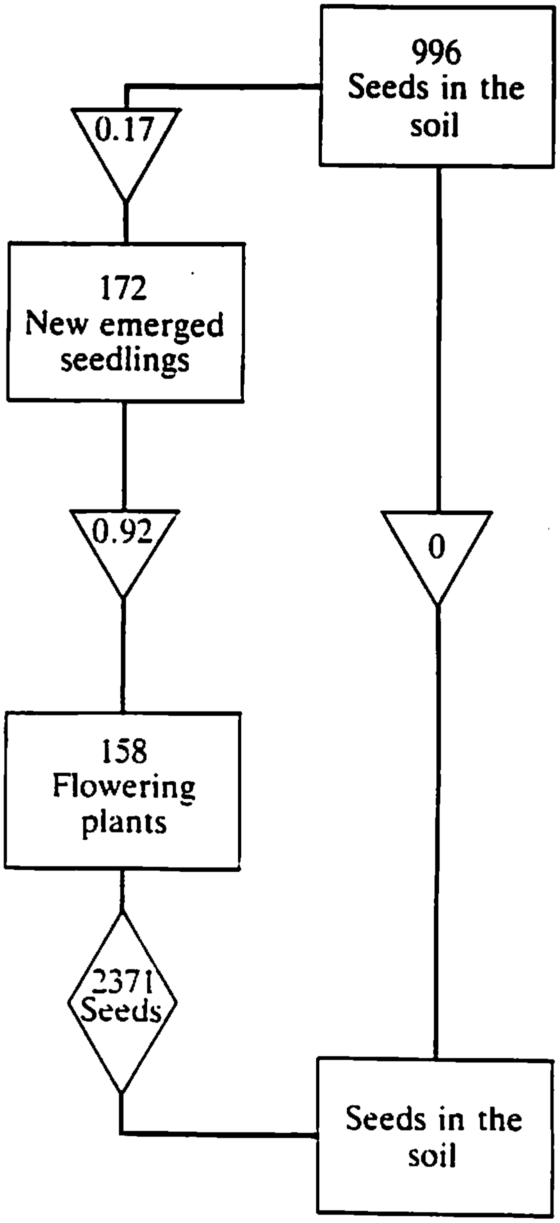


Fig. 2.1 Diagrammatic life table for *Phlox drummondii*. By convention, rectangles represent stages of the life-cycle, inverted triangles represent transition probabilities between stages and the diamond represents seed production.



③

REGULATION : Processes which control (regulate) the abundances, distributions, and dynamics of populations

Density Independent Processes

: Regulation caused by abiotic process, e.g. hurricane disturbance

= Changes in resources

+ Controllers

Density Dependent Processes

= Regulation caused by the proximity of neighboring plants.

=Changes in Resources

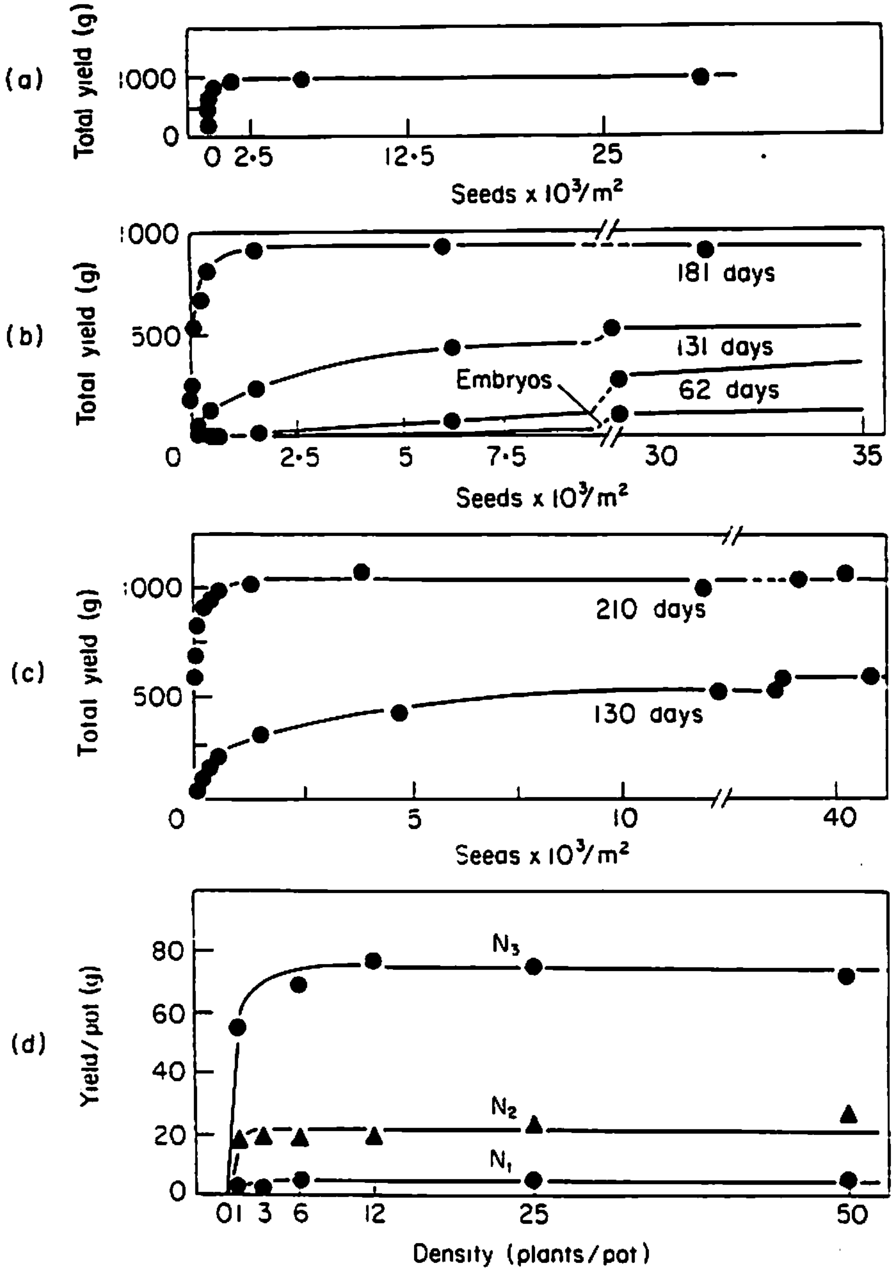
+ Controllers

+ ....

Interactions between plants can be both competitive and beneficent.

⑥

Law of constant final yield



time adds the effect of density

# of plants r. high but biomass is same.

Fig. 6/1. Some relationships between yield of dry matter per unit area and the density of seeds sown.

(a) *Trifolium subterraneum* at the post flowering stage

(b) *Trifolium subterraneum* at various stages in development (note the break in the scale of density)

(c) *Lolium loliaceum* at two growth stages.

(d) *Bromus unioloides* at three levels of nitrogen fertilization.

(From Donald, 1951)

⑦

Fig. 4.16 Yield/density relationships in four crops. See text for further details. (From Willey and Heath 1969, after various authors)

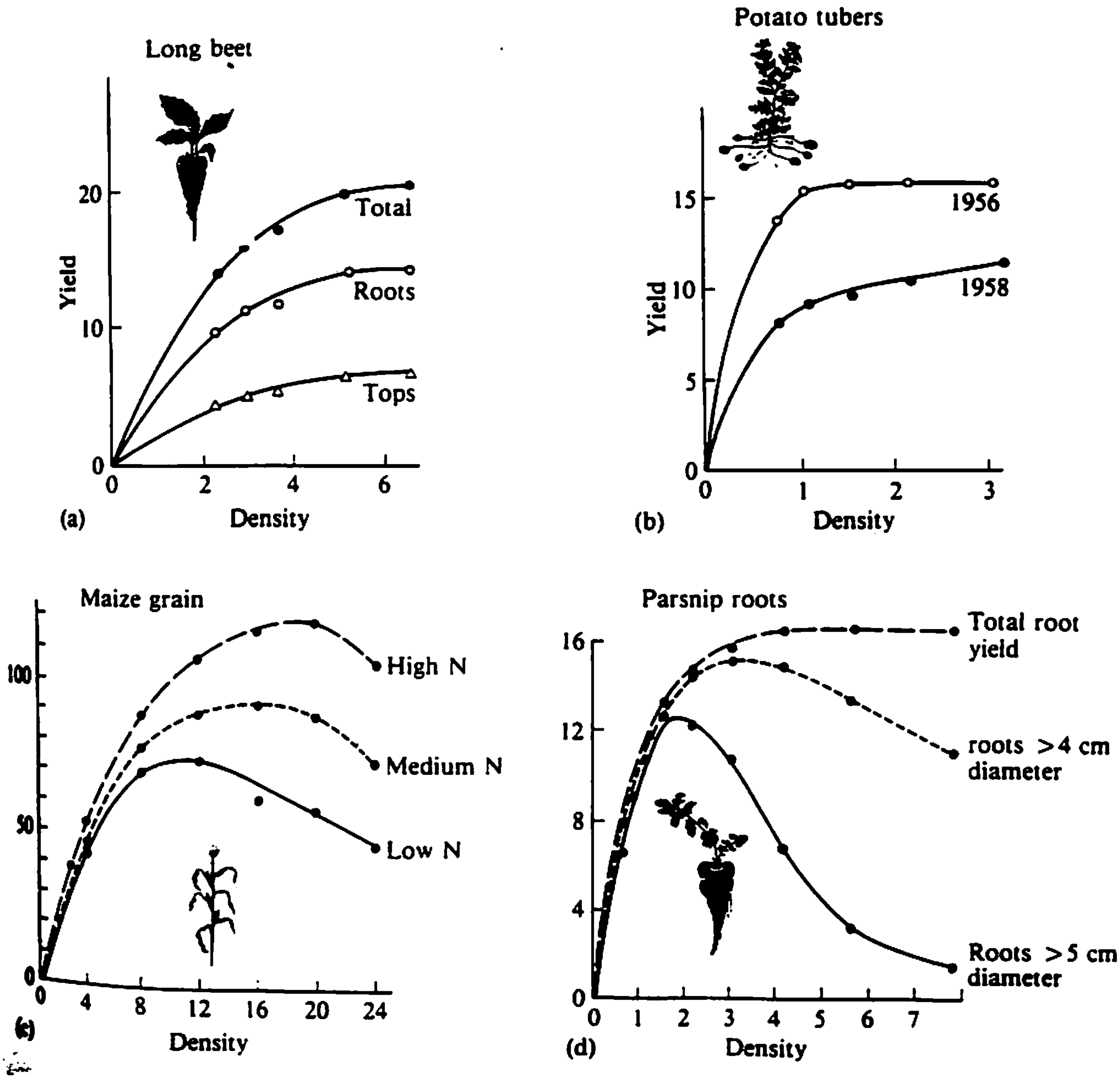
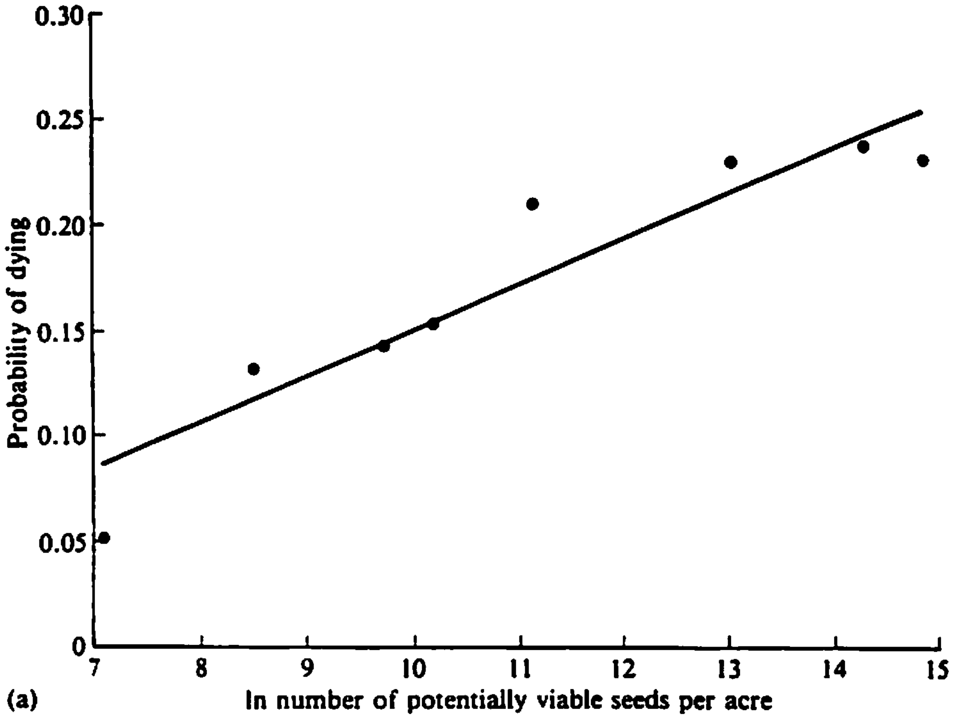


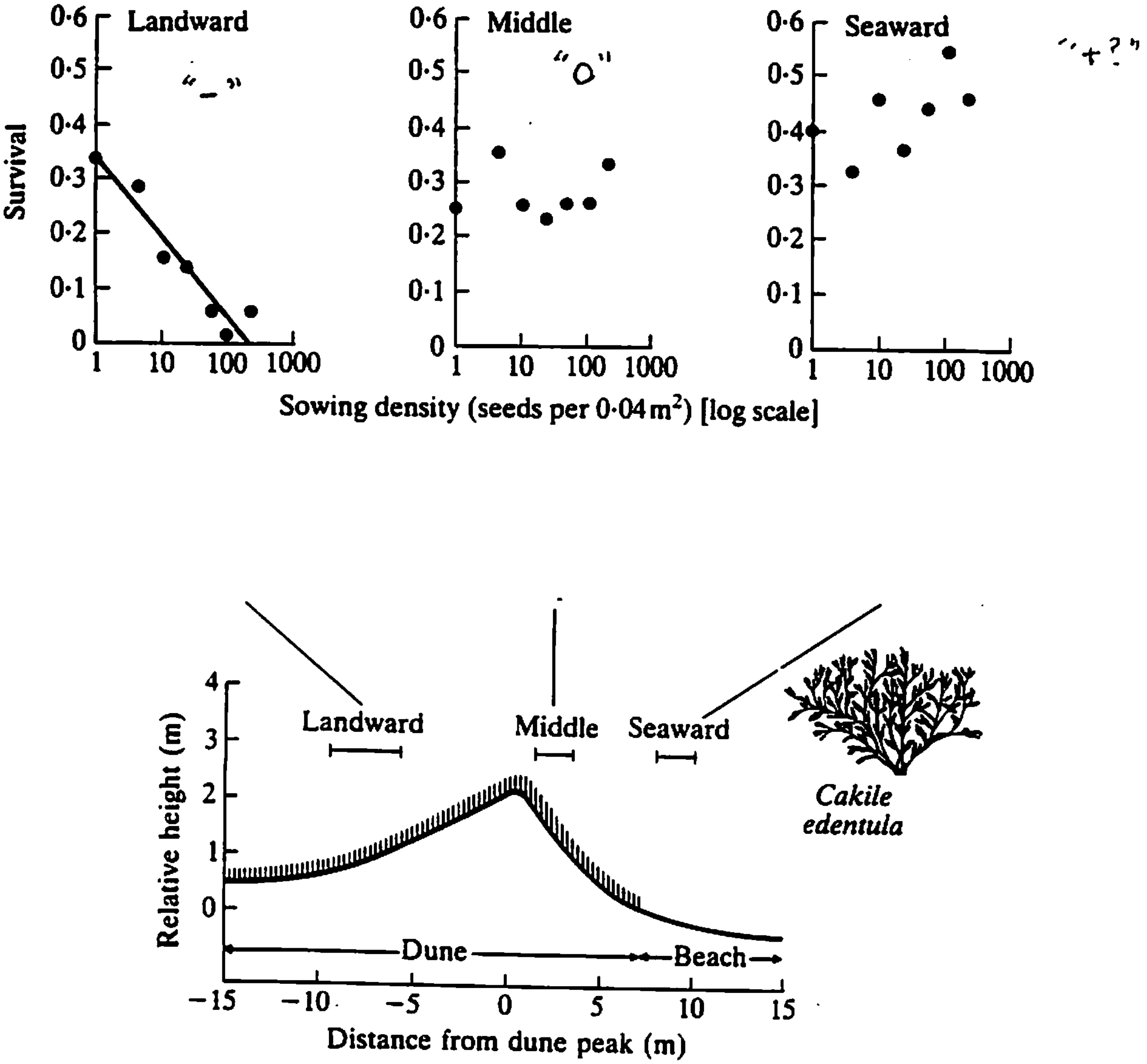
Fig. 4.1 Density-dependent processes in two plant populations: (a) mortality in a population of sugar maple establishing from seed (Hett 1971); (b) fecundity in experimentally manipulated natural populations of *Vulpia fasciculata*. (Watkinson and Harper 1978)



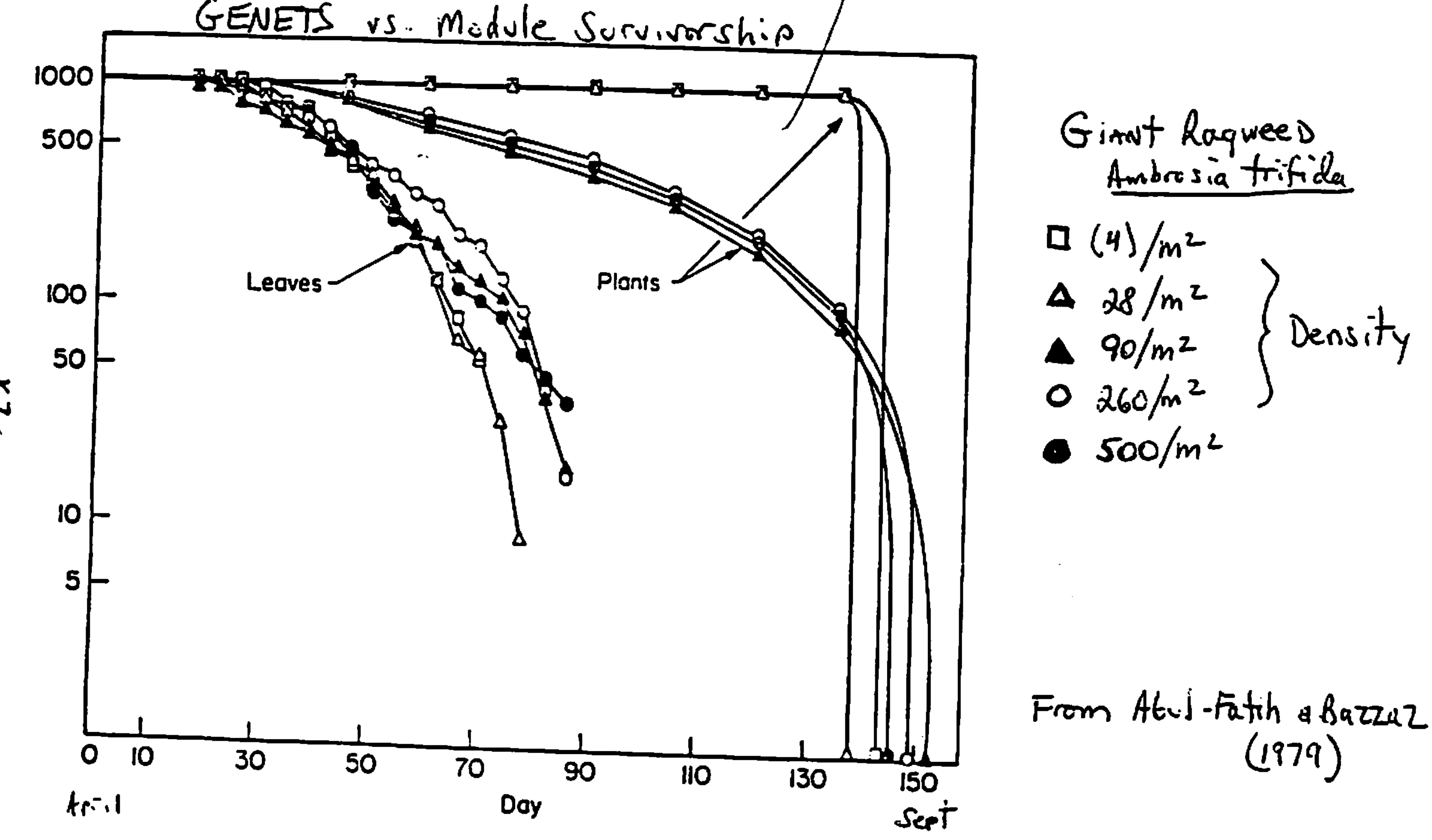
log scale

perhaps there is some threshold needed for seeds to survive.

Fig. 4.6 The relationship of fecundity and mortality to density in experimental plots sown with *Cakile edentula* at three sites on a sand dune. Statistically significant density-dependent relationships are shown by a regression line. There is no significant difference in levels of density-independent mortality at the three sites but there is a significant difference in the level of density-independent fecundity. The size and fecundity of solitary plants is far greater on the beach than elsewhere. (From Keddy 1981)



may be threshold here that has nothing to do directly w/ density.


GENETS vs. Module Survivorship

From Abul-Fatih & Bazzaz (1979)

w/ higher density "mortality" depends on mortality of leaves or indiv.

Table 1. *The cumulative percentage germination of seed of eleven herbaceous species aggregated to varying degrees; the time indicates the number of days elapsed from the beginning of the experiment*

	Light or dark	Seeds used per set	Time (days)	Percentage germinated in sets of: 1	5	10	25	χ^2	Response†
(a) Weedy species									
Erysimum asperum (Nutt.) D.C. (Cruciferae)	Light	200	5	48	52	42	39	4·5	0
			14	70	69	60	61	1·6	0
Kochia scoparia (L.) Schrad. (Chenopodiaceae)	Light	200	7	37	30	33	35	1·3	0
			14	53	50	59	51	2·0	0
Lolium multiflorum Lam. (Gramineae)	Light	200	7	53	56	54	60	1·0	0
			14	65	69	65	72	0·9	0
Taraxacum officinale Wiggars (Compositae)	Light	300	7	41	38	33	31	5·0	0(−)
			14	68	64	54	41	22·3**	−
Veronica peregrina L. (Scrophulariaceae)	Light	400	7	68	66	68	63	0·9	0
			14	76	72	76	66	3·6	0
	Dark	400	7	27	28	31	26	2·0	0
			14	30	28	32	29	1·0	0
(b) Cultivated species									
Agrostis tenuis Sibth. (Gramineae)	Light	200	7	11	20	20	25	11·4**	+
			14	34	52	65	50	19·3**	+
	Dark	200	7	47	53	50	53	0·7	0
			14	67	70	72	67	1·6	0
(c) Species of closed communities									
Boisduvalia glabella Walp. (Onagraceae)	Light	200	7	9	20	17	35	33·7**	+
			21	16	54	64	77	79·0**	+
Downingia concolor Greene (Campanulaceae)	Light	250	7	6	14	20	25	30·7**	+
			28	44	76	79	75	28·7**	+
	Dark	100	7	1	5	4	3	2·7	0
			28	15	21	12	17	2·6	0
Heterotheca villosa (Pursch.) Shiners (Compositae)	Light	250	4	6	12	12	14	7·8*	+
			20	12	15	18	19	4·9	0(+)
Lasthenia fremontii (Torr.) Gray (Compositae)	Light	200	3	40	48	42	36	3·6	0
			14	43	52	53	45	2·9	0
Panicum virgatum L. (Graminae)	Light	150	14	3	8	5	6	4·0	0
	Dark	300	7	21	27	26	29	3·9	0(+)
			14	26	33	35	35	5·2	0(+)

Significance levels for χ^2 with three degrees of freedom: * $P<0{\cdot}05$; ** $P<0{\cdot}01$.

† Five type of responses are indicated: 0, no statistically significant differences between sets; − and +, response statistically significant; 0 (−) and 0 (+), trend is suggestive but not statistically significant.

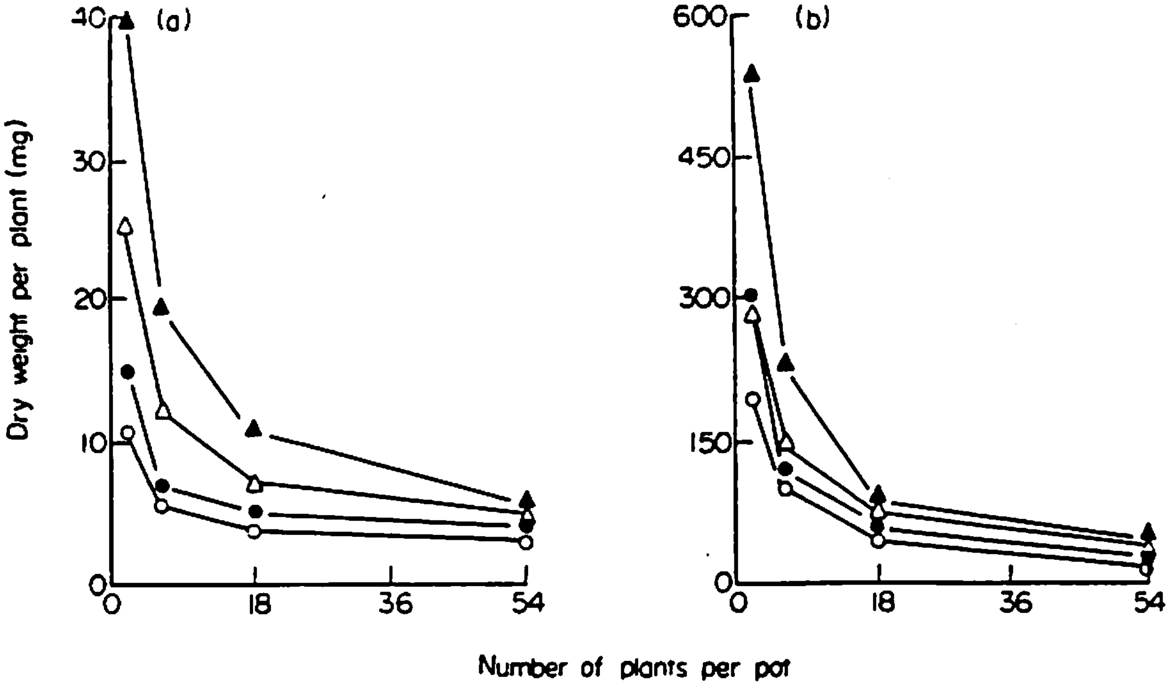


FIG. 1. Effect of density and nutrient regime on dry weight per plant in pure stands annuals: *Aira caryophyllea* (●), *A. praecox* (○), *Cerastium atrovirens* (△), *Vulpia men branacea* (▲). (a) Low nutrient regime; (b) high nutrient regime; note the differenc in scale on the vertical axis in (a) and (b).

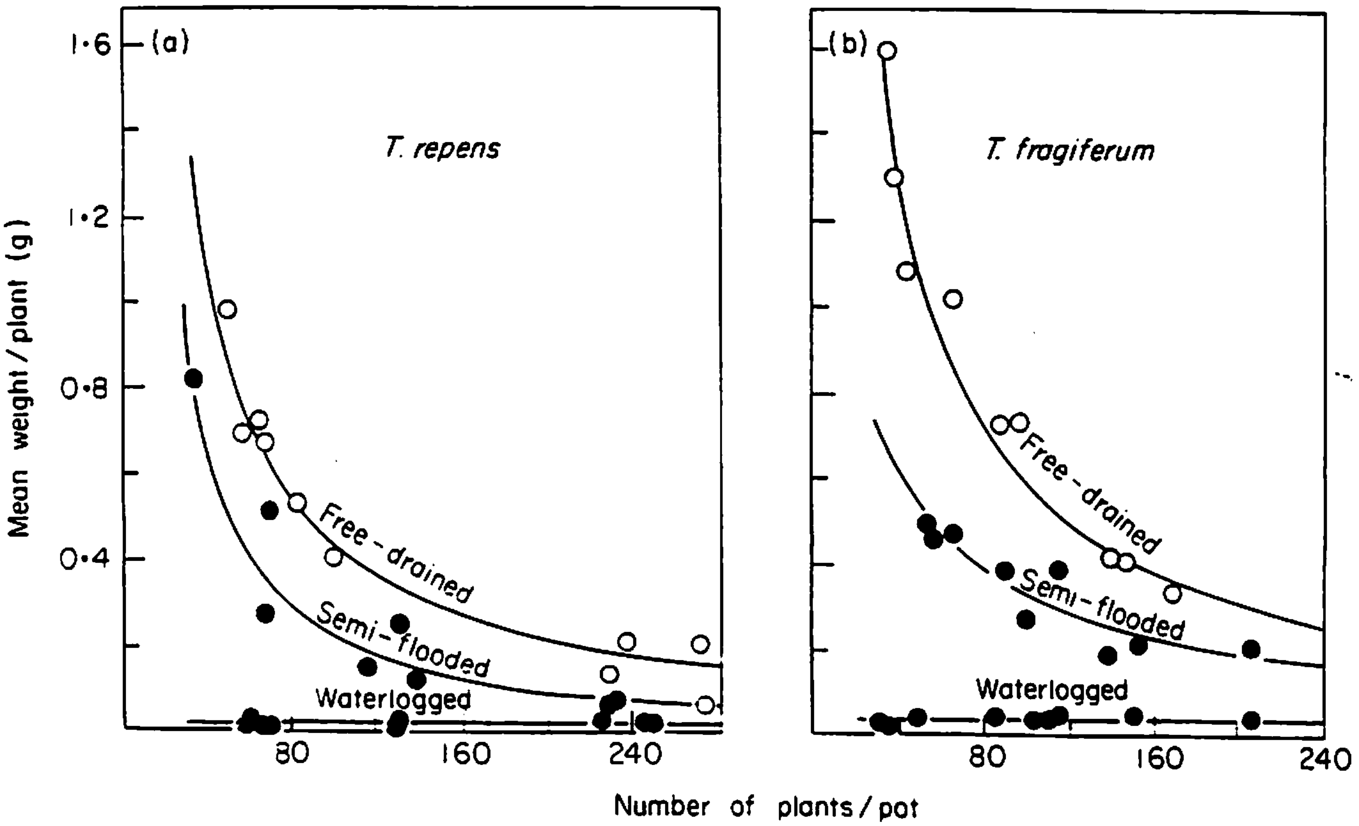
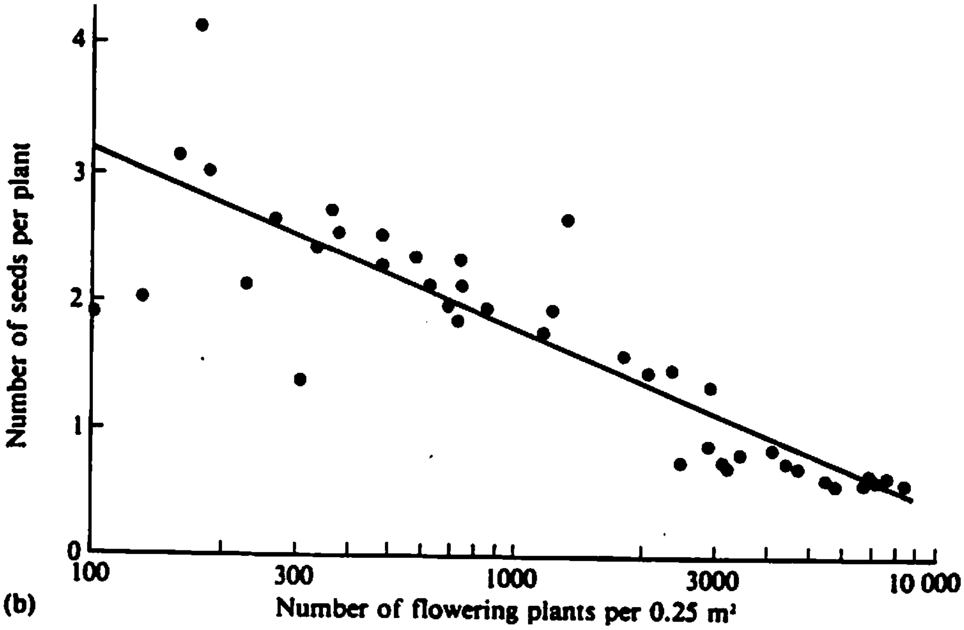
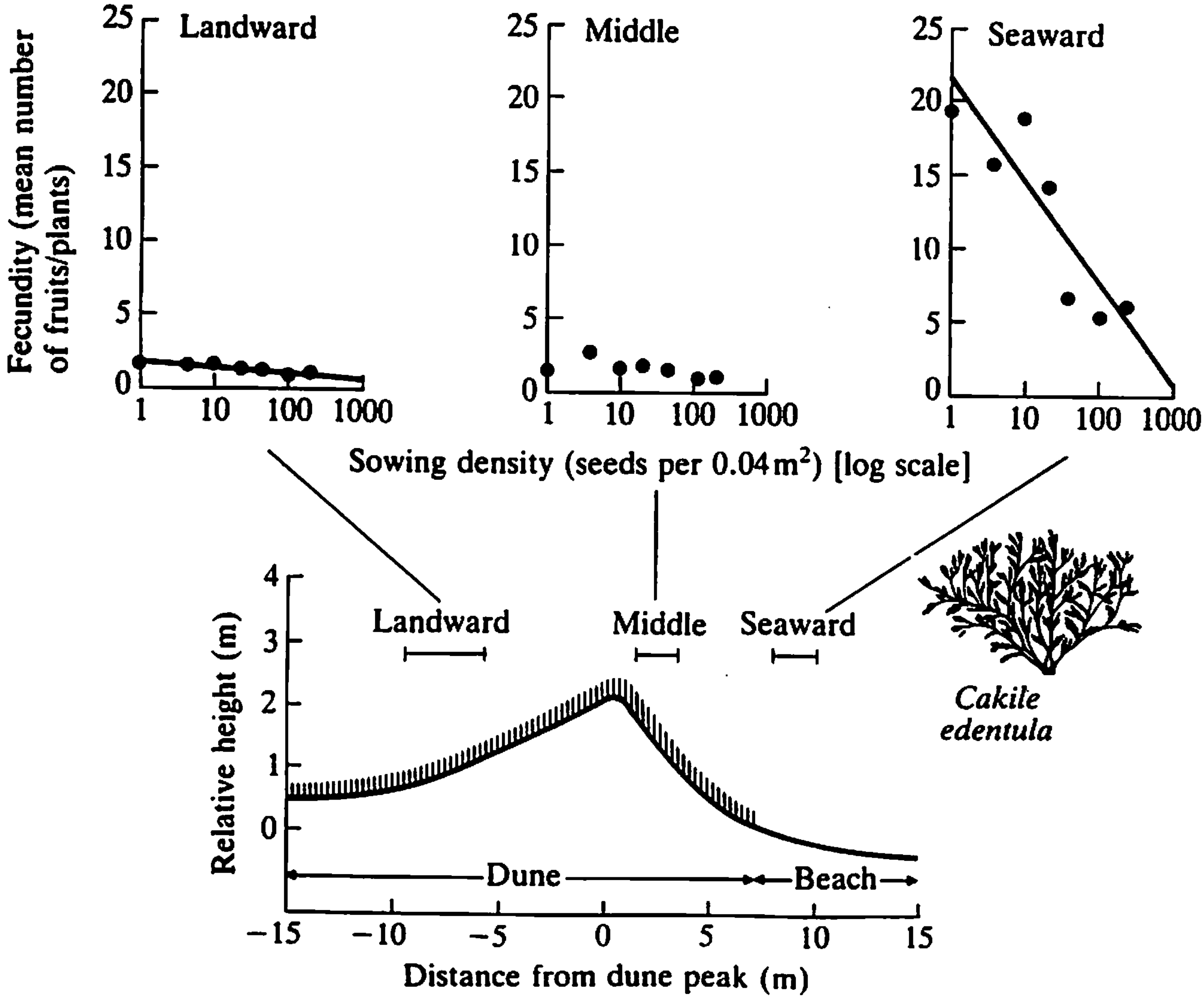


Fig. 6/2. The effect of plant density upon the mean dry weight of plants of (a) *Trifolium repens* and (b) *T. fragiferum* grown in pure stands under three water regimes. (From Clatworthy, 1960)



Number of seeds per plant
4
3
2
1
0
100
300
1000
3000
10 000
(b)
Number of flowering plants per 0.25 m²

$y = mx + b$



Fecundity (mean number of fruits/plants)
25
20
15
10
5
0
Landward
Middle
Seaward
1
10
100
1000
Sowing density (seeds per 0.04 m²) [log scale]
Relative height (m)
4
3
2
1
0
Landward
Middle
Seaward
Dune
Beach
−15
−10
−5
0
5
10
15
Distance from dune peak (m)
Cakile edentula

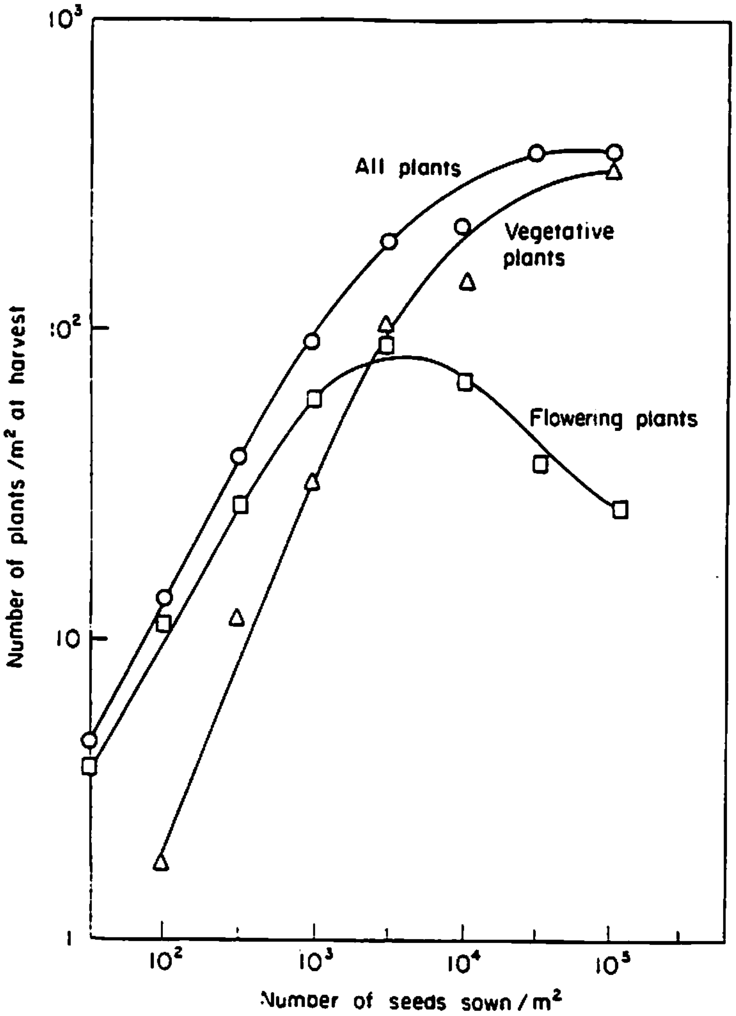


Fig. 7/8a. The influence of sowing density on the behaviour of populations of the foxglove, *Digitalis purpurea.* (From Oxley, in preparation)

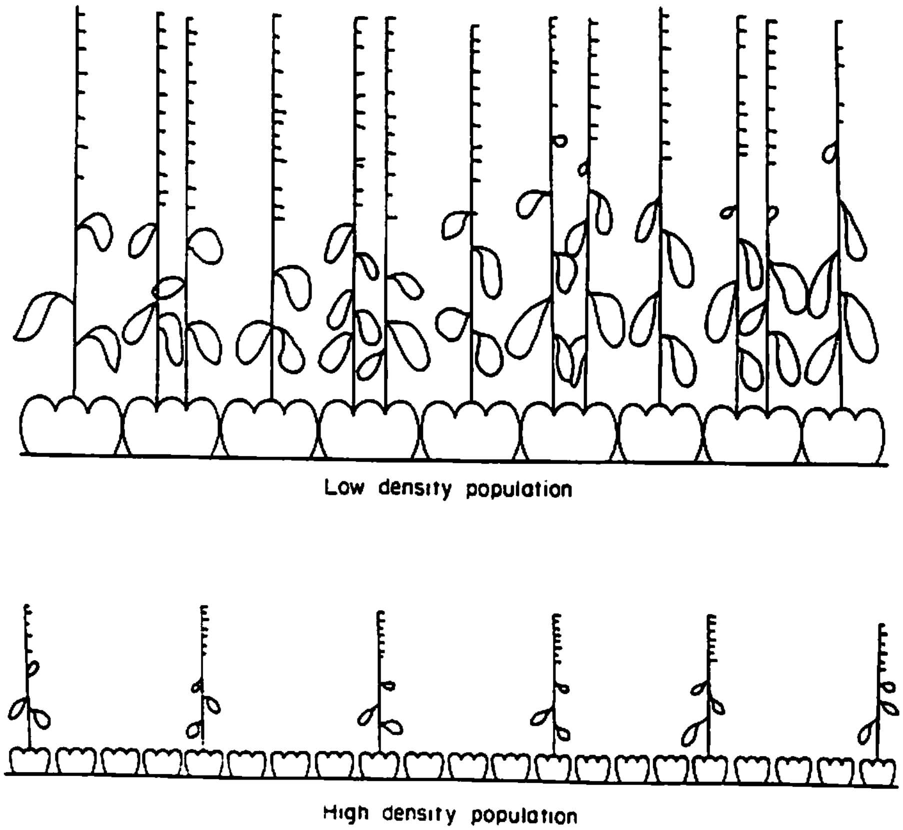


Fig. 7/8d. Diagrammatic illustration of the patterns of growth and flowering in populations of *Digitalis purpurea* at high and low densities. (From Oxley, in preparation)

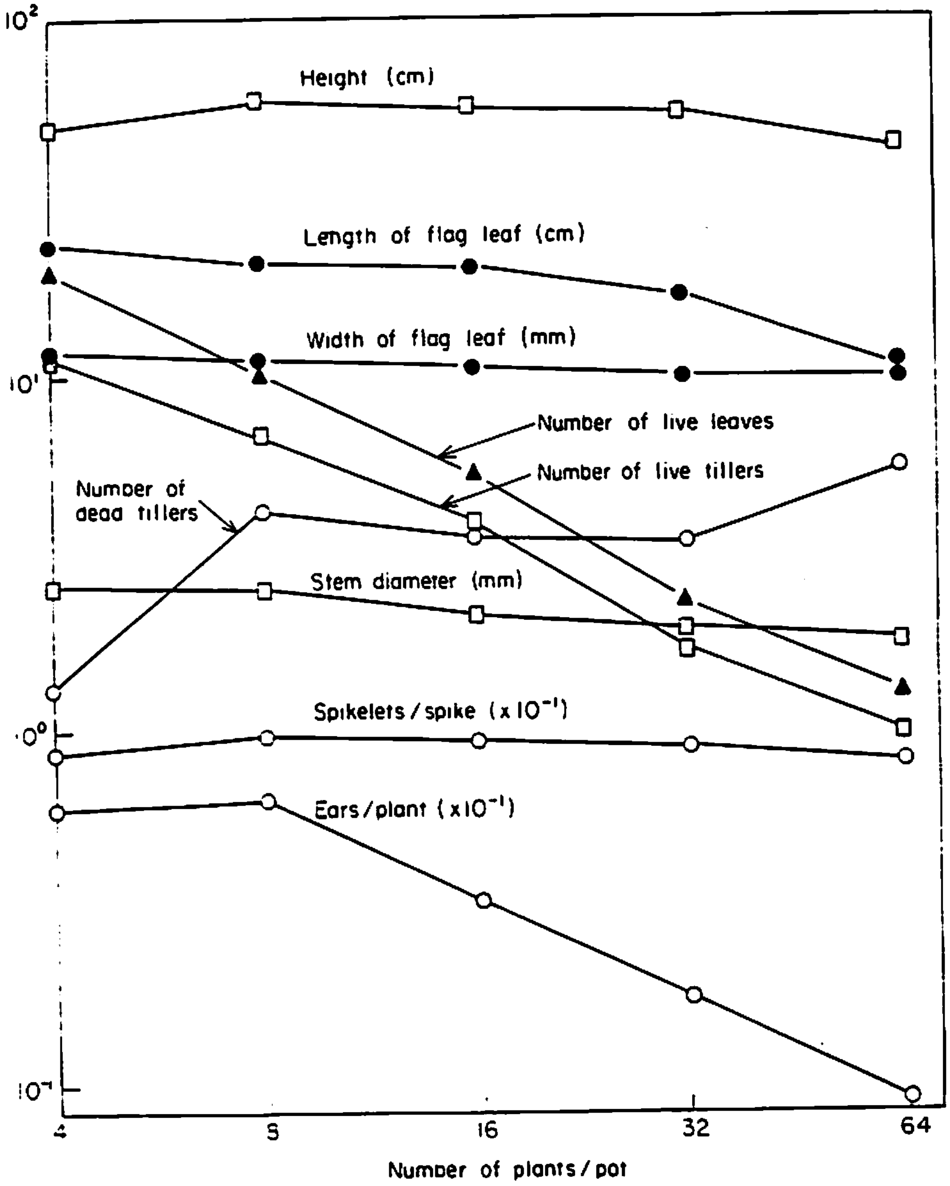


Fig. 7/3. The plasticity of the components of form and seed yield of wheat sown at a range of densities. (Drawn from data of Clements *et al.* 1929)

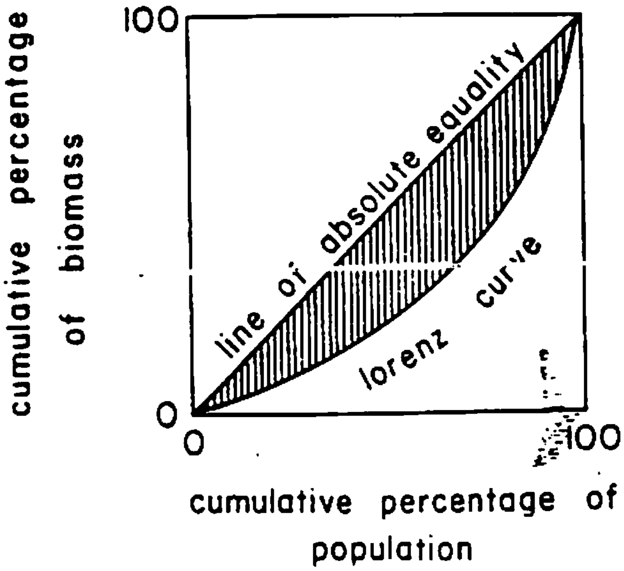


Fig. 3. The Lorenz curve as applied to size inequalities or hierarchies in plant populations. The area between the curve and the line of perfect equality expressed as a proportion of the area under the diagonal is called the Gini Coefficient and is a measure of inequality (after Sen 1973)

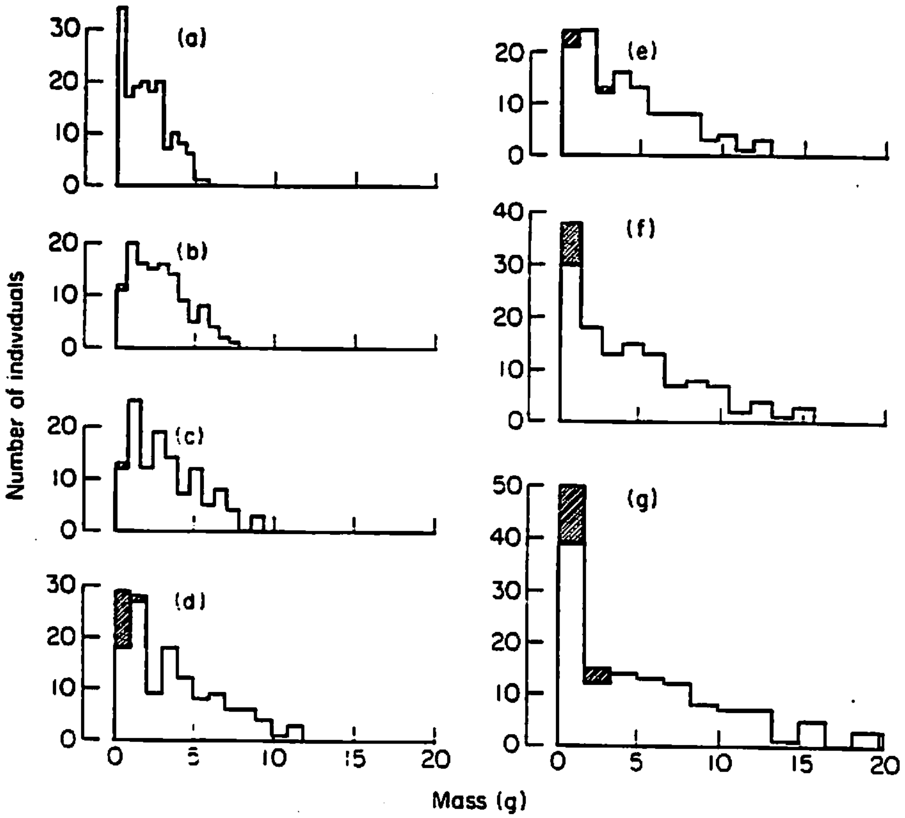


FIG. 4. Changing size distributions for an *Impatiens pallida* population in which individual fate was monitored weekly from (a) 23 July to (g) 11 September 1984. Initial and final distributions are based on direct size measurements. The intervening histograms are based on the assumption that individuals have linear growth (Fig. 2), and that individuals that subsequently died did not change in size (see text). Shaded columns represents individuals that died during a given time interval.

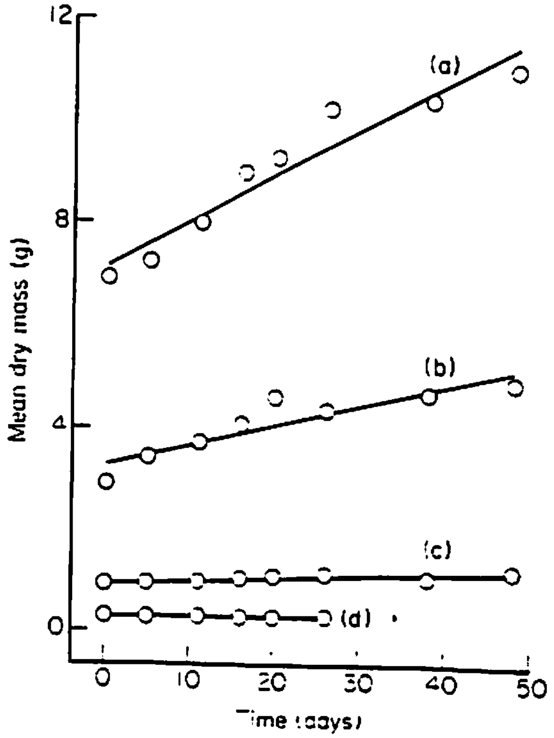


FIG. 2. Growth curves for groups of five out of twenty *Impatiens pallida* individuals repeatedly measured in 1985. (a) Mean for five largest individuals: (b) next five largest: (c) next five largest: (d) five smallest.

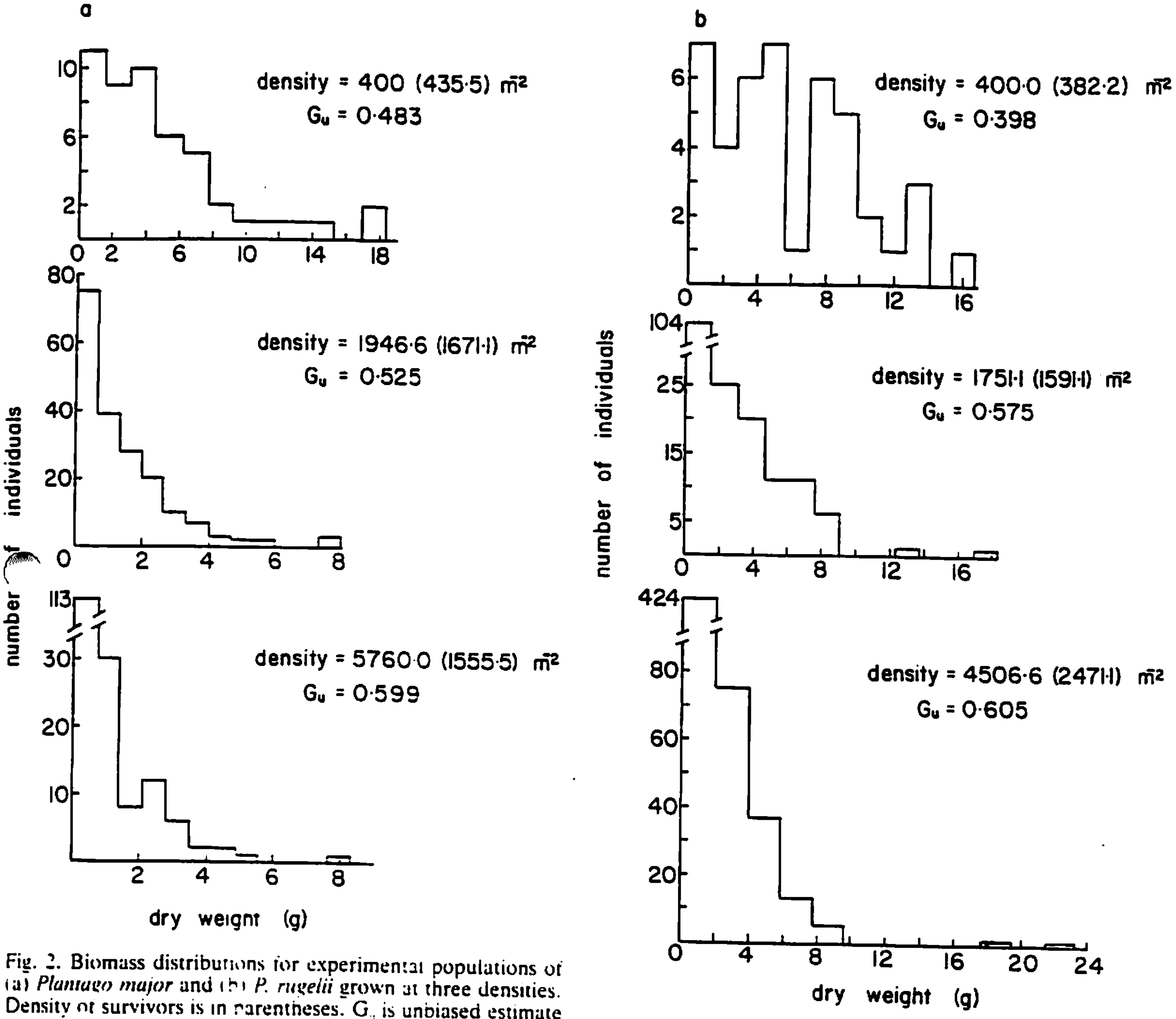


Fig. 2. Biomass distributions for experimental populations of (a) *Plantago major* and (b) *P. rugelii* grown at three densities. Density of survivors is in parentheses. G$_u$ is unbiased estimate of the Gini Coefficient (after Hawthorn and Cavers 1982).

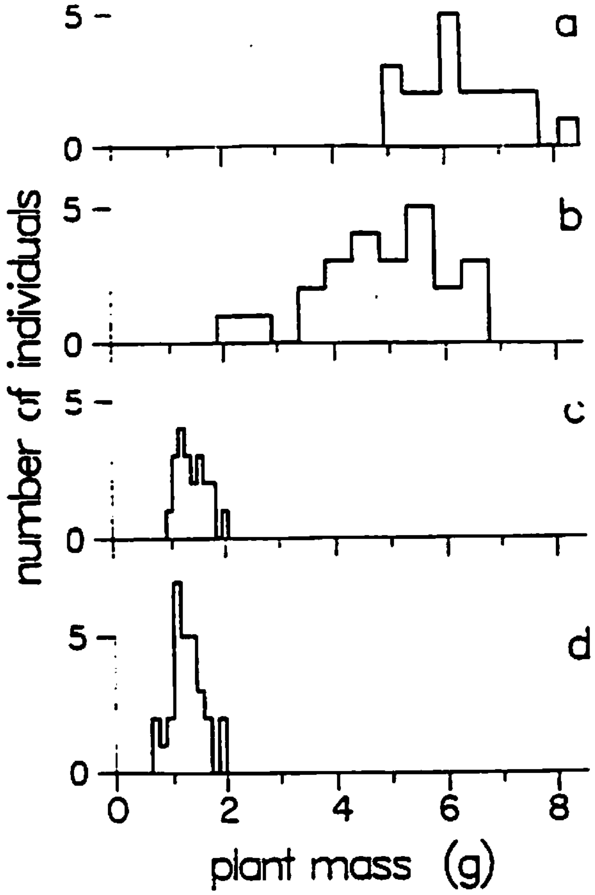


FIG. 1. Dry mass distributions for experimental populations of *Ipomoea tricolor* grown (a) without competition. (b) with shoots competing, (c) with roots competing. (d) with both shoots and roots competing. Each population is divided into 10 equal size classes. from the minimum to the maximum value.

	Treatment			
	Individually grown	Shoot competition	Root competition	Shoot - root competition
No. plants	21	24	21	29
Dry mass of aboveground plant tissue (g)				
Mean	6.34	4.84	1.42	1.26
Median	6.28	5.05	1.37	1.26
	*			
CV (%)	14.0	24.5	19.4	25.1
	**			
	*			
G	0.081	0.139	0.112	0.143
	**			

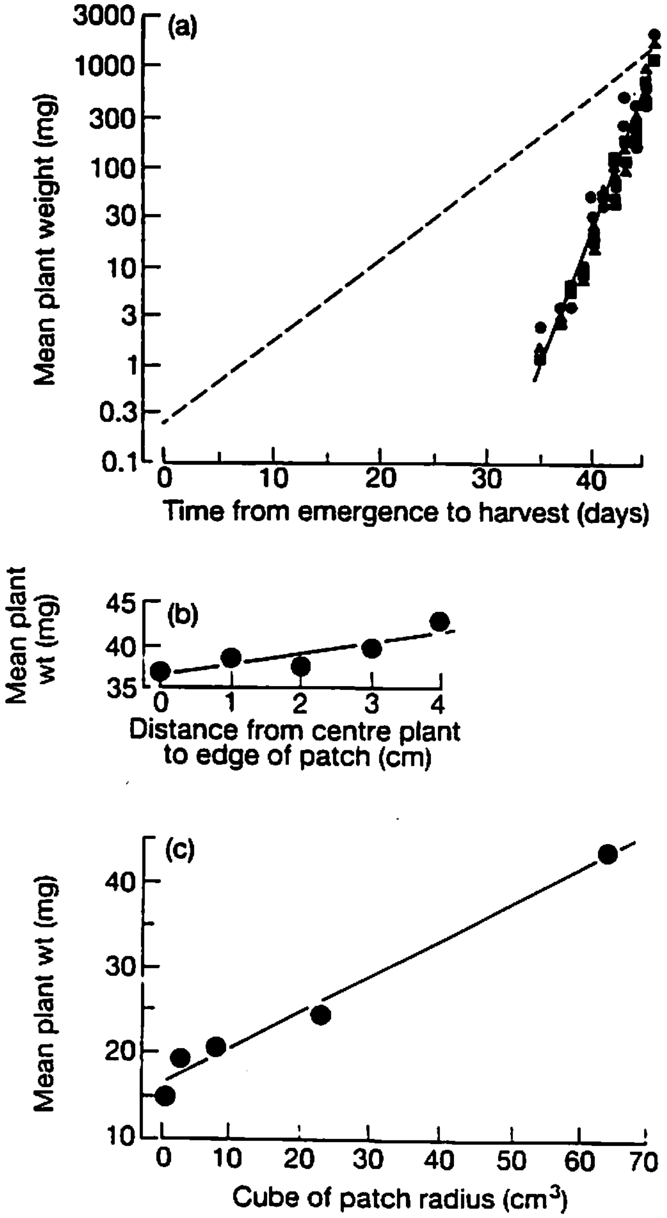


Fig. 4.2. Gap size and seedling establishment. (*a*) Mean weight of groups of plants emerging at different times in 3 populations. The dotted line indicates the weights of plants growing for different lengths of time in the *absence* of competition. (*b*) Response of individual plant weight to varying the distance of the centre plant from the perimeter of patches of a given size, showing the rather slight effect of distance. (*c*) Response of individual plant weight to varying sizes of patches. showing a much more pronounced effect. From Ross & Harper (1972).

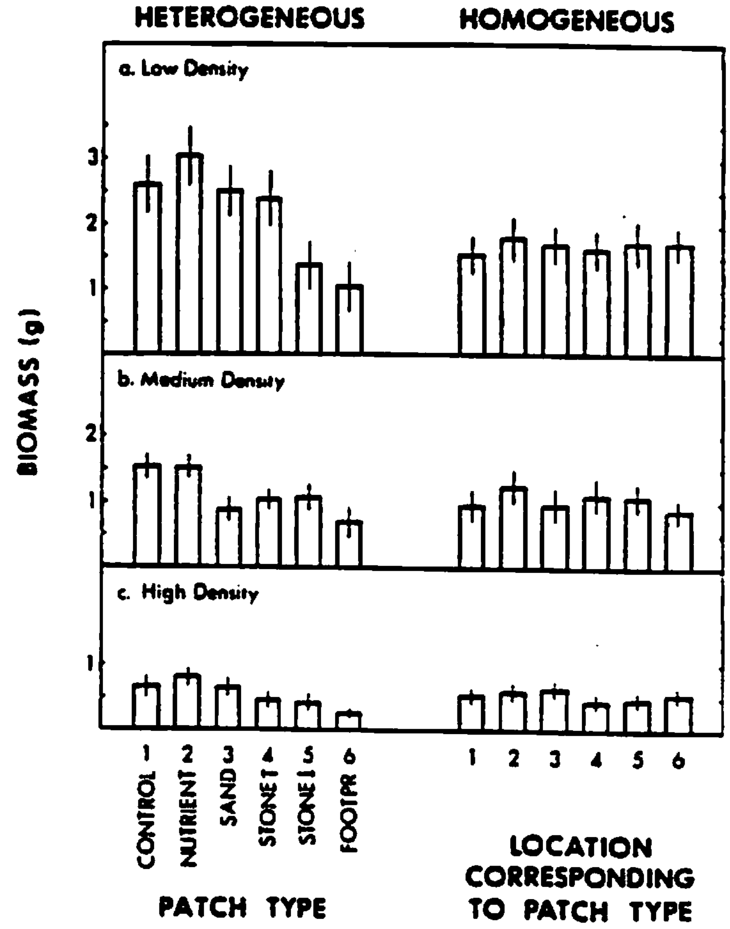
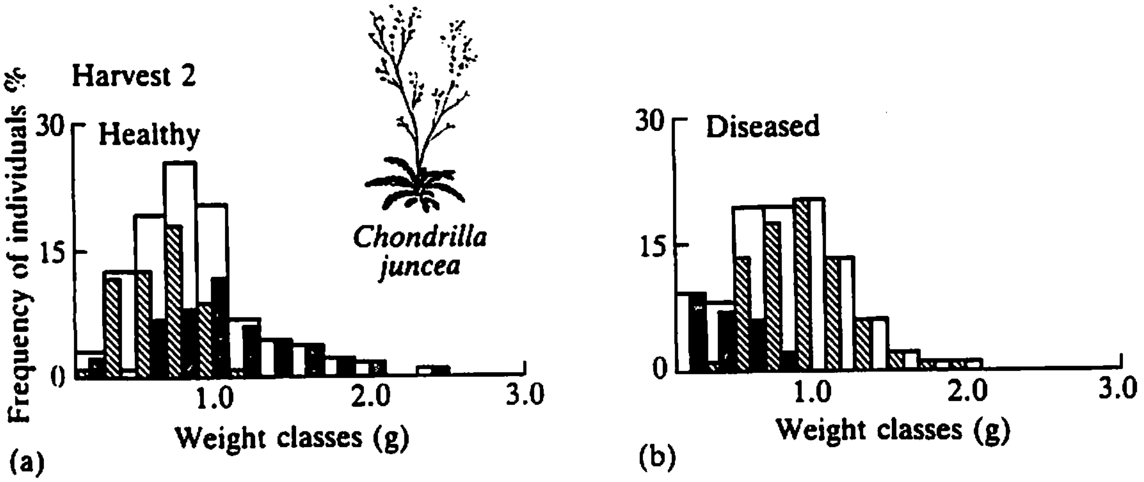


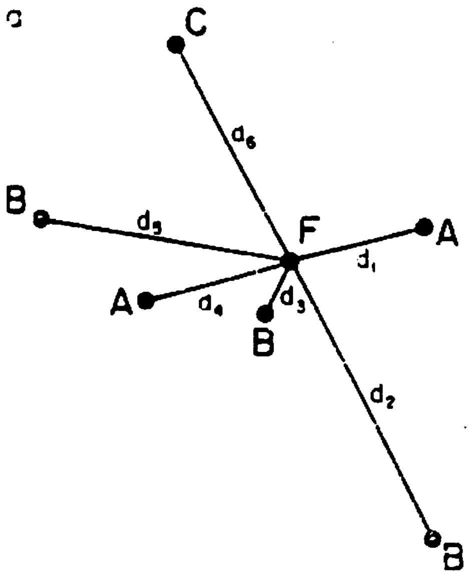
FIG. 1. Mean aboveground biomass (±2 SE) of plants grown on each patch type on heterogeneous substrate or, at corresponding locations in the container, on homogeneous substrate in 1977. The effects of density and of the patch type × heterogeneity interaction were significant at $P < .001$ and $< .025$, respectively, with three-way ANOVA. (a) Low density, 130 plants/m². (b) Medium density, 410 plants/m². (c) High density, 770 plants/m². $N = 20$ for each bar. STONE ↑ indicates a ceramic tile placed above the seed; STONE ↓ indicates a tile below.

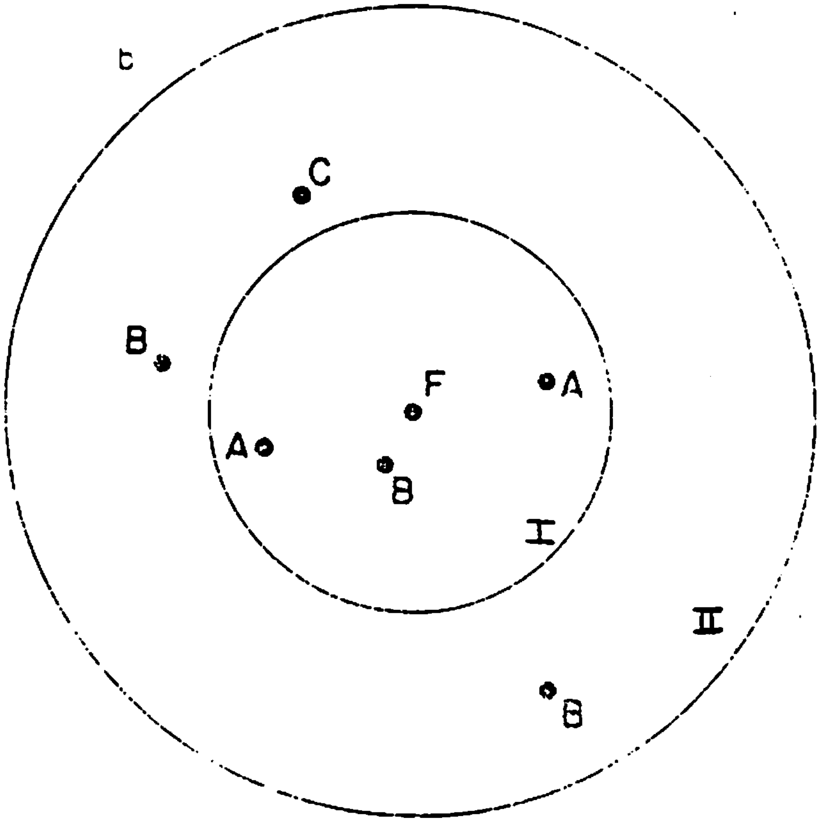
Fig. 4.15 The frequency distribution of plant size in dense mixtures of two genotypes of *Chondrilla juncea* that were (a) disease-free; and (b) infected with a rust. Hatched columns are plants with a resistant genotype, stippled columns are susceptible plants and open columns are the sum of the two. (From Burdon *et al.* 1984)



Neighborhood Analysis

* Wiener (1985)





$$W = C_j\left(\frac{N_1}{d_1^2} + \frac{N_2}{d_2^2} + \cdots \frac{N_n}{d_n^2}\right)$$

where:

W = "competition measure

d = distance to neighborhoo

C_j = competition coefficient for sp j

N_n = # individ in neighborhood$_n$

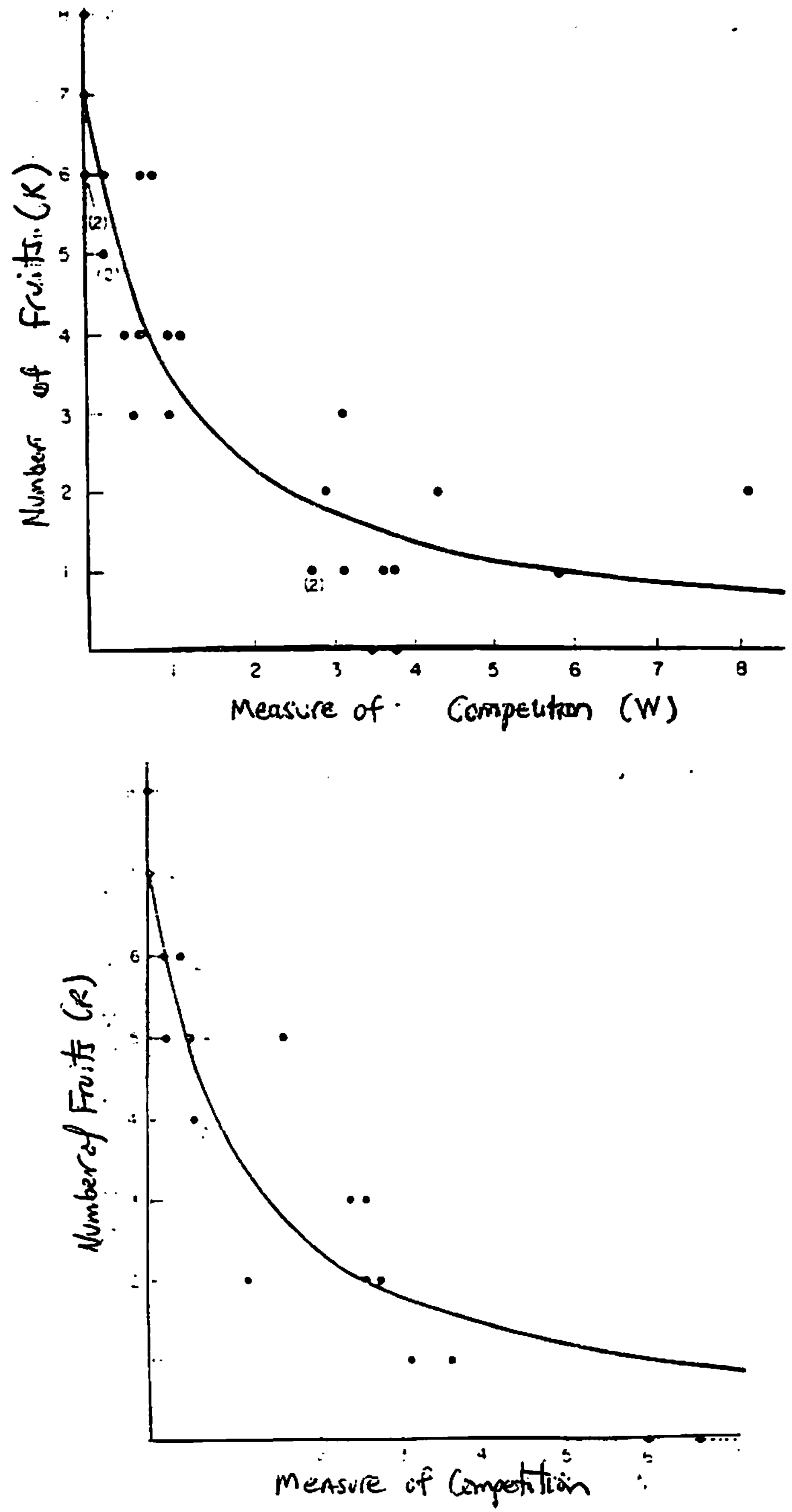


FIG. 2. Seed production (*K*) as a function of the measure of competition (*W*) for individuals of (*a*) *Polygonum minimum* and (*b*) *P. cascadense*. Each point represents an indi-

Thiessen Polygons

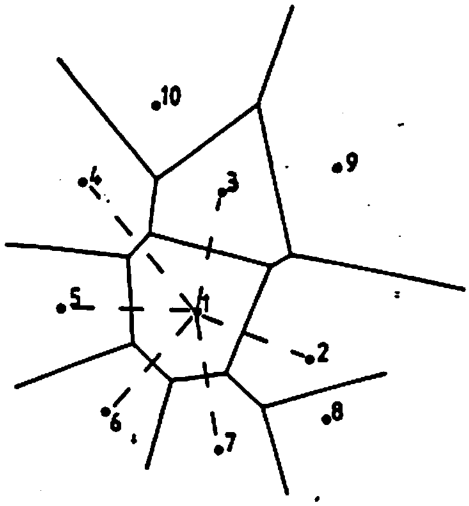


Fig. 1. The construction of Thiessen polygons. The perpendicular bisectors of the lines joining adjacent seedlings (dashed) form the polygon and define which plants are neighbours. Thus, plants 8–10 are not neighbours

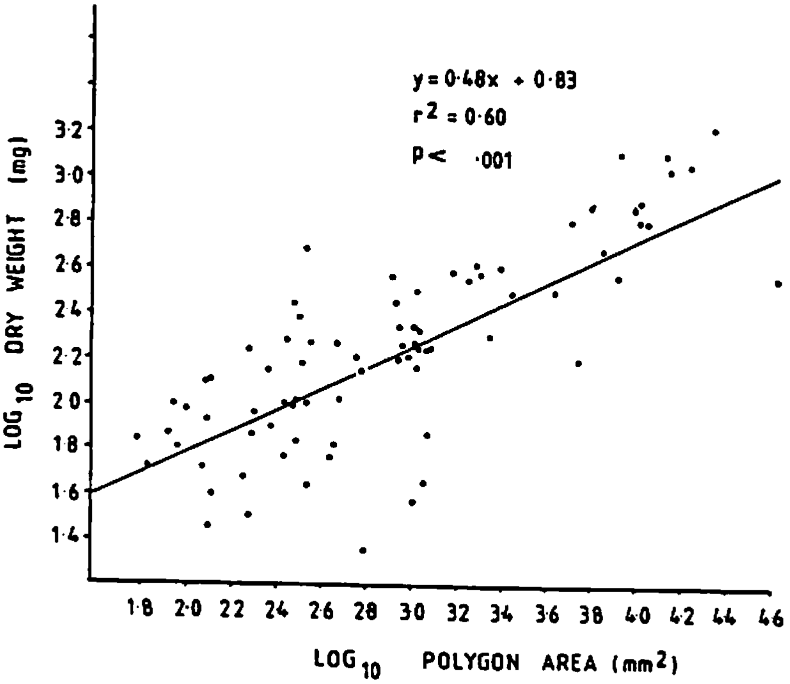
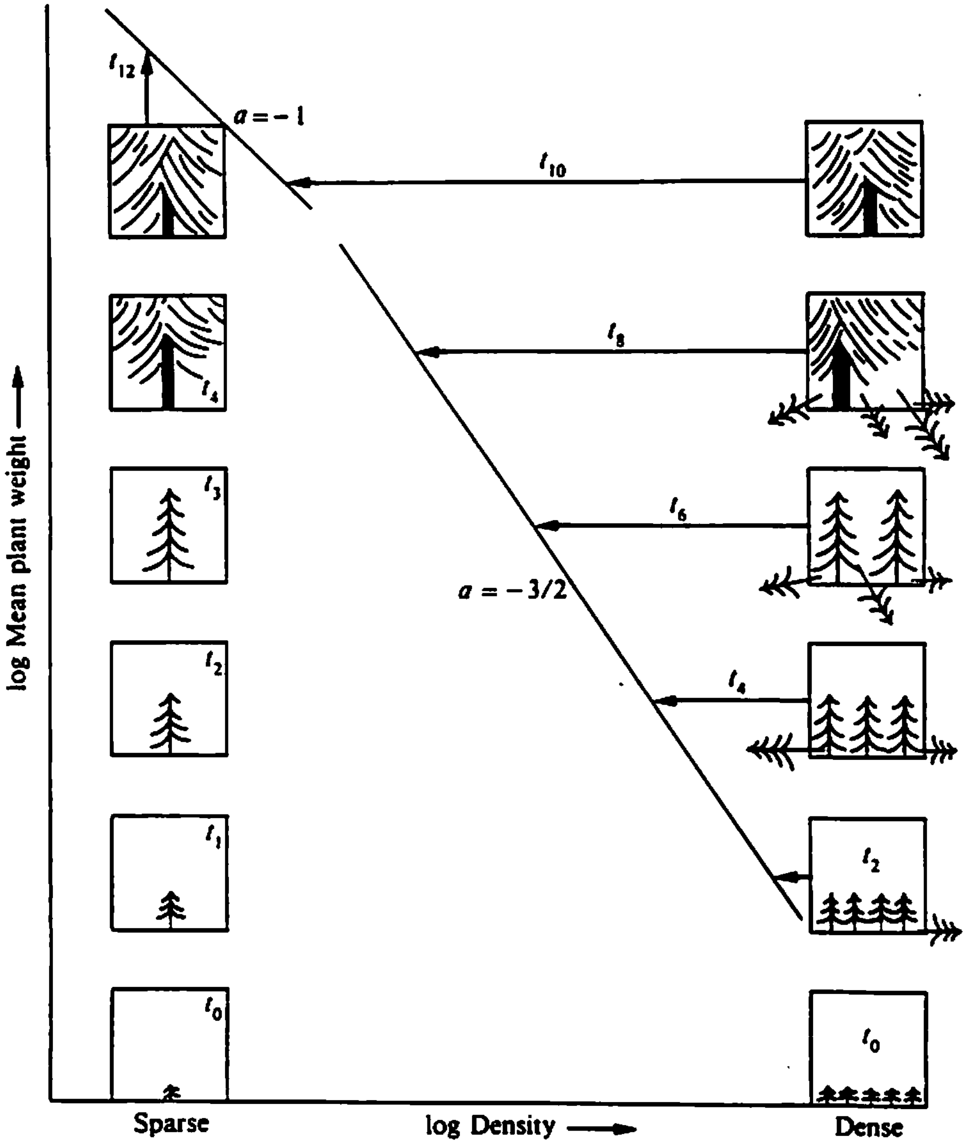


Fig. 5. Relationship between the dry weight of individual plants of *Lapsana cummunis* and the polygon area the plants occupied (harvest 1)

Self Thinning

Fig. 4.8 The progress of a sparse and a dense tree population through time, illustrating the main features of the −3/2 thinning process.



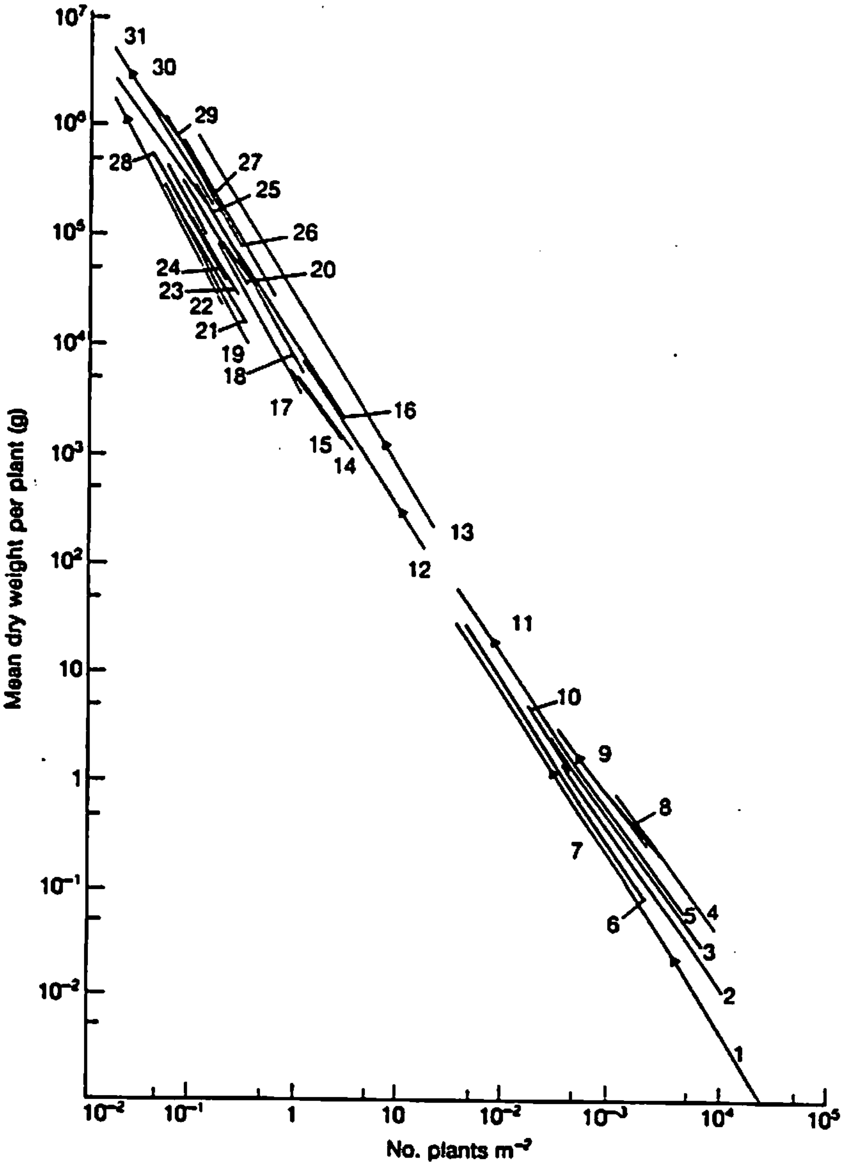


Figure 6.35. Self-thinning in a wide variety of herbs and trees. Each line is a different species, and the line itself indicates the range over which observations were made. The arrows, drawn on representative lines only, indicate the direction of self-thinning over time. The figure is based on Figure 2.9 of White (1980), which also gives the original sources and the species names for the 31 data sets. Note that all lines have a slope approximating to −3/2, and that their intercepts also fall within a relatively narrow band.

Fig. 4.10a Self-thinning in four populations of *Lolium perenne* planted at four different densities. H1–H5 are replicates harvested at five successive intervals. (From Kays and Harper 1974)

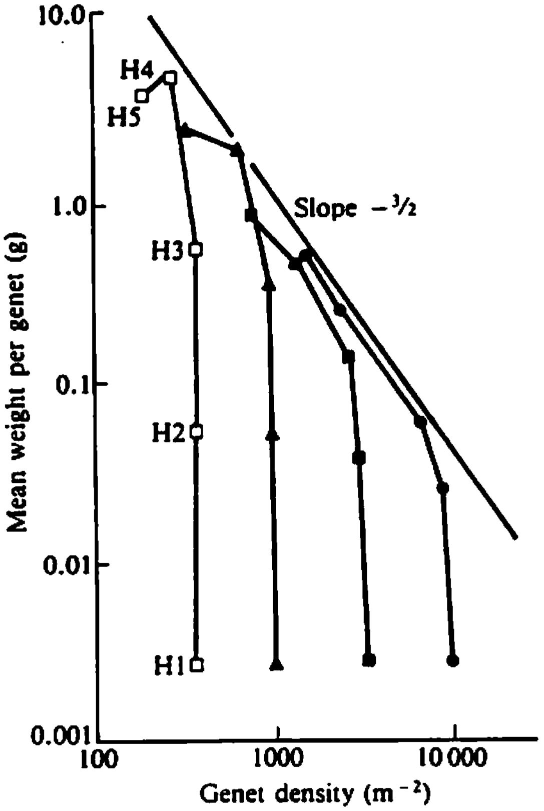
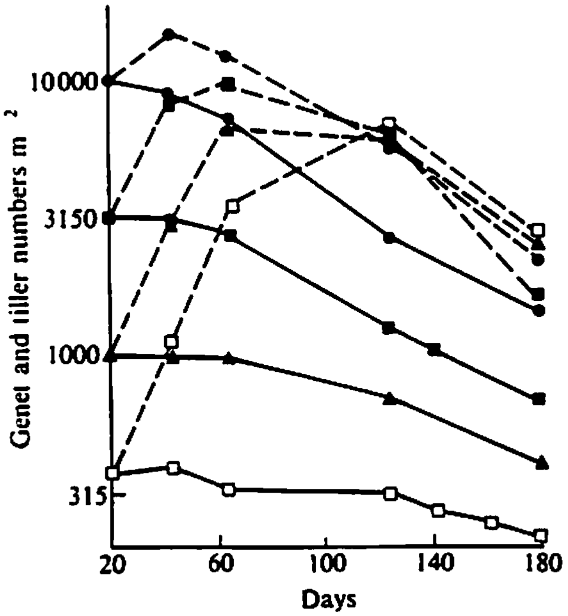


Fig. 4.10b Changes in the density of genets (continuous line) and tillers (dotted line) with time in populations of *Lolium perenne* sown at four starting densities. (From Kays and Harper 1974)



11/30

FAB'S
lecture
~~[illegible]~~

Dave Ackerly

Effect of Variable Environment

1) variable is not "extreme"
" " " " unpredictable

4 Dimensions x, y, z, time
- temporal & spacial heterogeneity
environment are interrelated but not dependent

scale time & space
.. lots at fine scale (forest) none at large scale
.. lots at ~~fin~~ coarse scale .. " " ..
time works this way.

space & time are mostly distinct

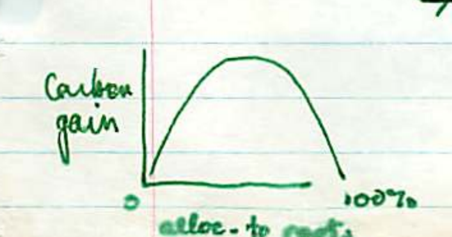
~~daily~~ T° variation
peaks at 1 yr, 1 day, 6 months

2) Plants
- phenotypic plasticity - As, germination ...
-

Characters

Performance - any measures of growth - assume growth is good
- but what about cancer

Optimum



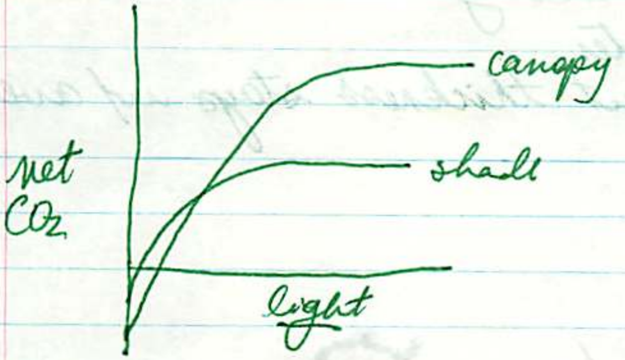
So what is the use of these "characters"
① to see if plasticity is useful

③ Scale of environmental variation
① must be relative to plant
algae vs. tree

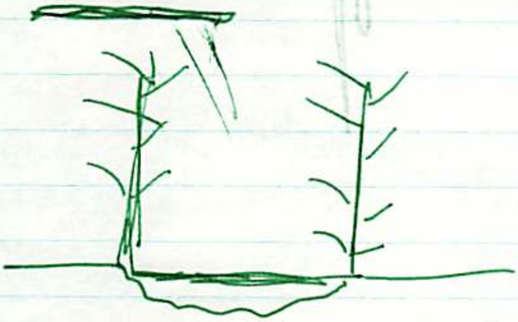
but variation w/in plant even if external is constant.
eg light, T°, ...

so can the idea of sun/shade chloroplasts w/in on leaf be used to describe all plasticity of chloroplast ... so if put plant in shade all leaves act as though they ~~are a~~ have leaf above them.

《idea = tape leaves to each other and see what happens》



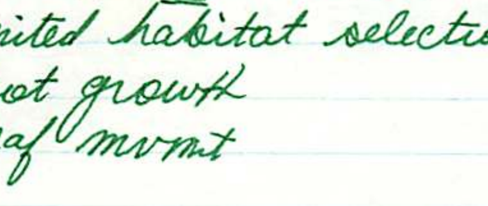
Clonal plants
:same genotype w/ variable phenotypes
·w/ connections ramets can help each other



when connected
see handout

plants are not sessile
-limited habitat selection
-root growth
·leaf mvmt

experiment



Plants can respond to average
① Depends on character
Ls v. plastic but thickness stays w/ average

Longer time scale

Idea & experiment
-CA, ED rhythms

Bio 149 - November 30, 1989
David Ackerly

Environmental Heterogeneity and Plant Plasticity

Reading:

Hartnett and Bazzaz, 1983 - "Physiological integration among intraclonal ramets in _Solidago canadensis_"

Mooney and Chiariello, 1984 - "The study of plant function: The plant as a balanced system"

Lecture Outline:

1. Environmental Heterogeneity
    - Variable vs. Extreme environments
    - Temporal vs. Spatial
    - Variability vs. Predictability
2. Phenotypic Plasticity (Bradshaw, 1965)
    - Plasticity is the response of the phenotype to different environments
    - Performance and Optimum characters
3. The scale, or "grain", of environmental heterogeneity relative to the plant (Levins, 1968)
    - Coarse scale: Different plants, or plant parts, experience different conditions
    - Fine scale: Each plant, or part, experiences the full range of conditions
4. Some case studies, each with a lesson (•)
    - Spatial Heterogeneity
        - A) Gradients of light levels within a leaf (Terashima and Inoue, 1985)
            - • Heterogeneity is generated by the plant
            - • The same pattern can be coarse and fine scale for different parts of the plant
        - B) Leaves in different canopy positions of a tree
            - • 'Tracking' coarse scale heterogeneity - different traits in different environments
        - C) Ramets of a clone living in different microhabitats (Hartnett and Bazzaz, 1983)
            - • 'Integrating' fine scale heterogeneity - the plant averages the environment
        - D) Foraging for nutrients in patchy soils (Evans, 1989?)
            - • Plasticity of growth is analogous to foraging behavior of animals
            - • Habitat selection in plants

Temporal Heterogeneity

- E) Seedling growth in forest gaps (Chabot et al., 1979; P. Wayne)
  - Traits which respond slowly to changes in the environment will effectively respond to the average conditions over long time periods - fine scale heterogeneity is integrated
- F) Annual seasonality
  - Ecology of leaf life spans (Chabot and Hicks, 1982)
  - Temperature optimum of photosynthesis (Regehr and Bazzaz, 1976)
    - Slow, coarse scale changes are tracked by plant
    - Example of acclimation, an 'adaptive' response to environmental conditions
- G) Photosynthesis in sun-flecks (Gross, 1982; Pearcy, 1988)
  - Growth in fluctuating light environments of varying periods (Garner and Allard, 1931)
    - Dynamics of response can be important

5. The Plant as a Balanced System (Mooney and Chiariello, 1984)

Costs and Benefits of investment of available resources

Response of growth to increasing resources is always non-linear

- A) Water cost of carbon gain (Cowan and Farquhar, 1977)
- B) Nitrogen cost of photosynthesis (Field, 1983)
- C) Multiple resource limitation (Bloom et al., 1985)

*** Common result of economic models ***

Photosynthesis or growth is maximized when the additional cost required to gain each additional unit of growth is the same at all times (A), or in all leaves (B), or for all resources (C).

Bio 149 - November 30, 1989 - References for work cited in lecture

Bloom A J, Chapin F S, Mooney H A (1985) Resource limitation in plants - an economic analogy. Ann. Rev. Ecol. Syst. 16: 363-92

Bradshaw A D (1965) Evolutionary significance of phenotypic plasticity in plants. Adv. Gen. 13: 115-155

Chabot B F, Hicks D J (1982) The ecology of leaf life spans. Ann. Rev. Ecol. Syst. 13: 229-259

Cowan I, Farquhar G (1977) Stomatal function in relation to leaf metabolism and environment. Symp. Soc. Exp. Biol. 31:471-505

Field C (1983) Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program. Oecologia 56: 341-347

Garner W W, Allard H A (1931) Effect of abnormally long and short alternations of light and darkness on growth and development of plants. J. Agric. Res. 42: 629-651

Gross L J (1982) Photosynthetic dynamics in varying light environments: A model and its application to whole leaf carbon gain. Ecology 63: 84-93

Hartnett D, Bazzaz F (1983) Physiological integration among intraclonal ramets in Solidago canadensis. Ecology 64: 779-788

Chabot B F, Jurik T W, Chabot J F (1979) Influence of instantaneous and integrated light-flux density on leaf anatomy and photosynthesis. Amer. J. Bot. 66: 940-945

Levins R (1968) Evolution in changing environments. Princeton Univ. Press, Princeton, N.J

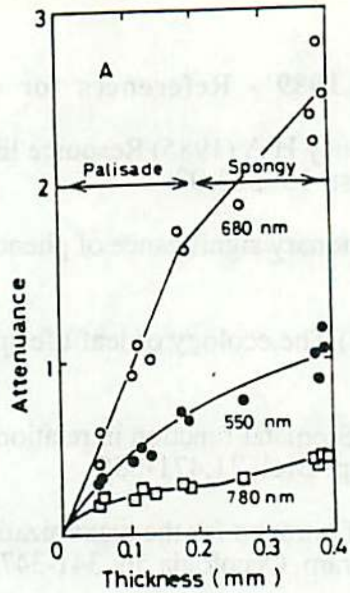
Mooney H, Chiariello N (1984) The study of plant function: The plant as a balanced system. Pp. 305-323 in R Dirzo, J Sarukhan, eds., Perspectives on plant population biology, Sinauer Assoc., Sunderland, Mass

Pearcy R (1988) Photosynthetic utilisation of lightflecks by understory plants. Aust. J. Plant Physiol. 15: 223-38

Regehr D L, Bazzaz F A (1976) Low temperature photosynthesis in successional winter annuals. Ecology 57: 1297-1303

Terashima I, Inoue Y (1985) Vertical gradient in photosynthetic properties of spinach chloroplasts dependent on the intra-leaf light environment. Plant Cell Physiol. 26: 781-785

Took diff. cuts
of leaves (diff thickness)



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Terashima and Inoue 1985

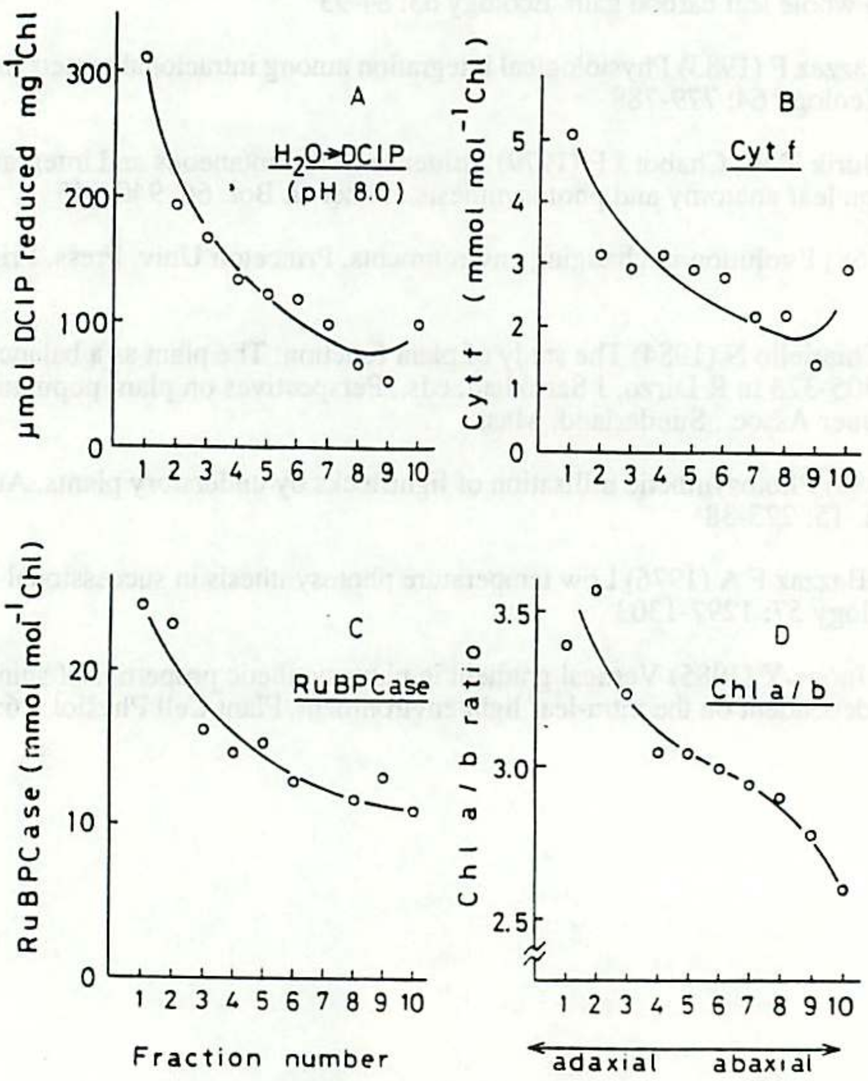


Fig. 1 Light-saturated rate of electron transport ($H_2O \rightarrow DCIP$, at pH 8.0) (A), content of Cyt *f* (B), content of RuBPCase (C) and Chl *a/b* ratio (D), in 10 planed mesophyll fractions of a spinach leaf. Fractions are numbered from the adaxial side.

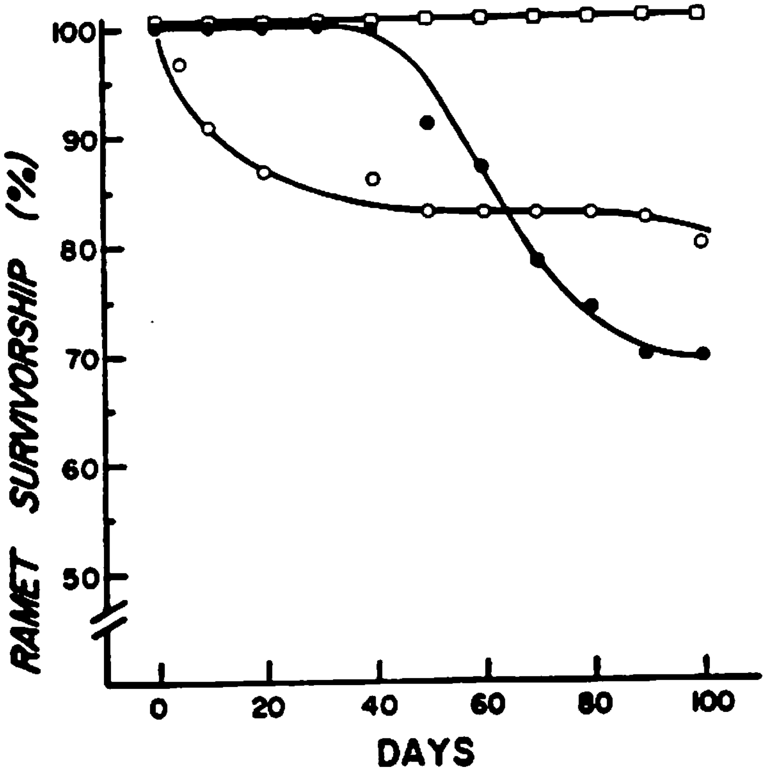


FIG. 6. Percent survivorship of *Solidago canadensis* ramets. □———□ - controls. (illuminated ramets with or without connections to illuminated siblings). ●———● = shaded ramets connected to illuminated siblings. ○———○ = shaded ramets severed from their illuminated siblings.

Hartnett and Bazzaz, 1983

Fig. 1.3 A map of the shoot system of *Ipomoea phillomega* on the floor of a tropical rainforest in Veracruz, Mexico. This plant originated at the 'manifold' which has an ascending shoot and a crown in the canopy. Liana crowns and ascending shoots are represented by circles. Stolons that have lost their tips end in a 'T' and those which are still growing are shown with a 'Y'. (Peñalosa 1983)

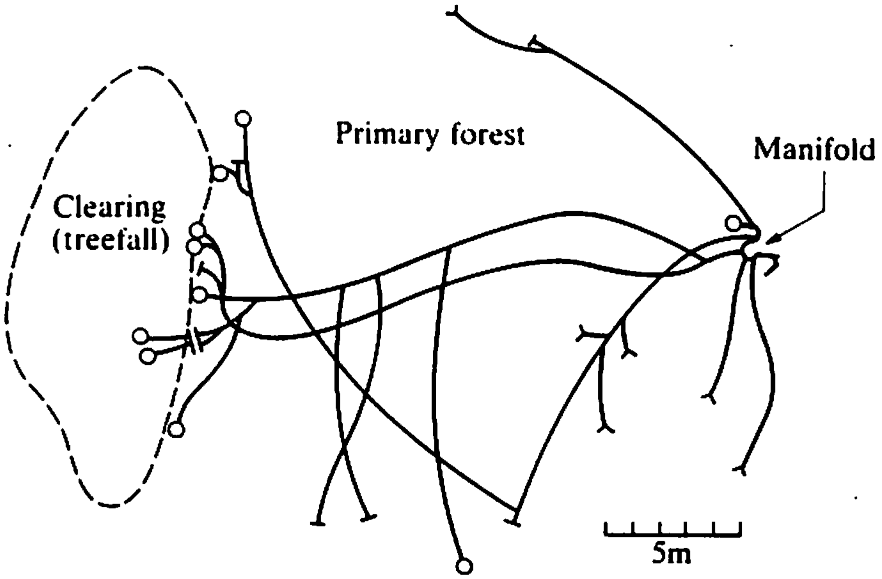


TABLE 1. *Apparent photosynthesis and leaf anatomy under conditions of constant daily PPFD but variable peak PPFD. Values in the same row followed by different letters are significantly different. Letters are not used in rows where there were no significant differences*

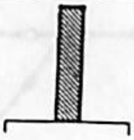
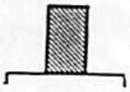
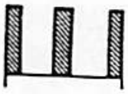
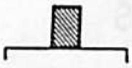
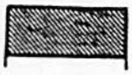
CHAMBER LIGHT REGIME					
LIGHT PATTERN					
PEAK PPFD ($\mu E \cdot m^{-2} \cdot sec^{-1}$)	560 ± 24	334 ± 13	154 ± 16	105 ± 9	186 ± 11
INTEGRATED 24-HR PPFD ($E \cdot m^{-2} \cdot day^{-1}$)	5.45	4.73	4.40	5.67	4.90

TABLE 2. *Apparent photosynthesis and leaf anatomy under conditions of constant peak PPFD, but variable total PPFD. Values in the same row followed by the same letter are not significantly different*

CHAMBER LIGHT REGIME					
LIGHT PATTERN					
PEAK PPFD ($\mu E \cdot m^{-2} \cdot sec^{-1}$)	305 ± 12	305 ± 10	302 ± 13	363 ± 10	371 ± 29
INTEGRATED 24-HR PPFD ($E \cdot m^{-2} \cdot day^{-1}$)	6.45	9.88	16.31	10.09	19.98

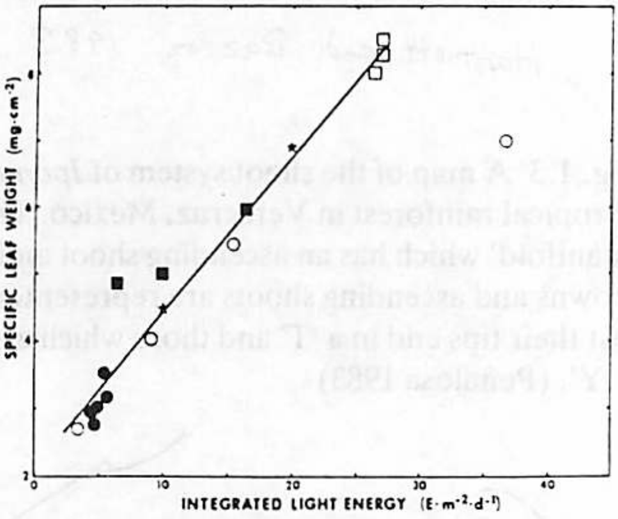


Fig. 7. Relationship between specific leaf weight and integrated light energy. Each point is the average for a different experiment where plants were grown under controlled growth chamber conditions. The regression line was fitted by least squares procedure excluding the point at 36 $E \cdot m^{-2} \cdot day^{-1}$ (see text). Growth conditions were approximately 25 C day/15 C night with a 15-hr background photoperiod using fluorescent/incandescent lamps (except where noted) for all experiments. Light conditions were: ●, this report, constant total quanta, variable PPFD; ■, this report, peak PPFD = ca. 305 $\mu E \cdot m^{-2} \cdot sec^{-1}$, variable total quanta; ★, this report, peak PPFD = ca. 370 $\mu E \cdot m^{-2} \cdot sec^{-1}$, variable total quanta; ○,

Regehr and Bazzaz 1976

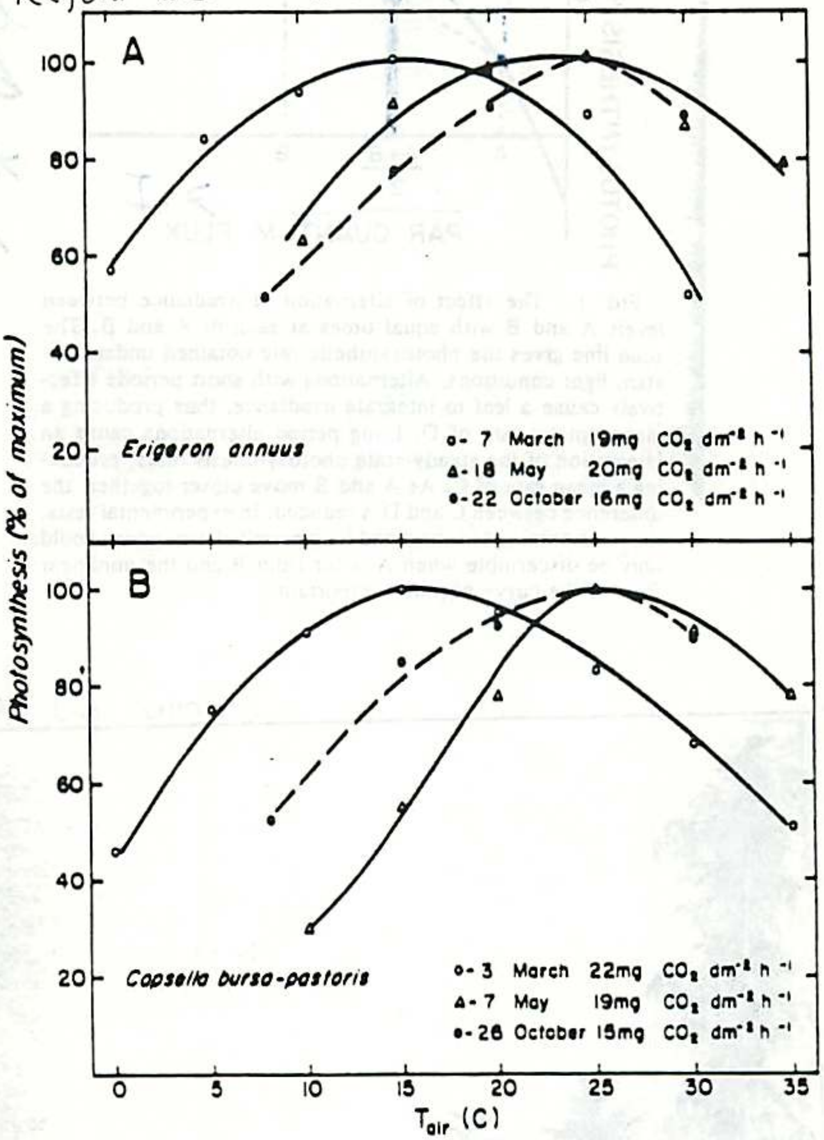
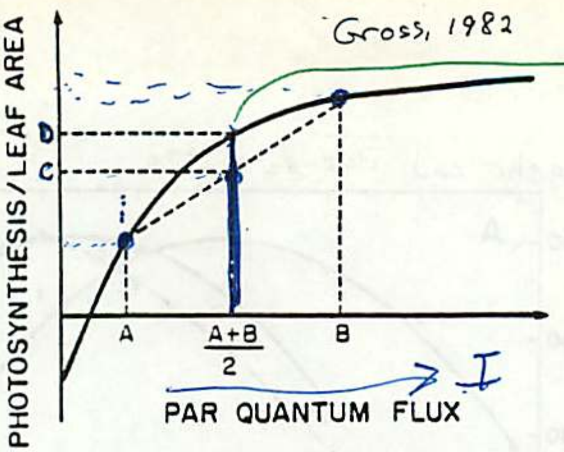


FIG. 4. Temperature response of P_N in *Erigeron annuus* and *Capsella bursa-pastoris* at different seasons. Solid curves are for the same individuals measured as winter rosettes and as bolted plants in spring. Dashed curve is for fall germinated rosettes before frost.

annual plants that keep leaves

Gross, 1982



of plants only see average light then may be higher Ps than if average Ps at each level.

FIG. 1. The effect of alternation of irradiance between levels A and B with equal times at each of A and B. The solid line gives the photosynthetic rate obtained under constant light conditions. Alternations with short periods effectively cause a leaf to integrate irradiance, thus producing a mean uptake rate of D. Long period alternations cause an integration of the steady-state photosynthesis rates, producing a mean rate of C. As A and B move closer together, the difference between C and D is reduced. In experimental tests, the rates obtained in short and long period alternations should only be discernible when A is far from B and the nonlinear form of the curve becomes important.

Garner and Allard 1931

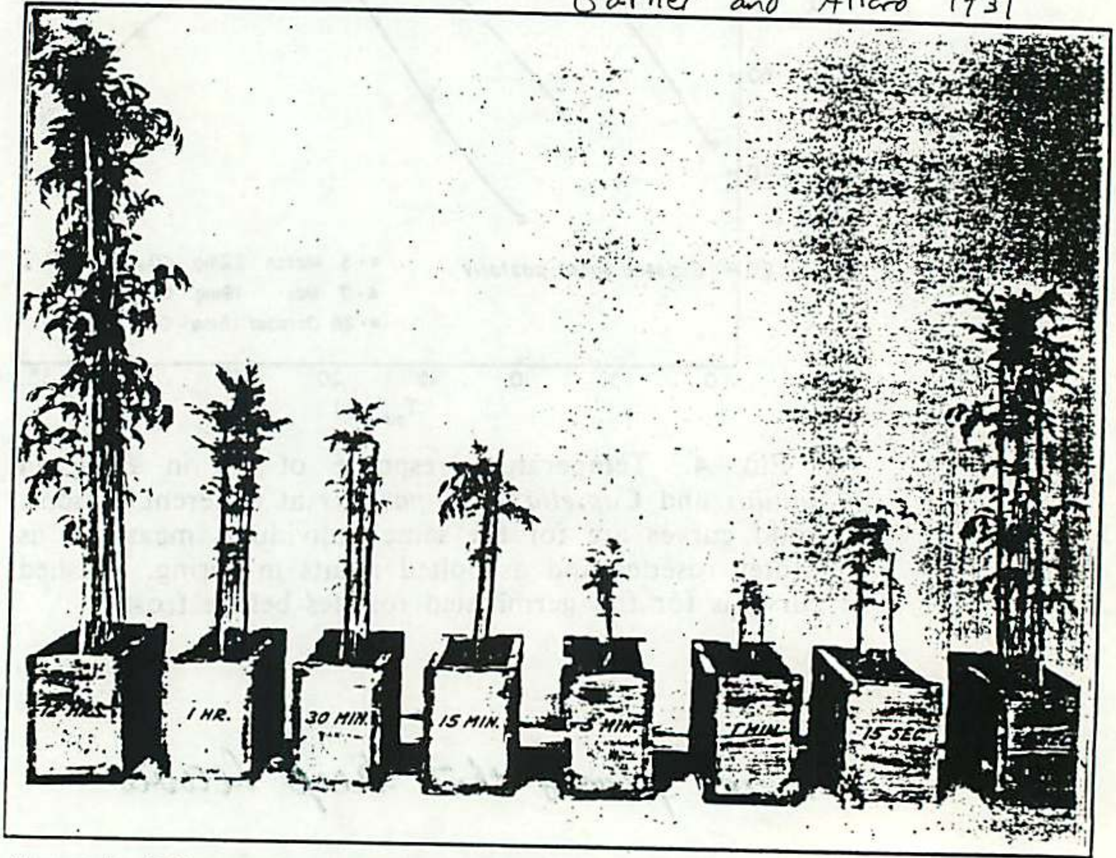


FIGURE 3.—Yellow cosmos (*Cosmos sulphureus* Cav.), a short-day plant, grown with equal alternations of light and darkness ranging from 12 hours to 5 seconds. With decrease in the intervals of light and darkness there is progressive decrease in height, size, and weight of the plants (see Table 6) and increase in etiolation and attenuation till the 1-minute intervals are reached. Further shortening of alternations causes marked improvement in growth and appearance of the plants. All intervals from 1 hour downward are almost equally unfavorable for flowering

11/28/89

Community Ecology

variations in "diversity" of vegetation
① species
② height

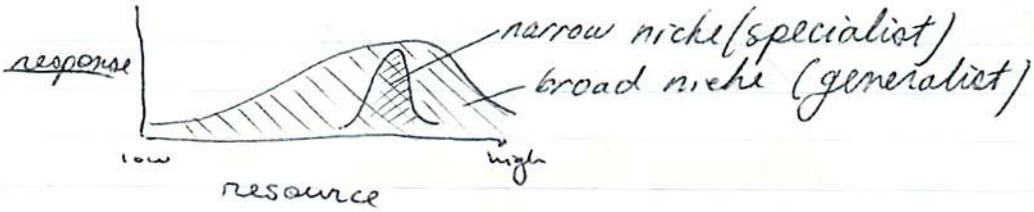
So How explain variations in diversity?

Community Ecology

① coexistence
- when do you determine coex. ; what is the time scale

Niche Differentiation

. "what does a species do?"
"where does it live?"
"how does it respond?" } diff. defintions



zoologists: considered food as main 'x' axis

how big a distance "should" there be betw. species using resources

but environment is very complex

N dimensional hypervolume

- too many factors
- factors affect other factors as well as affecting species
- can be generalist for light but specialist for N_2

so How many "dimensions"
- $h\nu \to$ intensity ...
- $N_2 \to NO_3 \to NO_4 \to$  ...

HOW COMPLEX DO WE GO?

·j19
1/27

·How do we determine which are important?
·Do we measure axis one at a time
or do light & water interact?

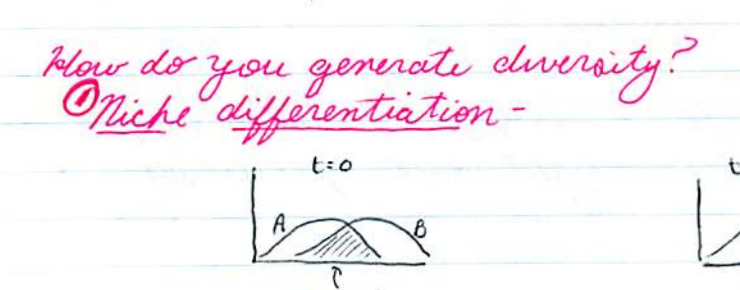
Can take subsets:
-1 response
-2 to 3 dimensions . . .

How do species diff. contribute to? ... huh

	C_1	C_2
1	16	1
2	16	40
3	16	3
4	16	19
5	16	17
6	16	20

Biomass seems to be more applicable than #'s
@ modular growth

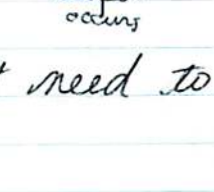
Dominance Diversity Curve

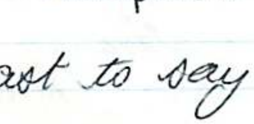


·w/low diversity

high diversity - many rare species, more equitable

How do you generate diversity?
① Niche differentiation -





- reciprocal selection

but need to know past to say whats happened

Niche separation: niches separate but don't know where came from.

② Fundamental vs. realized niche
- must look at reproduction two
- size threshold before repro.

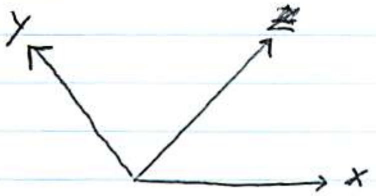
Patchiness

is very important

① physical
② H2O
③ Nutrient
④ Herbivores

Envir. variability → niche sep → variation

Time sep



x, y, z, time
\+
conditions at each } diversity

Succession

response breadth is greater in early succession

Bio 149 - December 5, 1989
David Ackerly

Niche Breadth

Reading:

F.A. Bazzaz and S.E. Sultan, 1987. Ecological variation and the maintenance of plant diversity

Lecture Outline:

1. Review of Niche and Niche Breadth Definitions
2. Components of population niche breadth:
    Niche breadth of genotypes within a population
2. Niche Breadth and Environmental Heterogeneity in Successional Environments
    Spatial and temporal heterogeneity is often higher in early successional and disturbed habitats
    As a result, early successional species tend to have broader niches - i.e. they can maintain performance across a broad range of environments
3. Why aren't niche breadths infinitely broad? The tradeoff between being a specialist and a generalist.

so how do you measure performance. Do we say a niche is broad if can survive constant H_2O. But what about H_2O changes.

Brown
Amer. Nat. 1986.

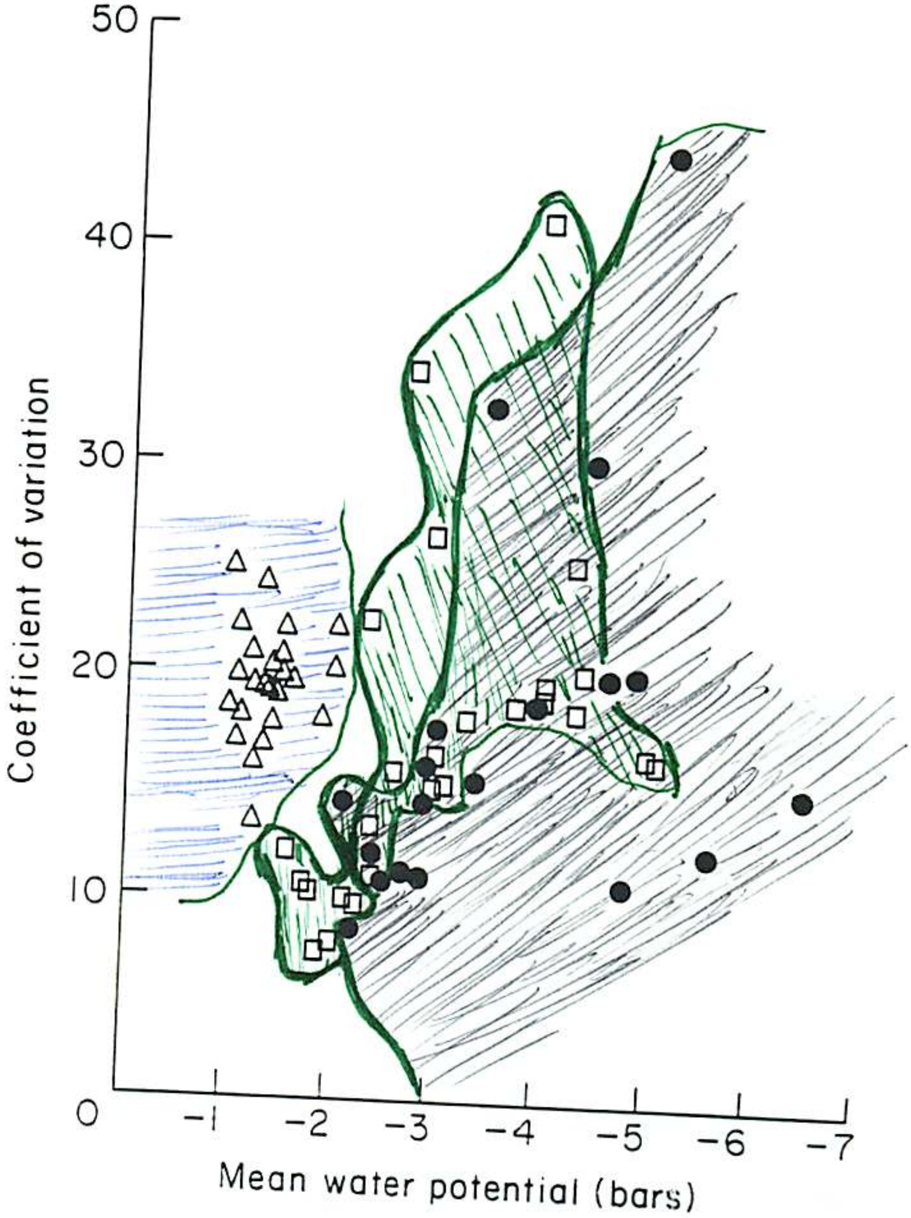
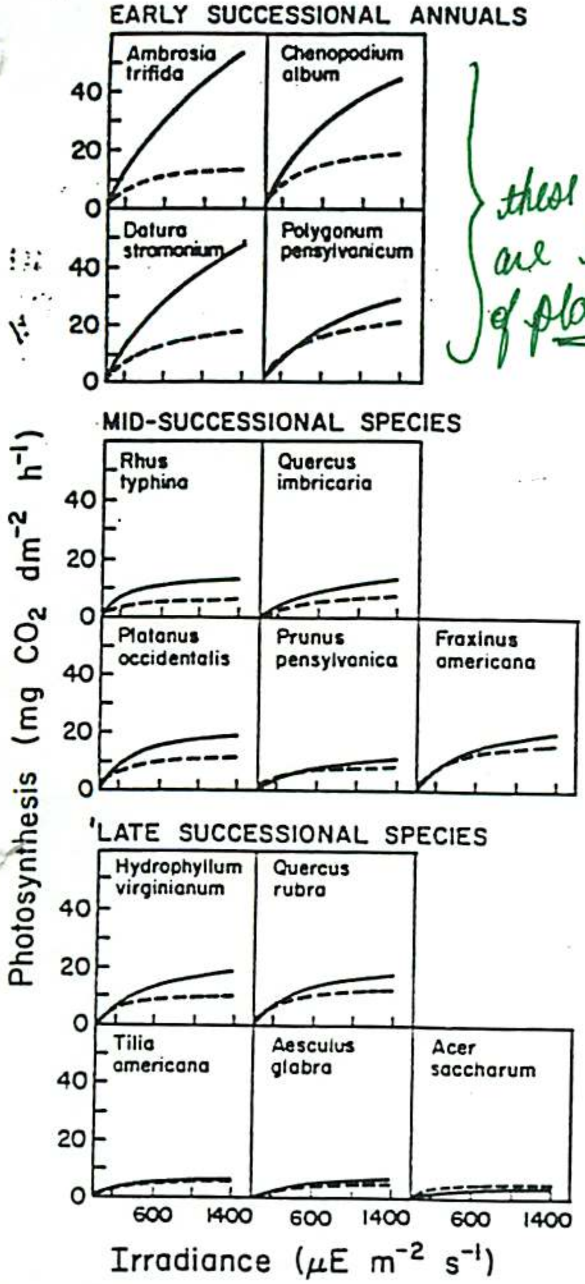


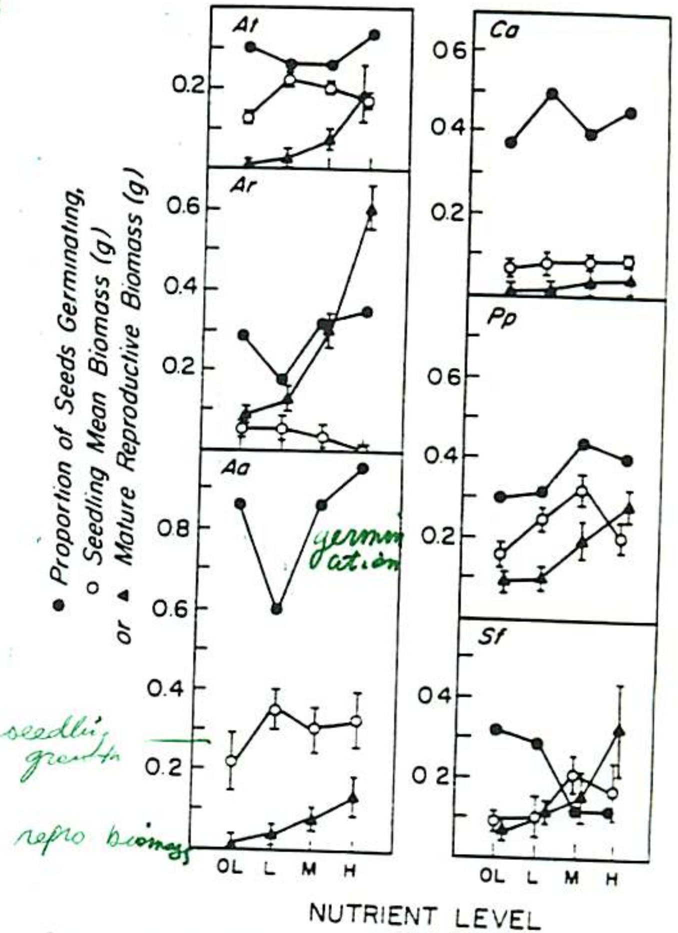
FIG. 12.1. Coefficient of variation in soil water potential of an early-successional field (●), late-successional grassland (□), and a late-successional deciduous forest (△) during a growing season.

open habitats are more variable



these differences are indicative of plasticity!

Fig. 1a–c. Photosynthetic response curves to light intensity for early successional annuals (a), mid-successional species (b), and late successional species grown (c) in full sunlight (solid lines) and in deep shade equal to 1% of full sunlight (broken lines)



germination

seedling growth

repro biomass

FIG. 1. Response of germination (●), whole-plant biomass for seedlings (○), or reproductive biomass of mature plants (▲) for six species on a nutrient gradient. Vertical bars represent ± two standard errors. Nutrient levels: H = high, M = medium (½ H), L = low (¼ H), OL = very low (⅛ H). *At* = *Abutilon theophrasti*, *Ar* = *Amaranthus retroflexus*, *Aa* = *Ambrosia artemisiifolia*, *Ca* = *Chenopodium album*, *Pp* = *Polygonum pensylvanicum*, and *Sf* = *Setaria faberi*.

- early successional species, since have to live in very vas areas tend to be more plastic.

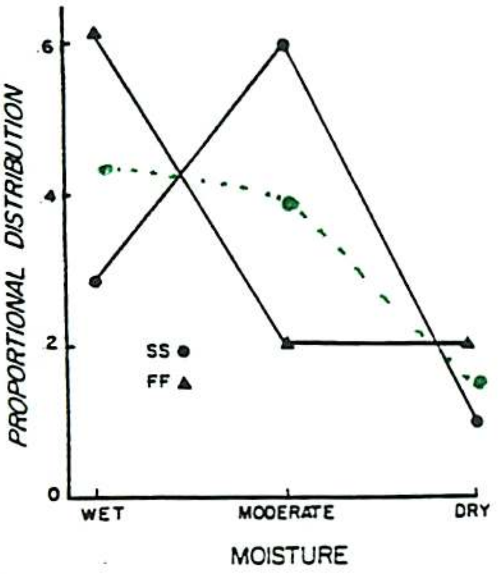


FIG. 2. Proportional distribution of total seed biomass i each of the two PGI homozygous genotypes grown togethe along the soil moisture gradient. The sum of proportions ove all three states equals 1.0 for each genotype.

PGI - two alleles

so - if always wet then ▲ is favored. If moderate then ● favored. But what if both environments.

but selection can favor multiple genotypes.

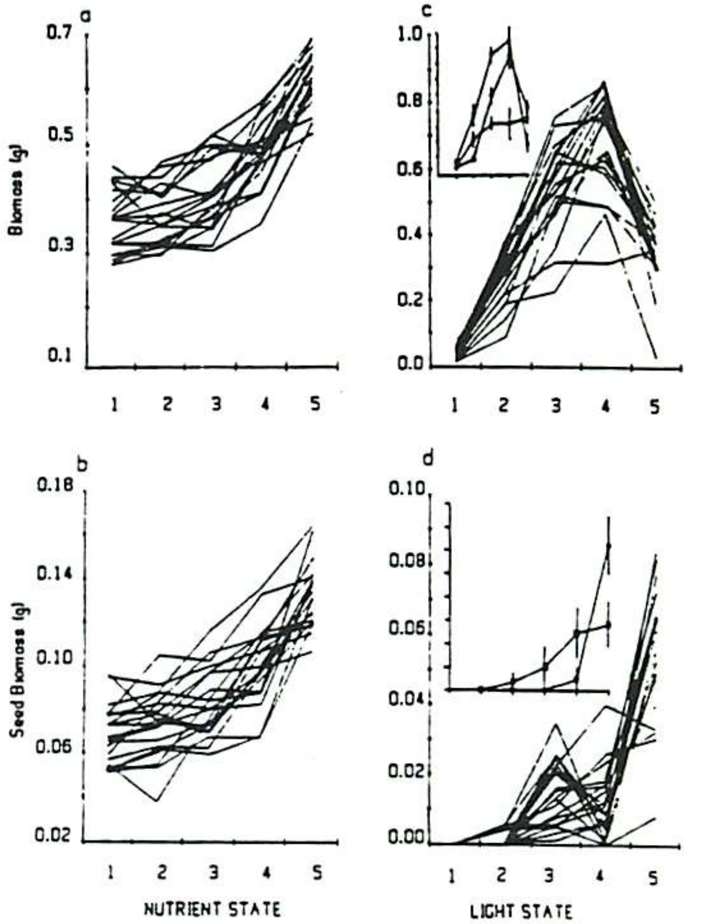
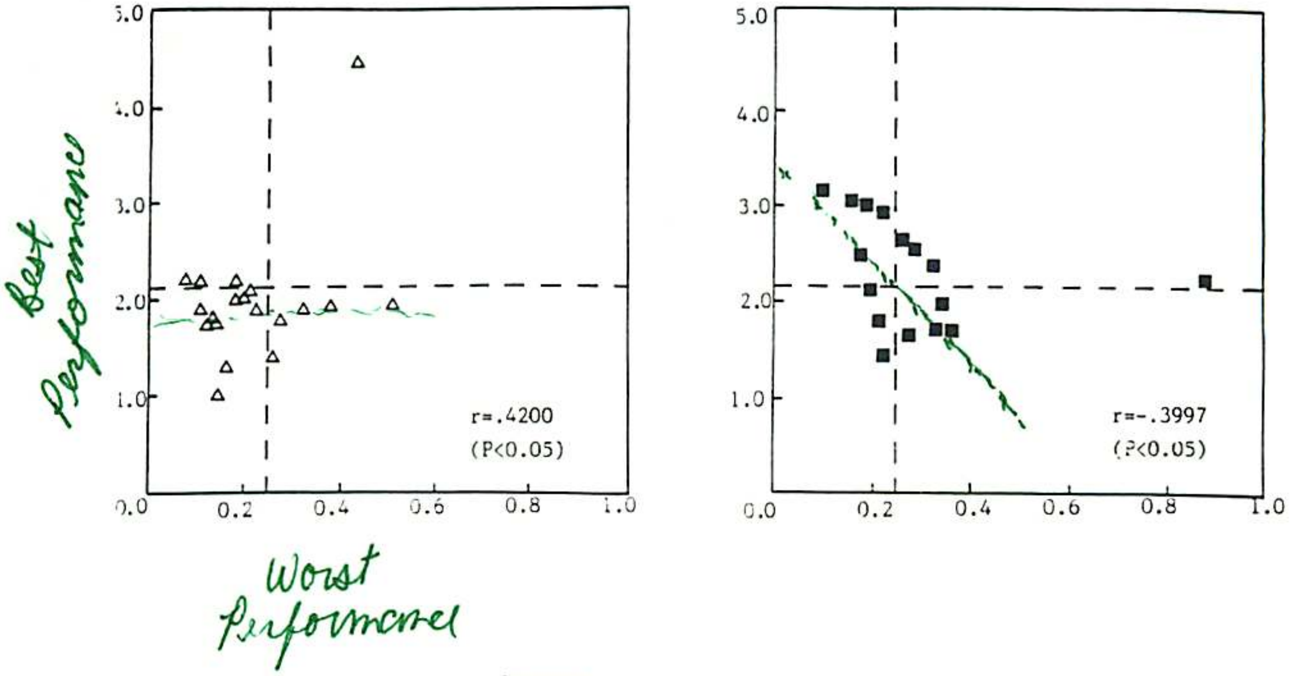


Fig. 1 a–d. The response of twenty maternal families of *Abutilon theophrasti* to a nutrient and a light gradient. State 1 is the lowest resource state, state 5 the highest. **a** Total biomass (*g*) on the nutrient gradient. **b** Mean seed weight (g) on the nutrient gradient. 1c Total biomass (g) on light gradient. *Inset* shows the response of three families in detail (family 2 ■, family 12 ▲, family 13 ●). *Bars* indicate two standard errors. **d** Mean seed weight (g) on the light gradient. *Inset* shows the response of two families (family 9 ■, family 13 ●) with similar total seed production over the gradient (see text). *Bars* indicate two standard errors

1984 1974 Taylor & Aarssen 1988



Turkington & Harper 1979

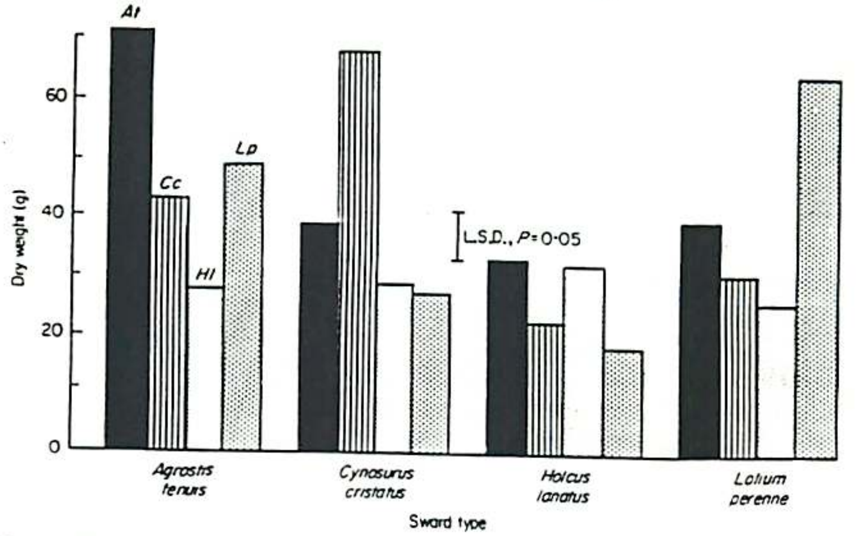
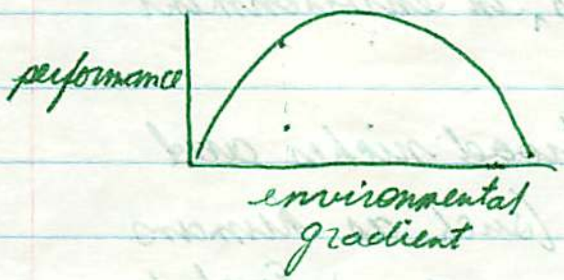


FIG. 1. The dry weight of plants of *Trifolium repens* from a permanent grassland sward, sampled from patches dominated by four different perennial grasses and grown in all combinations of mixture with the four grass species. Clover 'types': *At*, *Agrostis tenuis*; *Cc*, *Cynosurus cristatus*; *Hl*, *Holcus lanatus*; *Lp*, *Lolium perenne*.

12/05/80

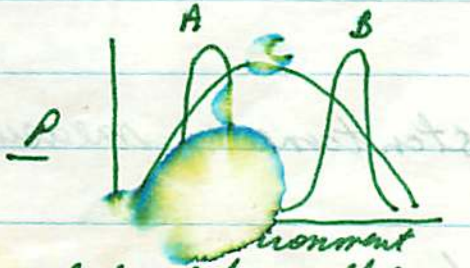
Populations



annual plants follow this pattern

Annuals: want to look at performance but what about seeds. Is # important, or is success of them important. ~~Constant~~ Measurements can't occur at one time.

must remember for each point on each graph there are multiple axis of other "environmental factors"



what get from this graph?

① narrow vs. broad

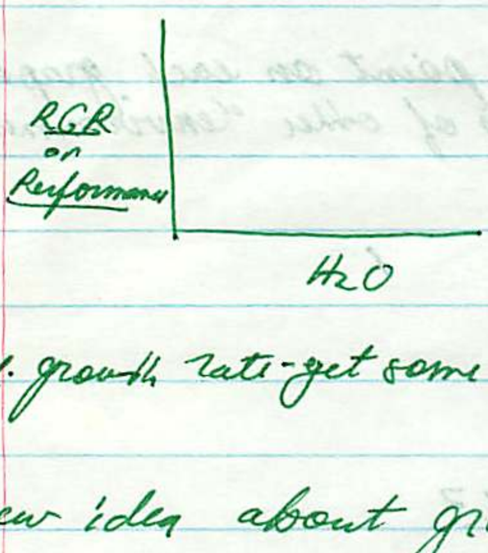
② range : A & B narrow but diff. areas

③ D : heigh important

use range of what is seen in environment

if species has many broad niches and one very narrow niche (such as humans can only survive on 1g). Evolutionary unimportant.

seed bank allow specialization.



w/ rel. growth rate - get some instantane[illegible] measurement

· new idea about graphs: areas

* maintaining performance in variable environments depends on plasticity (which is related to broad niche) *

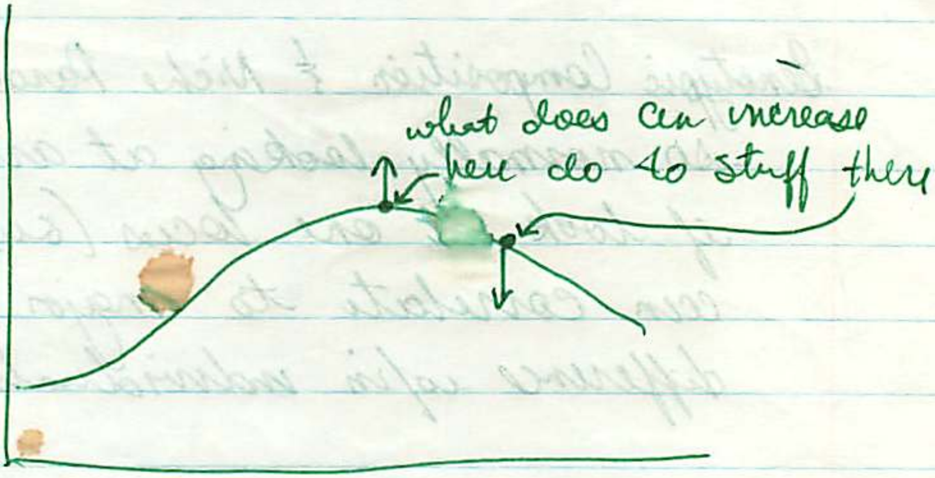
Genotypic Composition & Niche Parameters

- so normally looking at average but if look at one locus (such as PGI) can correlate to major internal difference w/in individuals.

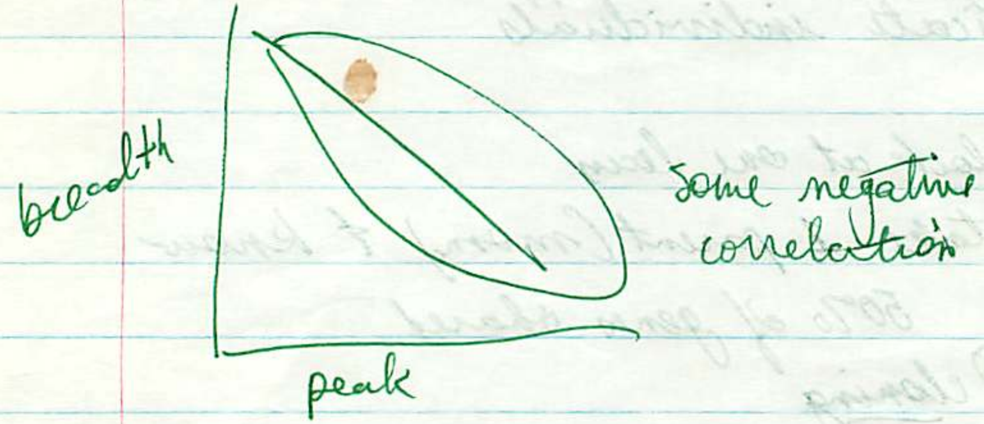
If every individual different then how replicate individuals

① look at one locus
② take 1 parent (mom) & know 50% of genes shared
③ cloning

norms of reaction



what does an increase
here do to stuff there



some negative
correlation

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Tim Sipe: Definition of Disturbance in Ecology

what is being disturbed?

Harper · v. complex at beginning (ecology)

-absolute vs. relative roles of major processes

INTRO -at level of community - ecological theory is in flux but this is the key goal of ecology.

Are ① young science in complex system

② maturing

③ disturbance is a visible symptom of study gaining maturity

2) Historical Trends in Ecology

TRENDS IN ECOLOGY

Simberloff - what you believe is what you see & what you see is data used for conclusions.

- recent trend away from simple predictable ecology to more complex theories with flux.

Plant Ecology

1890-1950 Biogeog, climate & response to climate "Community" concept was central. Climax types w/ recognizable association & if disturbed community would tend to succede back to dominant. type.

1950 - Individualistic Concept. Community is ideal preconception. Gleason.
So try to test these two.

1967 - Harper: Darwinian Plant Population Biology.
Life Histories

1978 - Patches. Non-equilibrium. Interactions not strongly deterministic.

Animal Ecology
Community: superorganism

Population: equations; L-V; compet; ...

THEORY.

1957. Hutchinson n-dimensional hypervolume. Mathematical Community Ecology. Niches. Diversity. Life Histories. Food Webs. MacArthur.

1980-90
- Are biotic interactions important? Is there order? Heterogeneity? Stochasticity?

Ecosystem
-1949 ....

1949 - Lindemann. Trophic Dynamic. Leap beyond taxonomy and into energy flows. Biogeochemistry.

Pollution lent support for this research.

1965 - IBP

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IBP
-attempt to model at biome level just didn't work

+ found out what they didn't know
①below ground

Ecosystems studies become more & more complex.

Can link physiological & ecosystem ecology easily because of emphasis on similar processes.

High-number systems : statistics works bec. so many components*
Low-number " " : number of components small.
linear equations. e.g. planetary motions.

w/in ecology there
e high/middle/low
systems too.

*like gas molecules. need sum of behavior.
Individual components unimportant.

ecosystem theory
es reduced
systems into
"low number"

Ecology is "middle number" system.
-because unpredictable and each component is quite different.

Sources of indeterminism
①evolution : species may change
②behavioral
③spacial heterogeneity
④non-linear
⑤chaos · simple equations put together may produce "random" results
* ⑥disturbance
⑦scale

Disturbance · see graphs

How know which ~~panel~~ change reflects disturbance.
①must know range of behavior of system before disturbance.

possible definition: sets a system outside range.
-but which "range" do you look at (see )
-but can you disturb a random system

②everything depends on what we look at
·scale : action potential vs glaciers
·what is being disturbed

③must define disturbance in relative terms so that it can be useful in many systems.

Emphasis recently on-

- size, shape, intensity, frequency, turnover time of disturbance

STRUCTURAL EMPHASIS OF DISTURBANCE

- so look at structural features of system
  eg - gaps; tidepool

- but ~~go~~ must go to functional forms of disturbance

So central theme is that all individuals organism need energy and resources, and if these energy & resources are changed from most probable behavior, ~~toh~~ this is a disturbance.

To understand disturbance in energy & resources must know how individuals respond.

NICHES - Do species need different niches to coexist?
- No - ① due to spatial heterogeneity, may always have another place to go.
  ② randomness

DISTURBANCE THEORY AND NICHE SPECIALIZATION AMONG FOREST TREE SPECIES

BIO 149, 12.7.89
T.W. Sipe

1. INTRODUCTION

Disturbance, Community Organization, Ecological Theory
Absolute vs. relative roles of major processes
Three main points

2. TRENDS IN ECOLOGICAL THEORY

Order to Disorder in Ecology and Other Disciplines
Major Trends in Ecological Theory, 1890-1990.
  Plant Ecology: 1890-1950, 1950-1967, 1967-1978, 1978-1980
  Animal Ecology: 1890-1957, 1957-1980, 1980-1990
  Ecosystem Ecology: 1900-1949, 1949-1965, 1965-1974, 1974-1990
State versus Process Emphases by Ecological Sub-disciplines
High-number vs. Low-number Systems
Sources of indeterminacy
Current Situation: Uncertainty over deterministic vs. stochastic organization of communities; emphasis on scales, disturbance, non-equilibrium dynamics
Efforts to move forward: Modifications to existing theory vs. Incorporation of new theory (hierarchy, chaos)
Agreement on the Importance of Disturbance

3. DISTURBANCE: GENERAL CONSIDERATIONS

The Essential Characteristics of Disturbance
Current disturbance theory:
  Impetus mostly from sessile communities, especially forests & intertidal zones
  Definitions
  Current disturbance regime descriptors
  Primary emphasis on structure, mortality, space, patch dynamics
The resource approach, and possibilities for linking levels.

4. NICHES, DIVERSITY, AND DISTURBANCE IN MOIST FORESTS

Current Debate: Niche specialization vs. Stochastic Disorganization, esp. in tropical rainforests
Importance of Canopy Gap Disturbances
Sources:
  Diversity-Stability relationships (1960-1975+)
  Evolutionary view of succession (Pickett 1976)
  Gap-understory environmental heterogeneity in tropics (Ricklefs 1977)
  Intermediate disturbance hypothesis (Connell 1977)
  Physiological ecology of succession (1979, 1980)
  Gap partitioning hypothesis (Denslow 1980)
  Non-equilibrium dynamics, disturbance (Connell 1979, Hubbell 1979,1986)

Essential Questions:

1. Must species have different niches to coexist?
2. Are closed forest environments diverse and recurrent enough to generate and/or maintain different tree species niches?
3. Do tree species have different niches?
4. Does the existing degree of niche differentiation contribute to coexistence?

Existing Data for Testing the Gap Partitioning Hypothesis

Potential Quantification: Advances in Instrumentation and Data Processing

5. GAP PARTITIONING AT THE HARVARD FOREST: MICROENVIRONMENTAL HETEROGENEITY IN SPACE AND TIME

Research Strategy
Research Components
Major Questions
Experimental Gap Creation
Measurements
Spatial and Temporal Microclimatic Patterns
Conclusions: Species Responses to Variables Environments

* * *

HISTORICAL EMPHASES BY SUB-DISCIPLINES WITHIN ECOLOGY

ECOSYSTEM	COMMUNITY	POPULATION	INDIVIDUAL (Physiological)
Energy Flow	Classifiction	Growth Rates	Energy Balance
Productivity	Succession	Demography	Carbon Gain
Biogeochemical Cycling	Competition	Regulation	Water Relations
Efficiencies	Coexistence	Life Histories	Nutrient Use
Homeostasis (Stability & Resilience)	Predation	Niche Dimensions	Allocation
	Diversity	Size Hierarchy	Efficiencies
	Trophic Structure	Genetic Structure	Homeostasis
	Physiognomy	Selection	

both are process approaches

	ECOSYSTEM SCIENCE	ANIMAL COMMUNITY	PLANT COMMUNITY	GENERAL CONCEPTS	RCE USE, ATEGIES	TECHNOLOGY	FORESTRY, esp. SILVICULTURE	ENVIRONMENTA ROBLEMS, CONSERVATION
1900								1900
	Lake Microcosm (Forbes) "Ecosystem" (Tansley) Trophic System (Lindemann)	Population Dynamics: Growth Models Competition Predation Coexistence (Gause) Niche Food Webs	Phytogeography Succession Climax Concept Individualistic Concept (Gleason) Pattern & Process (Watt)	Climate/Vegetation/ Geographic Correlation Limiting Factors Adaptation to Extreme Environments Life Forms (Raunkaier) Ecotypes (Turiessen, (Carnegie Inst.) Environmental Complex (Billings)	"Tolerance", esp. Shade Light vs. Moisture in Forests Individual Resource Requirements Shade Tolerance Rankings		Growth Rates Species-Site Relations Harvest Strategies Regeneration Economics etc. etc.	National Park Concept Dust Bowl Game Management (Leopold) A Sand County Almanac (Leopold)
1950								1950
	Ecosystem Analysis Linear Compartment Modeling	Life History Variation Niche Hypervolume	Individualistic Hypothesis Revisited Continuum Analysis Gradient Analysis Ordination et al. Succession Revisited	Diffusion Analog for Water (Gaastra)		Mainframe Computers Analog...Digital Lab-Based IRGA Growth Chambers Radioactive Tracers		
1960								1960
	International Biological Program (IBP) Perturbation Analysis Developmental Trends (Odum)	Mathematical Evolutionary Ecology (MacArthur) Island Biogeography	Darwinian Plant Population Biology (Harper)	Water Potential (Slatyer) Energy Balance (Gates)	Sun vs. Shade Syndromes (1962-75)	Pressure Bomb Thermocouples Remote Sensing, esp. Satellite		Silent Spring (Carson) Earth Day
1970								1970
	Diversity vs. Stability First LTER's Pattern & Process	Coevolution r-K Theory "Niche"?? Adaptationism Rejected Competitive Crunches	Plant Evolutionary Ecology Life Histories Succession Revisited Disturbance Non-equilibrium Patch Dynamics	SPAContinuum Hydraulic Conductivity PS Pathways Water-Use Efficiency Nutrieent-Use Efficiency Cost-Benefit Analysis Leaf g & A models	Adaptive Geometry, Architecture Physiological Ecology of Succession	Quantum Sensors Thermocouple Psychrometers Diffusion Porometer Autoanalyzer Microcomputers, esp. Dataloggers	Multiple-Use Forestry	EPA Major US Legislation Population Growth Tropical Rainforest Losses Extinction Rates Three-Mile Island Nature Preserve Design
1980								1980
	Global Questions Plurality, Scales, Hierarchy	Reassessment of Biotic Regulation	Disturbance vs. Diversity Spatial-Temporal Heterogeneity	Whole-Plant Integration Multiple Resources & Stresses	Resource Use Strategies: Conservative/Exploitive Equilibrist/Opportunist Large-Gap/Small-Gap	Portable IRGA's Stable Carbon Isotopes Fluorescence Spectroscopy	Forest Decline	Rainforest Diversity, Dynamics, Disturbance Nuclear Winter Global Warming Acid Precipitation
1989								1989
	↓ NICHES	↓ DIVERSITY niche? disturbance?	↓ DISTURBANCE	↓ WHOLE-PLANT PHYSIOLOGICAL ECOLOGY	↓ RESOURCE-USE CATEGORIES	↓ FAST, EFFICIENT FIELD SAMPLING OF MICRO-CLIMATES & LEAF GAS-EXCHANGE	↓ FOREST DECLINE, REGENERATION	↓ ROLES OF ALL COMPONENTS TO THE LEFT IN THE DIVERSITY AND GLOBAL BIOGEOCHEMICAL IMPACT OF FORESTED ECOSYSTEMS

DEFINITIONS OF DISTURBANCE IN ECOLOGY

GRIME (1979):

> "...*disturbance*, which may be said to consist of *the mechanisms which limit the plant biomass by causing its partial or total destruction*."

BAZZAZ (1983):

> "I define disturbance as a sudden change in the resource base of a unit of the landscape that is expressed as a readily detectable change in population response."

SOUSA (1984):

> "In the context of this review, a *disturbance* is a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established."

PICKETT & WHITE (1985):

> "In these cases, a 'perturbation' is a departure (explicitly defined) from a normal state, behavior, or trajectory (also explicitly defined)."

> "A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment."

SIPE (1988):

> **"A disturbance is a change** (*direction, magnitude and/or rate*) **in physical and chemical factors** (*spatial/temporal pattern of forces, concentrations, fluxes*) **that is judged by an observer to deflect an ecological system** (*individual, population, community, ecosystem*) **from its most probable behavior** (*state or series of transitions*)."

So how do you determine probable behavior. That still has scale problem. What about random?

Disturbance

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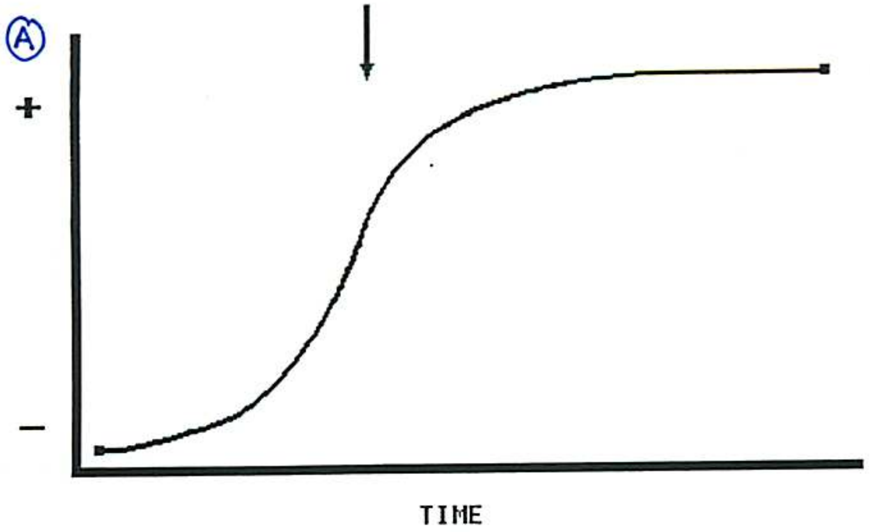
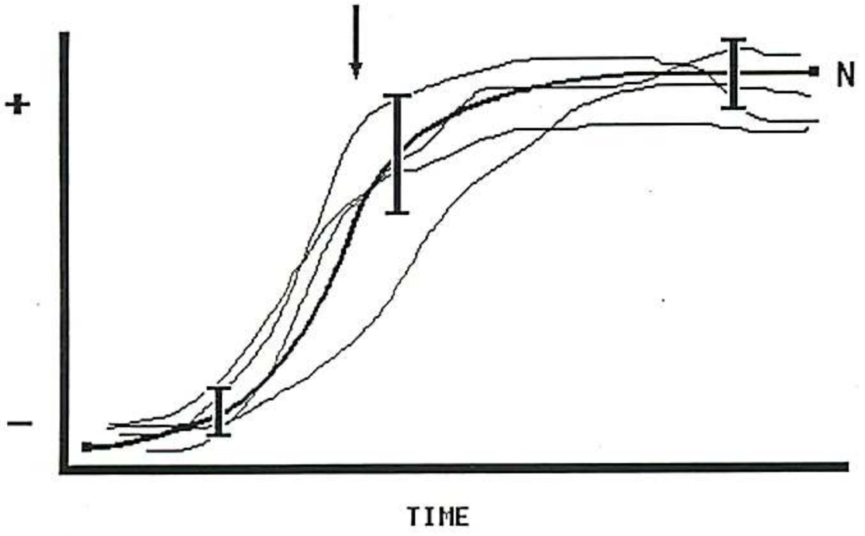
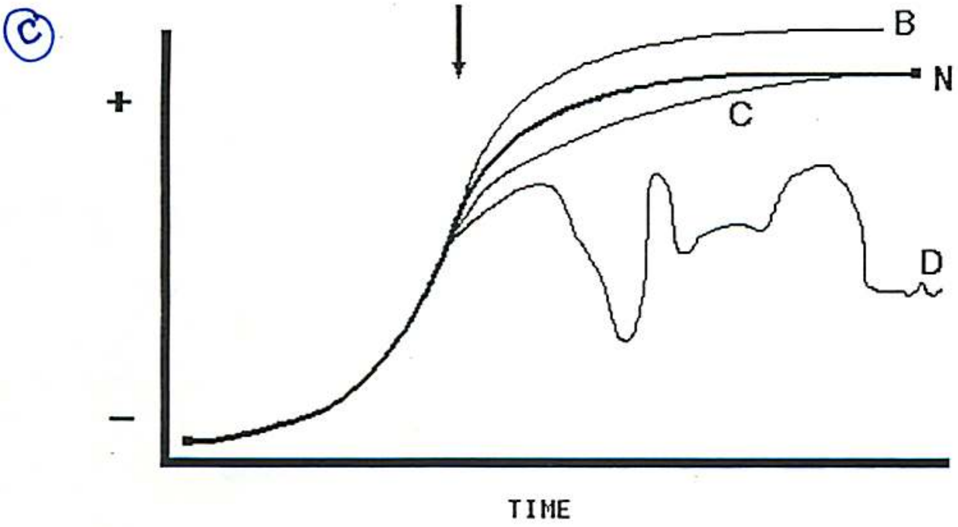


simpler log → equilib.

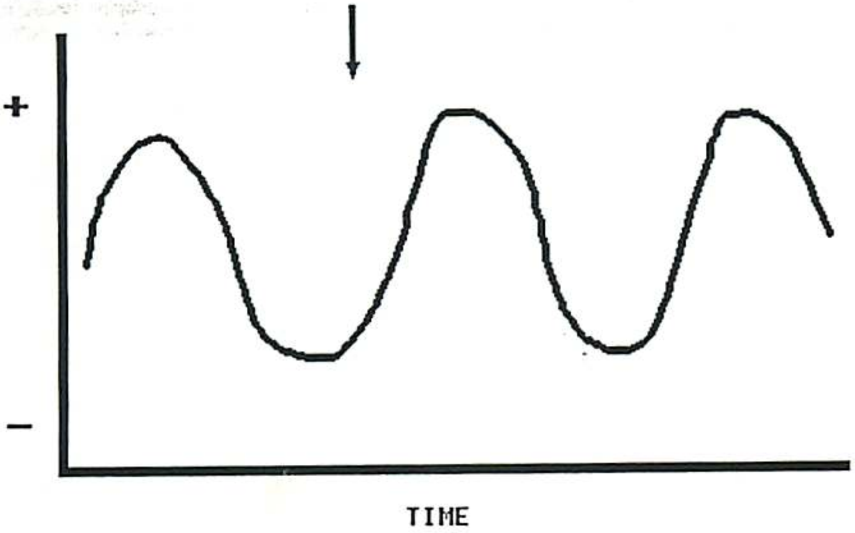




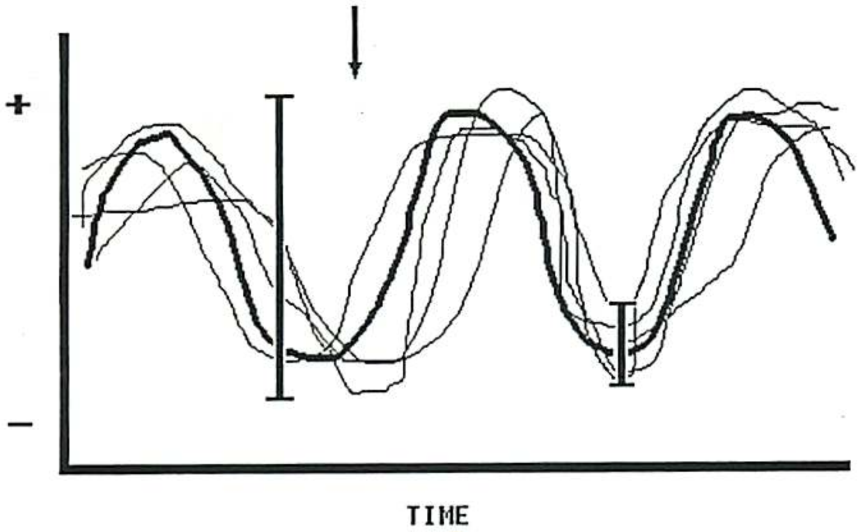
results of disturbance on Ⓐ

B = diff. equil
C = same equil
D = new system

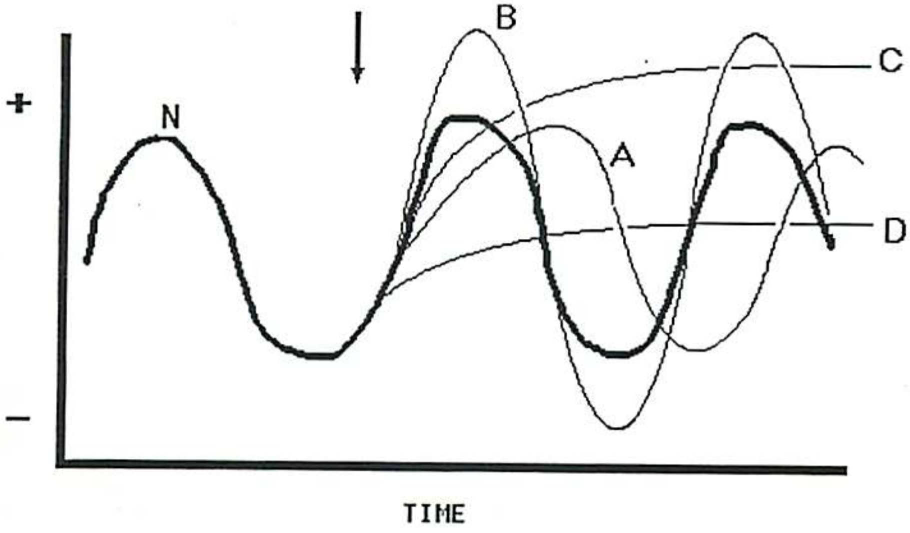
Ⓐ



Simple- predictable oscillation



Ⓒ

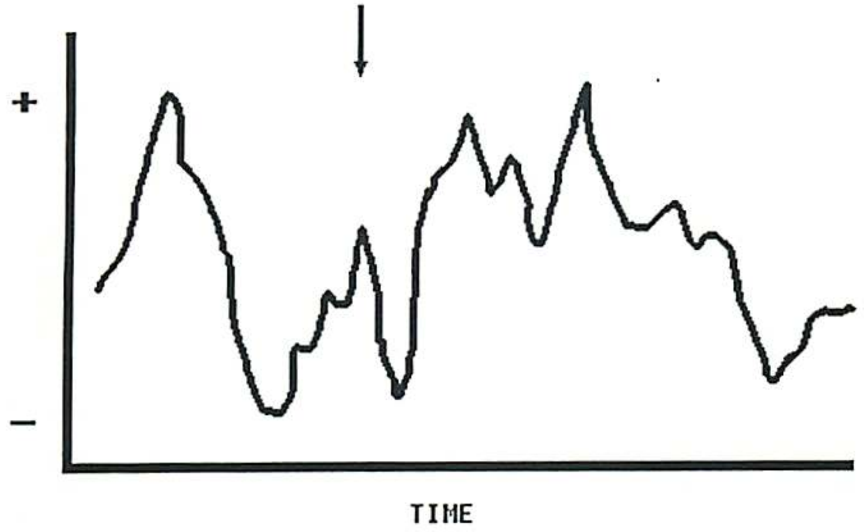


A - phase shift

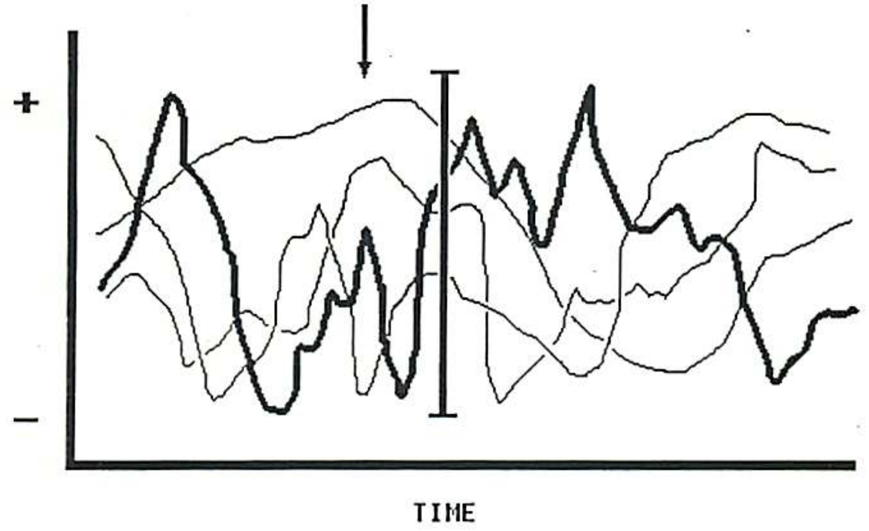
* B - higher amplitud

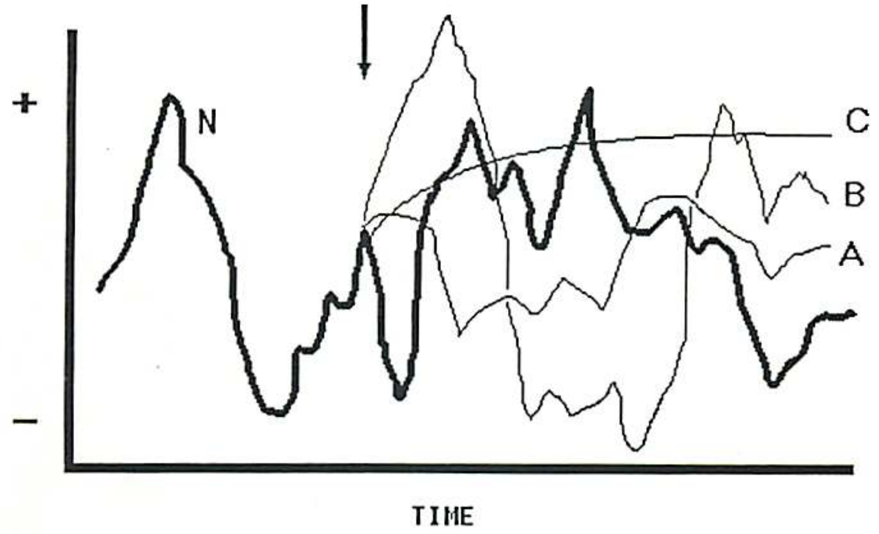
* C - new. equil.

D - no oscillation but average



“random”
curve





A - new amplitude
B - stable
C - wipe out
randomness

Biology 149, Plant Ecology
Succession Lecture outline
December 12, 1989

Historical development of the concept of succession (Cowles, Clements, Watt, Odum).

Relationship to the community concept

How is succession initiated? Disturbance (single tree -- fall, windthrow, earthquakes, fire, land clearing and degradation. Loss of soil, loss of organic matter, loss of seed bank etc.

The development of a general theory of succession: Determinism vs stochasticism

Causes of succession:
    Competitive exclusion, alellopathy
    Life history attributes

Models of succession

Scales of succession:
    Fungi on decaying leaves
    Intertidal algal succession
    Oldfield succession
    Forest regeneration

Attributes of early and late successional plants
    The individual level
    The community and ecosystem levels

Jon Eisén
B149
12/12/89

Succession

Historical confusion
how classify; possibility of general statements

J. Miles in
Colonization
Succession &
Stability
Gray, Edwards
& Crawley
Editors
1987.

H.C. Cowles 1899 & 1901
- observed changes in vegetation along shores of Lake Michigan
- oldest dunes were most complex
- so succession procedes from simple to complex

Clements U. Nebraska 1916. book about succession/classification

Watt - Britain, grazing

Odum Georgia. 1979. Science Emphasized ecosystems

Succession is change in species dominance in particular area.
- v. tied in to communities

COMMUNITY

Clements
- v. tight knit collection of organisms. Develop mature & die together.

Organism View

Gleason/Duminsky
- community is collection of species that happen to be overlapping, individualistically on resource gradient.

Individualistic Concept

Fight between Gleason & Clements groups

- but both views are incomplete
- organisms act as individuals but other species obviously modify environment so that each can be very dependent on each other

~~Gleason~~ Clement

Climatic Climax
- Climatic climaxes - if everything uniform then community will head towards specific "climax" Directional.

Dynamic
- but other view
  - bits & pieces & patches all in various stages of ~~non-equi~~ dynamic movement
-

When is succession succession? How many replacements needed?

Directionality Is succession direction - yes but not completely. Clements could incorporate everything by citing disturbance as holding back communities from climax.

Sub-climax: held back
Dis-climax: deflected in wrong direction

So Clements accepted other view.

Primary Succession

Primary Succession

- succession on land never occupied by plants
  ① sand ② rock ③ glacial till
-

New Land
↓
Primary succession
↓
Pioneer Seral Stage $\xrightarrow[\text{Stage}]{\text{Seral}}$ → Subclimax → Climax ⟲ these communities regenerate themselves

Secondary Succession

Succession where vegetation removed

Cyclic Succession

eg Chaparral - shrubs, oaks, v. low
- fuel accumulates - & fire wipes out
- site opens up w/ high nutrients
- annuals
- perennials → shrubs → ... chaparral

Allogenic - forces outside drive succession
Autogenic - forces w/in drive succession - use up nutrients

Disturbance v. important for 2° succession
Resources v. important for 1° succession

So 1° & 2° is irrelevent. Want to know
① amount of resource
② quantity and quality of propagules left

1° vs. 2° is a gradient of same thing.
-"erosion" leads to 1° succession
-so must consider level, timing, and type of succession; dispersal

Pattern of Succession

Pattern of succession v. dependent on initial colonizers due to Δ in light, T°, ... and ~~decre~~ change to non-random dispersal

Guild: a "bunch" of species doing same thing in a community.

Modeling

Modeling Succession

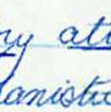
①Causes - why does it occur? -chem, disp, physiology
-when are these forces more important than others
- competition - A #1; but allows B to grow then B #2.
important but not enough
- life history attributes - all encompassing
- mechanistic explanations "How can A be able to replace B"

②Connell & Slatyer
inhibition - presence of A keep out B et al.
facilitation - presence of A helps B to enter
tolerance - no +/-
} not mutually exclusive
- can vary w/in "gap"

③succession as build up/decline of populations
- Lotke-Voltaire Equation

N_0 = unit # of pop.
r = intrinsic rate of growth

$$\frac{dN}{dt} = N_0 \times r \left(\frac{K-N}{K}\right)$$



but reaches a carrying capacity

problems
N - doesn't work for plant

- can use this to model succession

$$\frac{dN_1}{dt} = N_{0_1} r_1 \left(\frac{K_1-N_1}{K_1}\right) \quad \frac{dN_2}{dt} = N_{0_2} r_2 \left(\frac{K_2-N_2}{K_2}\right)$$

· convert N_2 to N_1. $\alpha_{ij} \neq \alpha_{ji}$

- can get α for one species or whole population

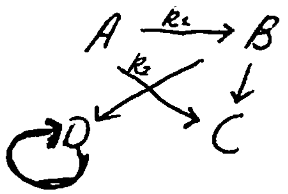
12/14

Succession - part II

-r (growth rate) becomes ∅ when N=K

Transition Probabilities

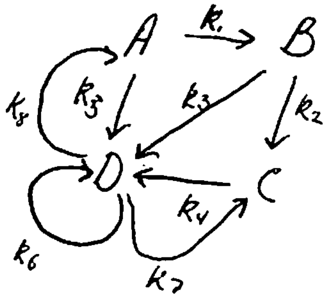
General



if $K_2 \gg K_1$ then likely go from A → B

Henry Horn - used Markov series
assumption - State 1 & 2 previous transitions have nothing to do with ~~previous~~ current probabilities but this doesn't work in nature

-article on Markov series - Usher, M Coloniz., Succession, & Stability



- if $k_3; k_4; k_5$ high and ~~[illegible]~~ ~~then~~ $k_6 \cong k_7 \cong k_8$ then D may be v. common but not climax

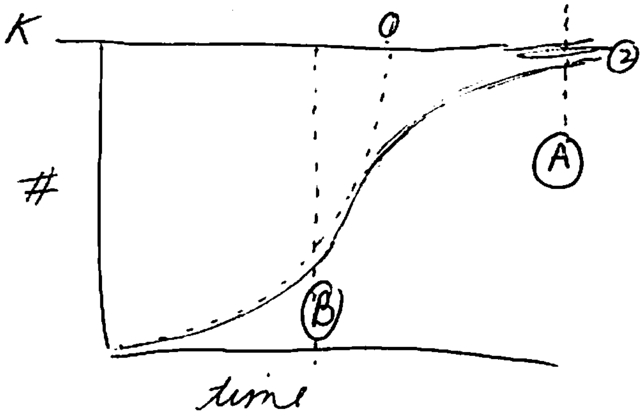
Numerical problems
① How define which community is which
② vary w/ weather

but these probabilities aren't "cumulative"

A → B → A → B
A → A → B → B

Forest succession:
one forest tree replaces another

Pioneer vs. Forest (mature)



desper..

① $\frac{dN}{dt} = r_0 N$

② $\cancel{\frac{dN}{dt} = r_0 N(K - \frac{K}{N})}$

$\frac{dN}{dt} = r_0 N\left(\frac{K-N}{K}\right)$

K Ⓐ - many species stay near K
always "competing"

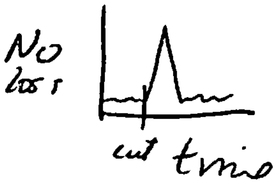
Ⓑ others due to "disturbance" never get near K

r always ~~selecten~~ trying to grow

Deforestation Bormann Likens Pierce & Fisher

- leads to NOx leaching
- which can affect other ecosystem

but regrowth is v. efficient in N. uptake



Vitousek & Reiners:
- mature phases: aren't growing & can't use new NOx
- pioneers grow v. fast;

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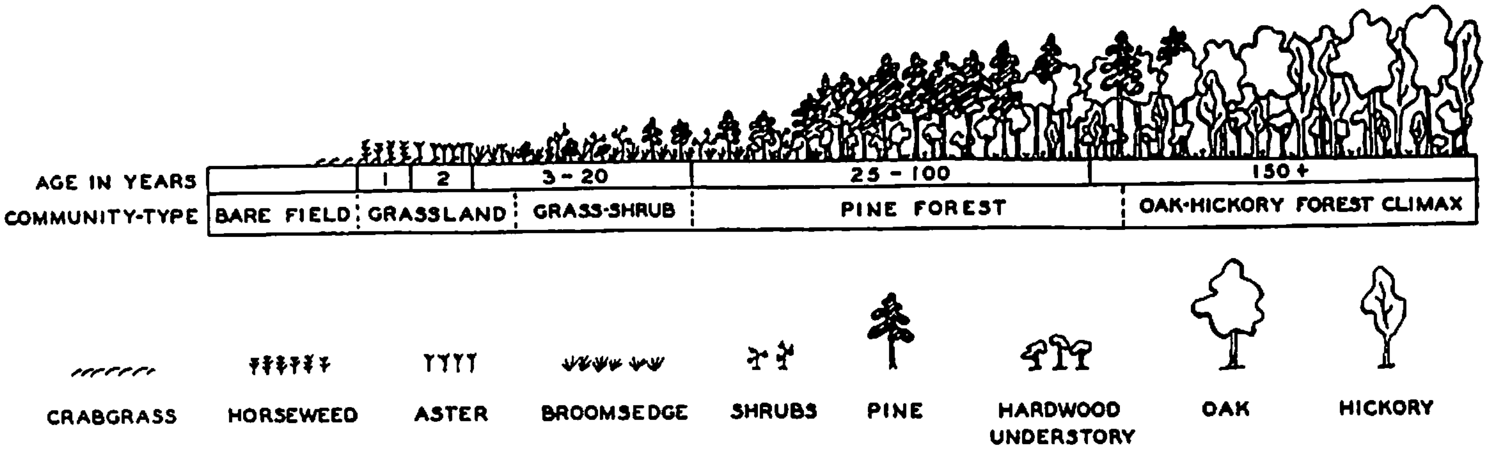
SUCCESSION



DEFINITION: **"...the process of succession is defined as the non-seasonal, directional and continuous pattern of colonization and extinction on a site by species populations"** --(Begon, Harper, Townsend, 1986).

WHAT DRIVES IT?

AUTOGENIC PROCESSES

ALLOGENIC PROCESSES

INDIVIDUALS RESOURCES

***Plant's Eye View**
?Hyphae's (Fungi's) Eye View?

SAPROPHTYIC FUNGAL SUCCESSION

a. Species Dynamics

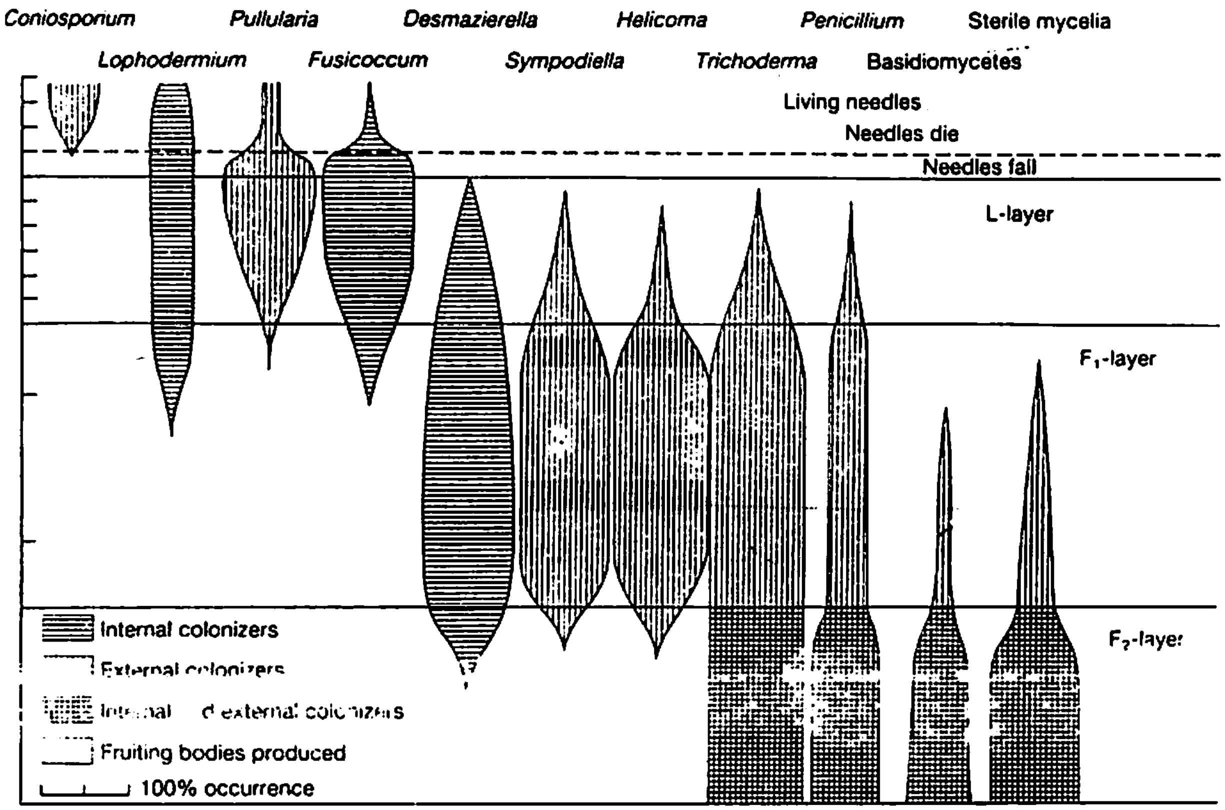
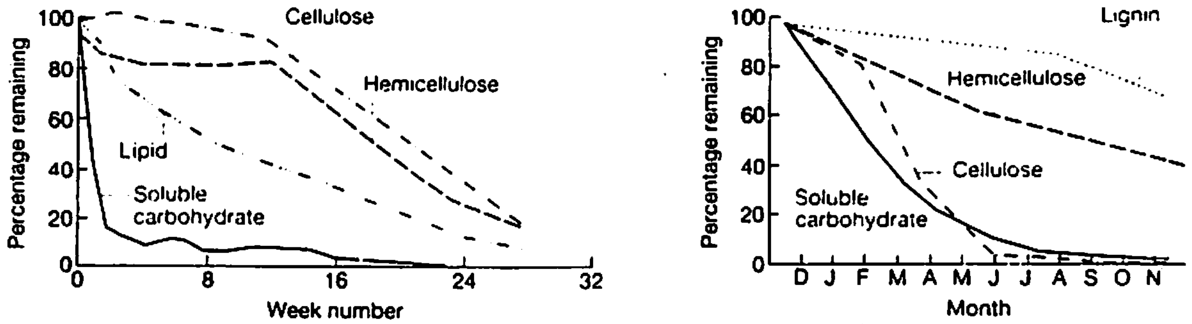


Figure 16.13. Temporal and spatial changes in fungal populations colonizing pine needles in litter layers beneath Scots pine (*Pinus sylvestris*) forest in England (from Richards, 1974, based on Kendrick & Burges, 1962).

b. Resource dynamics

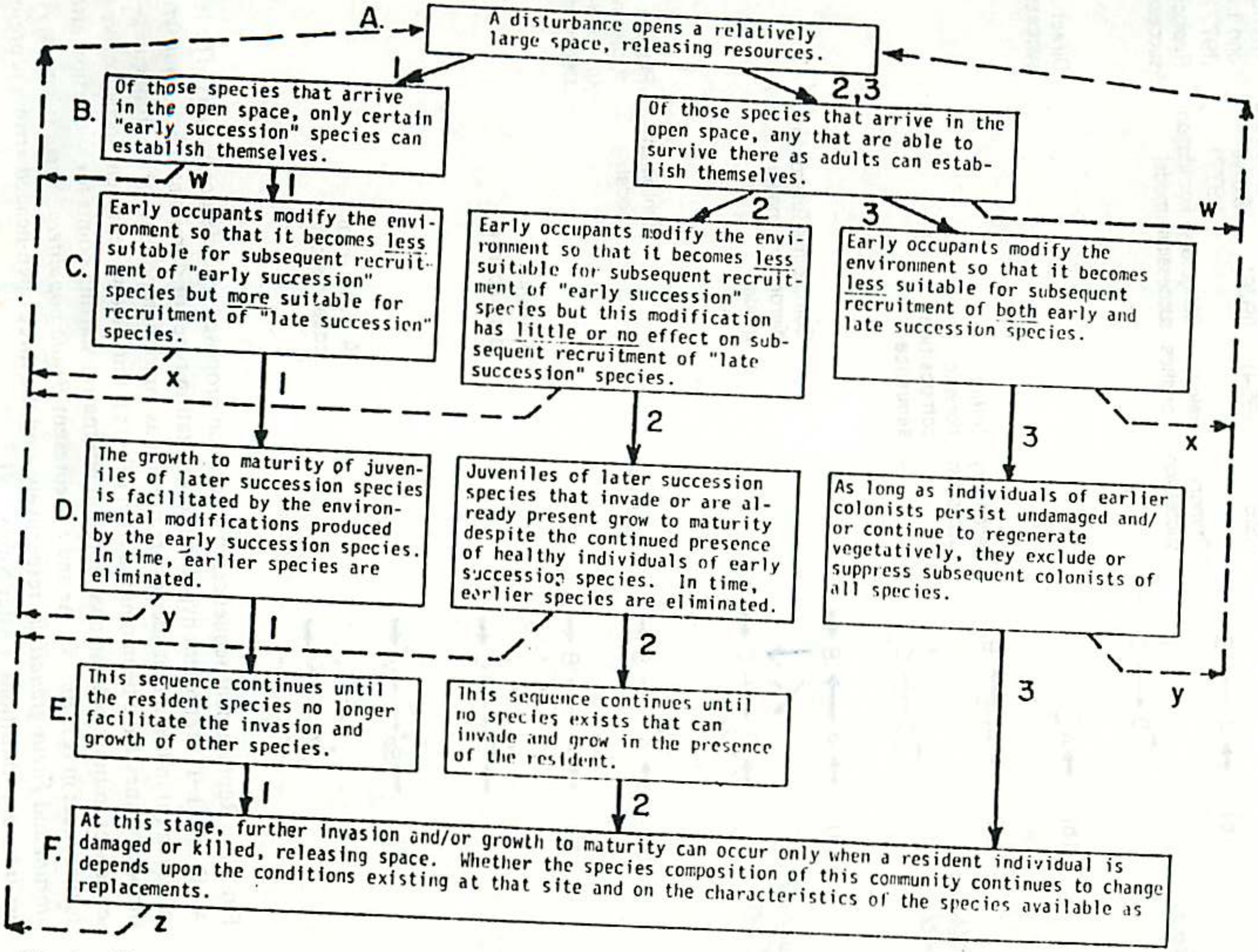


(b) *Quercus alba*
North American stream (Augusta Creek)

(a) *Quercus serris*
Hungarian woodland floor

Figure 11.3. Changes in composition of oak leaf litter during decomposition in contrasting situations: (a) leaves of *Quercus cerris* on a woodland floor in Hungary, through the year; (b) leaves of *Quercus alba* in a small stream in North America, during a 28 week experiment. Amounts are expressed as percentages of the starting quantities. (Respectively from Toth *et al.*, 1975; and Suberkropp *et al.*, 1976.)

space = space
+
resources



A disturbance opens a relatively large space, releasing resources.

Of those species that arrive in the open space, only certain "early succession" species can establish themselves.

Of those species that arrive in the open space, any that are able to survive there as adults can establish themselves.

Early occupants modify the environment so that it becomes less suitable for subsequent recruitment of "early succession" species but more suitable for recruitment of "late succession" species.

Early occupants modify the environment so that it becomes less suitable for subsequent recruitment of "early succession" species but this modification has little or no effect on subsequent recruitment of "late succession" species.

Early occupants modify the environment so that it becomes less suitable for subsequent recruitment of both early and late succession species.

The growth to maturity of juveniles of later succession species is facilitated by the environmental modifications produced by the early succession species. In time, earlier species are eliminated.

Juveniles of later succession species that invade or are already present grow to maturity despite the continued presence of healthy individuals of early succession species. In time, earlier species are eliminated.

As long as individuals of earlier colonists persist undamaged and/or continue to regenerate vegetatively, they exclude or suppress subsequent colonists of all species.

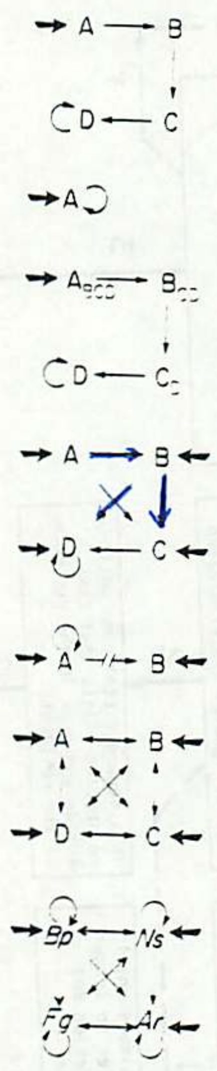
This sequence continues until the resident species no longer facilitate the invasion and growth of other species.

This sequence continues until no species exists that can invade and grow in the presence of the resident.

At this stage, further invasion and/or growth to maturity can occur only when a resident individual is damaged or killed, releasing space. Whether the species composition of this community continues to change depends upon the conditions existing at that site and on the characteristics of the species available as replacements.

FIG. 1.—Three models of the mechanisms producing the sequence of species in succession. The dashed lines represent interruptions of the process, in decreasing frequency in the order *w*, *x*, *y*, and *z*.

Vegetation succession



		Clements (1916)	Egler (1954)	Horn (1976)	Connell and Slatyer (1977)	Whittaker and Levin (1977)
· directional + climax	(a)	Primary succession	Relay floristics	Obligatory succession	Facilitation model	Replacement succession
. no succession	(b)					Direct succession
- secondary succession Δ in dominance	(c)	Secondary succession	Initial floristic composition sequence			
- deterministic ·A makes place bad for A but OK for B or C	(d)			Competitive hierarchy model	Tolerance model	
chronic	(e)	Subclimax			Inhibition model	Plateau succession (pseudo-steady state
chronic disturbance	(f)			Chronic disturbance		
	(g)			A quasi-real case history		

FIG. 1.5. Replacement sequences in succession proposed by different authors. The letters A–D in (a)–(f) represent hypothetical vegetation types or dominant species; subscript letters in (c) indicate that species are present as minor components or as propagules—for simplicity, they have been omitted from (d)–(g); thin arrows represent species or vegetation sequences in time; bold arrows represent alternative starting points for succession after disturbance; in (g), *Bp*, *Ns*, *Ar* and *Fg* represent *Betula populifera*, *Nyssa sylvatica*, *Acer rubrum* and *Fagus grandifolia* respectively, and the three open-headed arrows represent less frequent transitions. (After Noble 1981.)

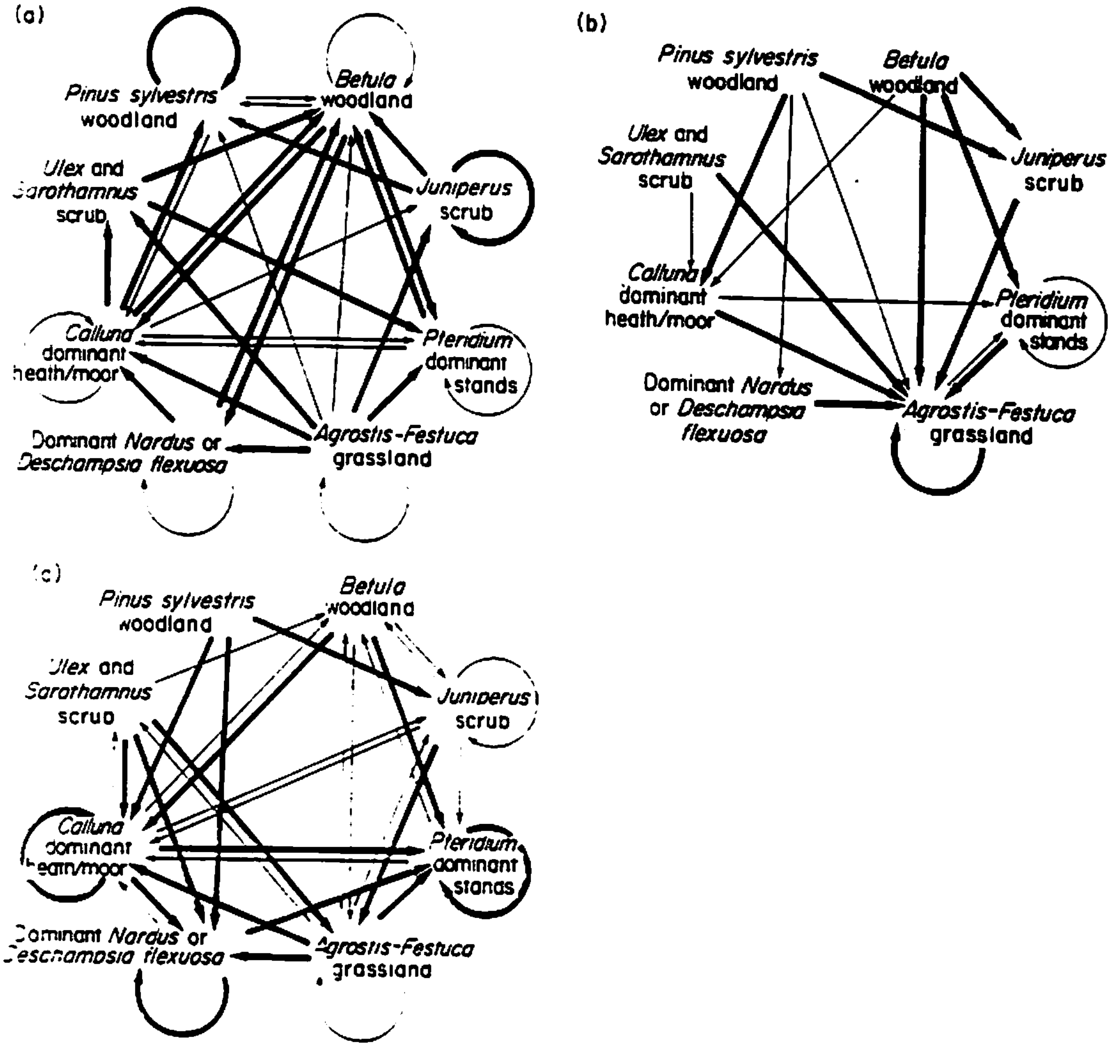


FIG. 1.10. Successional transitions in the British uplands (particularly north-west Scotland) between eight vegetation types given (a) low grazing pressures (<1 sheep equivalent ha^{-1} year^{-1}) and no burning, (b) high grazing pressures (>2–3 sheep equivalents ha^{-1} year^{-1}) and frequent burning, and (c) intermediate levels of grazing (1–2 sheep ha^{-1} year^{-1}) and occasional burning. Broad arrows represent common transitions, thin arrows less frequent transitions, and curved arrows self-replacement. The vegetation types are arranged so that types tending to podzolize and/or acidify soils are on the left, and types with contrasting pedogenic effects are on the right. (From Miles 1985b, courtesy of the British Society of Soil Science.)

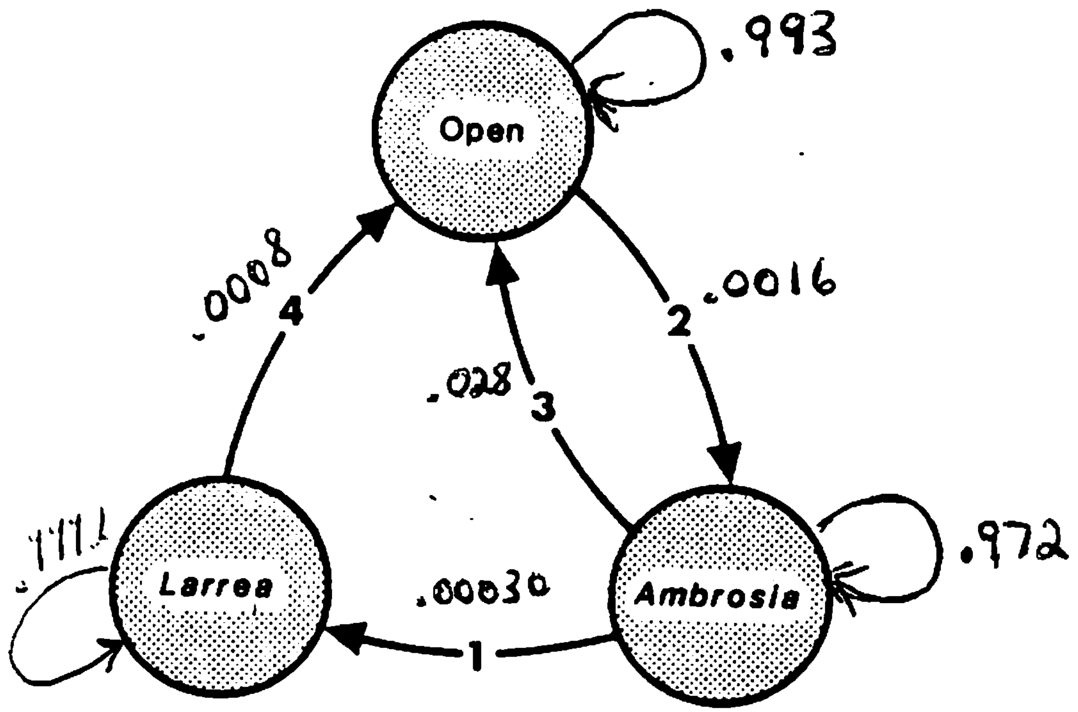


FIG. 2.—Simple digraph showing the principal transitions in the *Larrea-Ambrosia* communities at Dateland and San Luis.

Table 1 Empirically determined attributes of pioneer and mature forest tree species

Characteristic	Pioneer tree	Forest tree
Dispersibility of seed	To long distances wind/bird/bat	Short distance rodent/bird/none
Seed weight	Light to heavy	Relatively heavy
Seed germination:		
light-stimulated	Yes	No
inhibited by far red light	Yes	No
Longevity of individual	Shorter	Longer
Time to reproductive maturity	Shorter	Longer
Height growth	Fast	Slow
Height at maturity	Shorter	Taller
Resource acquisition rates	Fast	Slow
Photosynthesis light-saturated at	High light intensities	Low light intensities
Recovery from resource limitation	Fast	Slow

These categories represent the extremes of a spectrum of ecologies: pioneer is analogous to 'r-selected', forest to 'k-selected'. Reductionist authors assert that these differences between pioneer and mature forest species explain all the phenomena of succession (see also Fig. 1) (from

Table 16.2. Some representative photosynthetic rates (mg CO_2 dm^{-2} h^{-1}) of plants in a successional sequence. Late-successional trees are arranged according to their relative successional position. (From Bazzaz, 1979.)

Plant	Rate	Plant	R
SUMMER ANNUALS		EARLY SUCCESSIONAL TREES	
Abutilon theophrasti	24	*Diospyros virginiana*	17
Amaranthus retroflexus	26	*Juniperus virginiana*	10
Ambrosia artemisiifolia	35	*Populus deltoides*	26
Ambrosia trifida	28	*Sassafras albidum*	11
Chenopodium album	18	*Ulmus alata*	15
Polygonum pensylvanicum	18		
Setaria faberii	38	LATE SUCCESSIONAL TREES	
		Liriodendron tulipifera	18
WINTER ANNUALS		*Quercus velutina*	12
Capsella bursa-pastoris	22	*Fraxinus americana*	9
Erigeron annuus	22	*Quercus alba*	4
Erigeron canadensis	20	*Quercus rubra*	7
Lactuca scariola	20	*Aesculus glabra*	8
		Fagus grandifolia	7
HERBACEOUS PERENNIALS		*Acer saccharum*	6
Aster pilosus	20		

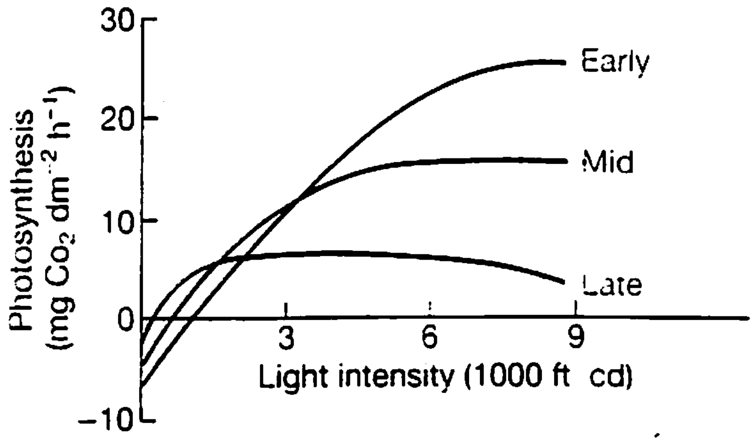


Figure 16.19. Idealized light saturation curves for early-, mid- and late-successional plants (from Bazzaz, 1979).

*See lecture outline from FAB

The design of the plant enables it to gain access to resources and to interact with controllers. Plants need to forage for resources, allocate these resources within themselves, and compete for the resources with neighbors, while at the same time fending off herbivores and reproducing.

Resources used by the plant (light, nutrients, water, CO2 etc) and **controllers** (temperature, light) both modify the plant and in turn are modified by the plant
--Resources usually are continuously available (not in packets), patchy, of varying quality, and the same ones are needed by all plants

The **biological environment** of the plant includes **neighbors** (many genetically related, competition, mutualism, resource modifiers/depletors); **pollinators** (plants need to attract them and optimize interactions), and **herbivores** (insects, grazers etc which may deter growth)

Plant Foraging strategies:
a) Temporal foraging - bloom or reproduce when resources are available
b) Specialized systems for dealing with particular environmental conditions (ie: C4 or CAM plants, leaf size versus light and water levels etc)

Special attributes of plants:
a) **sessile** so must be able to get resources from the surrounding area
b) **modular** - grow by adding new modules not by explanding like animals, usually die piece by piece, no senescence of genet
c) **indeterminate growth** - the number of modules added is not fixed so plant can reach any size, have any number of leaves etc.

There are some rules of branching, budding etc. but most plants are very flexible within these limits and are open to environmental influence **(plasticity = change in response to environmental conditions)**, they need this flexibility because some resources may be limiting in different circumstances and because seeds may fall in different environments and plants can't move away. **Timing of the expressions** of predetermined growth may also vary.

Some parts of a plant may be poorly adapted to an environment as long as the sum total of its effects is suited to the habitat (Adaptability)

Plants have adaptive responses that may result in a shift in the range of their resistance to environmental change etc., roots often have more flexible patterns than shoots since there is more variation in the soil.
---Plasticity may be expressed by a change in the amounts of enzymes produced, behavioral responses (sun tracking by flowers), production of different types of leaves in response to the amount of light received, etc. (See also Table 1.2 Fitter & Hay,). Plasticity may be more important in unstable habitats than in mature comunities.

Plants have **Resource Depletion Zones (RDZs)** around them from which they obtain resources. They need to **optimize resource gain and minimize overlap or competition within this zone** within one genet (between different modules) and/or between different genets, some modules may be deprived in order for the entire genet to have optimal resource gain, Plant's Eye View of a community : how may other genets will it encounter and have to compete with.

How plants may avoid overlap of RDZs:
a) branches may stop growing if it enters an occupied zone
b) old branches/leaves may die if a new branch enters zone
c) reoccupation of zone may occur only after the first occupant dies
d) angle of branching may be narrow so that reoccupation of zone is delayed
However, in nature, RDZs are usually taken over and each plant modifies the resources available to other plants

Compactedness strategies:
a) **Phalanx** - plants that develop closely packed modules that will overlap, take up all the space, and deny resources to other genets
b) **Guerrilla** - plants with long internodes and less branching, little overlap of RDZs, quick to invade then leave an area, can "move" to where resources are so that different modules may be very different from one another due to different environmental influences

One genet can have both phalanx and guerrilla forms (ie: tree with compact top leaves and more spread out leaves near bottom)

Principle of Allocation of Resources: What the plant does with the photosynthate: growth, defense, and reproduction are its options.
Allometric ratios dictate the rules which a plant must follow for structural purposes and survival. Once it is allocated to a certain purpose, cannot be used for another. Allocation depends upon the immediate requirements of the plant and thus on resource availability and environmental conditions.

Plants/Envi

Phys Ecol

· Resource. { adaptns & damage

Biol

Evolution

allocation

cost benefit

optm.

plasticity vs. program

depends on environ

· must be plastic in morph & physio

A unifying view of plant-environment, plant-plant, and plant-animal interactions is achieved through a precise knowledge of resource use.

Fitter and Hay

--Relative growth rate -- A measure of actual growth compared to potential maximum growth -- a useful indicator of the extent to which a species is using its photosynthate for growth and further photosynthesis -- the production and functioning of more chloroplasts as opposed to secondary functions, such as defense, support, reproduction, nutrient and water gathering.

-- The supply of resources is typically unbalanced, therefore in most cases a specific environmental factor limits growth; if that factor is alleviated then growth increases until another factor becomes limiting.
--Multiple limitations may require conflicting repsonses, for example, water and CO2 in determining WUE.
--resource variability demands that plants be flexible on several levels.

Environmental effects may be divided into damage effects and adaptive responses. -- individual responses

1) damage -- wind, ions, temperature, grazing etc.
    -- effects includes death or reduced growth rate
    -- damage implies plant lacks resistance -- molecular, anatomical, morphological, phenological.
2) adaptive -- fine control of plant resistance to damage, involves a shift in range over which resistance occurs.
    -- reversible -- usually physiological
    -- irreversible -- morphological
        both require phenotypic flexibility

Phenotypic plasticity -- widely recognized in morphology, but less often acknowledged in physiological functions, such as enzyme amounts, and various behavioral responses (flower and compound leaf opening and closing, sun tracking)

Population responses

-- Occur on a longer time or over a larger spacial scale than is encompassed by an individual (although definition of the individual if often problematic)
-- such gradual environmental change will result in genetic, and therefore evolutionary change.

--developemnt of ecotypes -- will occur if selection strength is sufficient to overcome gene flow (pollen flow, seed dispersal).
-- scale necessary to develop genetic discontinuities also depends on breeding system i.e. clonal, outbreeders, inbreeders.

When variation is unpredictable, ability to exist in a wide range of habitats is necessary, implying that species of more unstable habitats should be more plastic.

Adaptability and adaptedness

-- plants that survive in their habitats are clearly adapted, so to an extent the word is effectively meaningless.

--phenotypic plasticity confers implies greater adaptabiltiy to environmental change, and can be thought of as a character in itself that confers greater fitness on an individual because it allows an an organism to track environmental fluctuations.

--subject of adaptation and adaptability is a comparative one -- necessary to examine a wide range of species growing in a variety of habitats in order to see the diversity of physiological response that has evolved
-- danger in this approach: that it is easy to ascribe every difference to adaptation without defining precisely the criteria by which one can recognize it.

Manipulation of resources

--Cost-benefit analysis: global economic model
    -- an economic analogy, but definition of currency (carbon, nitrogen) can be tricky, for example, carbon assimilation is often used but photosynthesis may not be carbon limited but limited by a low utilization rate of the carbon fixed.

--Optimization: local model
    -- explain plant function in terms of its own consequences, for example, WUE is a plant's attempt to optimize its own function.

Harper

Clonal organisms

-- all are modular, iterative, and therefore branched

--ultimately the contribution of a genet to the next generation of genets is the integrated contribution from its various modules and the variety of their experiences

--particular genes or gene combinations are repeatedly expressed, so are repeatedly exposed to a variety of environments and selective forces.

modules, branches and resource capture

-- modular growth is basically capture of space

--modules = resource gathering centers

-- RDZ -- created by each module, overlap creates competition among modules

--ideally growth pattern would leave no zones unfilled, but would minimize overlap

--a branching pattern that achieves this may be one that continually changes its growth rules through feedback.

Phalanx: leaves no space unoccupied, deprives space to other genets
Guerilla: leaves zones unoccupied, occupation tends to be temporary
-- growth usually represents a continuum between the two

Avoidance of double occupancy achieved by:
1)branch stops growing when it enters an occupied zone
2) an old branch dies if a new one enters
3) new occupation is delayed until old occupants die
4) angle of branching may be narrow, increasing the time before RDZ is reoccupied.

Programmed growth -- results in species specific characteristic architecture
Responsive branching -- response to immediate environment -- plastic

programmed response is most successful in fine grained and predictable (in space and time) environments

not clear if behavior of clones when they meet is determined by programmed response or by the immediate local environment created when by the interaction between them

In most cases, RDZs are captured or overtopped when clones of the same or different species meet; modules interact by modifying each other's growth rates rather than by active inhibition.

GLOBAL CLIMATE AND VEGETATION PATTERNS

Reading. MacArthur Climates on a Rotating Earth. Geographical Ecology

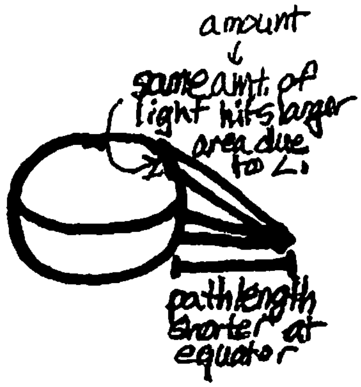
•**Climate Patterns** consequence of distribution of energy, geography

-**Circulation patterns** (MacArthur. Fig 1-5. p.11)

Equator highest energy 1 light has shorter path--less interference
2.light hits smaller area

Warm, high energy air rises 1. Rising air cools, falls over 30°N, S.
2 Trade winds blow to equator to replace rising air

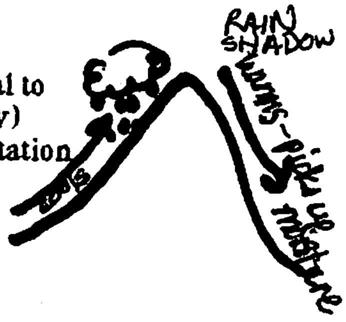
Creates one of three circulation cells in each hemisphere. Second cell, poleward winds from 30°, air rises at 55° Third cell similar to first.



-**Geography** 1 Mountains

Air colder at higher elevations. Moist=3°F/1000ft (Equal to cooling of 100miles of latitude-Hopkin's bioclimatic law)
Air condenses as it cools ascending mountain--precipitation
Dry when it reaches leeward side of mountain

2 Oceans--moderating effect on temperature.



-**Coriolis force**--winds, currents deflect to the right in both hemispheres.

Earth's surface moves west to east.
Surface at equator fastest at 24000 mi/day. Compare to 17,000mi/day at 45°N.
Air moving eastward with surface at the equator will keep its faster eastward speed as it moves North and thus blow to the east or right relative to the slower moving surface
Similarly, air from N moves slower than surface, blows west=right.

-**Example: Deserts.** 1. at 30° where warm air drops, picks up H_2O.

2. On west sides of continents.At 30°, air moving poleward. Deflects right=east. These westerly (from thewest) winds are cold and don't pick up much H_2O over cold ocean. Tend to pick up H_2O over warm land.

3.Usually to east of mountains--the little water westerlies picked up from ocean is lost on mountains.

•**Vegetation Types**	Climate & Location, Vegation Soil.
Tundra	Low temp. low precip. Arctic & alpine regions Veg: Lichens, mosses, sedges, dwarf trees Soil. cold& wet --low spp. diversity.
Deciduous	Seasonal temp., moderate precip. Midlatitudes. Veg: Mixed conifer, deciduous forest Soil. Better drained--higher spp. diversity.
Grasslands	Also seasonal temp., but lower precip. Midlatitudes. Veg: grasses and broad leafed, fire adapted.
Desert	No characteristic temp. low&seasonal precip 30°N,S Veg. shrubby, usually deep-rooted, annuals.
Tropical Rainforest	High temp., high precip. Equatorial region. Veg: extremely diverse Soils: weathered, leeched.

Global Change (Schneider article) Plant Ecology Outline

Since early 1800s, concentration of carbon dioxide in atmosphere has increased from
before IR → 280 ppm to 350 ppm of today (up to 600 by 2050)
due to: increased burning of fossil fuels
deforestation

at present rate of increase, predicted concentrations of 600 ppm by the year 2030

This could have severe consequences because of the GREENHOUSE EFFECT
to see this effect, must look at the earth's energy balance:

100% of incoming solar radiation
- 25% reflected back out by clouds (albedo)
- 5% reflected back out by soil
- 25% absorbed by clouds
- 45% absorbed by earth.
  - thus, 70% of solar radiation is absorbed

Is it just clouds.

eventually, this 70% radiated back out to maintain balance, but,

clouds and earth act as blackbodies, and reradiate absorbed solar radiation as infrared.
the clouds trap this reradiated energy and, acting as blackbodies, reradiate again again back down to earth.
this cycle of absorption and reradiation of energy is the greenhouse effect.
as a result of this, the earth is 33% warmer than it would be without clouds to trap and reradiate the infrared energy.
in fact, warm ages in past have been linked with heightened CO2 concentrations

Does this mean the earth will necessarily warm in the coming years?
Not necessarily. Climate models are still very crude, and increased cloud formation, for instance, might increase albedo which would cool the earth down. The models also do not adequately describe the ocean's role in climate or as a CO2 sink (ocean absorbs 50% of emitted CO2)
but if the earth does warm, and models predict 2-4 degrees by 2030,

will lead to:
- partial melting of ice caps--- increased ocean height
- more melting of tundra--- increased release of organic material
  - positive feedback

- shifting of climatic patterns--- wheat belt moves into Canada?
- change in plant-plant, plant-herbivore interactions
  - see notes on Fajer lecture
- change in mountains environments

The main point is that these rapid changes will disrupt ecosystems and have evolutionary consequences, but without the time scales normally associated with evolutionary change.

- e.g., growing conditions may favor plants migrating north, but soils may not be suitable
  - may cause wide-scale extinctions

hope for the future?

- maybe. From 1973-1987, USA net enrgy use remained constant, although global use increased.
  - energy efficiency is the short-term solution, though developing nations', such as China's and India's, use of fossil fuels and continuing deforestation may offset any gains in the developed world through reduced energy consumption.

Radiation ⟶ plant

Energy Budget

$$\underbrace{\text{Energy into leaf}} - \underbrace{\text{Energy out of leaf}} = \underbrace{\text{energy storage in leaf}}$$

Energy into leaf:

① Absorbed Solar irradiation
② Absorbed infrared irradiation from surroundings

Energy out of leaf:

① emitted IR radiation
② heat convection
③ heat conduction
④ heat loss accompanying water evaporation

energy storage in leaf:

①. Photosynthesis
② Other metabol.
③ leaf temp. change

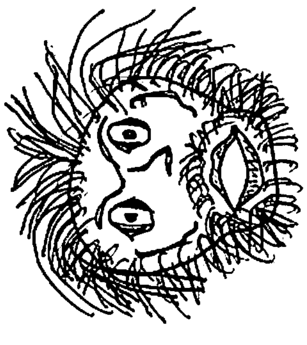
OR:

$$S_n + T_n + LE + H + P = 0$$

On a nice sunny day: (+) (+) (−) (−) (−)

Sn = Net Solar Radiation
Tn = Thermal Radiation – electro-rad. & re-radiation in long wavelength
LE: Latent heat of evaporation OR transpiration
H = Sensible heat transfer
    C = Convection – passive loss
    G = Advection – E lost by force
P = Photosynthesis (very small fraction (~1%))

what is K (extinction coefficient)



Interesting Points from the Readings:

Larcher: Ch. 2 Radiation & Temperature: Energy, Information & Stress

① Attenuation of radiation - different through different canopies

② LAI = $\frac{\text{total leaf area}}{\text{ground area}}$

③ Lambert-Beer Extinction Law : $\overset{\uparrow}{I} = \overset{?}{I_o}\, e^{-\enclose{circle}{k}x}$

where k = extinction coeff.
x = path length
I_o = incident radiati

④ Monsi - Saeki : $I = I_o\, e^{-k(LAI)}$

⑤ Exponential decrease in light intensity in diff stands of plants

⑥ Radiation that hits a plant can be: 1) reflected 2) absorbed or 3.) transmitted 4) reradiated

Region of Spectrum	Wavelength (nm)	% of total Solar Rad.	Mode of Action Photosynthetic	Photo-Morphogenetic	Photo-destructive	Ther- ma
Ultraviolet	290-380	0-4	I	M	S	I
Ph.A.R.	380-710	21-46	S	S	M	S
Near I.R.	710-4000	50-79	I	S	I	S
Long Wavelength	3000-10,000	-	I	I	I	S

I = Insignificant M = Moderate S = Significant

⑧ How plants avoid too much light - Avoidance / Reflect more ...

⑨ Adaptation of Plants to local radiation climate
1.) Environmental : a) Modulative = temporary (ie - turning leaves)
b) Modificative = adapt to average conditions (ie - Sun & shade leaves)
2.) Genetic ⇒ Evolutive (ie - Sun & shade plants)

⇒ Can Superimpose all 3 effects.

<u>Chiariello, Field & Mooney:</u> Midday wilting in a tropical pioneer tree.

full sun

↓

wilting

↓

intercepted PAR decreased 50-70%
& leaf temp. decreased 1-5°C

↓

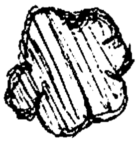
decreased photosynthetic rate by 20%
& decreased transpiration by 30-50%
(ie- photosynthesis decreased <u>less</u> than transpiration decreased)

⇓

∴ increased $\frac{\text{photosynthesis}}{\text{transpiration}}$ ratio = WUE

⇓

increased water-use efficiency.



8

Bill Calder

= evapotranspiration

$$E = \frac{VPD}{\text{resist.}} = \frac{\text{Force } (f(x) \text{ of } T°)}{\text{Resistance}}$$

~~VDP e_s (saturated) T_L~~

saturated vapor pressure

$$VPD = e_s'' (T° \text{ of Leaf}) - e_s (RH) \cdot T_a$$

because not saturated

e

SOLAR RADIATION: BIOPHYSICAL CONSIDERATION

I. How does radiation reach plants?

- Solar Radiation changes in quantity + quality as it passes through the plant canopy

A. Quantity Change

- Monsi-Saeki equation describes how much light is lost as it passes through canopy

$$I = I_0 e^{-\delta(LAI)}$$

I = incident irradiance

I_0 = incident irradiance at top of canopy

δ = extinction coefficient (varies with leaf orientation)

LAI = leaf area index

B. Quality Change

- Far red and infrared increase ~~in proportion~~ compared to other wavelengths
- Visible Red decreases

II. What does radiation do to plants?

A. Stimulates development

- example - germination stimulated by red light

B. Destructive

- ultraviolet light can break down tissues + enzymes

C. Source of energy

III. What do plants do with radiation?

- Plants actively control how much radiation they receive and how the energy is distributed in order to maintain their own proper environment
- Process described by energy budget

$$S_n + T_n + LE + H + P = 0$$

S_n = Total Solar Radiation Received - Radiation Reflected — Radiation Transmitted

S_n = Net Solar Radiation

T_n = Net Thermal Radiation (an energy loss to atmosphere)

H = Convection + Advection

H = Sensible heat transfer (energy lost to heating molecules immediately next to leaf)

LE = Latent Heat of evaporation (energy lost to evaporating water

P = Photosynthesis (energy used to make chemical energy

IV. How does a plant solve an energy budget?

- In general, responses are
    - A. Behavioral (temporary)
    - B. Morphological – sun vs. shade leaves
        heritage
- All responses are constrained by genetic heritage

A. Plant can change S_n

- Diaheliotropic leaf movements increase radiation received "sun tracking"
- Radiation load reduced by
    - Increased reflectance (albido)
        - leaf hairs, light colors, salt coatings
    - Paraheliotropic leaf movements
        - leaf is oriented $\perp$ to sun

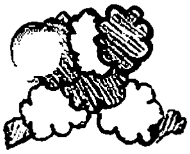
what have people done to show what causes this?

B. Distribution of radiation received depends on the plant's need to maintain proper temperature and water levels

- Maintaing Temperature
    - Evaporation cools plant
        - high LE = low temperature
          · more LE → decr T°
    - Maintaining boundary layer warms plant
        - shelter from wind reduces loss to advection
            - low H = high temperature
        - example, tundra cushion plants
          shield themselves from wind.
- Maintaing H_2O level
    - increasing LE = increasing H_2O loss
    - stomatal closure decreases LE and increases leaf temperature

Examples

- Midday wilting in a tropical plant
    - Wilted leaves decrease S_n
    - Decreased S_n decreases LE
    - Water-use efficiency increased
- Desert Annual with diaheliotropic leaf movements
    - Radiation received is enhanced until water stress causes wilting
    - Maximum photosynthesis occurs at high radiation levels



If a plant is under its <u>parent</u> then it may have all the usable wavelengths absorbed, unless juvenile is different from adult.

only studied as a population

SEED GERMINATION. Stuart Davies 25 October 1989.

Seed germination is the process in which the stored energy of a seed is utilized for rapid elongation of the embryo, resulting in the protrusion of the radicle through the seed coat, and a change to an existence where light is the energy source.

Seed dormancy involves a time delay from seed maturation to seed germination. As an ecological consequence of this inactivity period plants are able to disperse temporally. Three categories are often used to describe different types of seed dormancy (see Harper 1977, The Population Biology of Plants):

(i) innate dormancy - where a seed is incapable of germinating even if the appropriate conditions arise, and may be due to:
- a) embryo immaturity at dispersal (e.g. *Fraxinus excelsior*);
- b) hard-seededness (Fabaceae);
- c) chemical inhibition in seed coat;
- d) temperature requirement (overwintering in many summer species, and high temperatures in many winter germinating species).

(ii) enforced dormancy - where a seed is deprived of the requirements for germination, no specialized physiological mechanism is involved and the seed will (in theory) germinate when all conditions are satisfied.

(iii) induced (or secondary) dormancy - where a seed is without innate dormancy but due to unsuitable initial conditions 'acquires' a dormancy period which cannot be broken even if the appropriate conditions do arise.

(N.B. These categories are artificial.)

THE ROLE OF LIGHT IN SEED GERMINATION

The initiation of the germination response may or maynot be related to the light environment:

(i) positively photoblastic, (light utilizing)
(ii) negatively photoblastic, e.g. *Avena fatua*,
(iii) neutral response to light (less common).

Phytochrome is the major photoreceptor for germination responses to light. It changes in absorption properties after exposure to light. Two forms of the receptor have been identified, P_r and P_{fr}. Red

light (650-700 nm) converts P_r to P_{fr}, and far-red light (700-800 nm) converts P_{fr} to P_r. It is widely recognized that the P_{fr} form is the biologically active form of phytochrome.

Important aspects of the ecology of the phytochrome response:

(i) the P_{fr}/P_r ratio in the seed indicates the degree of shading in the canopy above, as live plant tissue absorbs red light;

(ii) the P_{fr}/P_r ratio in the seed indicates the degree of burial as red light levels decline more quickly than far red light levels.

(iii) P_{fr} reverts to P_r in the dark (more stable), hence photoperiodism.

Other Factors:

Seed light responses are markedly affected by other environmental factors:

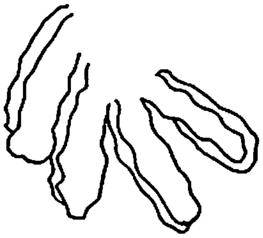
(i) ripening environment (e.g. seeds maturing in maternal tissue that is photosynthetic often require light for germination. Grime, 1981.);

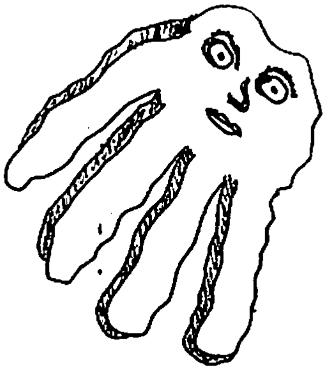
(ii) temperature;

(iii) plant hormones (gibberellins & cytokinins);

(iv) seed coat presence (e.g. presence of an inhibitor);

(v) water availability (e.g. P_r/P_{fr} reversibility does not occur below c. 20% moisture content, Hart,1988).





COMPARISON OF C3 AND C4 PHOTOSYNTHETIC PATHWAYS (ALSO CAM) AND THEIR PHYSIOLOGICAL AND ECOLOGICAL SIGNIFIGANCE

I. Basic Principles of Photosynthesis

-chloroplasts with chlorophyll pigment attract and capture light energy in chemical bonds which is in turn used to fixate carbon and manufacture the building blocks of plant tissue and function - sugars and starches

$CO_2 + H_2O = CH_2O + O_2$

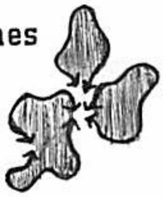
1.Light Reactions

-absorption of light energy by chloropyhll and conversion of energy into chemical bonds as described by the Z scheme - molecular energy raised via electrons in 2 stages ADP → ATP

NADP → NADPH (reduced)

2.Dark Reactions

-CO_2 fixed into molecules - sugars and starches



3.Photorespiration

-affinity of RuBP and rubisco for CO_2 and O_2

- competitive inhibition of rubisco caused by O_2 affinity and regulated by CO_2/O_2 concentrations (21% atmospheric O_2 - 40% inhibition)

-wasteful of plant resources

which is being produced

II. C3 vs. C4 plants

C4 plants

1. Anatomical Differences

-Kranz anatomy: decreases intercellular O_2

undifferentiated mesophyll: fix CO_2
bundle sheath:

2. Physical/Biochemical Pathway Differences

-photosynthetic process split into 2 separate pathways which are separated physically into 2 different cell types which are present together, linked by a shuttle service

-more predictable source and efficient use of CO_2

-dramatic reduction of intercellular O_2 (CO_2/O_2 ratio)

-some implications of above conditions : C4 plants use water, light, rubisco, and nitrogen more efficiently

3.Ecological Implications/Differences

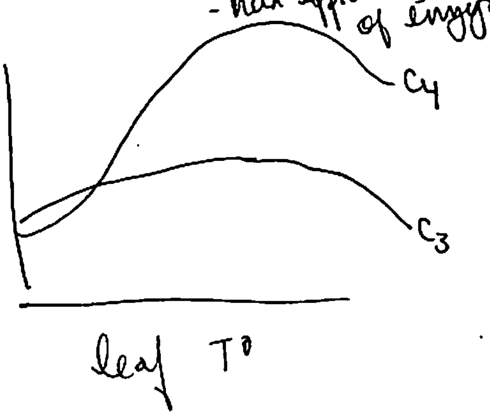
a) CO_2 concentration curves

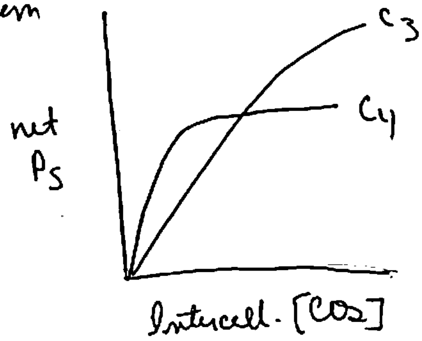
b) Light curves
c) Temperature curves - effect on photosynthesis rate and carboxylating enzymes
-PEP and rubisco
d) Water use efficiency and stomatal conductance curves

4. Habitat and geographic ditribution
- efficient adaptations at warm temperature, high light conditions
-sensitivity to chilling
-summer anual populations in hot desert areas

• PEP enzyme is more effective at high T° than Rubp

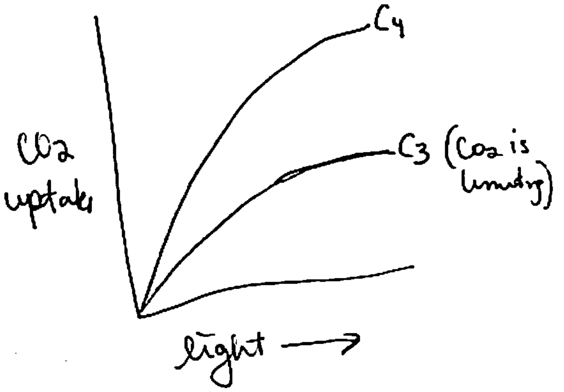
- max efficiency of enzymes other than them



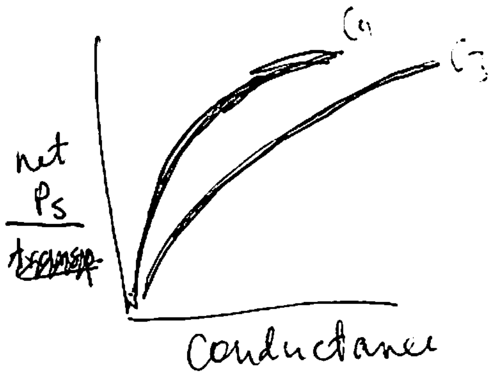


C3 - changes $CO_2:O_2$

C4 - don't suffer from CO_2 competition so CO_2 saturated and light limit,



C3 (CO_2 is limiting)



w/ incr in conductance cause small CO_2 incr. but C4 better prepared to use CO_2.

for a given Ps - C3 have to open stomata wider, and lose more H_2O.

Ruben Lubowski
BIO 149 review

Carbon Gain by Plants in Natural Environments--Pearcey & others

Intro

acquisition of other nutrients tied to C gain
water traded for CO2
C gain important to plant size, survival, reproduction
C gain=CO2 uptake rate/unit photo surface area minus C lost through respiration, herbivory

Leaf Photo capacity

-very variable--sun and shade grown leaves different
higher in plants from resource rich envts
highest in desert annuals and grasses, lowest in desert perennials
-ultimately limited by photo enzymes
    conductance responds to this, not main cause of lower gain
stomata work to minimize transp for daily C gain or maximize C
    gain for acceptable water loss

photo depends on RUBISCO
O2 leads to photorespiration--costs ATP to regenerate RUBISCO
photo limited by electron transport & photophosphorylation capacity
    -inorganic P supply impt
    -stomata keep CO2 in chloroplasts at limit between CO2 and
RuBP limitation
leaves in lower resource envts, lower photo rate
    not nec. true, sometimes 2 lower photo leaves beter than one higher

Alternate metabollic pathways

C4 vs C3 vs CAM
C4 for high photo when warm and sunny
C4 twice as high water use efficiency as C3 but lose ATP
    also use less RuBP
    -also C3 in desert, most perennials
C4 not in cold, succeptible to chilling
C4 ATP loss made up for loss through resp in C3

CAM very high water use efficiency
many plants switch from C3 to CAM or combo during drought
    --sucullents' "CAM idling" (stomata closed, recycle internal C)
        allows them to spring into action with first rain
CAM in epiphytes in upper dryer canopy parts
CAM in some aquatic plants in C-poor envts e.g. Isoetes which "traps"
    C at night cuz low in day

Coping w/ respiratory losses
    most losses from growth respiration
    also production of secondary chemicals for defense
    very little spent for maintenance
    in agric crops more correlation between high resp and reduce prod
    than photo rate and yield

Leaf carbon balance
    leaf C gain must > its C costs for construction, etc.
    resp higher during 1st pahses of leaf expansion
    photo decreases during senescence as N moves out

    evergreens--slower developmenr and lower photo rate
    envtl constraints impt in determining long-term C gain
    water stress, temp, light (too high leads to photoinhibition), humidity
        can reducedaily average photo by 40-70%

Allocation effects
    differences lead to large differences in growth
    optimize allocation so no resource more limiting than other
        consider lifespan of leaves, likely damage, support

Canopy structure
    design to max total plant C gain
    canopy closure to intercept light--optimizze LAI for more light
    leaf angle to sun lower leaves
    horiz. leaves shade competitiors
    leaf angles to avoid photoinhibition
    -need to max total short term C gain wo/ long term decrease fro stress

Conclusions
    C is currency of plants (sometimes N more appropriate)
    lot known of biochem but little understanding of much of resp
        e.g allocation

What are diff betw. enzymes
in diff areas

25th October 1989

R.Crabtree

Review Notes for Biology 149: Carbon Gain and Temperature

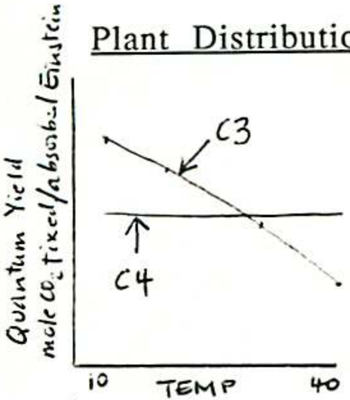
Remember: Net Carbon Gain = Gross Carbon Gain - Respiration

Carbon gain capability is a function of the concentration and activity of photosynthetic enzymes (RubisCo, PEP)^{C4} and substrate availabilities (CO2 and light). Net C gain also reflects respiration rates.

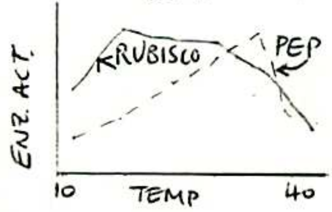
Temperature can have direct and indirect effects on C gain:
- direct - enz activity, rate of photorespiration, rate of dark resp.
- indirect - water status, leads to stomatal limitation

Effects on C gain are sometimes hard to attribute to a single factor, as factors so often interact. Light (? Call it radiation), Water and air temperature are all intimately connected in the leaf energy budget that gives you leaf temp, making response to leaf temp alone difficult to interpret.

Plant Distribution, C3/C4/CAM



Distribution of C3/C4 plants largely reflects the increased cost of photorespiration to C3 plants as temperature increases. RubisCo is not only a carboxylase, but also an oxygenase, and oxygen competition for the active site increases with temperature. See changes in Quantum yield efficiency per unit Light absorbed.



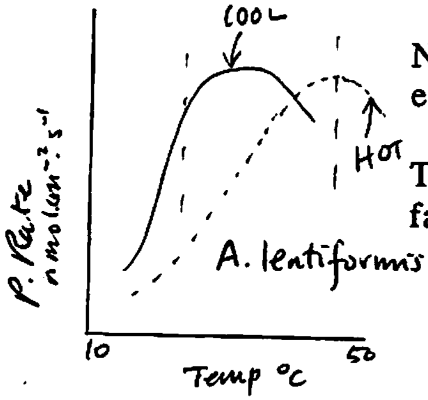
The temperature response of the different carboxylase enzymes also affects C gain capability. PEP is more active at higher temp.

CAM plants respond to a temperature x water problem - opening stomata at night under cooler conditions allows CO2 uptake with less water loss. When temperatures drop and water is plentiful, some CAM plants switch to straight C3 metabolism.

Note that plants have architectural adaptations to reduce heat load - i.e. temperature problems, to maximize C gain, eg inclined leaf angles in desert shrubs, wilting in Piper.

Plant/Leaf level considerations

Measure: Temperature response curves (cf Light and CO2 response curves) to see effects of temp on Photosynthetic rate.

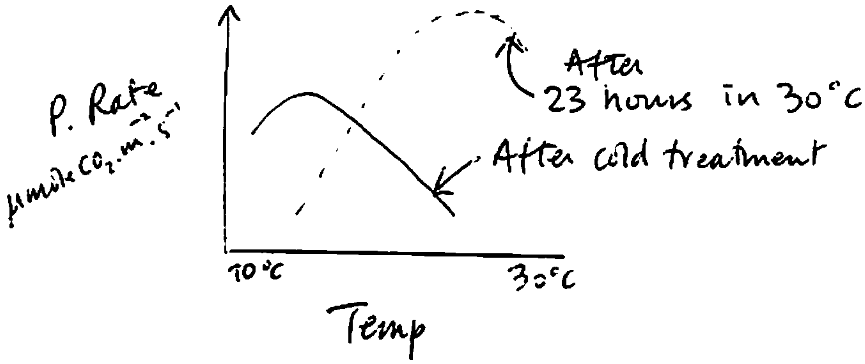


Note that optimum is coupled to growth environment, and that plants can acclimate.

Temperature response is also affected by other factors eg Light level. See fig 3. (10/12/89)

Balsam fir seedlings from different altitudes have different temp optima - reflects mean day temp closely. These grow in short season.

What if temperature regime changes?
Plants from longer seasons, or envs with more variability are able to acclimate, eg seasonal shifts in Erigeron annuus, which probably reflect changes in enz activities, Chlorophyll content and water status.
Plants may acclimate even more rapidly - see Encelia example. (Note coastal env is more constant, plants acclimate less well).
Desert plant acclimation to inc temp is sometimes a function of the plant's ability to keep dark respiration constant as temp increases.



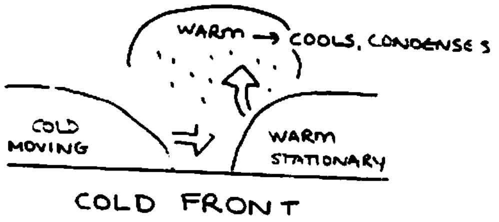
T° response depends on season too -

So - is there natural selection w/in individual - yes, such as Ab or possible things that make enzymes. Is this a "reason" for polyploidy

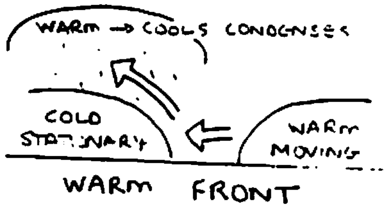
MIDTERM REVIEW: PRECIPITATION

Classes of Precipitation

I. **FRONTAL:** Results from the collision of two air masses of differing temperatures and therefore water content. The warmer air mass is forced to rise above the colder air mass and as it does, it cools, condenses and it rains.

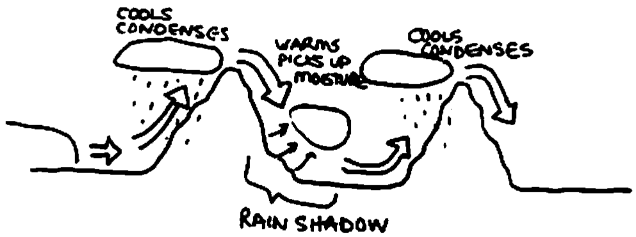


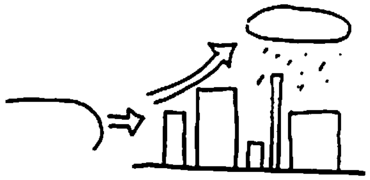
COLD FRONT



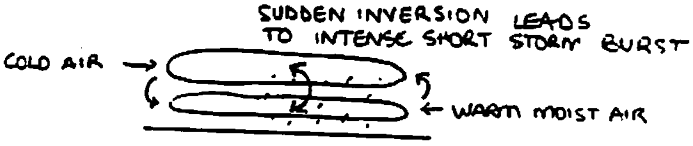
WARM FRONT

II. **OROGRAPHIC:** Results when an air mass encounters an obstacle (mountains, cities) and is lifted up. When it is, it cools, condenses and rain falls on the windward side of the obstacle. In the case of mountain ranges often times a rain shadow develops on the other side as the air mass descends, warms and picks up moisture again.





III. **CONVECTIONAL:** Results from intense surfacing heating which leads to evaporation. The resulting warm moist air rises until it is cooled and condenses to form precipitation.



Types of Rainfall

I. Rain: Get run off. Can lead to soil leaching.

II. Snow: Usually accumulates. Typical ratio of amount to available moisture = 10:1. More gentle water release and therefore doesn't cause drastic soil leaching. Also a good insulator.

III. Hail: Rain drops form and freeze. Crystals get heavy, fall, get pushed back up by wind currents. More layers of ice accumulate and they increase in size. The process repeats until the ice drops become so large the wind cannot lift them again and hail occurs. Can be very destructive.

IV. Glaize: Rain falls, touches cold surfaces and freezes around them. Insulates on cold nights and may protect fragile buds.

V. Dew: Accumulation of moisture on cool sufaces. Commonly occurs in drier habitats on clear nights via radiative cooling. Water condenses on the plants resulting in a major souce of moisture in dry habitats. Often plant structure may be such that the plant can direct watering of itself via dew accumulation.

Quantity and seasonality of rain fall are important when considering patterns of precipitation. Quantity of rain fall, intensity and electrical activity are a function of the size of the air masses involved, their differences in temperature and the speed at which they are travelling. Moisture is therefore important to the determination of vegetation distribution patterns.

Climate diagrams help in accessing the water budget of a region. They reveal the distribution of rain fall temporally, the quantity and what times during the year water deficits and excesses occur. (budget: amount of rain fall, amount of evaporation, run off, distribution)

Phenology, the timing of life history events may be closely linked to moisture availability.

Plant-Water Relations

Nan Arens 5-7602

A) Water Potential (Ψ)

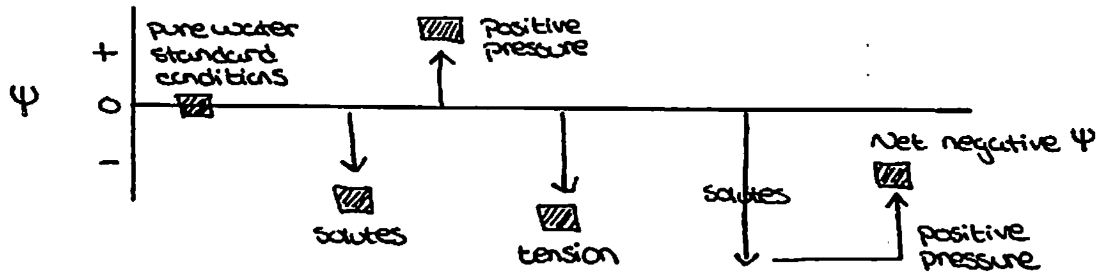
Water potential is the chemical potential (free energy per mole) of water in a system. In other words, how much work the water can do.

Components of Water Potential

$$\Psi = P + \pi + \overset{\rho}{q}gh + \tau$$

1. Pressure (P). Pressure may be positive (turgor) or negative (tension).

2. Solute concentrations (π). Solutes make water potential more negative.



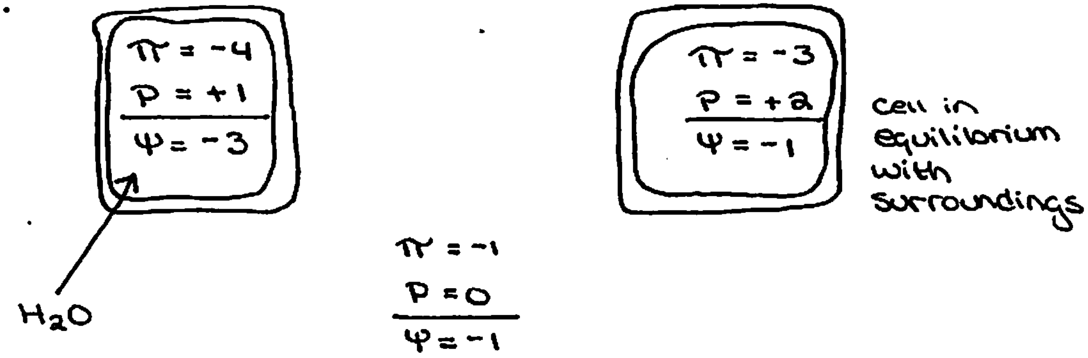
3. Gravitational component (ρgh) where ρ = density of water and solutes, g = gravitational constant, h = height. Important for trees.

4. Matric Potential (τ). Matric potential is the attractive force between soil particles and water. Think of it as extra tension that makes Ψ more negative by making it difficult for roots to extract water from soil. Usually minor.

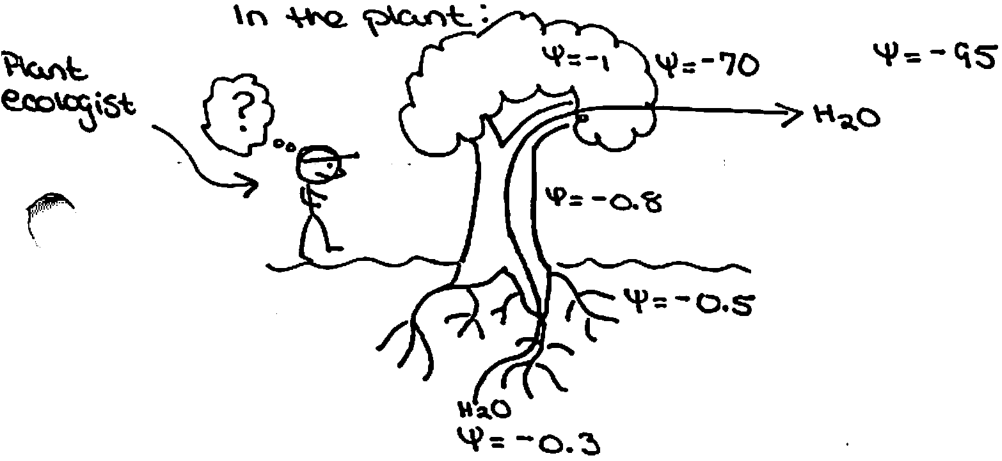
23 October 1989

- Differences in water potential set up a gradient from the soil, through the plant, and into the air. Water moves down this gradient, thus up the plant.

In the cell:



In the plant:



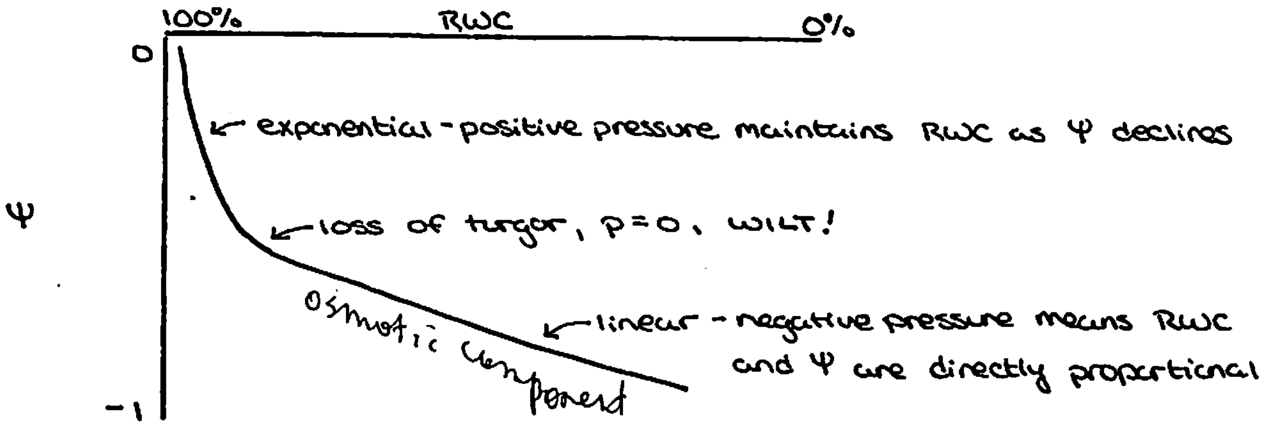
Water moves down the gradient and out of the plant.

B) <u>Relative Hydration</u>

Relative water content (RWC) tells how close the plant is to saturation. Most plants operate between 80% - 100% RWC. This may be a more accurate expression of plant water status (as perceived by the plant).

$$RWC = \frac{\text{Fresh Wt.} - \text{Dry Wt.}}{\text{Saturated Wt.} - \text{Dry Wt.}}$$

Dehydration Curve - relates water content (RWC) to water potential



c) Factors Generating Water Potential Gradient

1. Resistance of water moving through plant plumbing
2. Moisture content of the air (relative humidity) — this is the major driving force of water movement in the plant.
3. Temperature - affects the ability of roots to take up water and transpiration rate (due to effect of T° on RH)
4. Solute concentration w/ more solutes holds H_2O tighter
5. Soil moisture
6. Height of the plant

D) Since water is essential for many aspects of the plant's life, water conditions can impact many plant "activities" that, in turn, have ecological implications. Some examples:

1. Cell division and growth / whole plant growth
2. Germination timing and percent
3. Photosynthesis / carbon assimilation
4. Stomatal conductance
    - influence of roots
    - water storred in stem as "buffer"
    - impact on carbon gain
5. Biosynthesis
6. Phenology of flowering, growth, seed-set, germination etc
7. Embolism = air bubbles in xylem → too much tension causes water column to break, conduction disrupted (CAT)
    - angiosperms (vessels) vs. gymnospers ect. (tracheids)
8. Canopy size / leaf area
9. Leaf absorbancy controls – leaf angle etc.
10. Community effects – niche displacement ect.

E) Water Relations are Dynamic!

1. Varies from tissue to tissue within the plant.
2. Varies through the <u>Soil</u>-<u>Plant</u>-<u>Air</u> <u>Continuum</u> (SPAC)
3. Varies diurnally
4. Varies seasonally when precipitation is seasonal – plant conditions parallel soil conditions
5. Different species (often in the same community) respond differently

F) Examples – Controlling Water Relations – Strategies

1. Cactus – high tissue Ψ even when soil Ψ is very negative.

2. Hydraulic Lift in sagebrush – water brought up from deep soil and lost to shallow soil at night, recovered during the day.

3. Tropical deciduous trees

4. Mid-day wilting (implications for temperature and energy budget).

5. Winter wheat – Fall germination and spring flowering.

✻ Water Stress is important even in the most moist habitats so water relations must always be considered when evaluating plant performance.

✻ Keep in mind the old tradeoff of massive water loss for relatively small carbon gain when stomata are open.

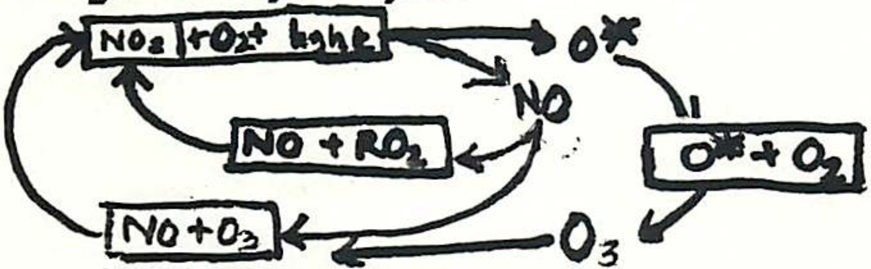
SO_2, NO_x, & OZONE

OZONE	SO_2	ACID RAIN
•2°	•1°	•2°
•regional	•local	•regional
•troposheric O_3 precursors: NO, NO_2, RO_2	•SO_2	•NO_x, SO_x

Point sources of SO_2: coal burning, smelting factories.
Sources of SO_x, NO_x, RO_x: power plants, industry, transportation.

SO_2 is a primary (1°) pollutant: directly from smokestacks.
Acid rain is 2°: from reactions after emitted from source.
Ozone is 2°: from atmospheric reactions - the ~~NO_2 Hydrolytic Cycle~~. NO_2

THE NO_2 PHOTOLYTIC CYCLE



Increased production of RO_2, NO, and NO_2 increases O_3 levels

EFFECTS ON PLANTS

OF SO_2 & O_3

- cuticle damage, needle yellowing, death.
- dissolve epidermal wax-->susceptibility to pathogens - "cumulative poison" - bec. damage potential incr. w/ more NO_x SO_x
- reduce photosynthesis by:
    - ~~decreasing~~ stomatal conductance
    - directly affecting light and dark reactions
    - acute damage

  Faster growing and C3 are harder hit.

- Lower root to shoot ratio.
- O_3 to O* in plant --> cell death.
- SO_2 to H_2SO_3 in plant --> dissociates to S_2 --> destroys enzymes.
- Can handle some SO_2 by S metabolism. Don't have O_3 metabolism.

OF ACID RAIN

- Direct: Cuticle damage, needle yellowing, canopy leaching.
- Indirect: leaches cations from the soil,
  adds N and S compounds
  increases solubility of Al, Fe (toxic)
  changes microbial activity

EFFECTS ON POPULATIONS, COMMUNITIES.

- SO_2 induces rapid resistance, increases ~~genetic~~ phenotypic variation. - incr. magnitudes
  Selection for resistant genotype.
- Community simplification, more sensitive killed.
- Decrease in productivity of system.

Soils

Andrea Arenovski
508 548 1400 (w) x2737

Weathering:

Physical:
- -wetting-drying - disrupts layer lattice
- -heating-cooling- disruption of rocks in which parts have different responses to temperature changes; or surface flaking due to sun
- -freezing- frost shatter due to ice's lower density then liquid water
- -glaciation- grinding
- -solution- removal of ions such as Ca, Cl ...
- -sand blast- erosion of upright rocks in arid areas
- -water-erosion

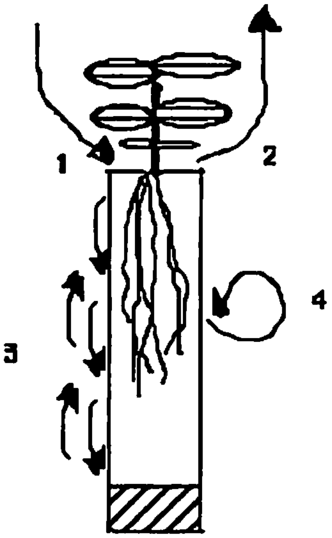
Chemical:
- -hydration- Fe_2O_3 »»» $Fe_2O_3(3\ H_2O)$
- -hydrolysis- silicate breakdown (lose K, Si)
- -oxidation/reduction Fe^{3+} »»» Fe^{2+} (latter is more soluble - disrupts cementing)
- -carbonation- $CaCO_3$ »»» $Ca(HCO_3)_2$ leads to loss of limestone, latter is more soluble
- -chelation - various metals dissolved as chelates with organic material

<<note - chemical/physical not completely separate>>

Parent Material - two kinds:
- -residual- soil is formed at its current location
- -transported- rock »»» finer rock »»» soil »»» moves
  - -water movement
  - -glaciers (cannot separate degradation and transport)
  - -wind
  - -gravity
  - -all types of mvmt. lead to "sorting"

Soil Formation Processes: the main influences
- -parent material- very variable in type, uniformity, quantity, quality
- -climate-temperature, water, sun (all interact with each other as well)
  - -direct and indirect effects
  - -high T° »»» faster decay ««« high water (also leads to more leaching)
  - -high T°, high humidity leads to deep profile
  - -low T°, low humidity leads to shallow profile
- -topography- determines drainage and therefore leads to differing rates of oxidation (oxidation higher where less water)
- -biota- flora and fauna
  - -circular, soil and biota influence each other
  - -different turnover rates leads to different nutrient qualities
  - -different plants leaves and biomass have diff. properties
  - -e.g. coniferous needles very acidic
  - -deep roots can bring up "chemicals" from below
  - -diff. plants grab diff. chemicals
  - -earthworms

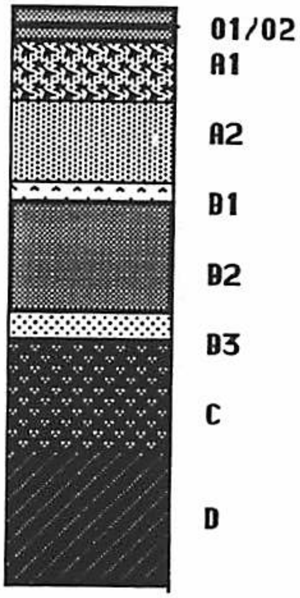
-time- serves to enhance effects of all of the above, esp. weathering
- glaciation, very long term event- new soil develps where old stripped off



Soil Development:

1) additions - organics, nitrogen, sulfur, ...
2) deletions & removals - minerals, water, herbivory, leeching, evaporation
3) translocation - minerals, organics, particles (finer material down)
4) transformation - dacay, hydration, ...

so - start with relatively uniform material but then develop layers



O1 -litter
O2 -humus
A1-mixed mineral and organic
A2-sift from A1, site of maximum leaching
B2-maximal deposition of fine grained
C- unaltered parent rock]
D- bedrock

There is a great variety in this "pattern" depending on site, climate, ...
In addition the boundaries between layers are not always so distinct.

Classification of soil forming processes:
- -<u>gleization</u>- occurs in cold/relatively wet climates
  - organic accumulates
  - sticky clay layer in B
  - w/o oxidation- lots of hydrated iron-oxides (gray, green, blue)
  - common in tundra & bogs
  - not very deep
  - freeze fracturing
- -<u>podsolization</u>- occurs in cool, wet (less than above) climates
  - <u>true podsolization</u>- in Northern regions
    - acidic litter
    - covers large areas with great internal variety
    - slow decay
    - litter/humus layer very prominent
    - A2 very leached (H in for Mg, K)
    - color - ash gray
    - B2- high iron - red or brown (depending on amount of water)

gray-brown podsolics- in warmer areas (South)
deciduous forests
deeper than true
A1 thicker, A2 less leached; B - Al, Fe w/o much water -
lighter in color

yellow podsolics-
better drainage- more oxidation - yellow/red

~~-laterization~~ calcification
warm, low water - grasslands, deserts
carbonates leach and end up in B horizon
depth of B depends on water level, water leaves deposits of solutes

laterization - high Al, low Si, v. deep; tropics, high leaching

Physical and Chemical Properties of Soil:

Physical:

-texture: only concerns mineral part, distribution of diff. sized particles
clay smallest, then silt,sand,gravel,rocks

-structure: aggregation of soil particles together
-structureless: no connections
-aggregation- attached to each other through bonding or glue or roots
-small round "PEDS" in A1
-platy PEDS in A2
-blocks, columns in B - offers resistance

-color: affects energy balance

Chemical:

-clay minerals and lattices:
1° minerals lead to 2° lead to clay paricles
-silicon tetrahedrons, aluminum octahedrons
-clay has multiple meanings (texture, size, ...)
-lattices 1:1 implies one silica sheet and one aluminum sheet
-substitution- Si replaces Al
-charges will attract ions, so if not 1:1 then more of one charge, and will hold ions better
-low pH (acid - high H+) hydrogen will replace cations

Etherington: Chapter 4, chemical and physical properties of soils. The root environment

Soil -- has solid, liquid and gaseous components
solid -- sand silt clay
clay -- major source of ion exchange capacity, along with organic matter; ion exchange capacity and weathering -- replenish soil-plant mobile nutrient pool.

1. Cation exhange complex (CEC) -- clay and organic matter
--unsatisfied neg. charges loosely bound with metals and H+ ions, exchange with ions in bathing solution
--cations -- most metalic elements taken up by plants as cations exists in three forms
a. as sparingly soluble components of mineral or organic material
b.adsorbed onto CEC
c.in soil solution

--in solution are freely leached, but exchange complex forms a resevoir
--plants acts as biocyclers, the root systems extracting nutrients from deeper horizons, returning them to soil surface in litter, decomposition returns them to exchange complex
--acidification - metal cations replaced by exchangeable hydrogen

2. Anion exchange-silicate clays and organic matter that have free positive charges on surface

3. Soil solution -- aqueous component of soil
--dissolved electrolyte content a function of the exhange equilibria of cations with the exchange complex, the solution equilibria of soluble inorganic materials, and microbiological mineralization equilibira of such materials and nitrogen and sulpher containing organic compounds
--components may move through the soil by mass flow with soil water or by diffusion

4. Soil Acidity
--associated with Hydrogen and aluminum on exhange complex and equibrium of solution of H+ ions in soil interstitial water
--pH strongly correlated with soil type, vegetation type, profile horizon

--natural soils range from 3-8.4
3: soil soln in equil with H+ saturated soil
8.4 calcium carbonate in equilibrium with atmospheric CO2
--calcicoles -- generally in cation saturated soil, usually occur above pH of 6.5
--calcifuges -- below 3.8-4.0 and are strongly desaturated

--pH 5-8: bacterial and fungal decomposition rapid,
-- below 5.0: decomposition activity reduced

-- long-term water-logging lowers pH of alkaline soils and raises pH of acid soils -- most anaerobic soils around 5-7

-- value of soil pH -- can be considered an index of its exchangeable cation saturation -- low saturation results in large equilibruim complex of H+ and with low conc. of metals such as calcium, magnesim and potassium (which are supplied to plants through CEC)

--Biological consequences for: (details in ch. 9 of reading)
a. solute availability
b. toxicity threshold
c. growth, through impeded N fixation, nitrification and denitrification (Mb deficient at low pH, needed by nitrogenase and nitrate reductace enzymes)
d. calcium deficiency

5. Soil organic matter
-- nature governed by vegetation, climate, parent material and topog.
A. formation
1. transport and breakdown of plant fragments by earthworms centipedes, fly larvae, mollusks. These also carry fungal and bacterial inocula
2. old litter: animals that feed on micro-micro-organisms -- protozoan, nematodes, springtails, mites
B Humus formation and pedogenesis
1. raw humus (mor)
--forms in low pH, below 3.8-4 in nutrients deficiency,
-- slow bacterial activity, thus decomposition, earthworms absent accumulation of deep O layer, plant roots confined to O or A
2. Mull humus --
-- above 5.0
-- rapid decomposition, earthworms, many deep-rooted plants active in nutrient cycling and porduce easily decomposible litter, which is

encorporated by worms into A and B layer

--pedogenesis--
  --affected by parent material, climate, topography, plants and animals and micro-organism species composition
--podzolization
  --promoted by low nutrients content, high lignin (fiber), decreased palatibility of plants, micro-organism inhibition

C. Nature of soil organic matter
  --represents equilibria between litter imput and degredative and resynthetic processes
  -- Minor constituents -- carbohydrates, lignins, fats, proteins, amino acids etc, decomposed quickly
  --Major contituent: Humic complexes, which are macromolecules bount to clay colloids = clay-humus complex

D. Properties of humic complexes: clay-humus complex = network of clay particles and macromolecules
  --converts mud-like mixture of compacted mineral matter to structurally aggregated, easily deformable, with pore spaces that provide aeration.
  --amount varies with depth and soil type
  --cation exchange component of humus -- less important in clay soils, but may be the main source in sandy soils

  --tropical soils
    -- tendency for degredation of organic matter to outstrip production as temperature increases
    --but this is overlaid by a wetness effect -- high water content lowers 02 content, lowering decomposition
    --lower pH reduces bacterial activity and ecourage organic matter accumulation

6. Soil particle size distribution
--texture influences soil-water relations, aeration and penetrability through relation to pore space
-- indirectly relates to nutrient status- clay main source of many nutrients
--sandy soils tend to be nutrients deficient, and lose nutrients to leaching
-- water infiltration affected -- panning: closing of pores
--protection by a vegetative canopy and good soil structure stabilizes soil against panning, run-off and soil erosion.

7. Soil structure: aggregation and porosity
--aggregates of ind. mineral particles= peds
--soil structure due to pores -- areas between peds, created by roots, animals and shrinkage of clays in dry weather

-- pores -- impove aearation, pathways for infiltration of water, allow easy movement of roots and animals
--structure and plant roots -- root growth can occur only of soil particles can be parted by extending roots -- requires pres to absorb the deformation.

Plant Demography from November 14, 1989 Diana Lane

Relevant Readings:
Bazzaz, F.A. Demographic consequences of physiological traits in *Perspectives on Plant Population Ecology*, R. Dirzo and J. Sarukhan editors.
Silvertown, J.N. The Demography of some plant populations in *Introduction to Plant Population Ecology*, 1st Ed.
Additional Reading:
Barbour, Burk, Pitts. Population Structure and Plant Demography (chapter 4) in *Terrestrial Plant Ecology*.

"Demographic features of populations are based on individual responses which have physiological bases." (Bazzaz, p. 546)

Relevant Definitions:

Population

Genetic: A group that interbreeds

Ecological: A group found in a common locale at a common time, defined by the investigator

Deme: Sub-unit of a population with frequent gene exchange

Genet: A genetically identical unit arising from a seed

Ramet: Vegetatively produced population units

Cohort: All of the seedlings germinating or being recruited at the same time

Demography: The study of ~~changes~~ births, deaths, emigration, immigration in populations through time

Demographic characteristics of populations include:

AGE STRUCTURE - How many individuals are in each age class

Two different methods for determining age structure

1. For short-lived species, an observer can follow a cohort of seeds or seedlings until all individuals die
2. For long-lived species, sample a population at a single time and determine age structure by dating individuals

What information do we gain from an age structure?

1. Knowledge of recruitment to population
   Episodic recruitment is common because seeds may be dispersed irregularly in large crops ("masting") or because environmental fluctuation may prevent annual recruitment
2. Knowledge of future age structure of population
   Example: seed and seedling suvivorship curves of many tree populations resemble a reverse "J", which implies that regeneration is occurring

SIZE STRUCTURE

1. Because of developmental plasticity in plants, size can be a better indicator of demographic status than age
2. Charting height and weight can reveal:
   a. If tree seedlings remain suppressed in understory for many years
   b. How many members are at reproductive stage

SPATIAL STRUCTURE

1. Reveals intensity of neighbor interactions

2. Gives information about how population was dispersed and about resource patterns

GENETIC STRUCTURE

1. Important to know because all genotypes will not have equal rates of growth and survivorship

Note--Determining the **absolute numbers** of individuals in plant populations is **generally not important** because deciding who qualifies as an individual is subjective, and because population size will not necessarily correlate with productivity or biomass

except genets

SURVIVORSHIP CURVES

Life tables can be used to create survivorship curves which plot the log of the number of survivors at each age interval vs. time

Extremes orginally described for animals

1. **Type I**--Low initial mortality, but rapid mortality in older age classes, ex. annuals in open situations
2. **Type II**--constant mortality rate
3. **Type III**--Rapid initial mortality followed by period of low mortality,ex. large forest trees with high seed mortality

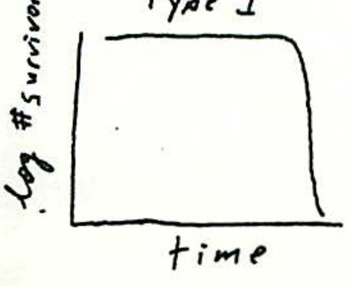
Note--Large long-lived animals are often type I, while large long-lived plants are often type III

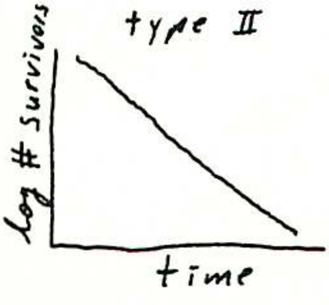
MODULAR DEMOGRAPHY

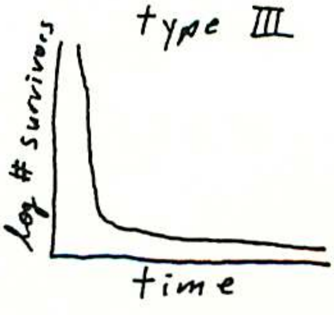
1. **Survivorship** curves can be constructed **for growth modules** such as **leaves, branches, or roots**
2. Important because plants can respond to changing environmental conditions by changing number and size of modules
3. Example--Age structure of a population of leaves of an <u>Ambrosia trifida</u> plant gives information about resource allocation and contribution of leaves to photosynthesis(see Bazzaz pp.336-340).

IMPORTANCE OF DEMOGRAPHIC MODELS

1. Helps to **identify population limiting step**
2. Indicates stage of greatest **selection pressure**
3. Allows **rate of** natural **replacement** to be monitored (useful for managers)
4. Extremely useful when **causes of mortality** can be added to mortality tables







NICHE

Bazzaz, F.A. 1987. Experimental studies on the evolution of niche in successional plant populations. In: A.J. Gray, M.J. Crawley, and P.J. Edwards (eds) Colonization, Succession and Stability. Blackwell Scientific, pp. 245-272.

A fundamental question in ecology is how do species coexist in communities. One answer is that species partition the environment so that everyone will have a bit of their own--out of this arises the concept of **niche.**

Major Concepts of Niche

1. The habitat in which a species makes its living (preferred habitat).

2. The role of the species in the biological environment (what the species does).

3. An n-dimensional hyperspace composed of a set of ecologically-relevant resource/controller axes (physical and biological).

4. The way a species' population is specialized within the community (relies heavily on interaction with neighbors).

*Niche has been subdivided into "life-form" niche, "phenological" niche, "habitat" niche, and "regeneration" niche to reflect the many components that must be considered when discussing niche.

The commonly held paradigm is that competitive interaction and selection will shape the niches of species in a community so as to minimize future competition. However, there are some problems with plants.

Problems with Niche Differentiation in Plants

1. Plant resources are continuous, not discrete.

2. Autotrophy limits resource-gathering possibilities.

3. Plants compete for space as well as other resources.

4. Biotic interactions may be more important than competition for physical resources.

5. Sessile - so local selection high

Things that Must be Considered with Respect to Plant Niche

1. There are many resources and controllers (physical and biological) all impinging on the organism simultaneously. And biological factors are probably more important in determining niche.

2. The organism's response to each resource and controller is rarely equable across the gradient.

3. More than one resource determines whether organisms can coexist in a community.

4. Resource axes are unlikely to be simple or orthogonal. And the multidimensional approach is necessary to understand the species response.

5. All of the above may be influenced by neighbors.

Therefore, **niche can be defined as the pattern of response of an individual, population, or species to the physical and biological gradients of its environment.** Responses on single gradients do not define niche, but rather define **niche breadth** or **response breadth** for a single niche axis.

Niche differentiation refers to differential resource use that results from competitive interactions between species in a community (coevolutionary displacement). **Niche separation** refers to differences in resource use between species that are not coevolutionary (fitting together "preadapted" species).

Niche Breadth and Successional Status

Early Succession: Communities made up of broad-niche species and usually having low diversity because each species occupies a large portion of total available niche space. High competition because of extensive niche overlap. Reduced biomass. Coexistence is promoted by species having narrower responses (refugia) within their total niche where they can escape from competitive interaction and reproduce.

Late Succession: Communities made up of narrow-niche species, usually with higher diversity because more species can be packed along the gradient. Competition reduced. Higher biomass.

*While these generalizations hold for the community as a whole, individual species within them may have varied responses to each gradient.

Niche and Competition

*Since there are real limitation to niche differentiation among plants, it is possible that competition may not be of primary importance in plant community development.

Conclusions

Niche differentiation has occurred in late-successional communities and is the basis for clear niche separation in these communities (especially biological factors like pollinators). In contrast, much less differentiation has occurred in early-successional communities and that many of the observed differences in response among species within these communities is likely caused by difference these species evolved elsewhere.

Therefore, in early-successional communities, the physical environmental variation may necessitate broad niches and preclude coevolutionary niche differentiation (ties in with idea of plasticity), while in late-successional communities coexistence may be promoted by some niche differentiation.

* early successional species have MORE competition but the nature of competition varies through ontogeny and diff. areas so much that directional selection is diminished

mean response breadth higher in
early successional

<u>but</u> w/ competition - total production
reduced due to less refugia
coevolution in late succession
- niche shifts during ontog
- more comp. in early success
bec. less selection in past
this doesn't make sense - then why
shouldn't there be more differentiation.

Disturbance and ecosystems

The actual definition of a disturbance is problematice because it depends on your frame of reference and the actual system.

> That is, you need to know the original range of behaviors within a system to detect a disturbance.
> Depending on the system studied, a disturbance could range temporally from an ice age to a sun fleck.

DEFINITIONS

> Bazzaz defines disturbance as a sudden change in the resource base of a unit of the landscape that is expressed as a readily detectable change in population response.
> emphasis on functional change

> Tim ~~Brian~~ Sipe uses a more probabilistic approach, defining a disturbance as a change in a system that deflects it from its most probable course.
> look for change in acquisition of energy and resources

disturbance occurs at some level in all ecosystems, and is important in the generation and maintenance of speceis diversity and environmental heterogeneity.

> always keep succession in mind when thinking about disturbance

The nature of disturbances

SIZE and INTENSITY

> compare a single defoliation with mass herbivory and its effect on gap size, or a high intensity fire versus low intensity for clearing understory and leaf litter.
> ------importance of environmental heterogeneity

FREQUENCY and REGULARITY

A number of systems are dependent on periodic disturbance
    fire in the California chaparral every 30 years leads to stable system.
    regulates age structure and life history strategy within the population
        e.g., plowed fields are dominated by annual

SEASONAL TIME OF OCCURENCE

> can species take advantage of resources made available?

Reproductive Strategies Dependent on regularity and nature of disturbance

in fire regime, early reproduction is advantageous (may be serotinous cones, as well)
    size may be more important than age in determining time of reproduction

Effect of Disturbance

modification of physical environment
    change in light, wind, temp, carbon dioxide, relative humidity
    -----act as selective force

--- pioneer species (r-species)
    seed germination keyed to disturbance
    effecient dispersal in space and time
    broad niches to cope with high level of variability and unpredictability

SUCCESSION - the directional change with time of the species composition and vegetation physiognomy of a single site - Finegan 1984

Historical development of the concept of succession
Cowles, Clements - introduced dynamic principles to a static field of vegetation mapping

Clements (1916) irreversible direction; progressive - from lower to higher life forms; predictable - convergence of successions to the regional climax, therefore deterministic; driven by "reaction" (site modification by plants present)

Egler (1954) Initial floristic composition - all spp. in a succession are present at the site at initiation of succession; sequential dominance of plants with different life histories and sizes at maturity; autogenic change may inhibit rather than facilitate species transitions

Odum (1969 Science) Presents table of trends (community energetics, structure, life history, nutrient cycling, overall homeostasis) expected in the development of ecosystems - subsequent testing supports some expectations and disproves others. He believes succession is community controlled and culminates in a stabilized ecosystem which is most resistant to outside perturbations.

Walker (1970) acceptance of multiple pathways of succession

Divergent views of the community underlie different schools of succession theory.
Clementsian view of community: superorganism; plant associations are discrete, integrated units repeatable in a particular habitat (stresses determinism).
Gleason (1937) individualistic concept of the plant association; associations are not discrete entities, but depend solely on the coincidence of environmental selection and migration (stresses stochasticism)

Determinism vs stochasticism - the development of a general theory of succession
--determinism (see Clements) autogenic change + facilitation
--stochasticism (see Egler) autogenic change - tolerance, inhibition; path of succession based on the stochastic nature of the initial floristic composition
Finegan (1984) theories are not mutually exclusive; "facilitation, tolerance, inhibition, allogenesis are interdependent mechanisms and may affect same individual successively or simultaneously during its life cycle"; fruitless to search for a general, universal theory of succession, a synthetical approach should be sought

Causes of succession - relative importance unknown & variable
competition - pioneers colonize because quick arrival, preemption of resources; replacement of pioneers with spp. of increased competitive ability (in the changing environment)
alellopathy - maintains present spp. by directly inhibiting other spp. or inhibiting nutrifying organisms thus changing the resource base perhaps favorable to a replacing species
life history attributes -

Models of succession
-Population models - concerned with the rate of change of numbers of a single species over time
-Markovian models - concerned more abstractly with the state of the system; displays probabilities that certain events will happen (rates of changes not considered)
-Compartment models - JABOWA, FLORET

Attributes of early and late successional plants
*Individual level (life history traits; physiological traits) see Bazzaz, F. A. 1979. The physiological ecology of plant succession. Ann. Rev. Ecol. Syst. 10:351-71.

*Community and ecosystem level - changes in total biomass, productivity, diversity over time (Bormann & Likens, Loucks)

Additional notes:
Succession is initiated by disturbance; to understand succession, it is important to evaluate the type and severity of disturbance and what changes that disturbance has had on the resource base to which plant populations will respond. What propagules are present and viable in the soil following disturbance? Importance of biological neighborhood and dispersal mechanisms in subsequent succession.

Scales of succession - fungi on decaying leaves; intertidal algal succession; oldfield succession; forest regeneration

Susan Bassow
23 January 1990

Plant-Plant Interactions -- Part 2

Normal vs Skewed Distributions

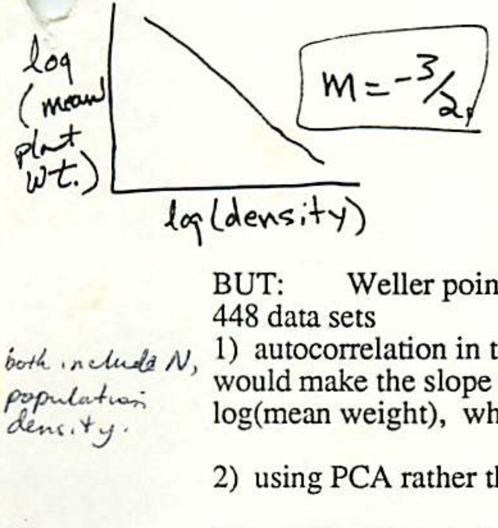
Ways to measure degree of skewness -
1. Skewness - visual
2. Gini Coefficient -
3. C.V. (Coefficient of Variation)

Thomas and Weiner, 1989
Hartgerink and Bazzaz, 1984 - 50-70% of size variability is explained by microenvironmental heterogeneity

Causes of Plant Hierarchies (many are not just competitive)

1) log nature of plant growth -- big plants grow faster -- this alone will lead to a skewed nature of the population
2) Genetic Variablity
3) Maternal Effects
4) Timing of Emergence
5) Environmental Heterogeneity (Hartgerink and Bazzaz, 1984)
6) Resource Competition
    - dominance and suppression
    - asymmetric vs symmetric competition (directional or non-directional resources) Silvertown

Self-thinning "law" (or "non-law") (Yoda, 1963)



$$wt = C d^{-a}$$
$$\log(wt) = \log C - a \log(d)$$

where:
wt = mean dry weight
d = density
C = constant
a = const $\approx -3/2$

Block Model
w = wt
l = length
s = surf. area
$w \propto l^3 \quad s \propto l^2$
so: $w \propto s^{3/2}$
when @ 100% cover, $s \propto 1/d$ so
$$\boxed{w \propto d^{-3/2}}$$

BUT: Weller points out major flaws:
448 data sets

1) autocorrelation in the x and y axes -- Weller suggests plotting log(N) by log(total biomass). This would make the slope = -1/2, rather than the traditional -3/2. [rather than the original plot of log(N) by log(mean weight), where mean weight is total biomass/N]

both include N, population density.

2) using PCA rather than regression because both axes have measurement or sampling error

3) questions how to test if slopes of empirical studies are significantly different (a. slight differences in slopes of log-log plots would mean big differences linearly; and b. earlier work tended to ignore contradictory data)

4) tolerant species vs. very intolerant species - can vary this

Response of Individuals to Neighbors
    Nearest Neighbors
    Theissen Polygons
    Multi-species neighbors

Plant-Plant

Regulation of birth/death

①Density independent - no effect of neighbors

②Density dependent

processes are complicated
-negative interactions aren't always only thing occurring
-pos
①vines
②pollen tubes
③attraction
④shade

see graph

①"Density-effects"
-e.g.-Pollination - greatly affected by density

-++-attraction of pollinators } emergent property
---" " of herbivores }

-not affected of resources

②Plant-plant interactions
-resource dependent
-+++ - intercedence
"---" = interference, ~~intercedence~~
competition - for something in particular
- ~~effect~~

parasitism is just different spacial relationship of competition. It is just competition for nutrient/etc. that one organism already got a hold of - Sort of like interception vs. fumble.

Environmental Heterogeneity ⊕ Plant Plasticity
(Bazzaz + Sultan article)

Ecological variation = differential performance (i.e. growth, physiology + reproduction) of a given organism under various environmental conditions
- different plant species, population + genotypes exhibit different growth responses to various env. factors → plasticity
- fitness characters reflected in present distributions + have implications for future selective outcomes → ecological + evolutionary consequences
- description of plant variation must look at ① plant response to env + ② description of env. encountered (influences on development - seed size + quality)

Patterns of Environmental Heterogeneity
All environments are heterogeneous to some degree - element of plant habitats
- early ⓥ late successional habitats → early ones are spatially + temporally more variable than grasslands + grasslands more variable than forest floor (measurements: light, soil water potential, temperature, nutrients)

Causes of env. patchiness / heterogeneity:
- Variability of soil + nutrients - tree falls
- Soil chemistry, microflora, microfauna - differential uptake + release, accumulation + breakdown of debris, of coexisting species
- Vegetation - variation influences plant establishment + stand composition
- Distribution of herbivores - differential damage in space + time
- Pathogen distribution - varies w/ microsite humidity

→ Fitness implications of variation of above env. factors as encountered by plants

Plant Responses on Environmental Gradients
Env. factors vary from broad to fine scales, spatially + temporally, from seasonal variation to variation as encountered by different parts of an individual plant to env. shifts as experienced by changing life history of plant

Ecological response breadth as determined along environmental gradients = linear range of controlled env. states from low to high levels
- measure plant growth and reproduction as broad to narrow response curves
- response curves connote actual distribution pattern spatially + temporally

→ Species may consist of diverse narrowly specialized genotypes or broadly generalized genotypes - evolutionary predictions of selective divergence

Study: early successionals have broader + more overlapping response patterns
- each species exhibited unique response to each env. gradient
- broad responses in some factors ≠ broad responses in others
- many showed restricted range response for sexual reproduction ⓥ vegetative growth
- competitors, presence of particular species, compressed response for some, not others

→ relationship to observed community diversity patterns

Genetic Variation in Plant Populations

▲Natural selection ⓥ maintenance of genetic variation (specialization ⓥ generalizat

→ Consistent, strong selection pressure will evoke genetic changes or selective differentiation which enable organisms to accomodate env. demands = mechanism of adaptive change

- would expect fitness-related characters of growth + reproduction to be strongly selected for, yet evidence for abundant variation -

Question: Under what circumstances will genetic variation for ecologically meaningful factors by winnowed out by natural selection? or directional selection constrained, + variation maintained?

Environmental Variation + Diversity

Env. heterogeneity + patchiness as promoting species diversity / richness

- Temporal - successional sequence generates increasing microenvironmental variation thru increased species diversity + structural complexity - exploited by species of diff. response patterns -
- Rainfall + temperature flunctuations - elicits diff. dominant species in diff. years
- Genetic longevity greater than scale of environmental variation - env. changes result in differential seasonal reproductive success ⓥ diff. mortality of genotypes

Conditions needed for selection for multiple niches: constant spatial diversity + variation, large selective differentials, restricted gene flow

Frequency dependence of env. factors affecting fitness parameters: if not fixed but contingent on relative competitive success (as influenced by genotype, microsite, neighborhood), complex + flunctuating selective pressures result (v. one-directional + consistent), promoting maintenance of genetic variation. ▲Increase fitness value of genotypes w/ broad eco. response capacity

- in field, not complete correspondence between env. differences and population response - "failure" to produce complete "adaptation"
- seasonal changes affect community composition and buffer selection pressures - patches dominated by diff. species at diff. times → leaves record of flunctuation in seed bank - evidence of variation of annual abundance yearly
- unpredictable variability + frequency opposes evolutionary specialization in seedling response

Other Ecological Mechanisms Important to Maintenance of Genetic Variation

Phenotypic plasticity = flexibility in size, morphology + physiological behavior in response to environmental variation = flexible expression of individual genotypes = mechanism by which a population can accomodate environmental stresses (patchiness) w/out selective/directional change, ∴ maintaining existing genetic variation → buffers against selection, yet plastic responses themselves may be selected for -

Examples: Individual Response Flexibility

- Response to density stress
  - avoid death thru reduced growth rates. Maintain reproductive output thru increased allocation to reproductive ⓥ growth biomass
  - developmental flexibility thru plasticity in sex expression. Monoecious plants produce only female flowers – invest more energy in seed production
- Low soil moisture stress
  - increase biomass allocation to roots
  - CAM plants switch metabolic pathway (physiological plasticity)
- Light / temperature variation (morphological plasticity)
  - change leaf angle
  - change petiole length
  - sun ⓥ shade leaves
- Pathogens or herbivores
  - plasticity of defence capabilities - synthesis of compounds
  - w/in plant variability - protects against herbivores ⊕ evolution of defences -

Clonal Integration

Clonal plants can integrate spatial heterogeneity encountered by diff. ramets
→ physiological integration buffers genets against patch-specific fine-scale selection pressures & distributes probability of success evenly among genotypes. + so most maintained w/in a site

Evidence: • translocation of photosynthate from parental to developing ramets
- w/ ↑ density, interconnected ramets larger & more equitable in size → buffering of variation in biotic neighborhood
- differential response of "phalanx" ⓥ "guerrilla" forms - former more plastic + eco. tolerant, more equal expansion

Non-clonal perennials integrate variation in time & space thru
- storage organs
- woody species - cumulative growth
- seasonal variation of reproductive allocation

} buffers w/in + between seasons-

Environmentally Imposed Determinants of Fitness

Non-heritable influences may obscure or override genotypic diff.s & oppose directional/disruptive selection
- Env. stress affects seed size which affects many factors - generational carryover
- Microsite conditions - minute scale, depth of seed burial, pattern of soil disturbance, emergence timing
- Different age classes of individuals coexisting w/in a population - diff responses of diff. ontogenetic stages - obscure genotypic differences

- Patterns of herbivory - distribution + behaviour, plant location + apparency - not necessarily genetically correlated - direct + indirect effects, costs of producing defences + reflected in seed production
  - better competitor can equal preferred food species - offsets competitive differential to maintain diversity

→ env. inherently random in many aspects so that responses to on one gradient don't necessarily align w/ other varying factors -

Life History Characteristics

- Seed bank - storage of genetic material/variation prevents genetic losses due to drift.
  - env. variation which may reduce present populations don't nec. reduce genetic material because of stored variation in *underground* population
  - → population *resistant* to genetic response to short-term env. variation
- Immigration thru pollen/seed dispersal
  - important means of maintaining genetic variation - lost variants reintroduced from nearby populations
  - continued gene flow

Conclusion

Complexity of interactions in nature between heterogeneous plant env., plant's response pattern, + structuring influence of gene flow, may mitigate force of natural selection..

Bio149: Experimental Plant Ecology Fall 1989

Lecture Outline for Dr. Jim Coleman ("Jimbob")

Ecological Consequences of Atmospheric Pollution to Plants

1. What are O3, SO2, and Acid Rain, and How do they Differ?
    - a. O3
        - -Troposheric vs stratospheric O3
        - -Secondary pollutant
        - -NO2 Photolytic Cycle
        - -Sources of ozone precursors (NOx; CH2...)
        - -Regional scale
        - -Other oxidants (PAN; H2O2)
        - -Most important pollutant (e.g. agricultural losses)
    - b. SO2
        - -Primary pollutant
        - -Point source (local)
        - -Sources
    - c. Acid Rain
        - -Catch all phrase?
        - -NOx + SO2 + O3 + H2O
        - -Secondary pollutant
        - -Regional

2. Direct Effects of Pollutants on Plants
    - I. SO2 + O3:
        - a. General mechanisms of action
        - b. Acute damage
        - c. Reduced photosynthesis
        - d. Plant growth and resource allocation
    - II. Acid Rain
        - a. Cuticle damage
        - b. Nutrient imbalances
        - c. Release of toxic cations to soil

3. Implications for Plant Populations and Communities
    - a. Types of changes
    - b. Variability and selection for resistant genotypes
    - c. Community simplification (e.g. Forest Decline)
    - d. Research on O3

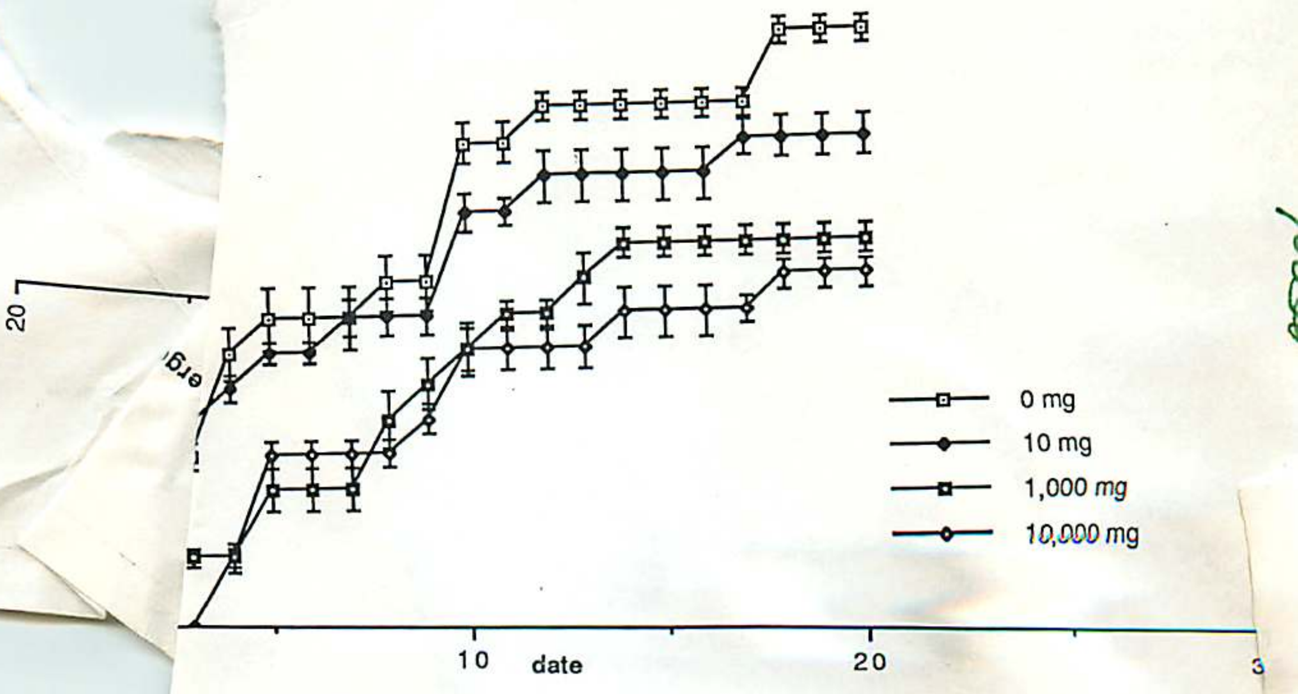
4. Trophic Level Interactions
    - a. Plant-Pest Relationships
    - b. Other: Litter decomposers; Mycorrhizal relationships.

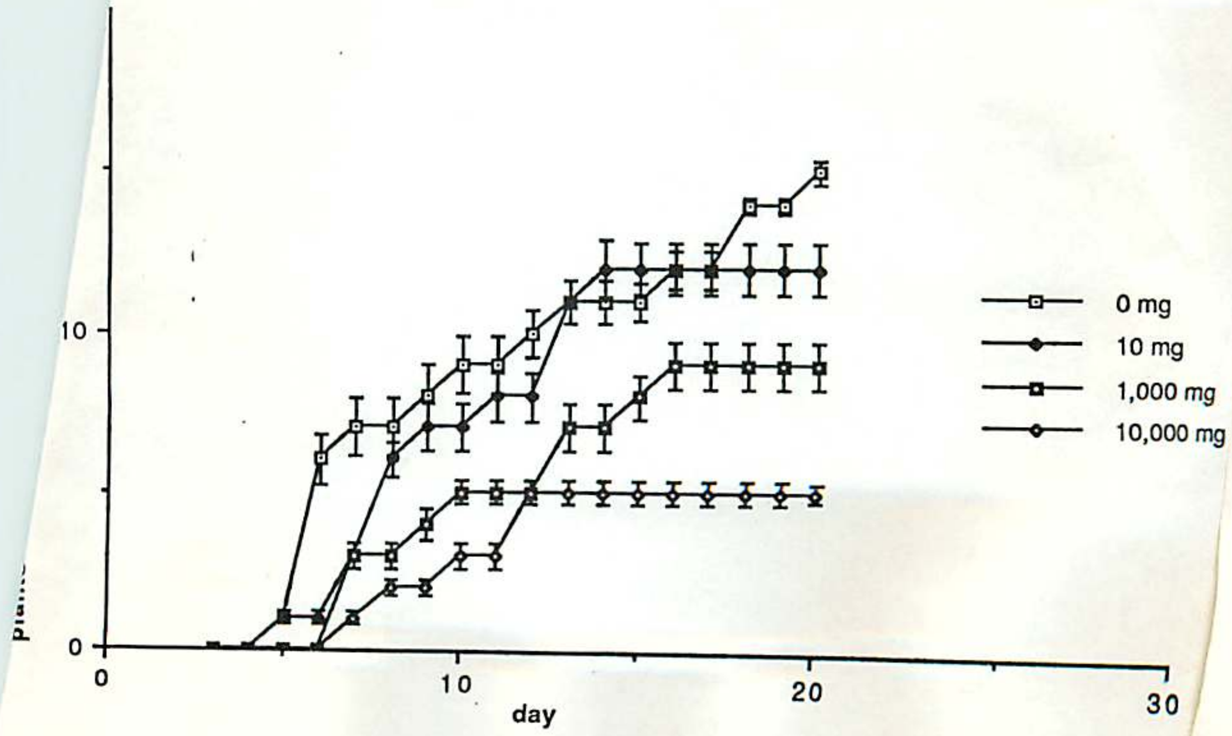
Reading

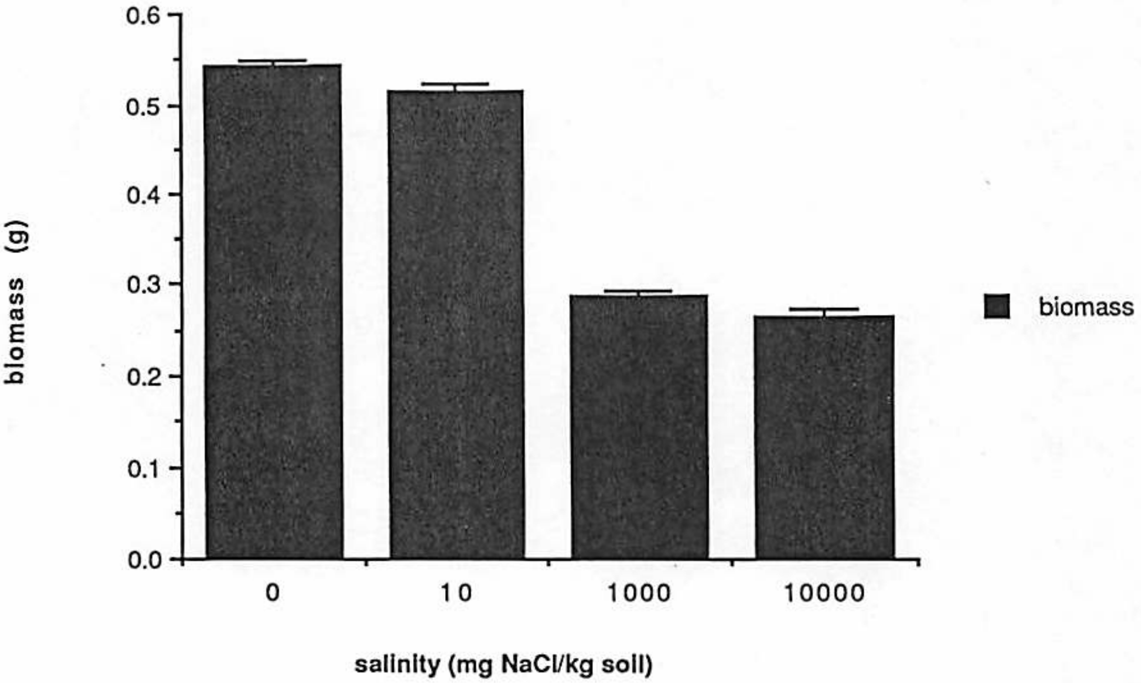
Reich, P.B. and Amundson 1985. Ambient Levels of Ozone Reduce Net Photosynthesis in Tree and Crop Species. Science 230: 566-570.

Effect of Salinity
on early growth of Abutilon

J. Salzman







Sam Pollock: Massachusetts Department of Public Works

Holmes, F.W. 1961. Salt injury to trees. Phytopathology 51:712-718.

Holmes, F.W. & J.H. Baker. 1966. Salt injury to trees II. Sodium and chloride in roadside sugar maples in Massachusetts. Phytopathology 56:633-636.

Pitelka, L. 1979. Salt tolerance in roadside populations of two herbaceous perennials. Bulletin of Torrey Botanical Club 106:131-134.

Pollack, S. 1974. Retention of chloride in the unsaturated zone. Journal of Research of US Geological Service 2:119-123.

Walton, G.S. 1969. Phytotoxicity of NaCl and $CaCl_2$ to Norway Maples. Phytopathology 59:1412-1415.

Table 3.3 Weathering processes

Physical	Chemical
WETTING—DRYING E.g. Disruption of layer lattice minerals which swell on wetting	HYDRATION E.g. Reversible change of haematite to limonite which is accompanied by swelling and so disrupts cementation of sandstones etc. $Fe_2O_3 \rightleftharpoons Fe_2O_3 3H_2O$
HEATING—COOLING E.g. Disruption of heterogeneous crystalline rocks in which inclusions have differential coefficients of thermal expansion. Surface flaking of large boulders, particularly in arid climates, due to sun heating	HYDROLYSIS E.g. Silicate breakdown $\underset{\text{Orthoclase}}{K_2Al_2Si_6O_{16}} \rightarrow \underset{\text{Kaolinite}}{Al_2O_3 2SiO_2 2H_2O}$ K and surplus Si are washed away in solution
FREEZING E.g. Disruption of porous, lamellar or vesicular rocks by frost shatter due to expansion of water during freezing	OXIDATION—REDUCTION E.g. $Fe^{3+} \rightleftharpoons Fe^{2+}$ causes disruption of cementation as Fe^{2+} is much more soluble than Fe^{3+}
GLACIATION E.g. Physical erosion by grinding process	CARBONATION E.g. $CaCO_3 \rightleftharpoons Ca(HCO_3)_2$ leads to solution loss of limestone or disruption of $CaCO_3$ cemented rocks as the hydrogen carbonate is more soluble than the carbonate
SOLUTION E.g. Removal of more mobile components such as Ca, SO_4, Cl etc.	CHELATION Essentially a consequence of biochemical activity, various metals being dissolved as chelates with organic products of plant and microorganism activity
SAND BLAST E.g. Erosion of upstanding rocks in arid, desert conditions	

rock becoming incorporated in what must now be recognized as a thin soil layer covering the surface.

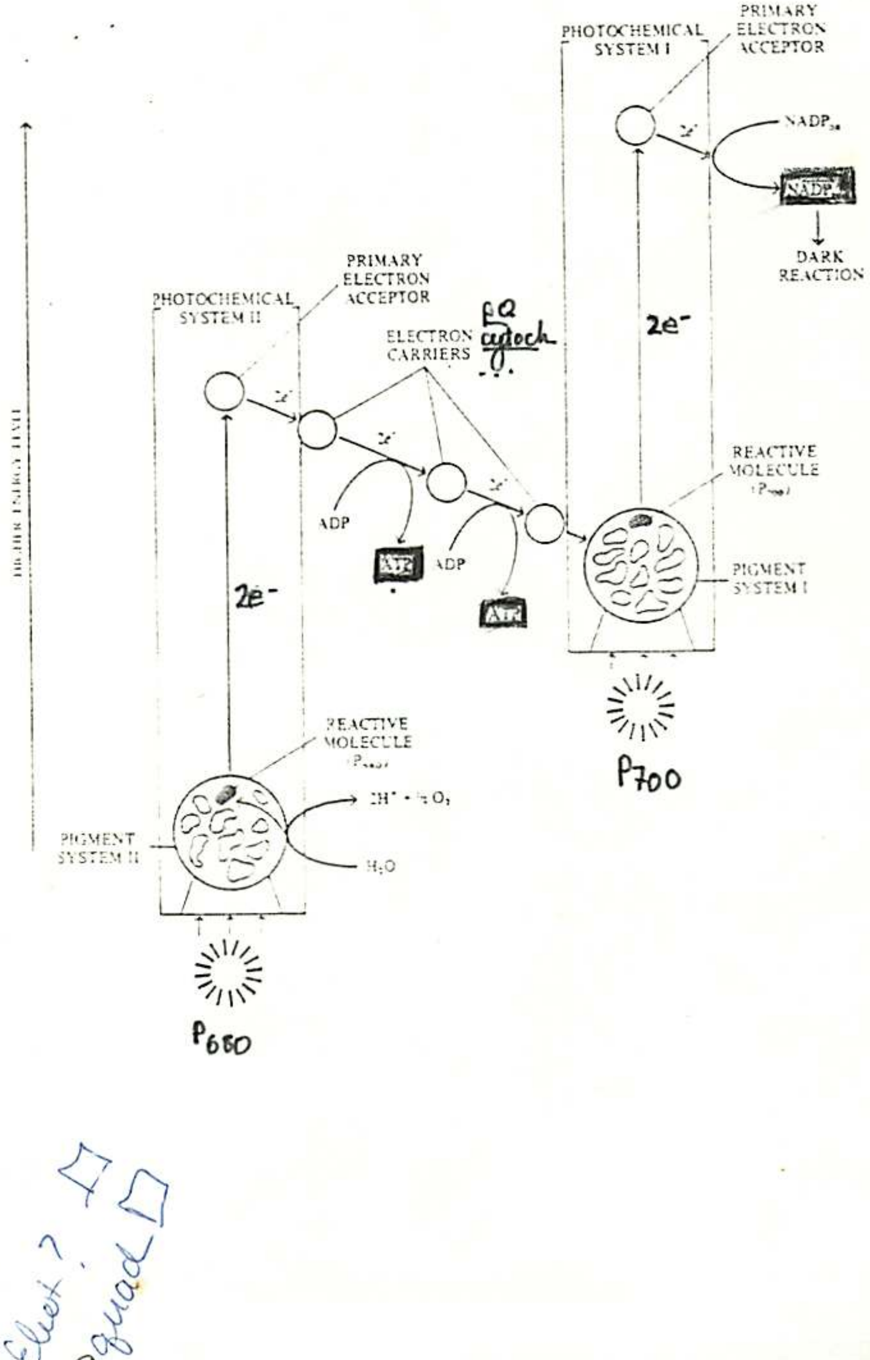
Various exudates from these organisms, other than respiratory CO_2 are likely to speed the pedogenetic process; for example, some of the lichen acids have strong chelating properties; organic acids generally are potent in dissolving mineral components, while some species of bacteria directly influence the solubility of nutrient elements and cementing compounds. Mulder *et al.* (1969) cite the solubilization of phosphorus by microorganism-formed organic acids and microorganism reduction of insoluble ferric phosphates. Further examples are the bacterial reduction of manganese and iron, increasing their solubility. The cycles of sulphur, nitrogen and phosphorus are all strongly governed by microorganisms through the sizes of the organic and inorganic pools and the rates of change between soluble and insoluble, available and unavailable forms. Further discussion may be found in Campbell and Lees (1967), nitrogen; Cosgrove (1967) and Halstead and McKercher (1975), phosphorus; Freny (1967), sulphur; and Ehrlich (1971), minor elements. Many non-essential elements are also biologically cycled and concentrated, for example Uernelöv (1975) describes the formation of mono- and di-methyl mercury from relatively immobile inorganic sources.

Colonization of a juvenile soil by higher plants adds yet another complication to the soil-forming process, greatly increasing the energy-fixing capacity of the surface and increasing the supply of decaying organic matter. Soluble organic compounds also diffuse into the rhizosphere zone from the roots and wash into the soil surface from leaf-drip. Deeper penetration of roots will tend to increase the depth range of the cyclic processes involving nutrient elements, soluble

Fig 2

6-6

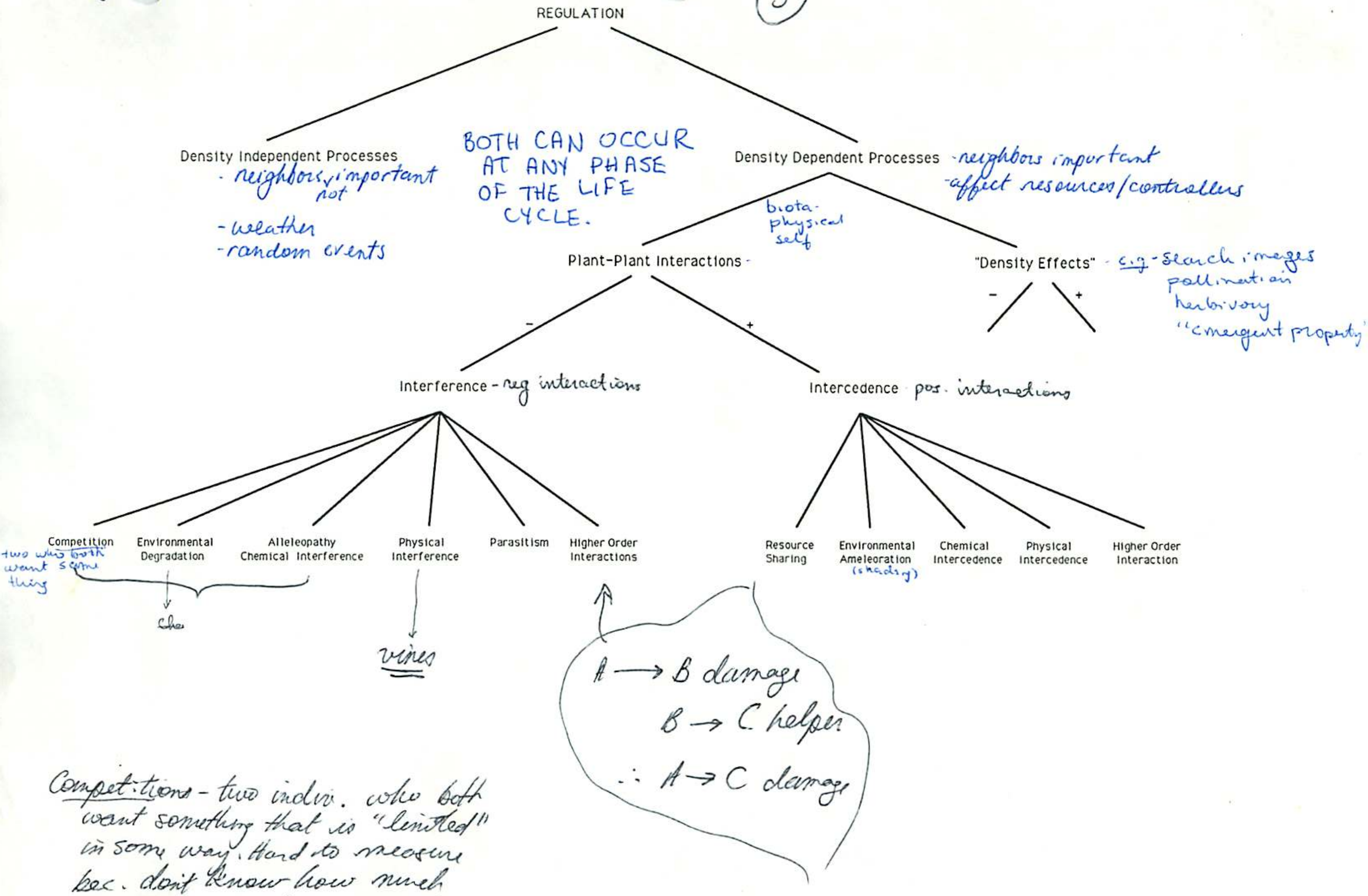
Light energy trapped in the reactive molecule of Pigment System II boosts electrons uphill from chlorophyll to a primary electron acceptor. These electrons are replaced by electrons pulled away from water molecules, which then fall apart, producing protons and oxygen gas. The electrons are passed from the electron acceptor along an electron transport chain to a lower energy level, the reaction center of Pigment System I. As they pass along the electron transport chain, some of their energy is packaged in the form of ATP. Light energy absorbed by Pigment System I boosts the electrons to another primary electron acceptor. From this acceptor, they are passed via other electron carriers to $NADP_{ox}$ *to form* $NADP_{red}$*. The electrons removed from Pigment System I are replaced by those from Pigment System II. ATP and* $NADP_{red}$ *represent the net gain from the light reactions.*



[illegible]-Eliot? ☐
Linnes? quad ☐

Pwayne

⑤



<u>Competitions</u> - two indiv. who both want something that is "limited" in some way. Hard to measure bec. don't know how much available vs. how much consumed. Also, may be replacements or may have 'variable effects'

Plant Ecology

Salt Marshes

- v. productive ecosystems

~short form in more reducing sediments

is there a steep gradient between tall/short forms

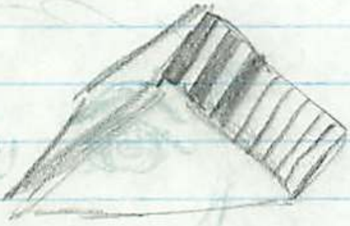
w/more evapotransp. then less H_2O in soil & more O_2.

Deicing Salts

++ salt
  ↓ dry matter prod.
  - change osmotic Ψ of soil

- hard to separate effects of salt w/ effects of pollution, light, T°

- amt of salt
- timing
- plowing
  - thaw timing
- runoff
- topography
  - dist from rd.



Nan Arens

= weight

Seed size in germination, emergence time, & early seedling vigor in low nutrient environment.

Factors influencing seed size.

① Zygote effects
- genetic potential of embryo
- ploidy

② Maternal effects
- environment
- mothers plasticity
- position of ovule on ovary

③ what about post-zygote effects

Effect of seed size on plants early life

Large seeds (cross species variation)

① larger independence from need to autogenerate ~~exgo~~ energy

← ② ???

③ light restricting envir. more easily for large seeds. Logarithmic growth.

④ large seeds in poor substrates

~~large~~ small seeds ~~in~~ in open envir.
maybe dispersal related

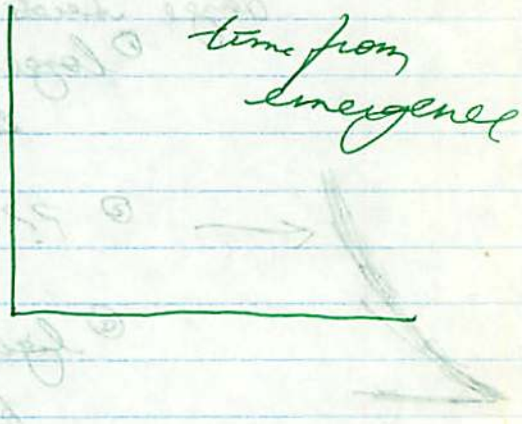
This is post evidence hypothesis generation or - actually - any of those open communities could have fit that hypotheses.

seed size important depending on conditions.

if seed size affects time of germination then it may <u>hurt</u> plants.

How this effect population

<u>Small</u>
suppressed
Self thinned



Has anyone done exp.
w/ filters at diff heights.

<u>herbivory</u> - timing, cant
frosts & other weather

Effects of N_2 / Herbivory on Plant Growth

How does plant use N_2?

① PS - rubisco
chlorophyll

② Growth
proteins

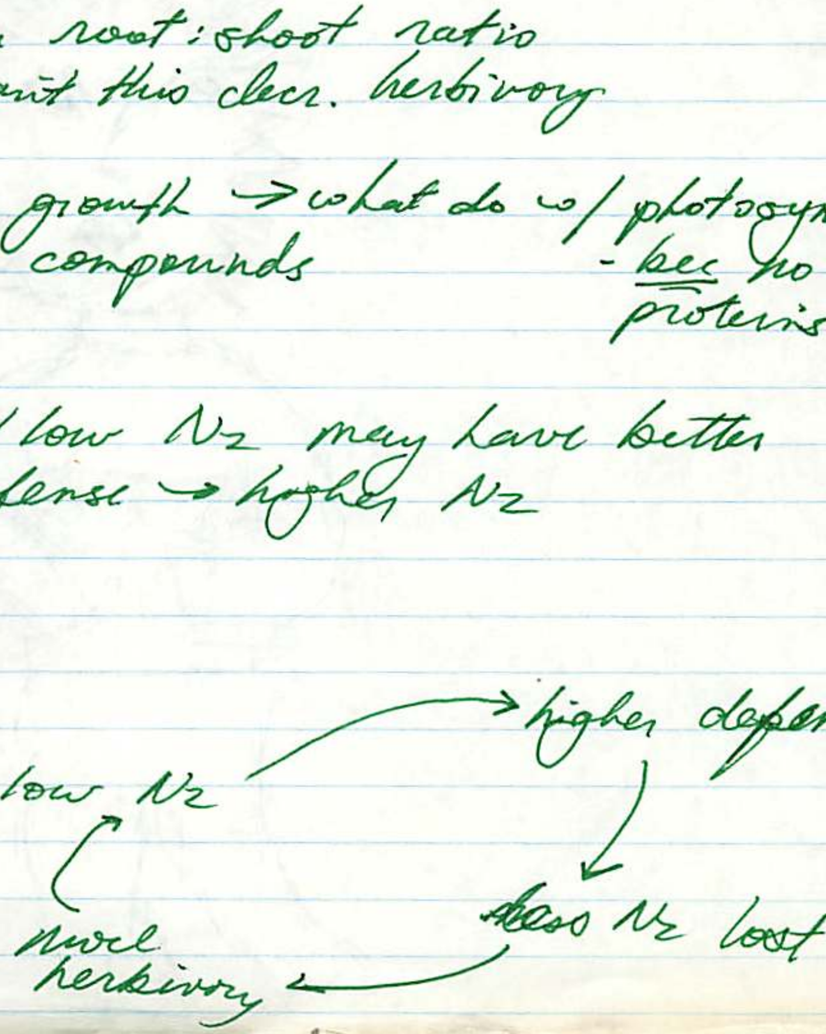
Low N_2 effects

① Low productivity (growth & repro)
prolonged life = more herbivory

② higher root:shoot ratio
can't this decr. herbivory

Lower growth → what do w/ photosynthate
- 2° compounds
- bec no N_2 for proteins

so w/ low N_2 may have better defense → higher N_2



herbivory
© ↓ Ps ↓ biomass
↓ seed prod
↑ mortality
↑ light
↑ H_2O balance
↑ [nutrients]

Plant Ecology - Lab #3

W

gas exchange

$$\text{Flux} = \frac{\text{Driving Force } (\Delta x)}{\text{Resistance}}$$ ← gradient

boundary, stomate...

photosynthesis = carbon gain

net *assimilation* ($C_{gain} - C_{loss}$)

1) building/maintenance respiration
2) photo respiration (Rubp grabs O_2)

why measure photosynthesis?

① *growth* = Carbon gain

but...

② photosyn reflects *other* conditions

N_2, H_2O, timing

③ systematics; comparisons; convergence?

Measuring CO_2 uptake

① ΔCO_2

$\left.\begin{array}{l}\cdot CO_2 \\ \text{-time}\end{array}\right\}$ = net photosyn. rate

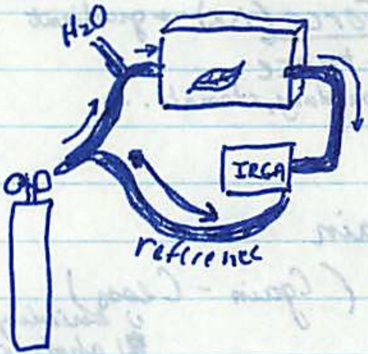
Infrared Gas Analyzer = $\boxed{\text{IRGA}}$; measured CO_2

$pCO_2 \sim$ IR absorbance

$$\text{Assim. Rate} = \frac{\Delta CO_2 \cdot v}{\Delta t \cdot SA} = \text{umoles}_{CO_2} \cdot m^{-2} \cdot s$$

but want steady state

Lab Machines



Portable

- neg: ΔCO_2; delayed RXN; plant not in equil
- pos:
  - v. fast

Closed system

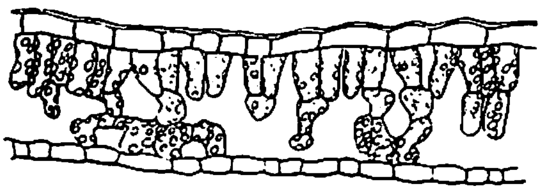
2) can bypass dessicant

$E = \frac{upd}{resis}$

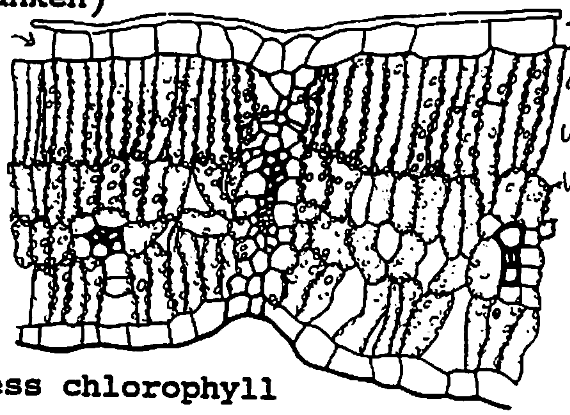
Sun/Shade Leaf Characteristics

** Sun and shade leaves may occur in two individuals of the same species grown in different light conditions. They may also occur in different areas in the canopy of one individual.

Shade leaf characteristics	**Sun leaf characteristics** w/in same species
Morphological & Anatomical	
leaves arranged within canopy with minimal overlap	overlap of leaves less detrimental
large surface area	relatively smaller leaves
thin leaf (short palisade layer, more intercellular space)	thicker, heavier leaves (tall palisade layer, cells tightly packed)
low specific leaf weight = g/m2	high specific leaf weight
thin cuticle	thick cuticle, (various epidermal coatings and appendages increase reflectance & decrease transpiration, stomata may be sunken)

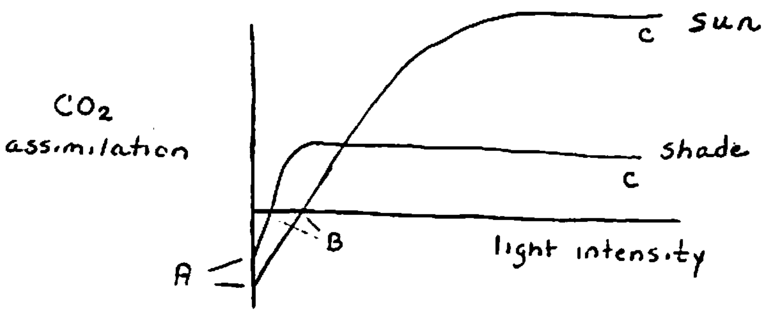


From Hart, J. W. A 1988 Light and plant growth. Boston. Unwin Hyman.



Is there a diff. in Chl a:b in diff layers of leaves.

Biochemical	
more chlorophyll (but less efficient)	less chlorophyll
more N allocated to chlorophyll vs. RUBISCO for light harvesting	more N allocated to RUBISCO for carbon fixation
* high chlorophyll A/B ratio ⟷ reversed	lower chlorophyll A/B ratio
lower maximum photosynthetic capacity	high photosynthetic capacity
A - low rates of respiration	higher rates of respiration
B - low light compensation point	high light compensation point
C - low light saturation level	high light saturation level



* in photosystems diff. proportions of Chl. a & b.

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3. Seeds, like those of <u>Ambrosia artemisiifolia</u>, fall from plants in late summer and become part of a seed bank in the soil. Many species require 'disturbance' in order to "trigger" germination.

a) What cues might germinating seeds in disturbed (vs. undisturbed) soil environments be responding to?

b) What mechanisms might seed's "employ" to prevent mistiming of germination?

c) What are the ecological consequences of such mechanisms combined with seed longevity of the order of 50-100 years?

Cues in disturbed

① change in red:far red ratio

- since plants tend to absorb more in the red area of the spectrum ~~them~~ in the far red, the red:far red ratio will be lower when there is much plant cover versus when there is little cover. Therefore if disturbance causes reduced cover (gaps) then red: far red ratio will increase. 3

② change in daily T° (temperature) fluctuations

- If seeds are buried in the soil, ~~deeper~~ they will experience different amounts of T° fluctuation depending on depth, soil type, water content, season, etc. Since disturbances, such as tree uprootings, might cause changes in seed position, the changes would also cause changes in T° fluctuations. 3
- In addition other factors, such as [CO_2], red: far red ratio, and light intensity vary with soil depth. All these cues could be perceived by a seed. 3

③ change in light intensity: with disturbance, such as tree fall, light intensity, and duration, as well as diurnal pattern, will change. All these may be influencial on germination.

Other types of disturbances can be important to germination. These include fires, floods, and freezing.

all types of disturbance can be perceived in different ways. For example:

fire → incr. T°
→ cracking seed coats 2
→ denaturing enzymes
→ reduced H_2O

If seeds, such as those of some savanna plants, use "fire" as a cue for germination, they could be perceiving any of a multitude of changes. This is the same for "treefall" as a disturbance. 1

b) Seeds would definitely want to prevent mistiming of germination - because mistiming could put a seedling in too dry or too wet or too anything an environment. Some of the ways to prevent this include

① dormancy

innate - plants may set seeds that automatically are dormant for a certain period of time, and then may need other cues to germinate, or may just need time. 2

enforced - if conditions are wrong (such as too low water) seeds may enter a dormancy, "coming out" when conditions are better 2

innate
↓
enforced
↓ if stimuli missing
induced

② all of the above cues - may be timing specific - such as water, or fire, and may lead to germination when conditions are right 2

③ stratification - seeds may need a winter to cause some changes such as cracking the seed coat, or changes ratios of promoter:inhibitor. 4

continued

3 continued

other cues may help with timing such as

① light period

② overall light received

③ temperature

④ $[CO_2]$ - which is higher in winter in deciduous areas bec. little is being fixed.

1(c)

Name: Jonathan Eisen   Bio 149

4. Global Climate Change is probably the most debated environmental issue facing our society today.

a) Describe putative sources of CO2 and their relative importances. ? 3
How might elevated CO2 lead to global warming?

b) Compare and contrast the C3 vs C4 photosynthetic pathways.

c) Draw and explain temperature response curves for net photosynthetic rates for a C3 vs C4 leaf.

− 3

d) Draw and explain CO_2 photosynthetic response curves for a C3 vs C4 leaf.

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Sources of CO_2

① fossile fuel burning - very important, esp. in developing countries where energy use in incr. greatly

② slash & burn removal of rainforests - relatively high source of CO_2 - may be important also because of what replaces ~~③ respiration~~ the forests. Crops may reabsorb a lot of CO_2 but cities do not.

③ respiration - high source but not directly in control of humans so not important to discuss.

relative contribution?

Elevated CO_2 might lead to global warming because of a few factors

① CO_2 is a greenhouse gas - it transmits most wavelengths but absorbs IR radiation. Since the earth, as a black body, ~~emits IR radiation [illegible] the sun~~ more IR than any other radiation, and CO_2 "absorbs" and then reradiates this IR, the earth warms up. In other words, the CO_2 reduces the transmission of IR back to space.

~~incr. CO2 may lead to incr.~~

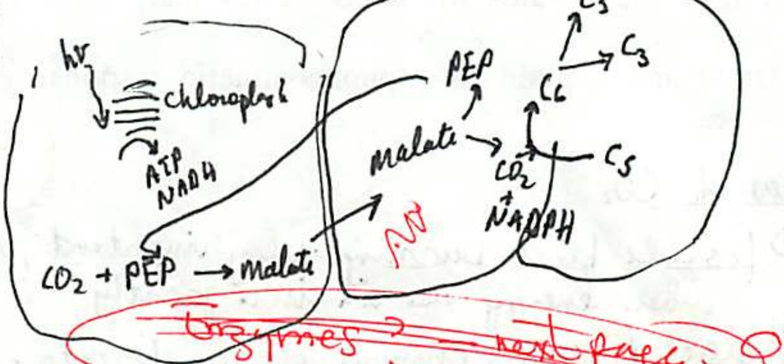
This incr. in ~~[illegible]~~ temperature may provide positive feedback by

① thawing out carbon sources in the poles so that they will be decomposed more rapidly

② melting of ice caps leading to a decr. in light reflected back to space

b) 4

C4



~~Enzymes? — next page~~ OK

in C4 the CO_2 fixation is decoupled from the calvin cycle. Thus CO_2 fixation occurs through PEP carboxylase and makes malate (C4) which is transported to the cells where the calvin cycle occurs. The malate is then converted ~~p~~ back to PEP & CO_2 and the PEP returns to its previous location while the CO_2 is incorporated into the calvin cycle. This system greatly reduces the amount of photorespiration.

continued

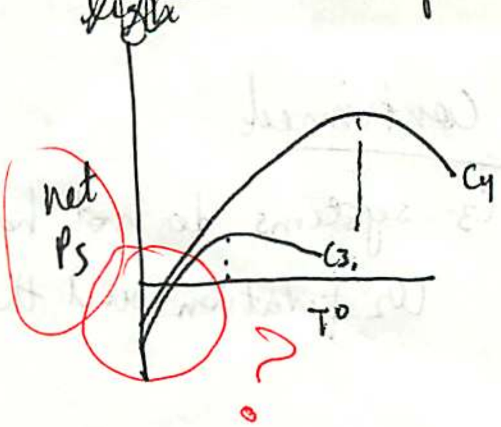
4 continued

C_3 systems do not have a decoupling of CO_2 fixation and the calvin cycle

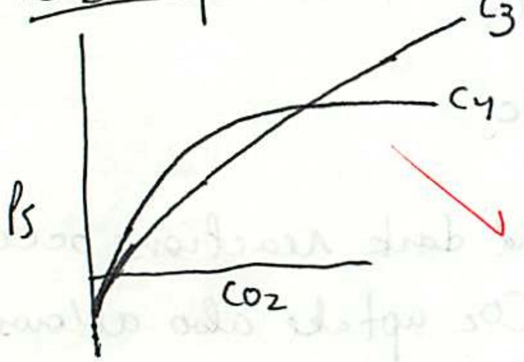
$$CO_2 + C_5 \xrightarrow[ATP,\,NADPH]{rubisco} C_6 \begin{array}{l} \nearrow C_3 \\ \searrow C_3 \end{array}$$

In this system the light and dark reactions occur in the same cells. Since CO_2 uptake also allows O_2 uptake, a great deal of photorespiration can occur. In C_4 Pep carboxylase is exposed to O_2 but it is not sensitive like rubisco. C_4 photosynthesis is less efficient because more ATP is used overall, <u>but</u> it reduces the energy loss of photorespiration. ~~this~~ By concentrating CO_2 in the area of the calvin cycle C_4 plants can greatly decrease the opening of stomata and thereby decrease water loss.

Temperature response



CO2 response curve



* note this graph would vary with light intensity.

C3 plants will have higher net Ps at high CO_2 because they are limited by CO_2 concentration and not light. With higher CO_2 - there will be lower amounts of photorespiration.

C4 plants which concentrate CO_2 will be efficient at low CO_2 concentration but will not benefit ~~ma~~ as much from incr. CO_2 concentration

Temp response

C4 plants are able to do better than C3's at higher temperatures bec. ① pep carboxylase is not as sensitive to T° as rubisco, and in C3's rubisco is one of the limiting factors ② pre adapted to higher temperatures ③ T° influences other factors like H_2O levels, soil H_2O ψ; respiration rates

Diff. in Temp. sensitivity of the enzymes.

35/40

Name: Jonathan Eisen Bio 149

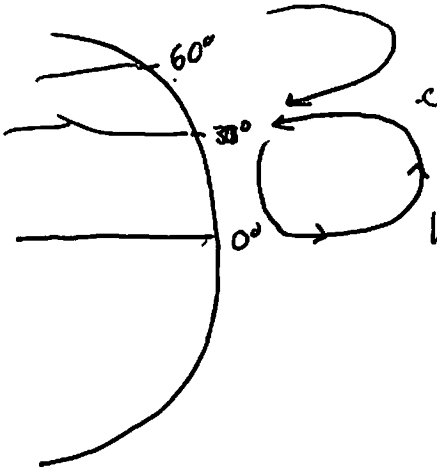
5. Water is perhaps the most important ecological factor determining the productivity of ecosystems, and distributions, and abundances of organisms within communities.

a) At what latitudes should we expect to find desert biomes, and what climatological/meterological processes cause this?

b) What are two short-term (modificitive) physiological/morphological response of plants to water short term water deficits?

c) What are two long-term (evolutive) responses plant may employ to deal with periods of water deficit?

a)



cool air descends at ≤ 30°, absorbing water as it warms ✓

hot air rises at the equator, releasing water as it cools ✓

∴ at 30° N & S tatitudes there tend to be more arid areas because the air is descending and as it warms it can hold more water, and thus these areas stay dry.

b) two such responses are
① decr. conductance (& ∴ less H_2O loss) by shutting stomates.
② change in timing of photosynthesis - plants can expose their leaves to the sun when humidity is high and temperature is low ∴ reducing conductance.

via Δ's in leaf ∠'s w/ tilting parallels...

-5

c) long term

✓ ① deciduous - dropping of leaves greatly reduces water loss

* ✓ ② water storage - such as in cact: , allows plants to maintain a higher ψ than the soil.

* ✓ ③ C4 or CAM metabolism
these increase water use efficiency a

④ temporally distributed
-germinating when water is in abundance such as in desert annuals.

life cycle / phenological adaptations

R.C. Crabtree Nov 8,1989

Answers for Biology 149 Midterm

These are not definitive - credit was given for other answers I thought appropriate.

Q2 Swamp Thing and the energy budget director.

(a) First give energy budget equation: $S_n + T_n + LE + H + P = 0$

S_n = net solar radiation absorbed = total - reflected and transmitted
T_n = net thermal radiation
LE = Latent heat of evaporation
H = Sensible heat transfer, convection and advection
P = Energy stored by Photosynthesis

(b) How to alter leaves to make more efficient?
Swamp thing has a set of inter-related problems. You assume that it came from a shady, wet environment, and therefore probably has large, thin C3 leaves.
ST will have overheating problems (- leading to enz degradation etc), possibly UV problems, and will also need to gear up photosynthetic performance for the new env.

Heat load - reduce Sn term
Decrease interception area, make leaves smaller, intercept less radiation
Reduce amount of S absorbed, inc reflectance (hairs, cuticle), change leaf angle, or even go for -ve leaf tracking. (Leaf arrangement w/in a canopy to give self shading also possible)

LE, H
Increase evaporative cooling to reduce overheating in the short term. In the longer term, reduce leaf size, reducing boundary layer resistance, so that more heat can be dumped through sensible heat transfer, which also increases as boundary layer resistance drops.

P
Sun/shade type problem
Allocate more to RubisCo, less to Chlorophyll, as now carbon rather than light limited. (Could also inc # stomata). Decrease chl a/b ratio as fewer collectors and more processors needed.

(c)If little water available:
Keep LE increase minimal
Sunken stomata, -ve solar tracking, or steeply inclined leaves
Change photosynthetic pathway to C4 or CAM, depending on severity of heat load/water limitation. Taking up CO2 at night reduces water loss greatly. Other observations on water trapping, funnelling etc and dormancy were also credited.

Q3 Seed dormancy

(a) Cues for germ in disturbance species.

light quality, R:FR high, i.e. incoming light has not passed through a canopy
High Light (PAR) quantity
Increased temperature fluctuations, as the deeper seeds are buried, the less temp fluctuation there will be due to diurnal heating and cooling driven by sunshine.
Low CO2, as the closer seeds are to the soil surface, the lower the CO2 concs, as soil respiratory gases are lost to the atmosphere.

(b) avoiding germination at inappropriate times for plant survival.

Innate dormancy: requirements that have to be satisfied
eg. animal digestion, stratification (both probably loosen seed coat, leach out germination inhibitors), or embryo immaturity imposes a time requirement (after-ripening), while embryo finishes maturation.

Seeds that have satisfied an innate dormancy requirement may then enter a window of time where they are in enforced dormancy, and will germinate under right combination of resources or resource controllers. If appropriate combination not found in that window of time, then seeds may enter induced dormancy, and wait for next cycle, perhaps avoiding germination too late in a growing season.
Mechanisms for sensing appropriate conditions are sensing degree days, water quantities (desert plants for example), phytochrome.

(c) Ecological consequences of dormancy + seed longevity

Dormancy plus seed longevity generates a seed bank. This disperses seeds in time as well as space. This may be important to species that require disturbance to establish as such events may be spatially and temporally quite rare. Without a seed bank, these species would have to disperse in from other disturbed sites, at exactly the right time!

Maintenance of genetic diversity as different generations mix in the seed bank. Different genotypes may experience a wide range of env conditions - possibilities for selection.

Biology 149
F. A. Bazzaz

Final Exam
1/26/88

There are seven questions. The first question is worth fifty points; the others are worth 25 points each. It wouldn't be a bad idea to read them all over first before starting, so that you have a sense for what there is to do and so that you can choose a logical order in which to answer them (your answers do not have to be in order in the blue book, as long as you number them!). As in the first exam, more of the questions involve the integration of concepts and the logical defense of ideas than a doling back of facts. Take this as an opportunity to piece together relationships between the various concepts or processes we discussed in class.

1. Plants obtain resources from two very different types of environments: the soil and the atmosphere. Yet the functions and uses within the plant of the different resources obtained from these different environments are intimately related. Discuss how plants, through physiological and behavioral responses, integrate their soil, atmospheric and radiant energy environments to optimize growth and reproduction.

2. What are the different colloids present in soils? How do they differ in their properties and their abilities to supply plants with nutrients?

3. Write the set of Lotka-Volterra equations that describe competition between two species. Do you think that this model appropriate for describing competition between plants? If you do, why? If you don't, then discuss why not by comparing this model to one that you feel better represents plant competition. $\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$ $\frac{dN}{}$

4. Plant ecologists have often borrowed concepts and methods developed by or for the study of animal ecology and attempted to apply them directly to their work on plants. Recently, however, plant ecologists have begun to see that this can be a misleading practice because of some very fundamental differences between plants and animals. Discuss two ways in which plants and animals are fundamentally different and the consequences of these for the study of their population biology.

v. similar resource base - resources [illegible] dimensions / directions
- autotrophic
- sessile

5. Discuss the extrinsic and intrinsic factors which might determine recruitment and survivorship in natural plant populations.

[illegible] [illegible] Water
[illegible] [illegible] [illegible]

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6. Compare the physiology, growth, allocation patterns and reproduction of early- and late-successional plants.

7. Discuss the role of natural disturbance in the evolution of life-history traits, including reproductive patterns, niche relations, and resource uptake abilities.