The Dynamic Relationship Between Plant Architecture and Competition

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What is interesting about this subject?

What have population studies shown?

What have architecture studies shown?

Development of theory for effects of
plant architecture on competition

Conclusion

The Dynamic Relationship Between Plant Architecture and Competition

What is interesting about this subject?

Functional-structural plant models (FSPM) type models simulating competition, e.g.,

Dauzat et al. 2008. Cotton

Evers et al. 2007. Spring wheat

Letort et al. 2008. Beech

Mathieu et al. 2009. General

Sievänen et al. 2008. Scots pine

Sorrensen-Cothern et al. 1993. Pacific silver fir

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Academic: Stringent test.

Simulating competition (FSPM) requires increase in knowledge about the processes of integration of plant growth

Practical: Competition affects crop yield

Can an increase in planting density be used to increase yield?

What have population studies shown? And so what should FSPMs explain?

(a) Frequency distributions of plant size as a result of competition

(b) Spatial evenness of surviving individuals

(c) Relationship between mean plant weight and density of plants

Population studies provide descriptions of phenomena without convincing explanations for them. (***FSPMs must do that!***)

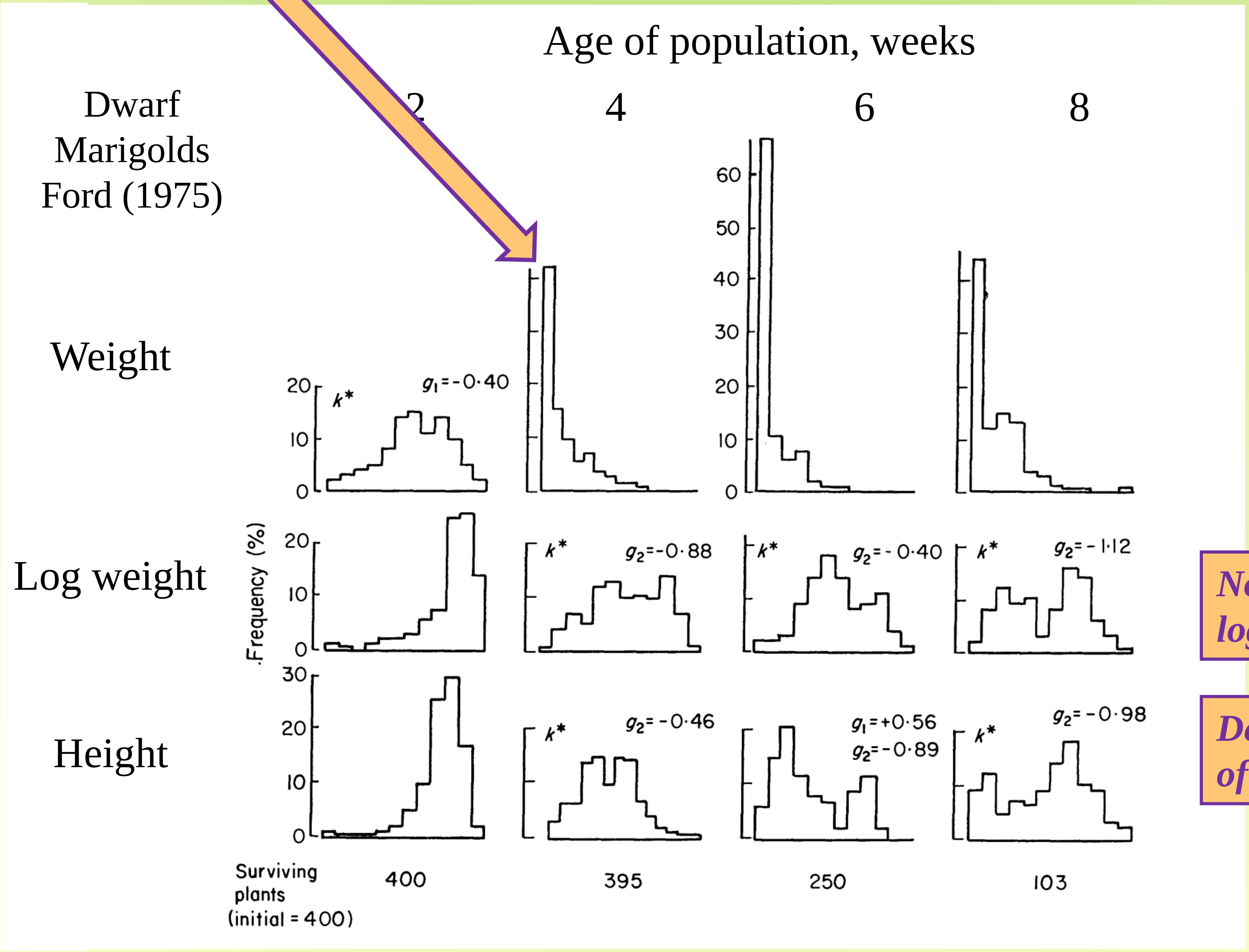
Dwarf marigolds (*Tagetes patula*) at 2 cm spacing


Day 28
2 cm

Arabidopsis: 2 cm hexagon lattice spacing.
From above after 6 weeks, short days, low temperature.

(a) Frequency distributions of plant size as a result of competition

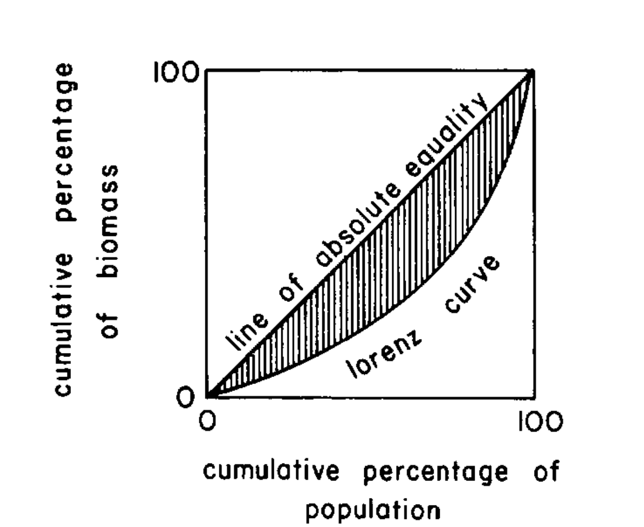
Koyama and Kira (1956): development of lognormal distributions of plant weight



Not strictly log normal

Development of bimodality

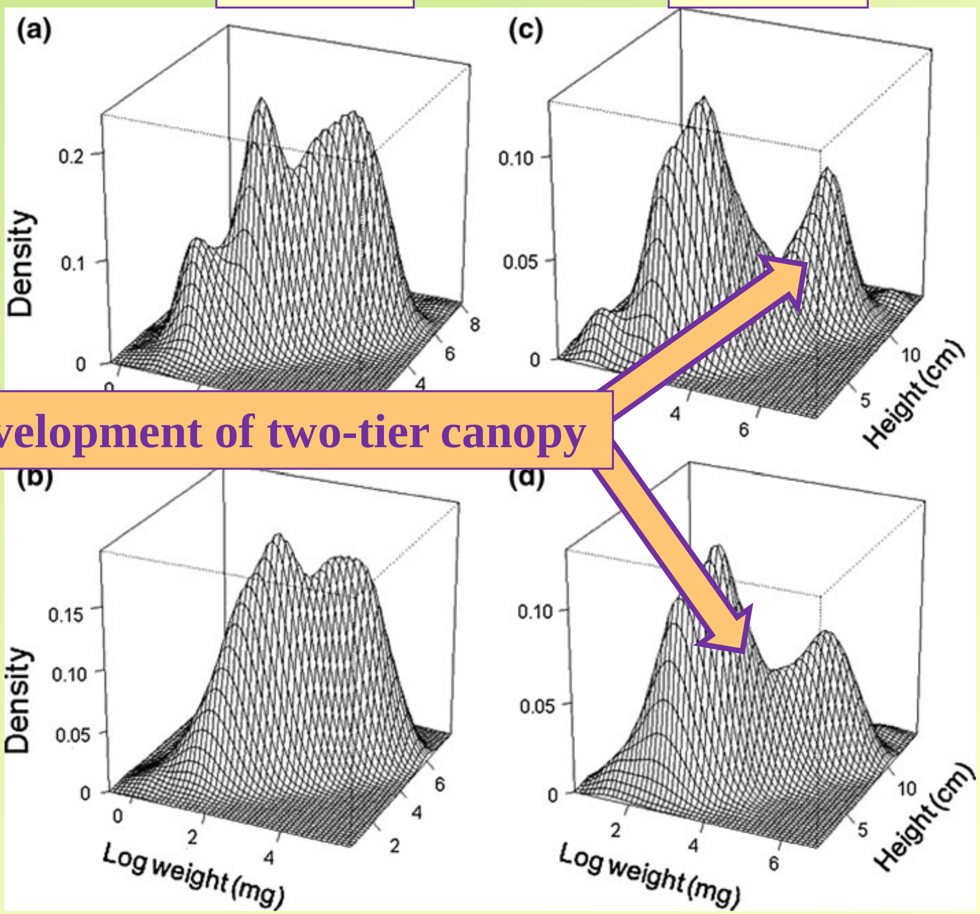
Simplified overall summary



Weiner and Solbrig (1984)

Lorenz curve – cumulative % plot: Area between curve and line of perfect equality expressed as proportion of area under the diagonal is the Gini Coefficient — a measure of inequality

4 weeks **6 weeks**



Development of two-tier canopy

Analysis of distributions

Turley and Ford (2011)

Kernel density of bivariate log plant weight:plant height

Replicate dwarf marigold, 2-cm initial spacing after 4 weeks (a, b)

and 6 weeks (c, d)

(b) Spatial evenness of surviving individuals

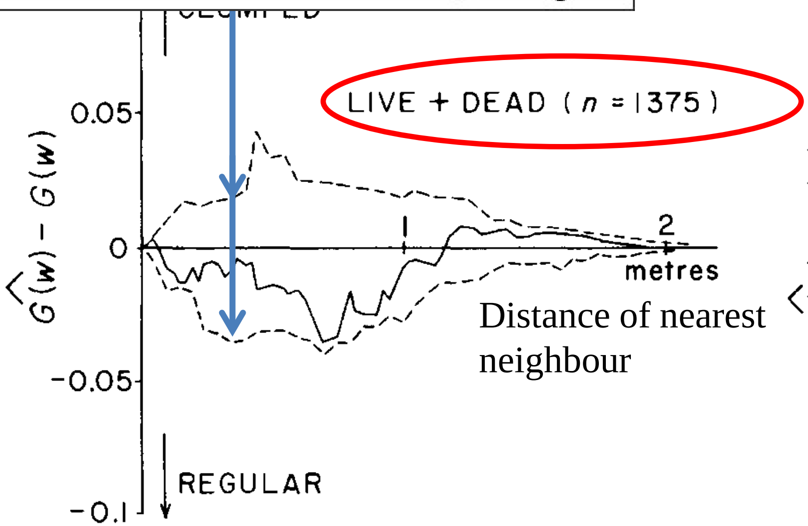
This jack pine stand needs thinning

Kenkel (1988) Spatial distribution of Jack pine after self-thinning

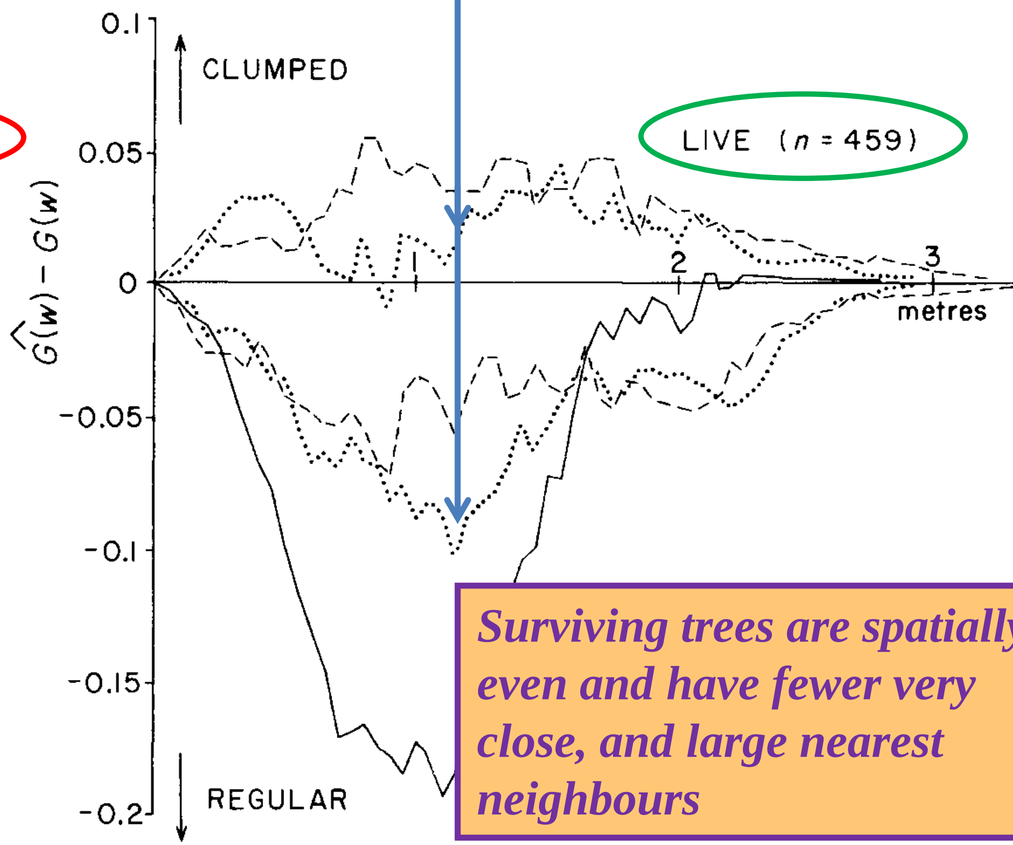
…ances, G, relative to that expected for a random distribution

S
9

Confidence interval for random mortality

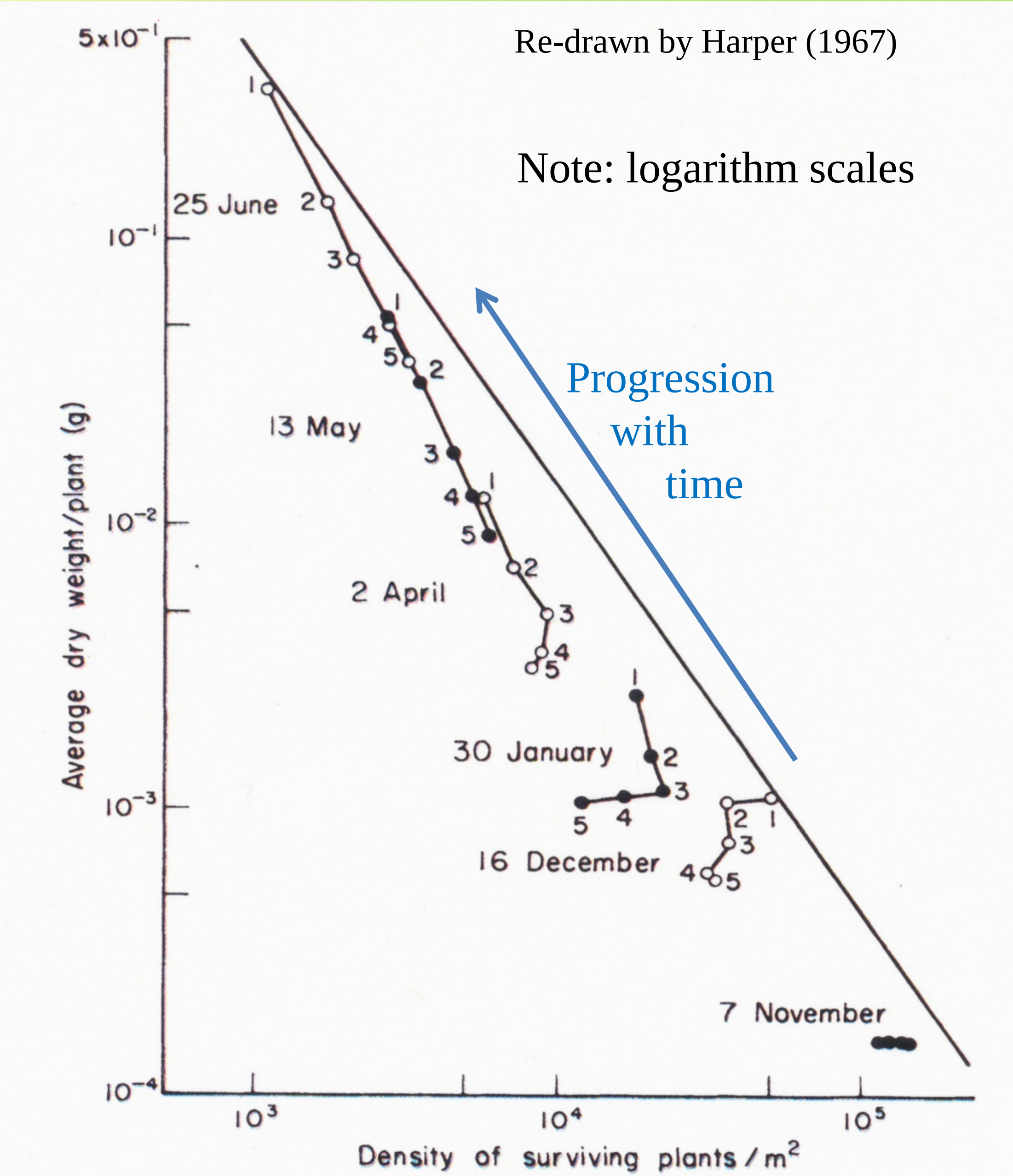


Distance of nearest neighbour



Surviving trees are spatially even and have fewer very close, and large nearest neighbours

(c) Relationship between mean plant weight and density of plants



Yoda et al. (1963)

Erigeron canadensis *(now Conzoya)* sown on an abandoned field at Osaka, Japan. Numbers 1-5 represent decreasing site fertility exaggerated by addition of N-P-K-Mg fertilizer in the ratio 5:4:3:2:1. Seed distributed evenly at1-2 x 10^5 seeds/ m^2.

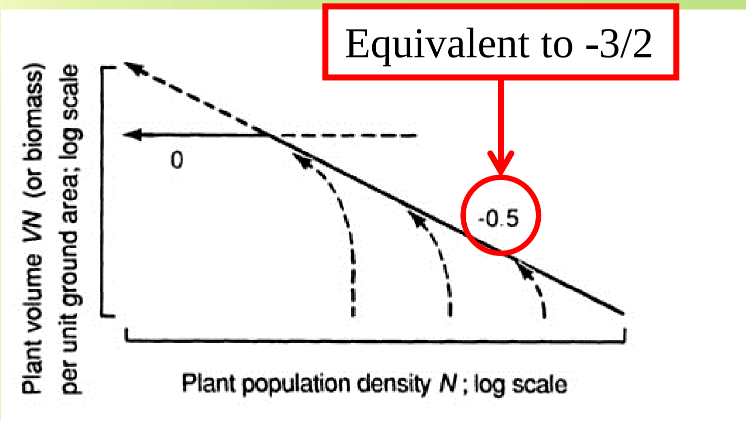
Empirically derived relationship of

$$w = Cp^{-3/2}$$

w = mean weight per plant,

p = existing plant density,

C = constant.

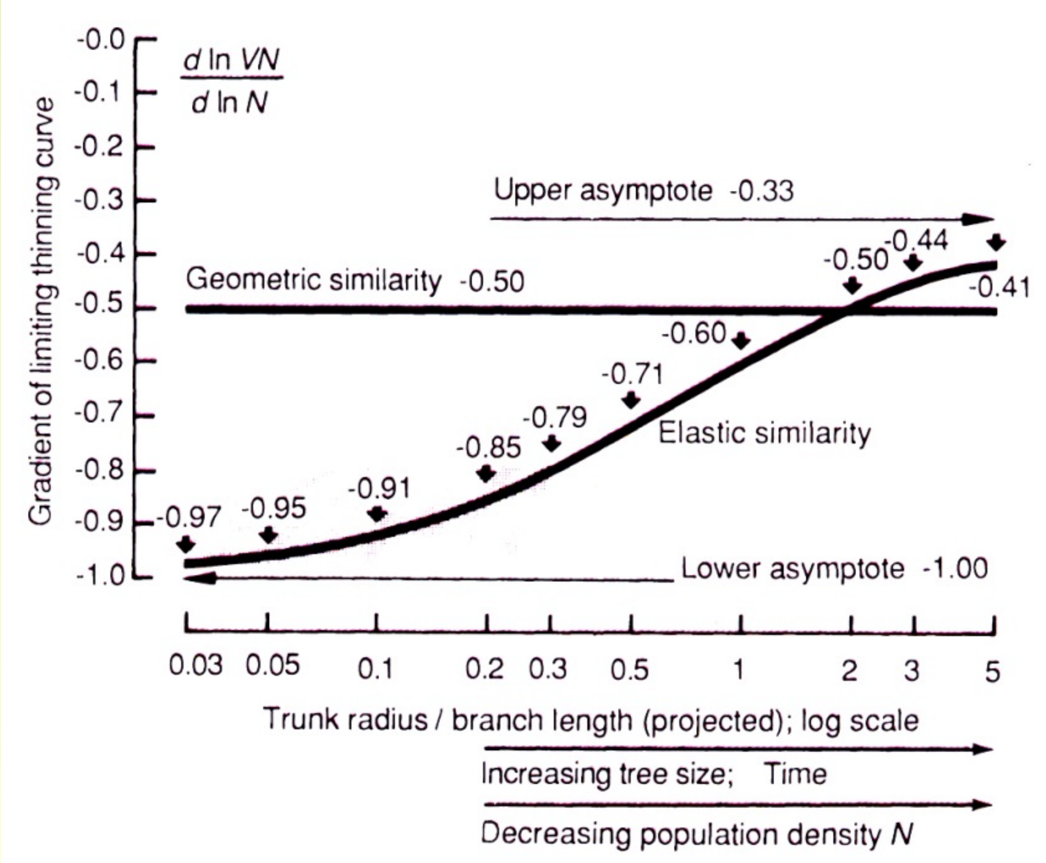


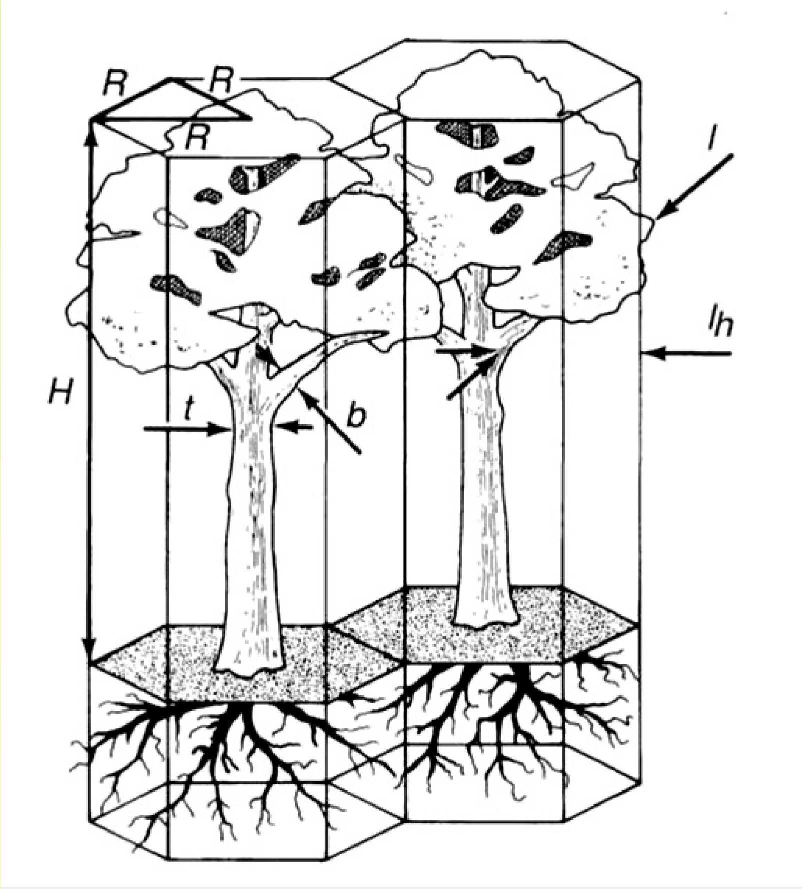
$$\log B = \beta \log N + \log K$$

where B is stand biomass density or yield in grams.m^{-2}, and *N* is plant density in individuals per square metre and ß and *K* are constants

Weller (1987): relationship varies with plant type

Norberg (1988): expected to vary theoretically





What have population studies shown? And so what should FSPMs explain?

Universal features:

right-skewed distributions,

self-thinning mortality,

spatial evenness of large plants/survivors.

FSPMs, with few exceptions, have not attempted to simulate these features.

BUT there are questions about:

consistency of bimodality and its significance,

continuing progress of spatial evenness as population develops,

species attributes that affect competition,

AND the subject needs a theory.

FSPMs should answer these questions and provide explanations.

Observations of the effects of competition :

need to become more precise in both experimental technique

and biometric analysis

The Dynamic Relationship Between Plant Architecture and Competition

What have architecture studies shown?

Three properties influencing competition as a 3-D process.

(i) Resource acquisition plasticity.

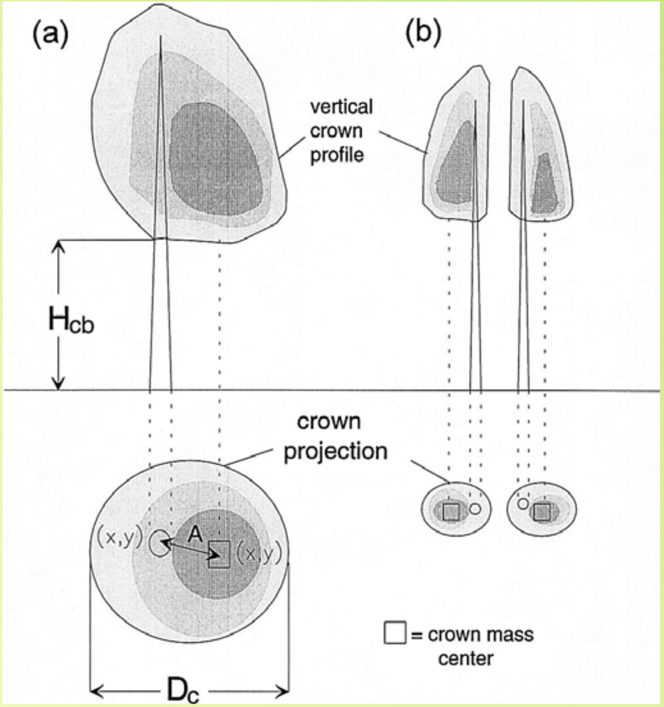
(ii) Morphogenetic plasticity.

(iii) Architectural variation in interception and utilization of light.

(i) Resource acquisition plasticity

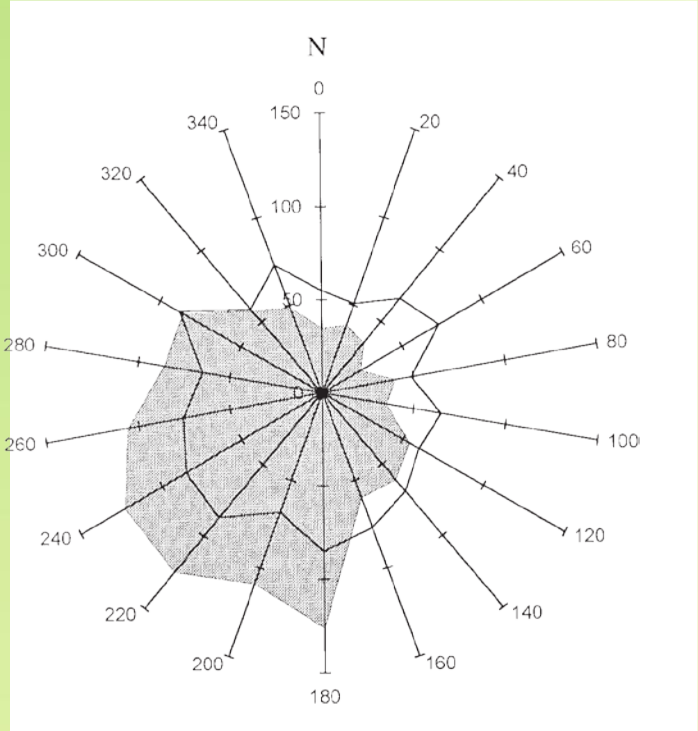
Rouvinen and Kuuluvainen (1997)
Scots pine, 150-200 y, Finland

Crowns are asymmetric in relation to local competition.



(a) Tree in a wide space with competition significantly lower on one side (e.g., a tree grown on the edge of a gap)

(b) Trees close together.



Distribution of crown mass center direction for 1251 trees. Shaded area is measured frequency distribution and solid line predicted frequency distribution based on 2-D competition model.

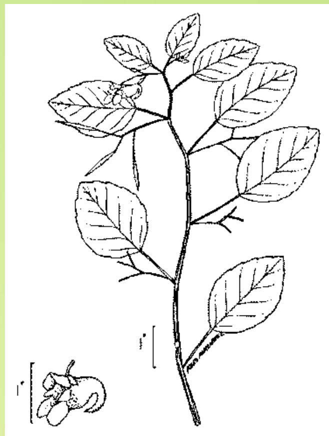
See also Umeki(1995) for crowns of *Xanthium canadense*

Koike (1989), *Quercus* species – no phototropic effect

(ii) Morphogenetic plasticity

Phytochrome mediated effects

$$R : FR = \frac{\text{photon irradiance between 660 and 670 nm}}{\text{photon irradiance between 725 and 735 nm}}$$



Schmitt and Wulf (1993)

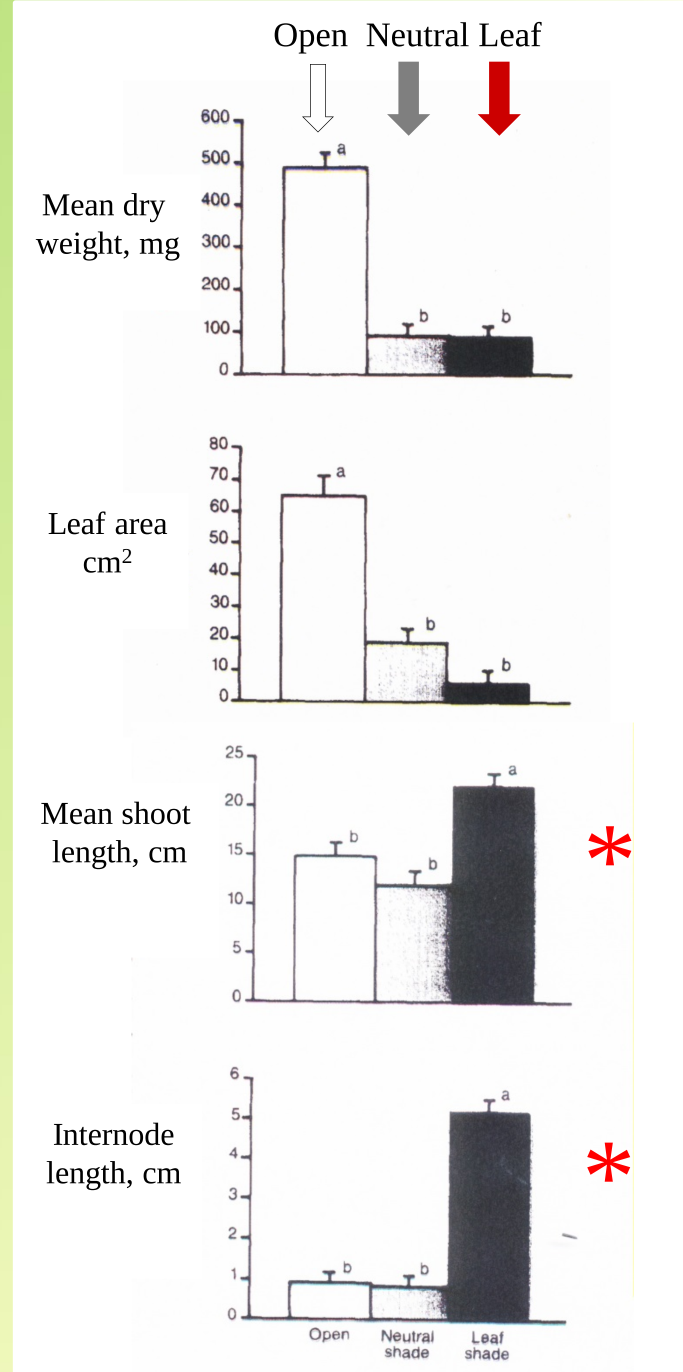
Morphological response of *Impatiens capensis* seedlings to reductions in irradiance and R: FR.

Three treatments:

open (covered with transparent plastic sheets, full sunlight, R: FR = 1.1);

neutral shade (neutral shade cloth, irradiance 6% of incident light R: FR = 1.1);

leaf shade (a layer of living banana leaves reduced irradiance to 6% and R: FR to 0.2).



Issues with morphogenetic plasticity:

Sometimes more is claimed for morphogenetic plasticity than is justified,

e.g., that it is ***the*** indicator for existence of competition.

The effect depends upon presence of adequate resources. Casal et al. (1986),

Transition of effects during canopy development.

In cotton Dauzat et al. (2008) suggest that while the pattern of increasing internode lengths early in development is consistent with decreasing R:FR this is counteracted by plant carbon limitations during the latter phase.

Dudley and Schmitt (1995) show populations of *Impatiens capensis* from more open conditions, where there was likely considerable competition for light, show photomorphogenetic-induced height growth, populations from more shaded conditions did not.

There is dispute whether height growth stimulation produced by decrease in R:FR has a cost in terms of reduced biomass growth in other parts of the plant.

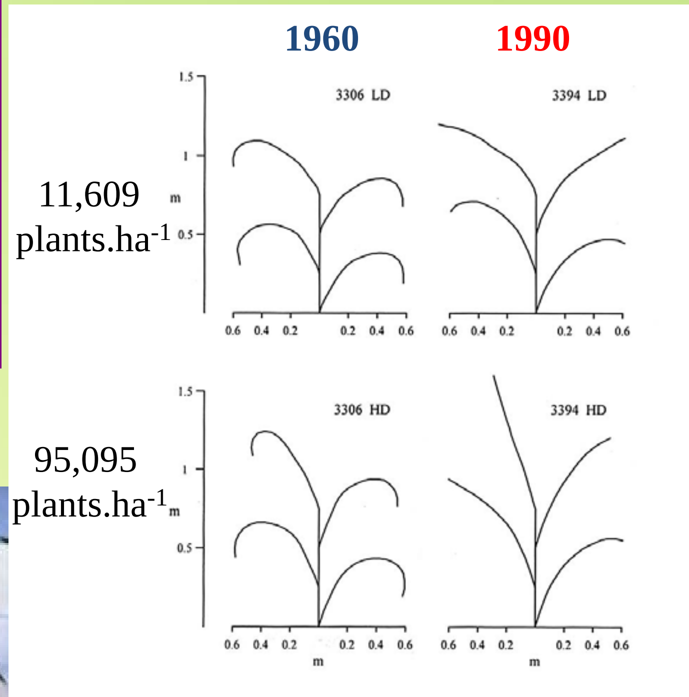
(iii) Architectural variation in interception and utilization of light

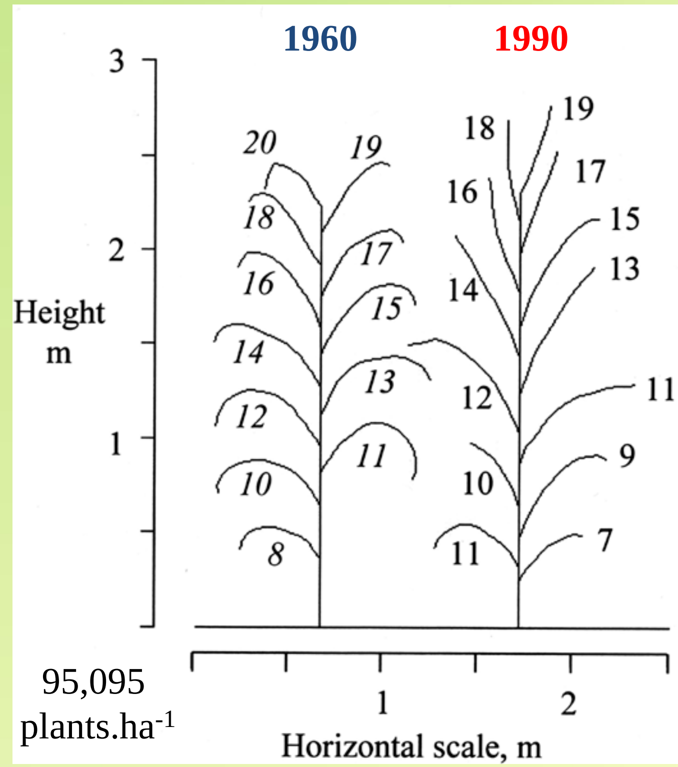
Central USA corn belt maize.

Selection for yield inadvertently led to more upright foliage and increased plasticity at higher planting density.

1960s (3306)

1990s (3394)





1990 hybrid shorter, more lanceolate leaves with smaller leaf area, Loss-of-function in auxin signaling which affects growth of the auricle to produce greater leaf uprightness and reduce leaf size

1990 hybrid, **less** total light interception, **greater** producton

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What have architecture studies shown?

Three properties influencing competition as a 3-D process.

(i) Resource acquisition plasticity: ***plants preferentially extend branches and/or foliage into regions where there are resources***.

(ii) Morphogenetic plasticity: ***plants respond to competition by changing morphology, e.g., the increase in relative height growth of shaded plants.***

Much focus on this aspect

(iii) Architectural variation in interception and utilization of light: ***absorption of light by one plant obviously makes it unavailable for another and so will affect competition but efficiency of utilization of light in growth may also affect competition***.

The Dynamic Relationship Between Plant Architecture and Competition

Development of theory for effects of plant architecture on competition

Five general groups of postulates to analyze effects of ***differences*** in architecture on competition. Specific postulates are needed for particular questions.

1. Competition for light takes place at the level of foliage and foliated axes rather than whole plants—except for small plants that have only a single foliated axis.

2. The outcome of competition is determined by interaction between two processes

Exertion of dominance through growth of foliage or a foliated axis that intercepts light that would otherwise could be utilized by neighbouring foliage.

Dynamics of the process—but constrained by spatial interactions

Reaction to shading through changing form and/or physiological characteristics.

Competition between large plants maintains a spatial even distribution

3. Architectural properties of a species determine both *Exertion of dominance* and *Reaction to shading*.

4. For an individual plant the outcome of competition depends upon integration of effects of *Exertion of dominance* and *Reaction to shading* across the component foliage and foliated shoots.

5. Mortality is a time-delayed response to suppression.

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Conclusions

Plant population studies have shown some features that develop during competition but they have not explained them. Variation due to species differences have not been well defined.

Architecture studies, and characterization of physiology relevant to competition, have tended to focus on just one process where attempts have been made to explain population processes. Dynamics of the competition process need to be studied explicitly.

Study of whole plant integration is a subject that may have to be studied directly by scientists interested in designing, constructing and using FSPMs.

Thanks to *Katrin Kahlen, Leo Marcelis, Hartmut Stützel* for helpful comments during the preparation of an article for Frontiers.

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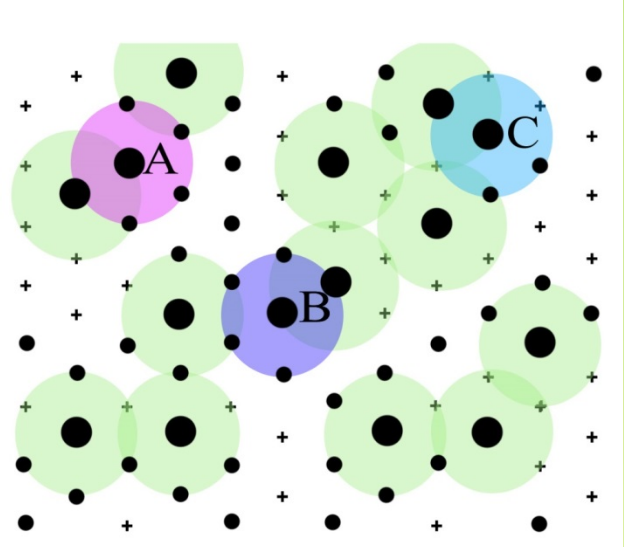


The spatial arrangement of large and small plants, represented by black circles of their respective sizes at the lattice points and dead plants indicated by +. Plants **A**, **B**, and **C** are each one of a pair of large plants that are within 2cm of each other, whereas other large plants are further than 2 cm from a large neighbour.

(ii) Morphogenetic plasticity

Ballaré, et al. (1988) many other papers since then.

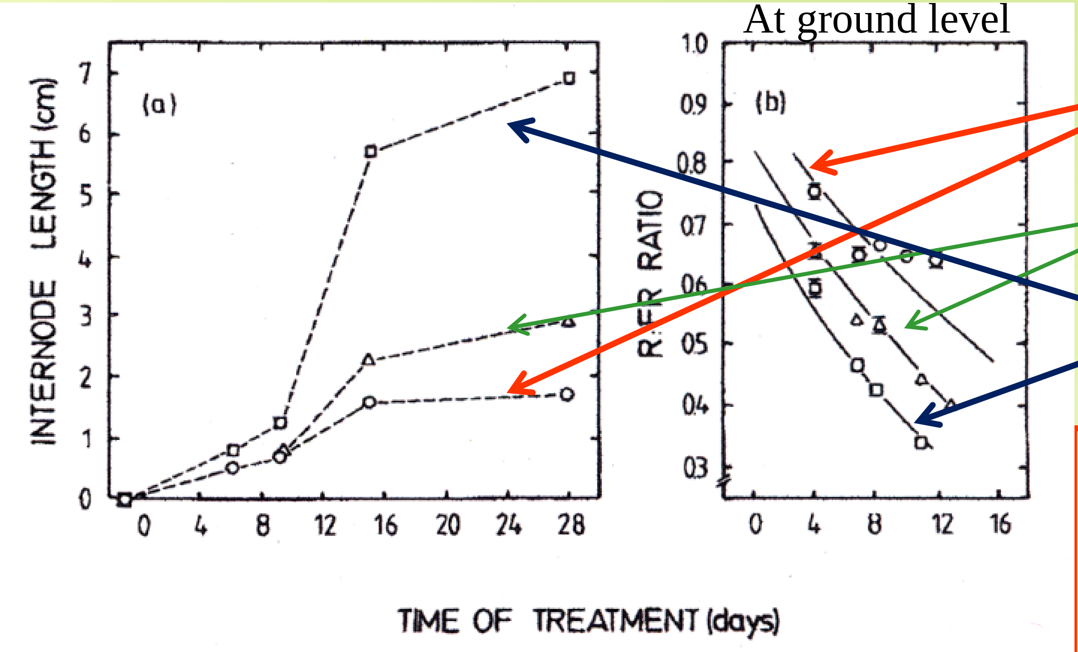
Phytochrome mediated effects

$$R : FR = \frac{\text{photon irradiance between 660 and 670 nm}}{\text{photon irradiance between 725 and 735 nm}}$$

Morphological responses of *Datura ferox* L. seedlings to the presence of neighbours

Seedlings respond rapidly (1-2 wks) to increased plant density by producing longer internodes and greater dry matter in stems.

Responses were observed before light interception or growth rate were reduced by presence of neighbours.



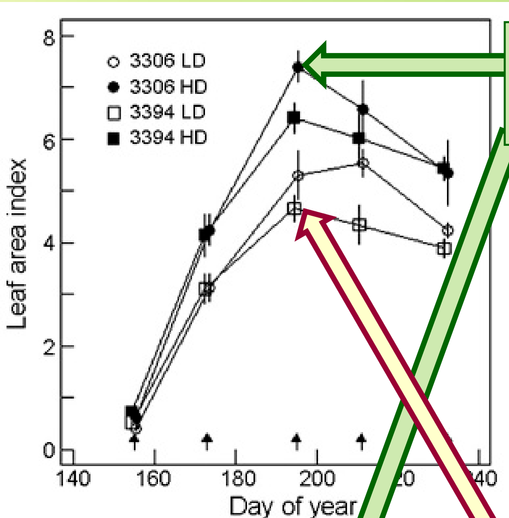
32 seedlings per square meter

100 seedlings per square meter

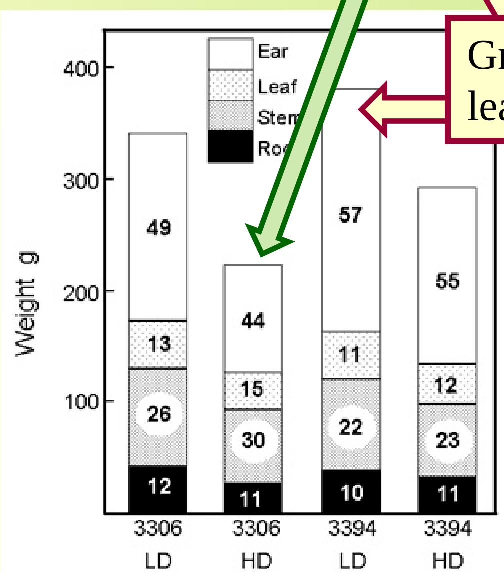
240 seedlings per square meter

Results support the idea that the drop in R:FR ratio is an early signal allows rapid adjustment of plan form to changes in canopy struc

Canopy development, crop production and light interception of 1960 (3306) and 1990 (3394) hybrid maize planted at 64,000 (LD) and 95,095 (HD) plants ha^{-1}.



Greatest L, least yield



Greatest yield, least L

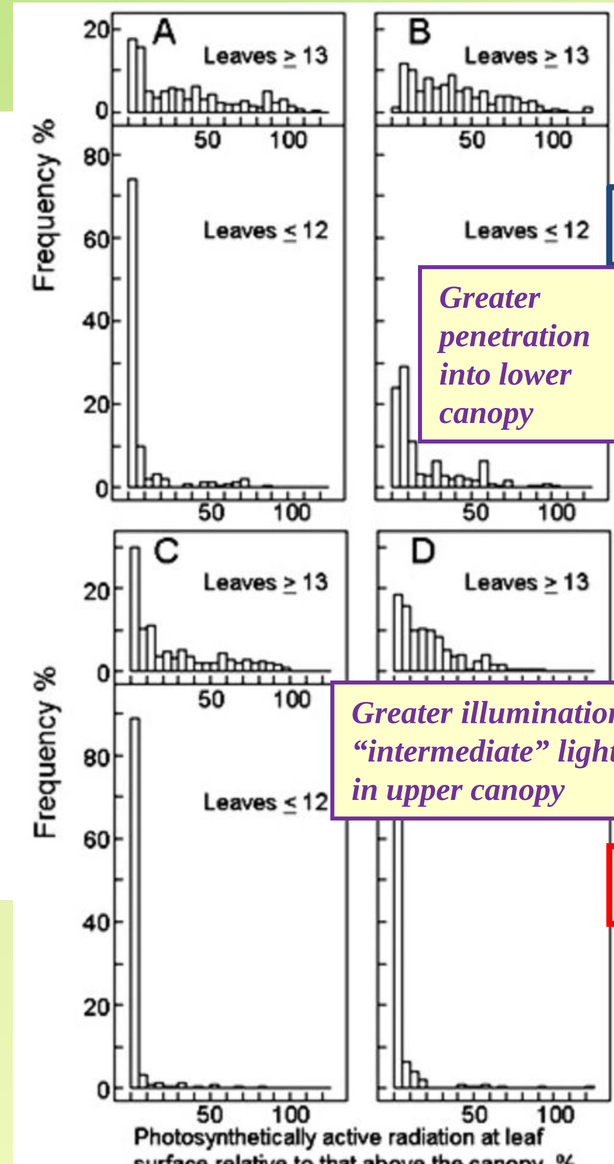
Distribution of foliage area according to percent light received on a horizontally upward pointing PAR meter above the canopy.

Upper row for foliage at leaf 13 or higher; lower row for foliage at leaf 12 or lower.

Columns on the left are hybrid 3306, on the right.

1960

1990



LD

Greater penetration into lower canopy

Greater illumination at "intermediate" light levels in upper canopy

HD