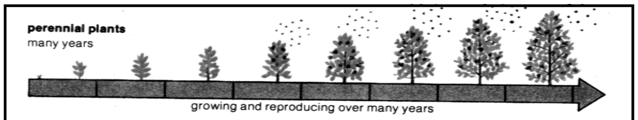


Growth and Allocation

1. Definitions
2. Mechanisms and measures of growth
    - at the cellular level
    - At the whole plant level
3. Adaptations associated with variation in growth rate
4. Allocation between growth and storage

What is plant growth?

A *permanent* increase in size or mass that may or may not be associated with change in form or anatomy

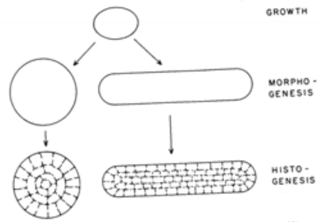
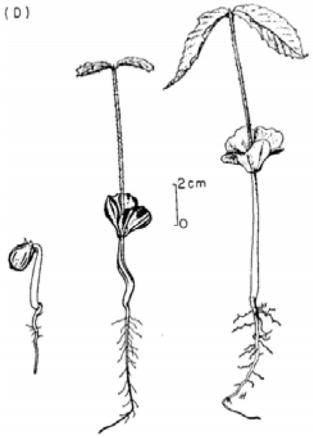


Figure 1.1. Schematic relations between growth and development (morphogenesis and histogenesis).

Plant growth studies provide:

- Insight into evolutionary strategies
- Indications of how plant function may change under environmental change
- Climate reconstruction uses tree growth rings
- Crop/timber yield

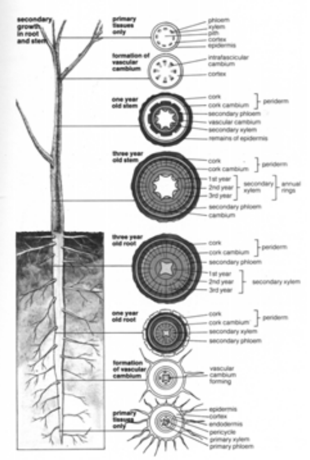
Growth includes processes of seed reproduction, germination and development, but we will not be considering those important processes here.



Tissue Growth:

Two main types of Growth in plants: Primary (“length”) and Secondary (“girth”).

These occur at “apical” and “lateral” meristems, respectively.



Primary growth and form is very sensitive to hormonal control (auxins) and physical alterations at growing tips (apical meristems)

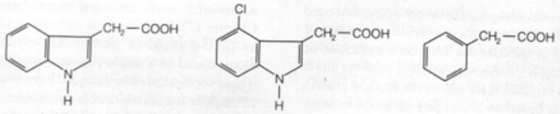
“hormone” greek: set into motion

Typically occur at low concentrations

Often moved from source of production to site of action

Animals have glands; plants don’t

Here are some natural auxins – note that they are acids – this is important to cell wall loosening and cell expansion, as we will discuss later



Indole-3-acetic acid (IAA)

4-Chloroindole-3-acetic acid (4-Cl-IAA)

Phenylacetic acid (PAA)

FIGURE 16.2. Structure of some natural auxins. Although indole-3-acetic acid (IAA) occurs in all plants, there are other substances in plants that have auxin activity. Pea plants, for example, contain 4-chloroindole-3-acetic acid. Other compounds that are not indoles, such as phenylacetic acid, also possess auxin activity. It is not clear what roles, if any, these other natural auxins play in plant development.

IAA is the most ubiquitous growth hormone – but there are many other important ones:

Gibberellins – a class of hormone that has the specialized function of promoting height growth.

Although acids, gibberellins appear not to acidify cell walls, but rather to inhibit calcium incorporation into cell walls.

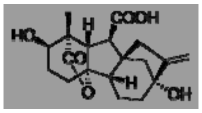


FIGURE 17.12. Cabbage, a long-day plant, remains as a rosette in short days but can be induced to bolt and flower by applications of gibberellin. In the case illustrated, giant flowering stalks were produced. (Photo courtesy of S. Wittwer, Michigan State University.)

IAA is the most ubiquitous growth hormone – but there are many other important ones:

Cytokinins – hormone implicated in promoting cell division.

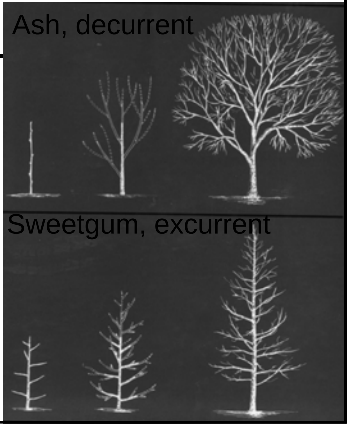
Ethylene and abscisic acid – responsible for growth inhibition (senescence, fruit ripening, abscission)

(abscisic acid also promotes stomatal closure)

Allocation is related to, but different from growth:

It is the partitioning of growth resources (e.g. “root allocation”, “leaf allocation”, etc.)

Allocation patterns can vary greatly over lifetimes, and among plant forms.



Changes in allocation and plant form over time may give clues as to the primary constraints on plant function (hydraulic, mechanical, nutritional, etc.)

For example, look at the overall form of juvenile plants and compare them with adults – what do you notice?

Allocation can in turn have a large impact on further growth and allocation.

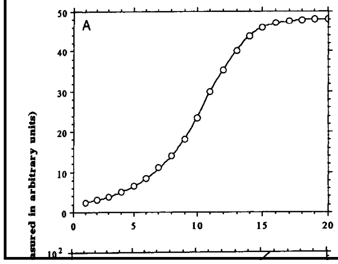
For example, relatively lots of allocation to leaves may promote even more absolute growth resources.

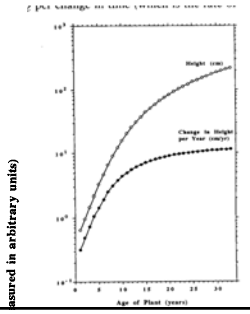
Growth and allocation are fundamentally circular processes

Growth is often mistakenly equated with photosynthetic rate

Allocation of photosynthate into structural components versus storage or metabolism can be highly variable.

"All" organisms cease growth at some point – we want to know why they stop where they do, and why they get there at the rate they do





Mechanisms and measures of growth:

At the cellular level

Cellular Growth

Cell Division: not necessarily mass or volume growth.

Cell Expansion: Size growth, but not necessarily mass growth.

Cell Growth: Cell Expansion

- **Turgor driven – hence growth inhibited by low leaf water potentials (drought, tree height)**

- **Dependent on cell wall extensibility (Lockhart Equation)**

$$dV/(Vdt) = \phi(\Psi_p - Y)$$

Where dV/Vdt = relative volume change/time
ϕ = yield coefficient ($MPa^{-1}\ s^{-1}$)
Ψ_p = cell turgor pressure (MPa)
Y = yield threshold (MPa)

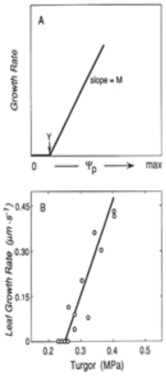


Figure 11.2 Relationship between turgor and growth. (A) Lockhart relationship showing yield threshold *Y* and wall extensibility *M* (slope of the line) obtained when the growth rate *G* is plotted as a function of the turgor Ψ_p. (B) Experiment showing growth of leaves at various turgor pressures in sunflower (from Matthews *et al.*, 1984). The experiment was done by withholding water from the soil and measuring growth for several days.

Cell Growth: Cell Expansion

Both ϕ and Y are dependent on cell wall extensibility, which itself can be varied:

Acidification (e.g., light caused) weakens microfibril bonds

Calcium removal weakens pectins/cell wall strength

Several enzymes and hormones can promote both acidification and/or calcium removal.

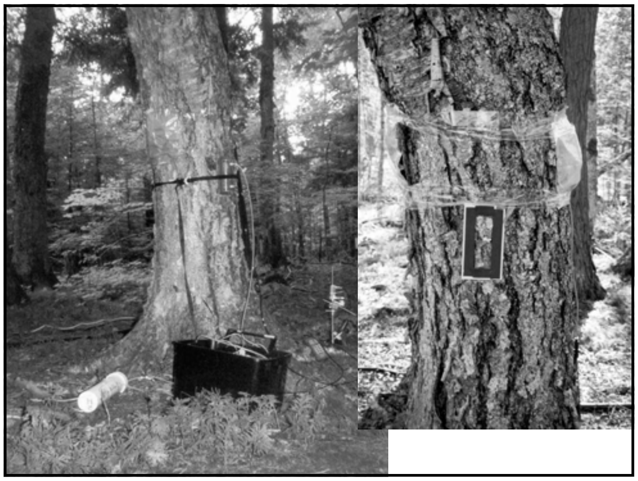
Whole Plant Growth: Relative Growth Rate.

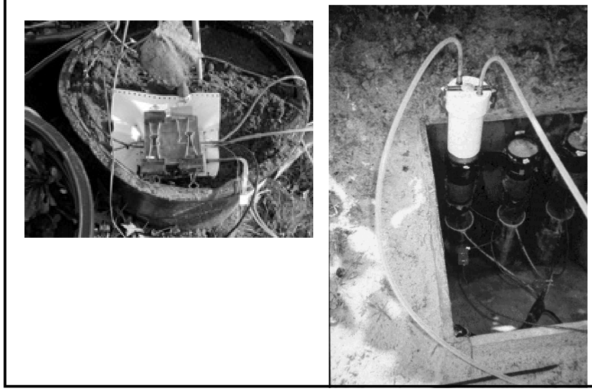
We've already dealt with RGR in the context of nutrients. Now lets take a closer look in terms of allocation.

While we discussed RGR in nutrient productivity terms we can also express it in terms of photosynthetic – respiration rates, per unit total plant mass:

$$RGR=(\underbrace{A_a*SLA*LMR}_{\substack{\text{Photosynthesis}\\ \text{Per plant mass}}}-\underbrace{LR_m*LMR}_{\substack{\text{Leaf respiration}\\ \text{Per plant mass}}}-\underbrace{SR*SMR}_{\substack{\text{Stem respiration}\\ \text{Per plant mass}}}-\underbrace{RR*RMR}_{\substack{\text{Root respiration}\\ \text{Per plant mass}}})/[C]$$

No surprise: higher leaf area and lower respiration support higher RGR. But this equation allows us to deconstruct the reasons for overall plant growth





Whole Plant Growth: Relative Growth Rate.

RGR = dV/Vdt : change in size relative to existing size.

What if a plant has constant RGR, say “a”?

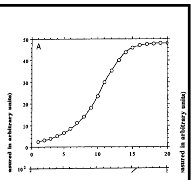
dV/V = adt

$$\int dV / V = \int a dt$$

$$\ln(V) = at$$

$$V = e^{at}$$ **Exponential Growth**

Most organisms show sigmoidal growth:



$V = k(1+be^{-rt})^{-1}$

where r,b,k are constants

$dV/dt = kbre^{-rt}(1+be^{-rt})^{-2}$

So RGR = dV/Vdt = $bre^{-rt}(1+be^{-rt})^{-1}$

RGR is maximum at the inflection point of the sigmoidal curve

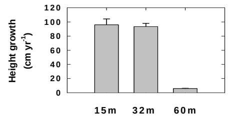
Space may be traded for time to see sigmoidal growth

Height growth, Wind River, Washington

15m, 20 yr

32m, 40 yr

60m, 450 yr



60m data from Ishii et al. (2000)

An operational definition of growth commonly used by foresters is “site index”:

Height of dominant trees at 50 years age. In the doug fir shown, SI ~ 100
(low: SI <= 105, medium: 105 < SI <= 125, high: SI > 125).

This is arbitrary, dictated mostly by the fact that foresters weren’t interested in rotations longer than 50 years

Back to sigmoidal growth: What do these parameters k, b, r, mean mathematically?

k is the maximum or terminal size of the organism.

b determines the organism size as t approaches 0 (“lag phase”)

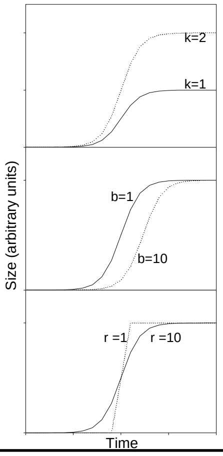
V= k/(1+b)

r determines the curvature of the sigmoid

Variation in k:

Variation in b:

Variation in r:

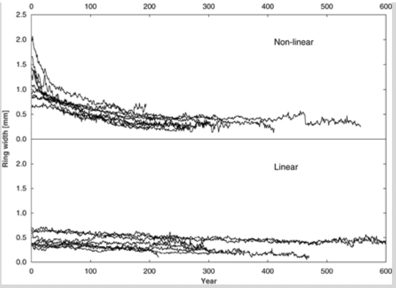


Modeling growth curves for long-lived trees is difficult.

How much does climate change affect a presumed sigmoidal growth curve? Not a lot known. (science paper)

FIG. 4.21. Very old, multiple-stemmed and branched *Pinus aristata* tree in California. Only one side of the tree is alive. (U.S. Forest Service photo.)

How much of the continued growth is due to CO2 vs. Temperature vs. intrinsic growth?



Supplemental Figure 1. Arithmetic mean curves of individual ring width series from different sites after aligning by cambial age. Athabasca, Mangazeja and Polar Urals are represented in both data sets, because some of the series from these sites belong to the linear and others to the nonlinear data set Esper et al. 2002

3. Adaptations associated with variation in growth rate

What do these parameters k, b, r, mean *biologically*?

k is the maximum or terminal size of the organism:

Clearly under genetic control – but genetics are shaped by natural selection (e.g. we would expect genetic control to allow taller trees to grow in moister environments).

Other hypotheses: Nutrient Limitation, Hydraulic Limitation, Metabolic Limitation, Biomechanical Limitation.

What do these parameters k, b, r, mean *biologically*?

b determines the organism size as t -> 0

V-> k/(1+b):

b relates to a generally exhibited ‘lag phase’ – or a quiescent period before rapid growth from the seedling stage. Often associated with shade tolerance.

Although quiescent in terms of net growth, this period is characterized by large developmental and allocation changes, including producing leaves.

What do these parameters a, b, r, mean *biologically*?

r determines the curvature of the sigmoid

r describes the maximum relative growth rate. Fertile sites favor high r species, and high r can lead to competitive advantages (e.g. access to light while shading neighbors).

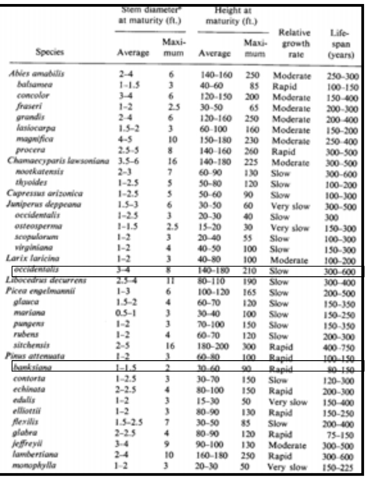
But as always, there are tradeoffs with high r…

High r is usually associated with large allocation to leaves, not much to stems, roots, or the “quality” of organs (strength, chemical defense compounds).

So high r trees may have shorter lifetimes due to mechanical failure, disease, herbivory, ability to withstand stochastic resource limitations.

Perhaps counter-intuitively, maximum tree size (k) is not well correlated with maximum growth rate (r) in trees.

Instead, max tree size appears more to be associated w/ longevity – which may be a product of low r!



Species	Stem diameter[a] at maturity (ft.)		Height at maturity (ft.)		Relative growth rate	Life-span (years)
	Average	Maximum	Average	Maximum		
Abies amabilis	2–4	6	140–160	250	Moderate	250–300
balsamea	1–1.5	3	40–60	85	Rapid	100–150
concolor	3–4	6	120–150	200	Moderate	150–400
fraseri	1–2	2.5	30–50	65	Moderate	200–300
grandis	2–4	6	120–160	250	Moderate	200–400
lasiocarpa	1.5–2	3	60–100	160	Moderate	150–200
magnifica	4–5	10	150–180	230	Moderate	250–400
procera	2.5–5	8	140–160	260	Rapid	300–500
Chamaecyparis lawsoniana	3.5–6	16	140–180	225	Moderate	300–500
nootkatensis	2–3	7	60–90	130	Slow	300–600
thyoides	1–2.5	5	50–80	120	Slow	100–200
Cupressus arizonica	1–2.5	5	50–60	90	Slow	100–300
Juniperus deppeana	1.5–3	6	30–50	60	Very slow	300–500
occidentalis	1–2.5	3	20–30	40	Slow	300
osteosperma	1–1.5	2.5	15–20	30	Very slow	150–300
scopulorum	1–2	3	20–40	55	Slow	100–300
virginiana	1–2	4	40–50	100	Slow	150–300
Larix laricina	1–2	3	40–80	100	Moderate	100–200
occidentalis	3–4	8	140–180	210	Slow	300–600
Libocedrus decurrens	2.5–4	11	80–110	190	Slow	300–400
Picea engelmannii	1–3	6	100–120	165	Slow	200–500
glauca	1.5–2	4	60–70	120	Slow	150–350
mariana	0.5–1	3	30–40	100	Slow	150–250
pungens	1–2	3	70–100	150	Slow	150–350
rubens	1–2	4	60–70	120	Slow	200–300
sitchensis	2–5	16	180–200	300	Rapid	400–750
Pinus attenuata	1–2	3	60–80	100	Rapid	100–150
banksiana	1–1.5	2	30–60	90	Rapid	80–150
contorta	1–2.5	3	30–70	150	Slow	120–300
echinata	2–2.5	4	80–100	150	Rapid	200–300
edulis	1–2	3	15–30	50	Very slow	150–400
elliottii	1–2	3	80–90	130	Rapid	150–250
flexilis	1.5–2.5	7	30–50	85	Slow	200–400
glabra	2–2.5	4	80–90	120	Rapid	75–150
jeffreyii	3–4	9	90–100	130	Moderate	300–500
lambertiana	2–4	10	160–180	250	Rapid	300–600
monophylla	1–2	3	20–30	50	Very slow	150–225

Ecologists separate inherently fast vs. slow growing organisms as being either “r” or “k” selected.

“r” selected means selected for maximum growth, “k” for achieving carrying capacity.

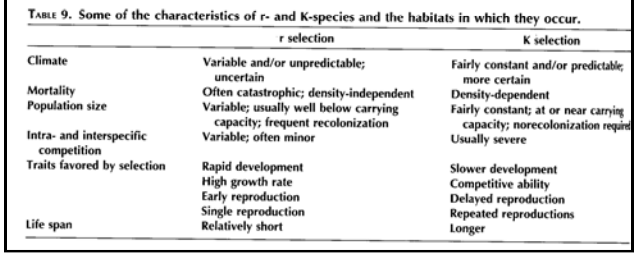


Table 9. Some of the characteristics of r- and K-species and the habitats in which they occur.

	r selection	K selection
Climate	Variable and/or unpredictable; uncertain	Fairly constant and/or predictable; more certain
Mortality	Often catastrophic; density-independent	Density-dependent
Population size	Variable; usually well below carrying capacity; frequent recolonization	Fairly constant; at or near carrying capacity; norecolonization requir
Intra- and interspecific competition	Variable; often minor	Usually severe
Traits favored by selection	Rapid development High growth rate Early reproduction Single reproduction	Slower development Competitive ability Delayed reproduction Repeated reproductions
Life span	Relatively short	Longer

Allocation to storage

Three forms:

1. **Accumulation (e.g. leaf starch)**
2. **Reserve formation (e.g. tubers)**
3. **Internal recycling (e.g. hypothesized reason for fall colors)**