Physiology of High Yielding Corn and Soybeans

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Outline

- Canopy photosynthesis and grain yield
  - vegetative and reproductive stages
- Yield formation
  - control of seed number
- Environmental limitations
  - seed number and seed size

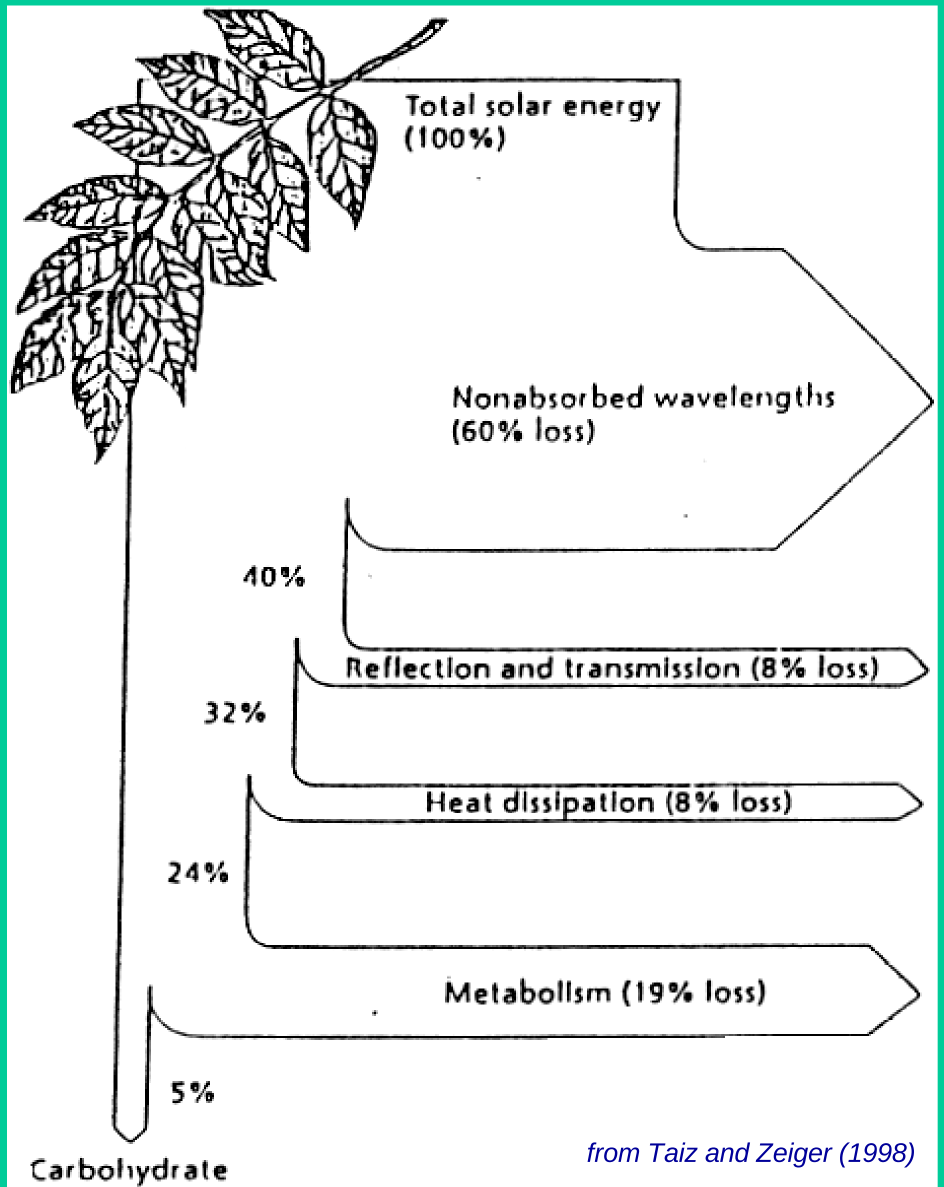
Photosynthate supply...

- Review factors limiting photosynthetic rates at the canopy level.
- Explore the relationship between canopy photosynthesis and yield formation.
- Suggest ways to manage corn and soybeans for high photosynthetic efficiency.

Crop canopies typically convert less than 5% of the incident solar energy available during the season into dry matter.

Only about half of incident solar is 'useful' for photosynthesis.

About one-third of the 'useful' radiation is not utilized for photosynthesis.

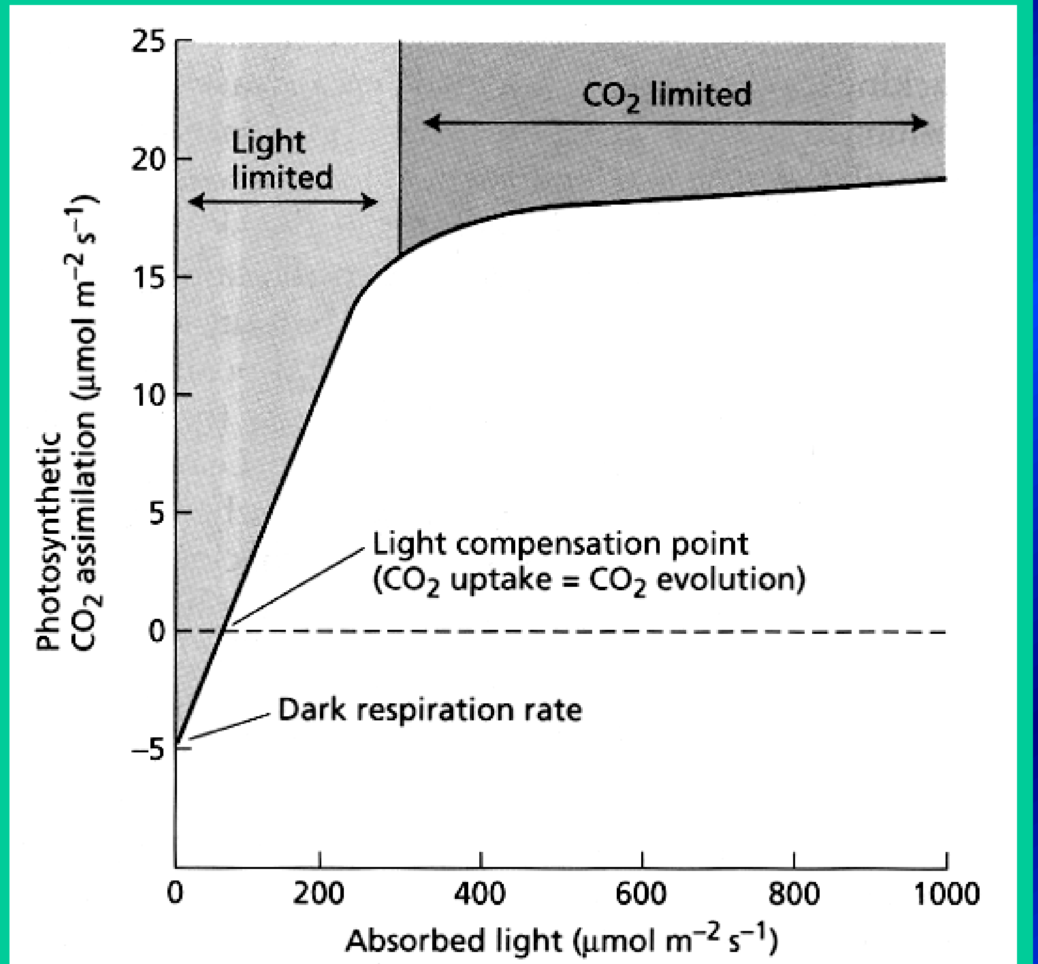


from Taiz and Zeiger (1998)

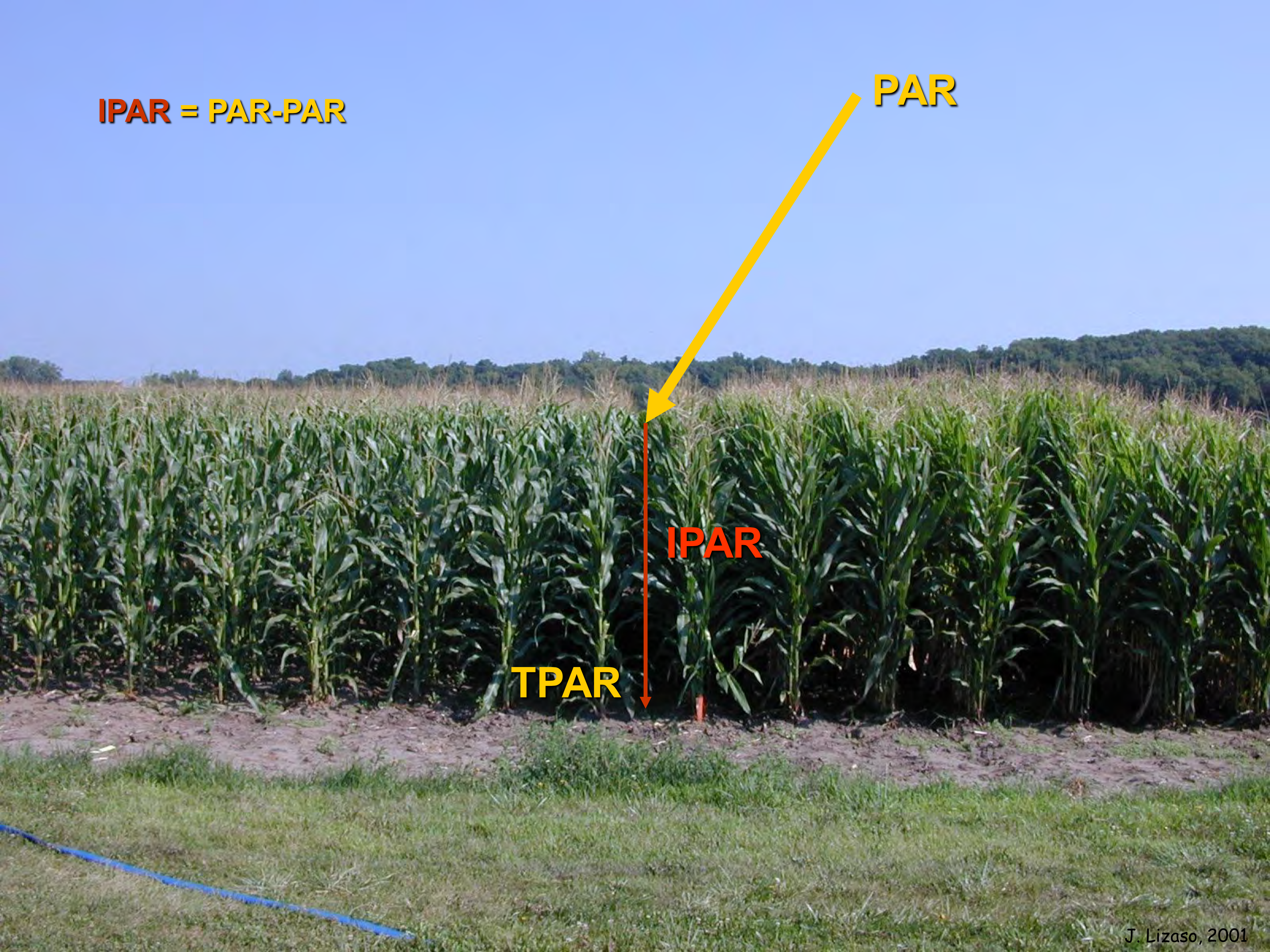
The photosynthetic rate of individual leaves is limited by the concentration of CO_2 within them, and by amount of light energy they can absorb.

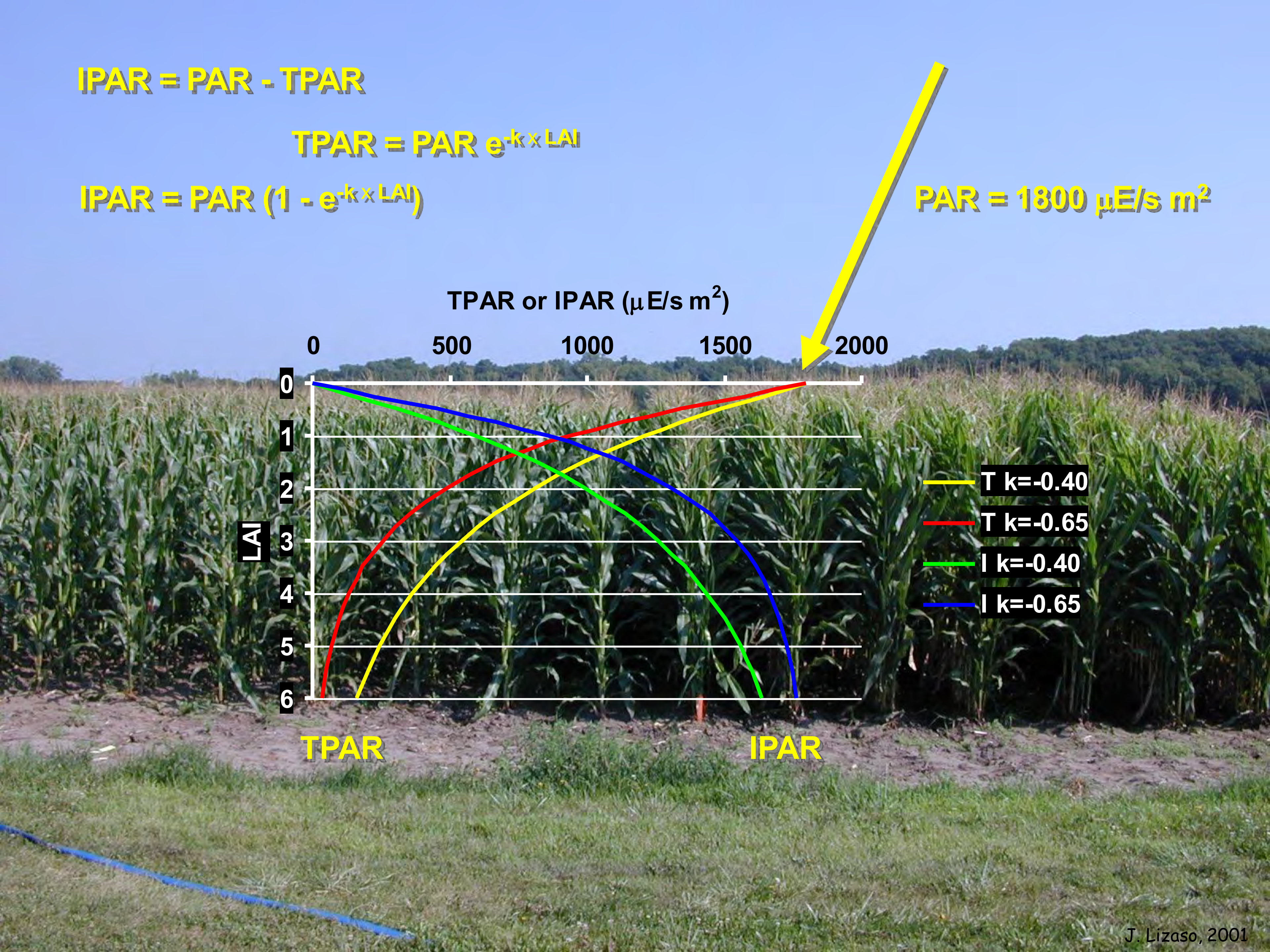
In the field,
Individual leaves become 'saturated' for light at ~ 500 μmol photons m^{-2} s^{-1}.

That's equivalent to about one-third to one-fourth of full sunlight.



from Taiz and Zeiger (1998)


IPAR = PAR-PAR
PAR
IPAR
TPAR
J. Lizaso, 2001


IPAR = PAR - TPAR
TPAR = PAR $e^{-k \times LAI}$
IPAR = PAR $(1 - e^{-k \times LAI})$
PAR = 1800 μE/s m^2
TPAR or IPAR (μE/s m^2)
0
500
1000
1500
2000
LAI
0
1
2
3
4
5
6
T k=-0.40
T k=-0.65
I k=-0.40
I k=-0.65
TPAR
IPAR
J. Lizaso, 2001

Decreasing spacing between rows…

How much does it improve light interception and radiation use efficiency in maize?

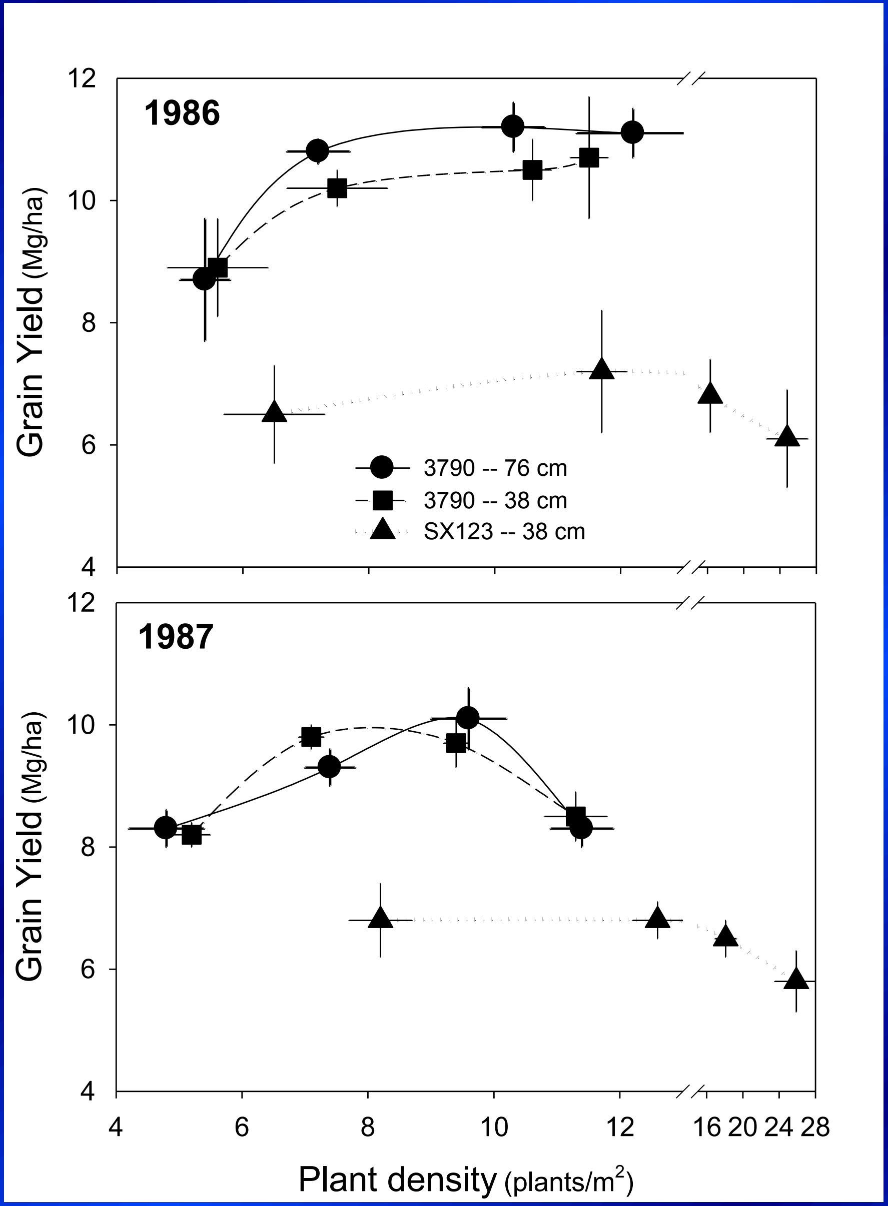
76-cm (30 in) rows
Light reaches soil between rows

38-cm (15 in) rows
Light reaches soil between plants

Most research on maize indicates maximum yield can be attained across a range of population densities and row spacings.

Optimum population -- 8-10 pl/m^2

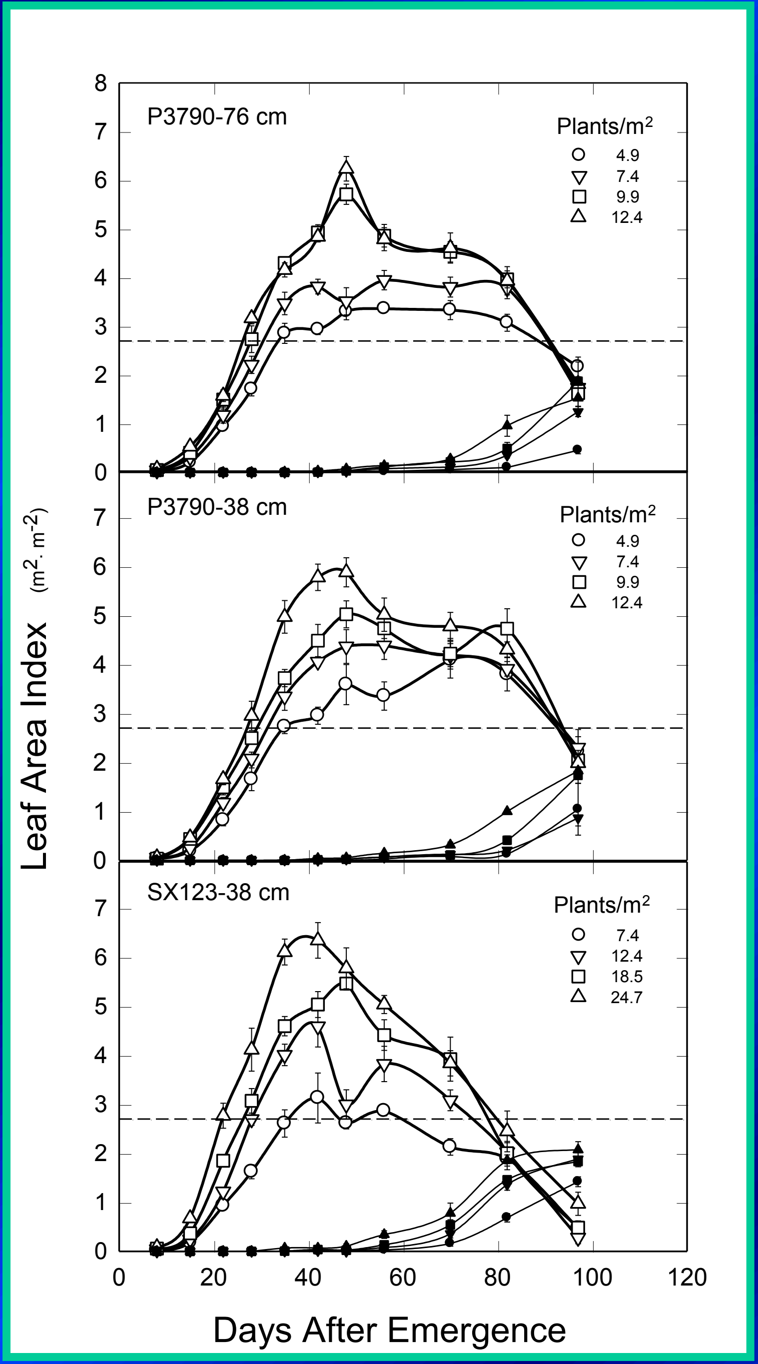
Optimum row spacing -- 50 cm



adapted from Westgate et al 1997

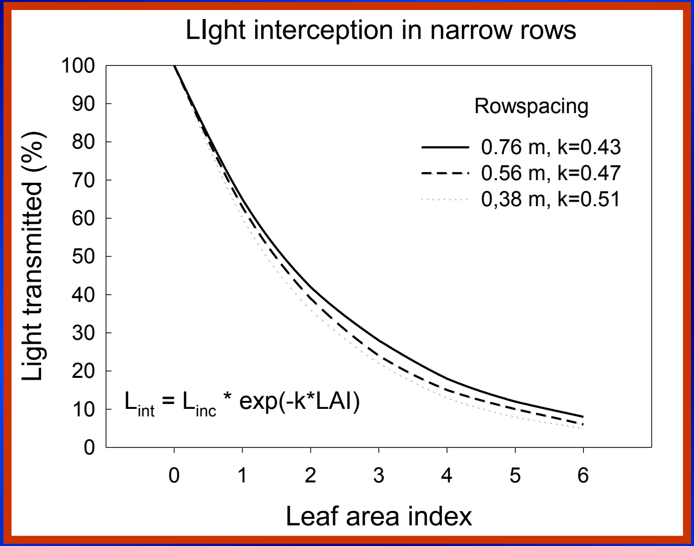
Row spacing and plant population density can be used to alter canopy development

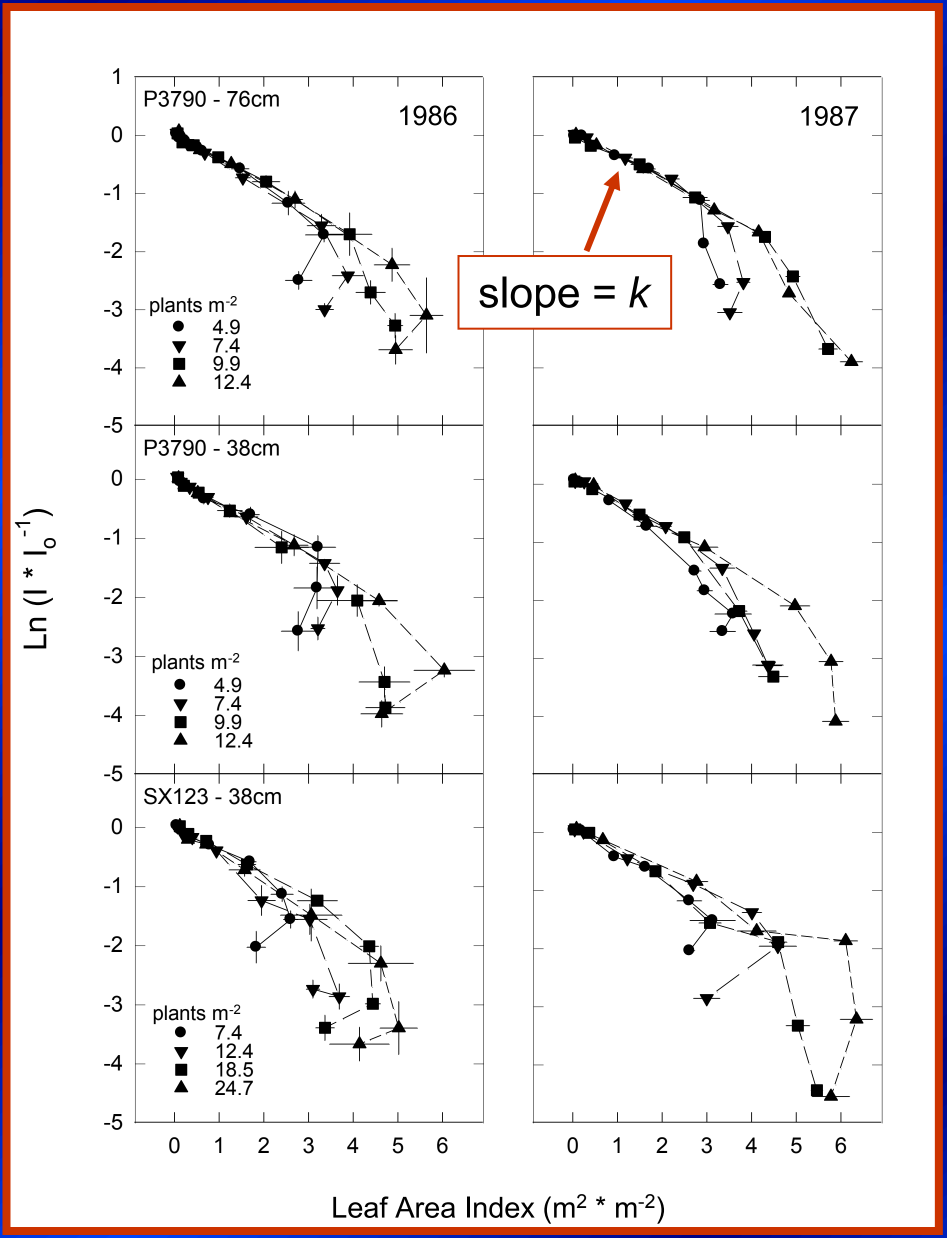
…and presumably, the efficiency of light interception and total seasonal photosynthesis.



Westgate et al 1997

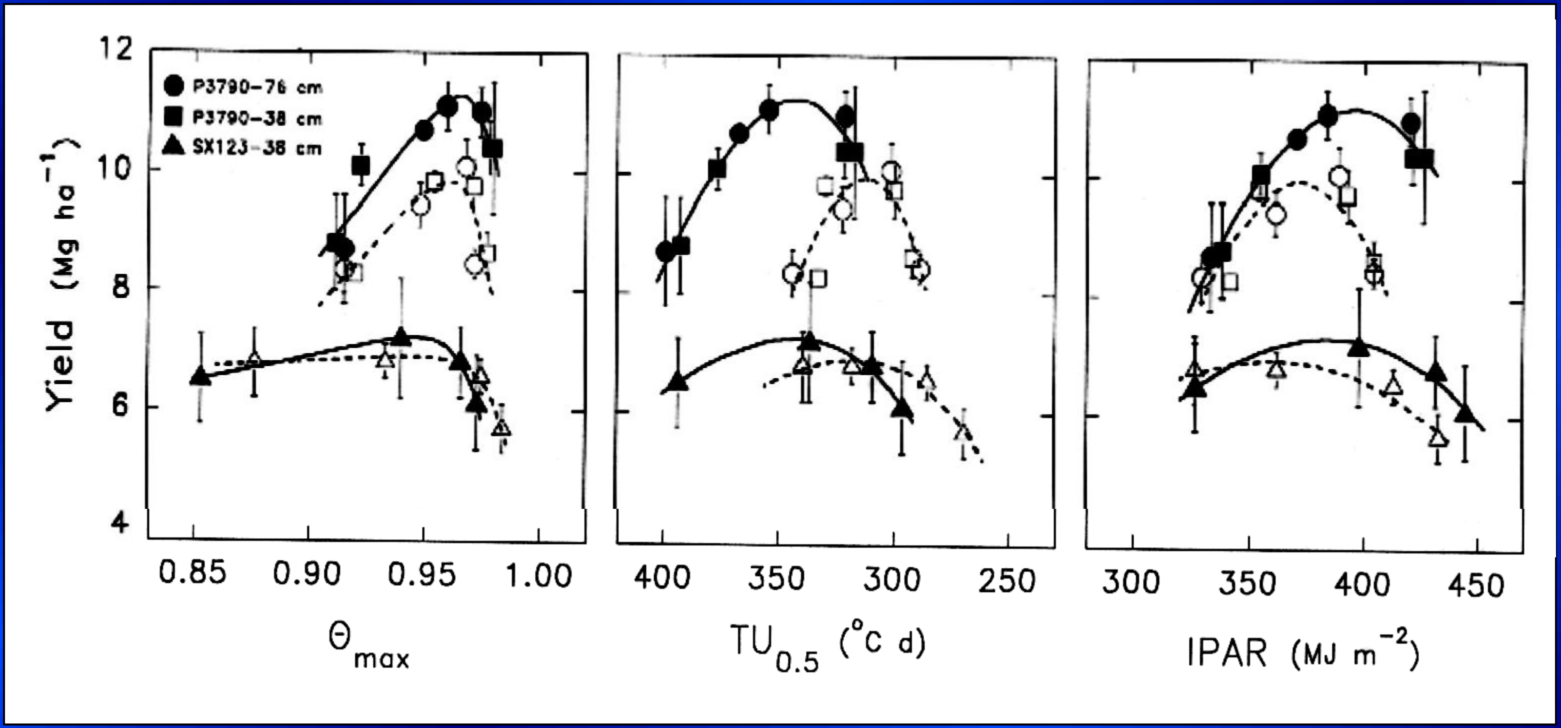
Increasing plant density improves light interception primarily by adding more leaf area, not by improving canopy efficiency per unit leaf area (*k*).





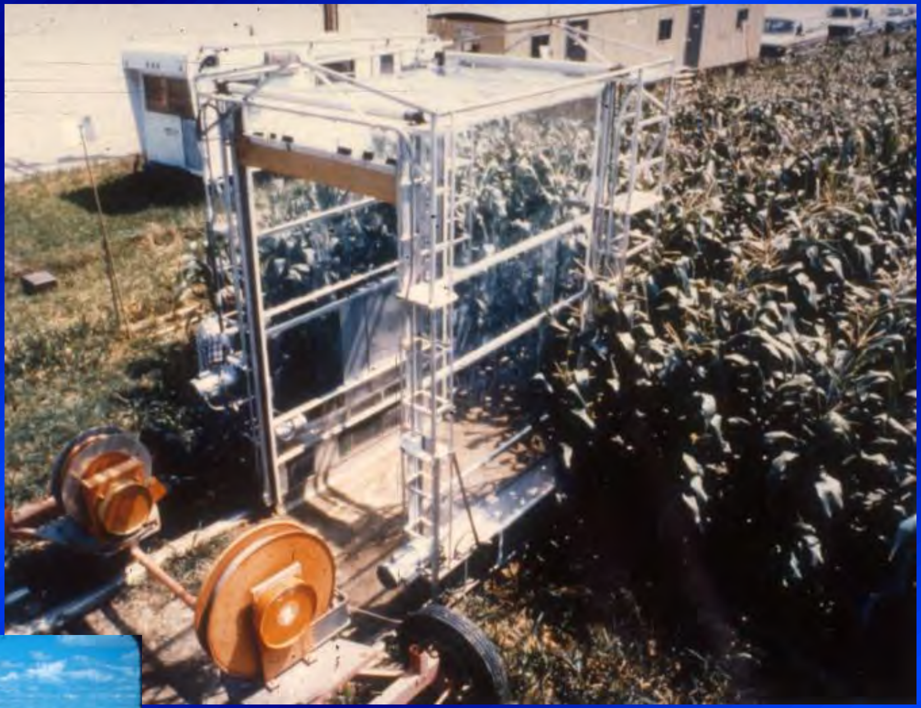
Westgate et al 1997

Maximum grain yield in maize reflects an optimum level of light interception, timing of canopy closure, and IPAR prior to flowering.



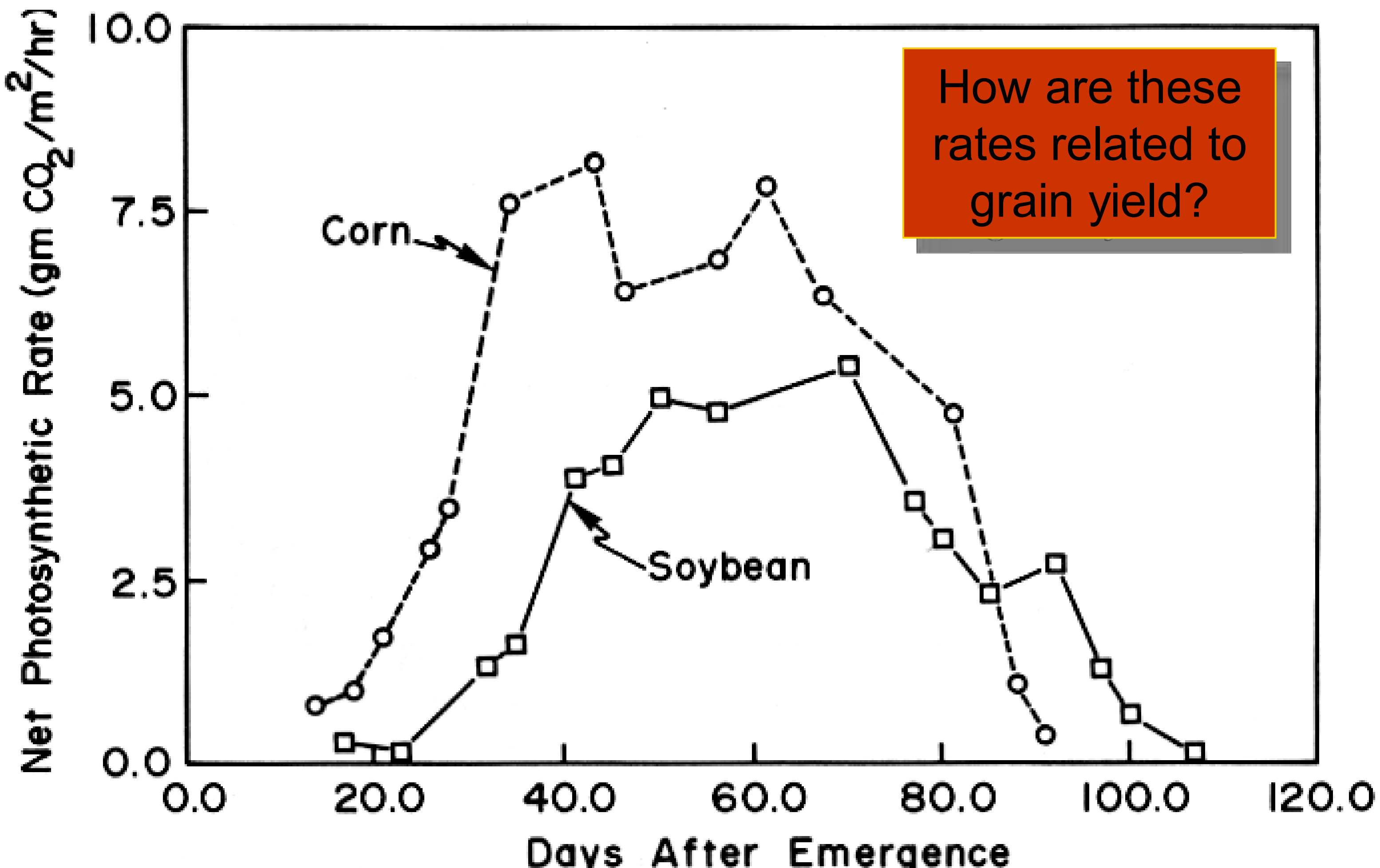
Westgate et al 1997

Chambers used to estimate "Seasonal Canopy Photosynthesis"



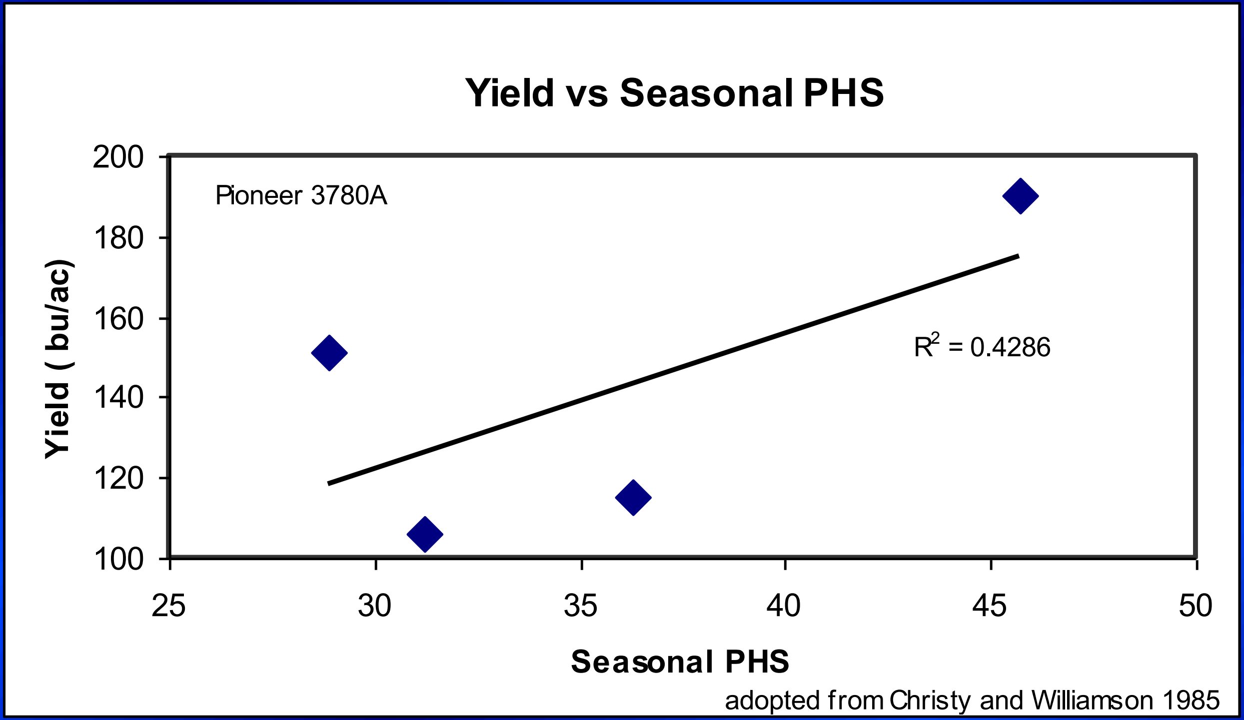
Measurements are made on clear days at maximum light intensity. These rates indicated the potential photosynthate supply for the season

Rates of canopy photosynthesis increase with LAI to a a maximum during flowering and seed set. Corn achieves higher rates than soybean at high light intensities.

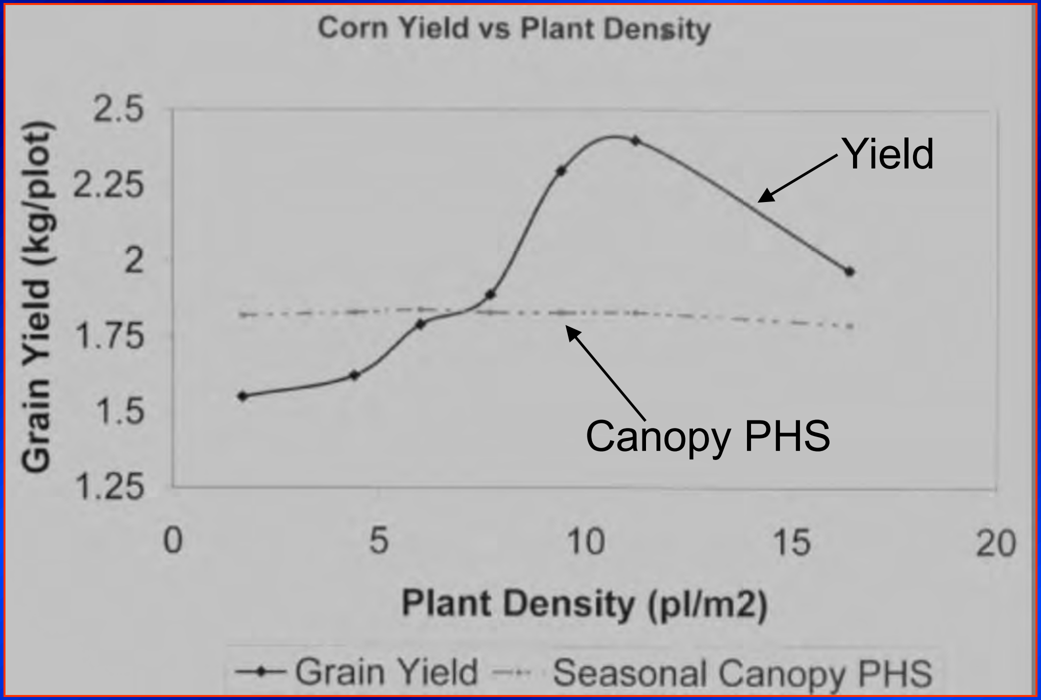


from Christy and Williamson (1985)

For maize, variation in grain yield across years is not closely related to maximum canopy photosynthesis during the season (one hybrid, four years)



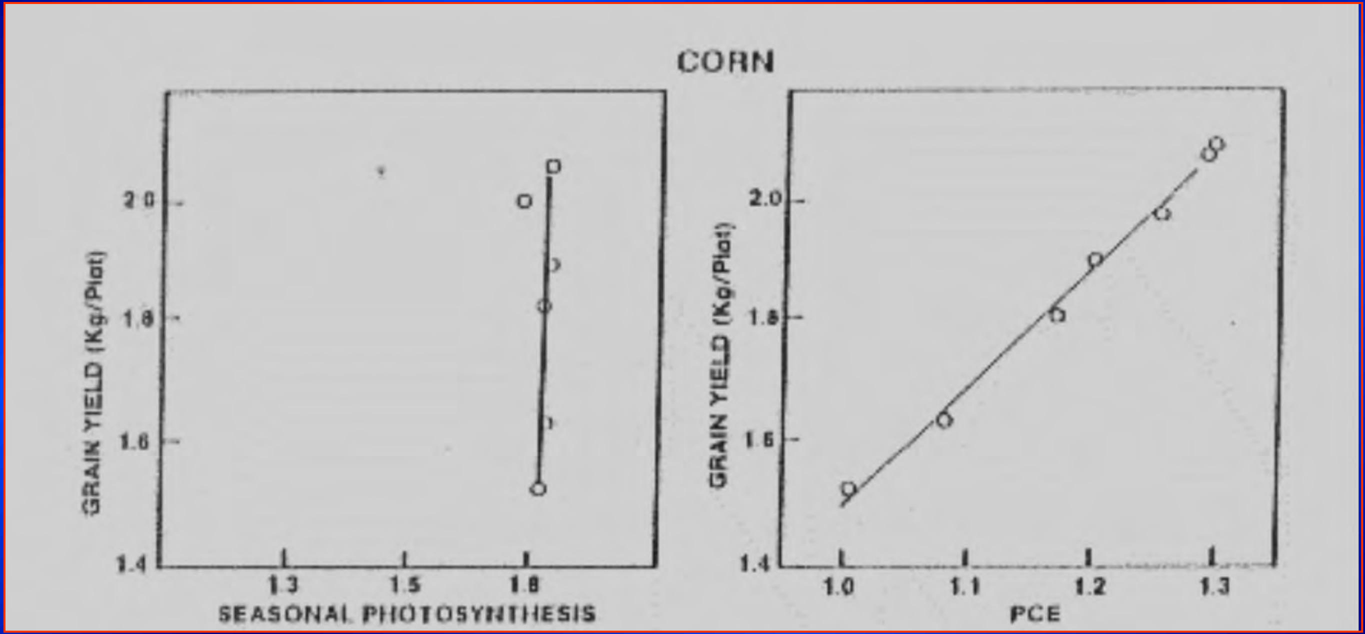
Modern maize hybrids generally achieve maximum grain yield at about 9 to 11 plants/m^2



Variation in grain yield with plant density is not reflected in the capacity for canopy photosynthesis

The increase in yield due to higher plant population is not solely a result of increased assimilate availability during the growing season.

Higher plant densities are more efficient at converting available assimilate into grain.

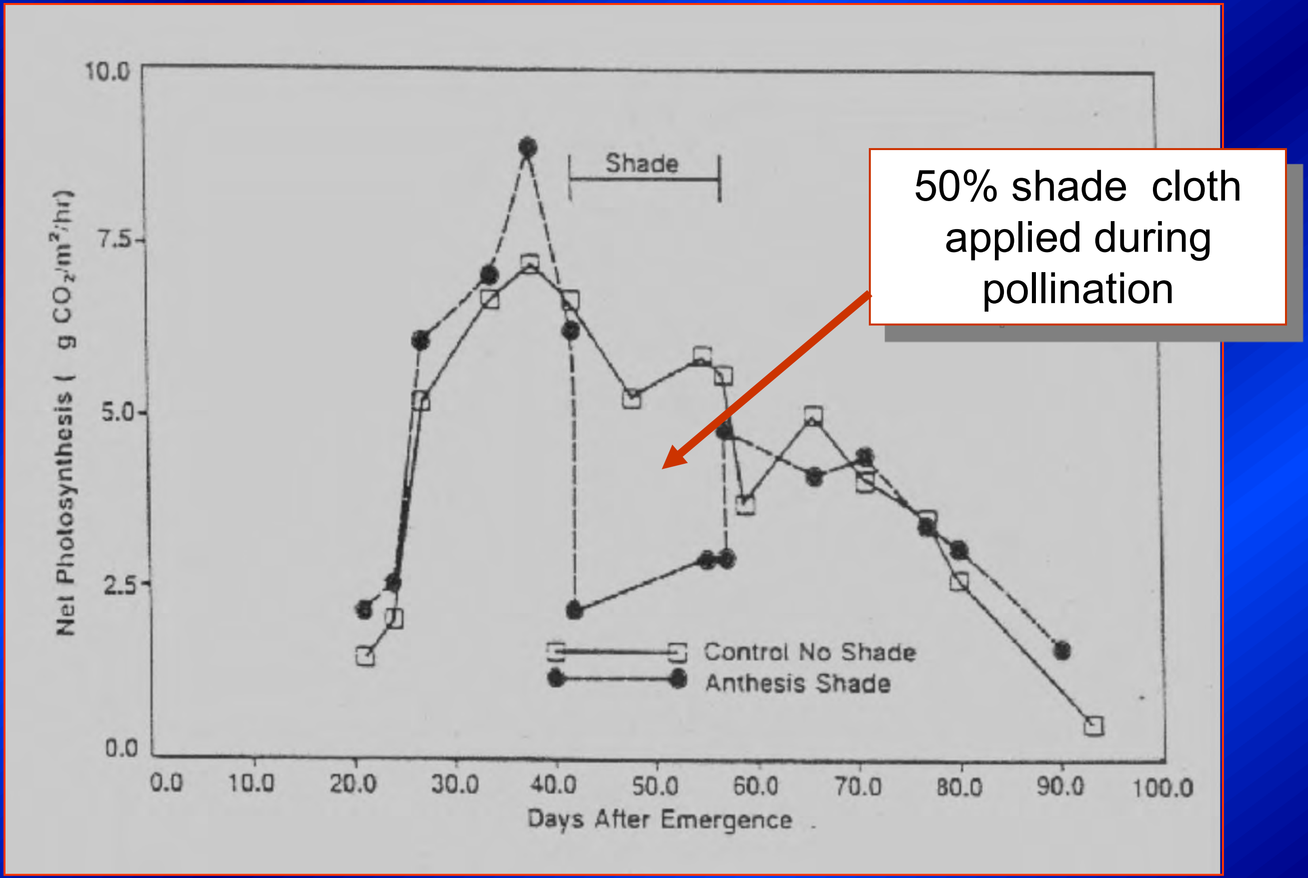


from Christy and Williamson, 1985

PCE = photosynthetic conversion efficiency

Shading Experiments:

Although grain yield in maize does not appear to be 'source limited,' there are periods during development when assimilate supply is critical



from Christy et al 1982

Shading Experiments:

Impact of shade before, during, or after flowering on grain yield varies with environmental conditions.

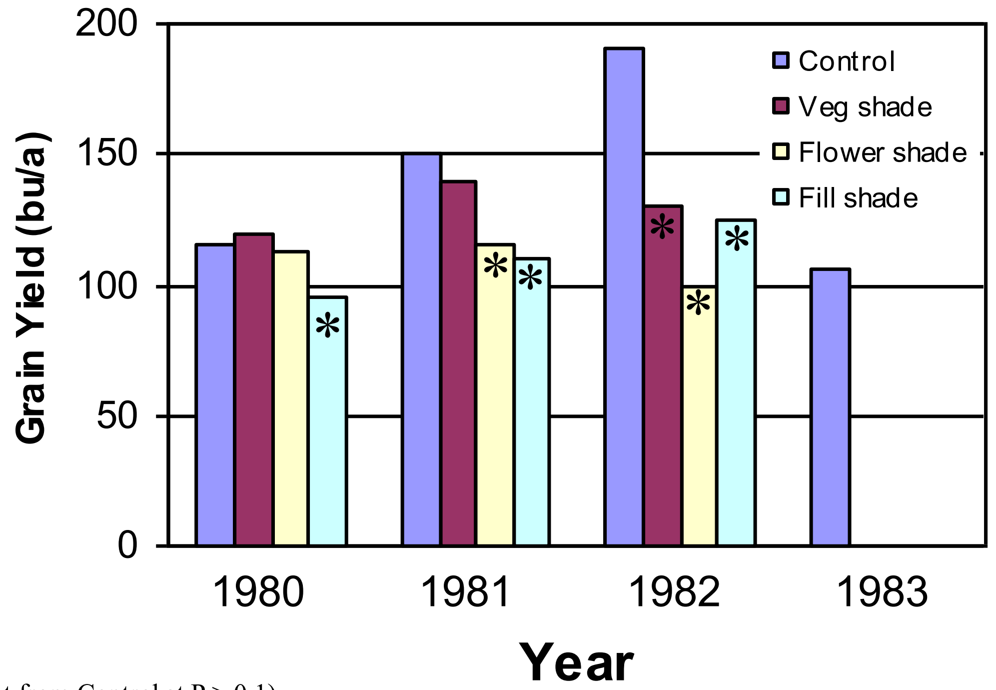
Yield variation between years was greater than shading effects within years.

1980: Hot
moderate PHS

1981: Cool
low PHS

1982: Cool
high PHS

1983: Hot
low PHS

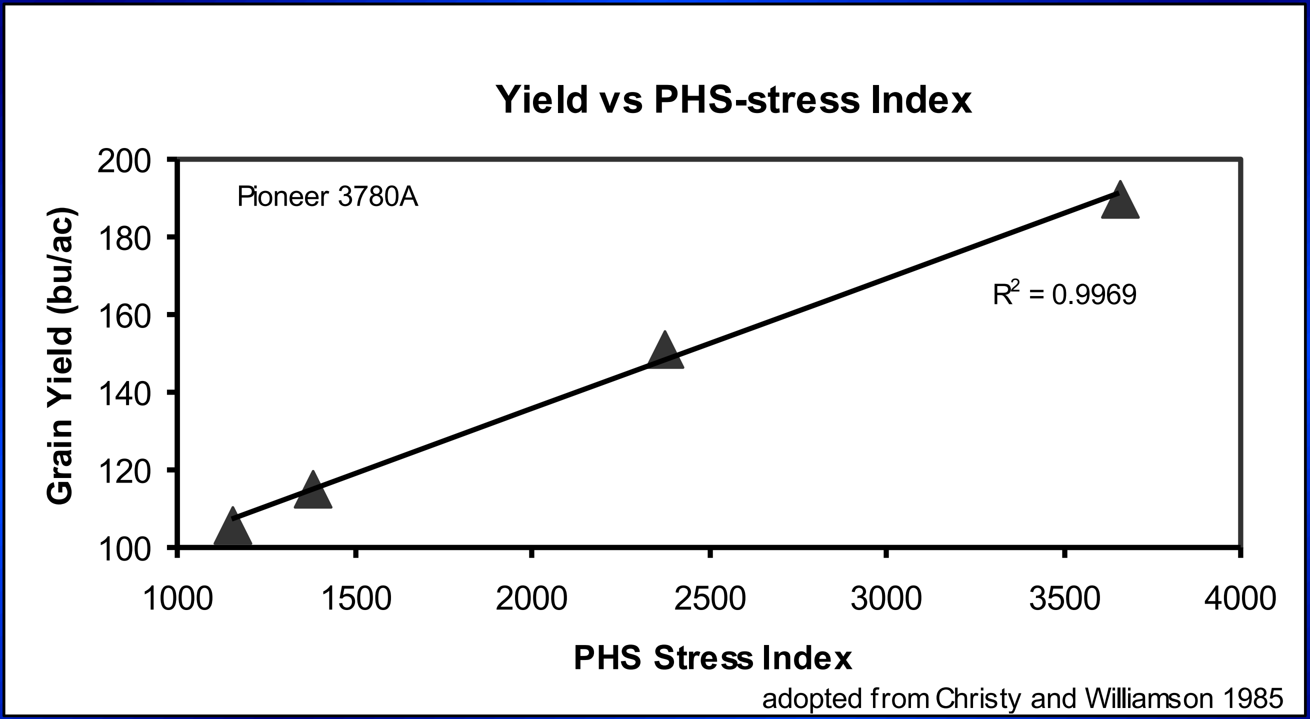


(* different from Control at P > 0.1)

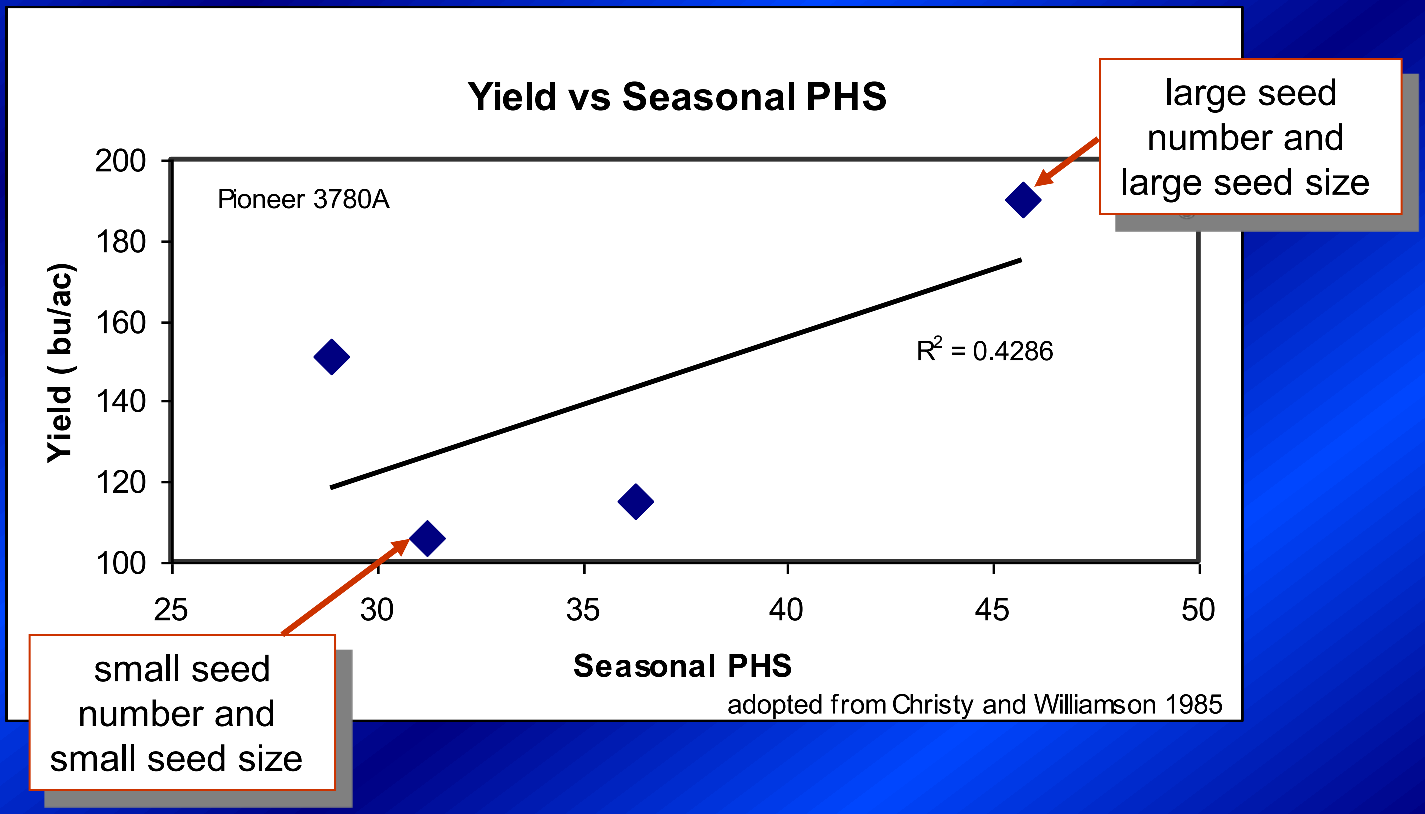
adopted from Christy and Williamson, 1985

When seasonal canopy photosynthesis is adjusted for accumulated stress days, there is clearly a combined effect of source capacity and sink demand on final grain yield

PHS Stress Index = Seasonal PHS • (100-days`> 32°C)

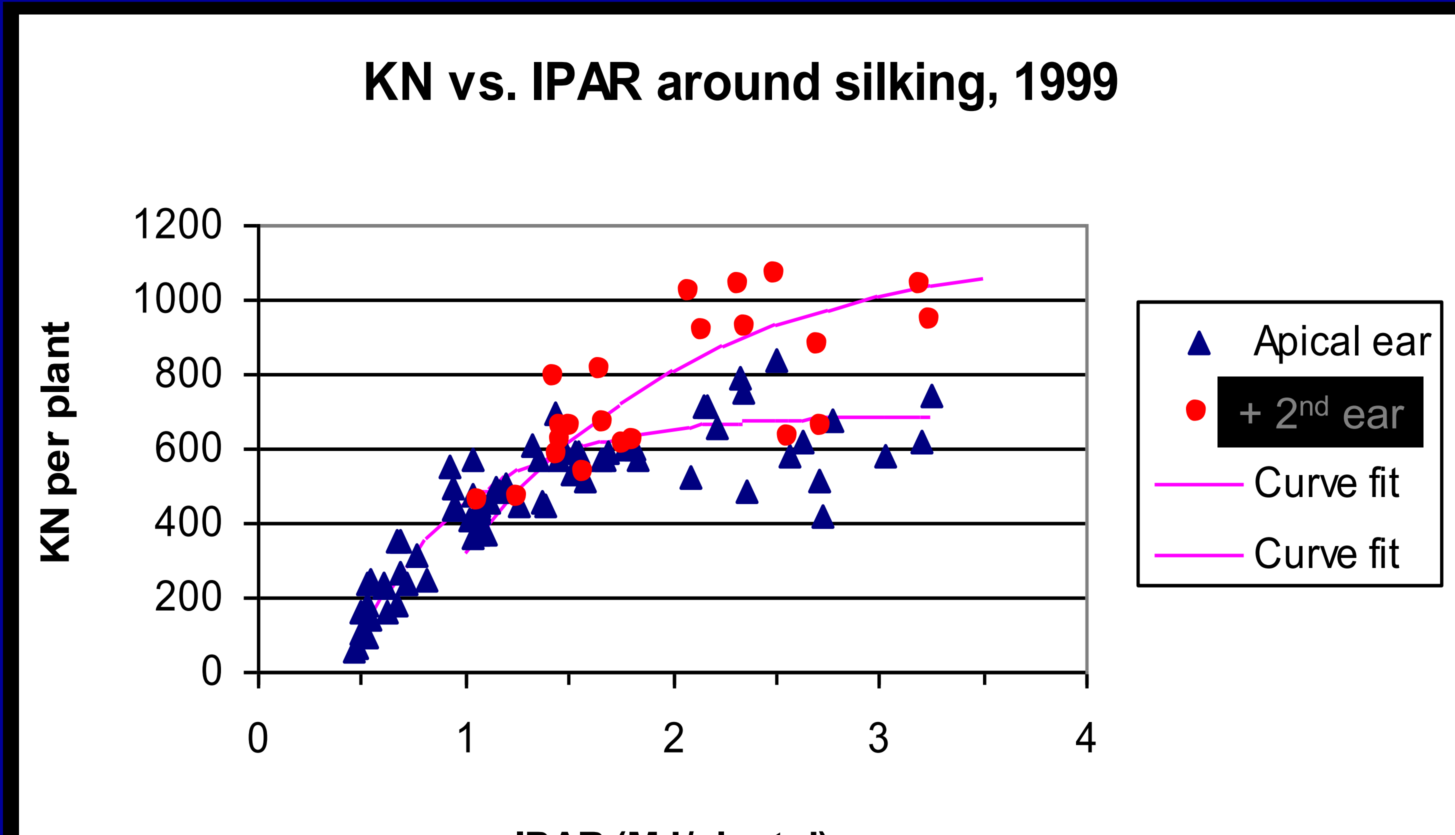


Differences in seed number per plant explain most of the variation in grain yield across years. Seed size is more stable, but also contributes to yield variation.



Numerous studies confirm that KN varies with IPAR during pollination and early kernel growth

Ames, IA 1999



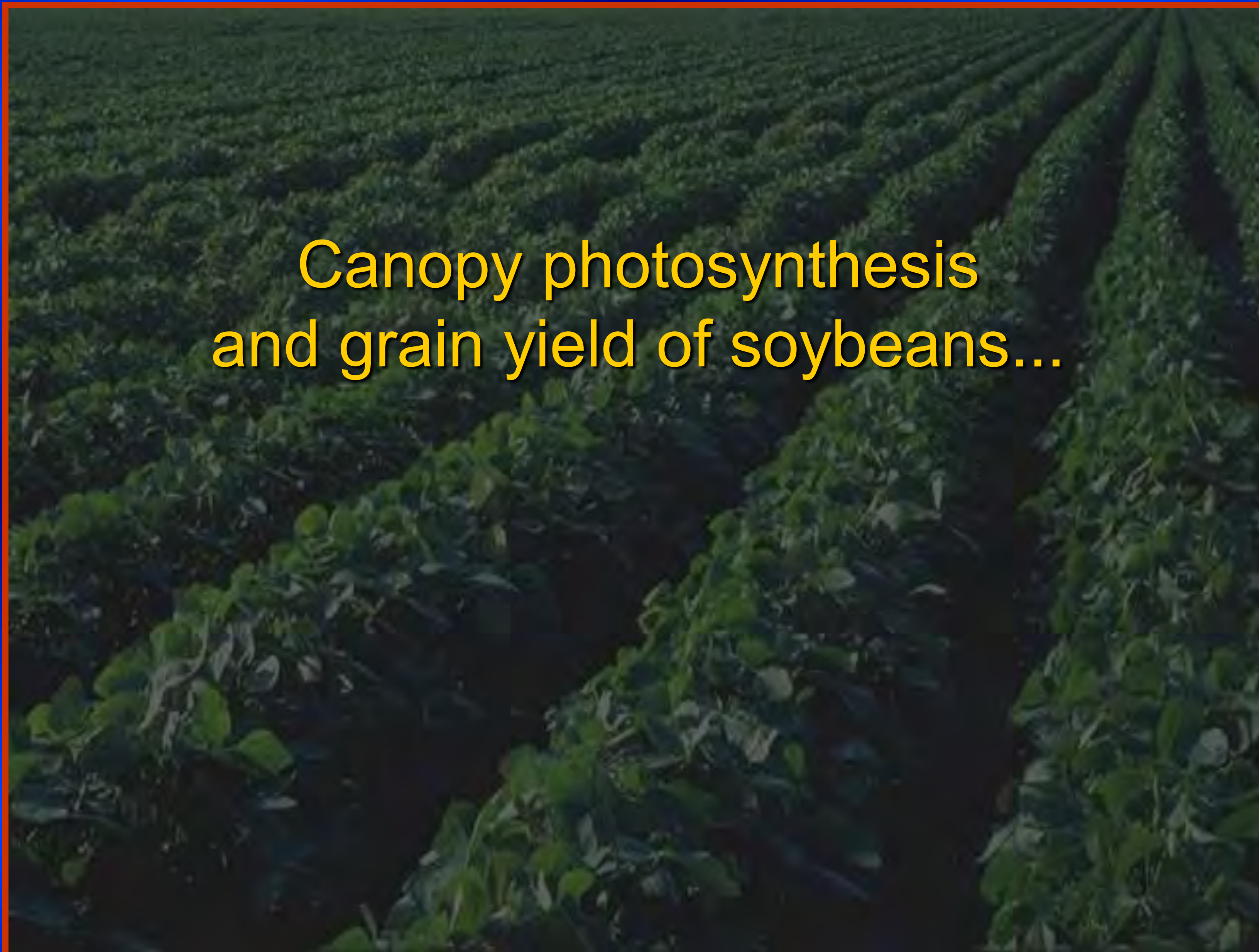
Lizaso et al unpublished

Summary:
– assimilate supply for high yield in maize

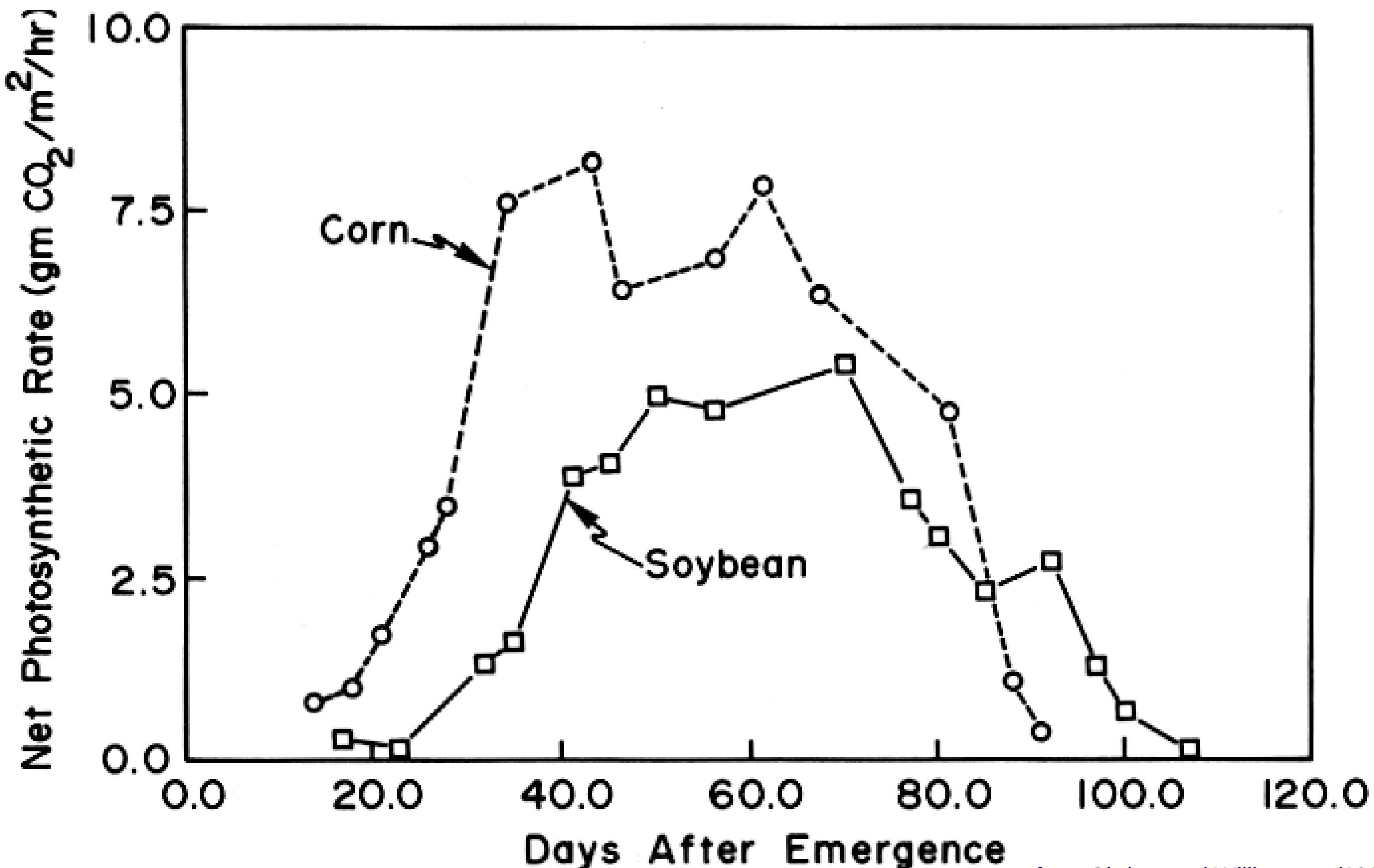
Grain yield in maize is primarily ‘sink limited.’

Attaining rates of canopy photosynthesis during the entire season are necessary, but not sufficient, to obtain high grain yield

Management strategies that increase seasonal canopy photosynthesis must not do so at the expense of establishing and maintaining reproductive sinks.

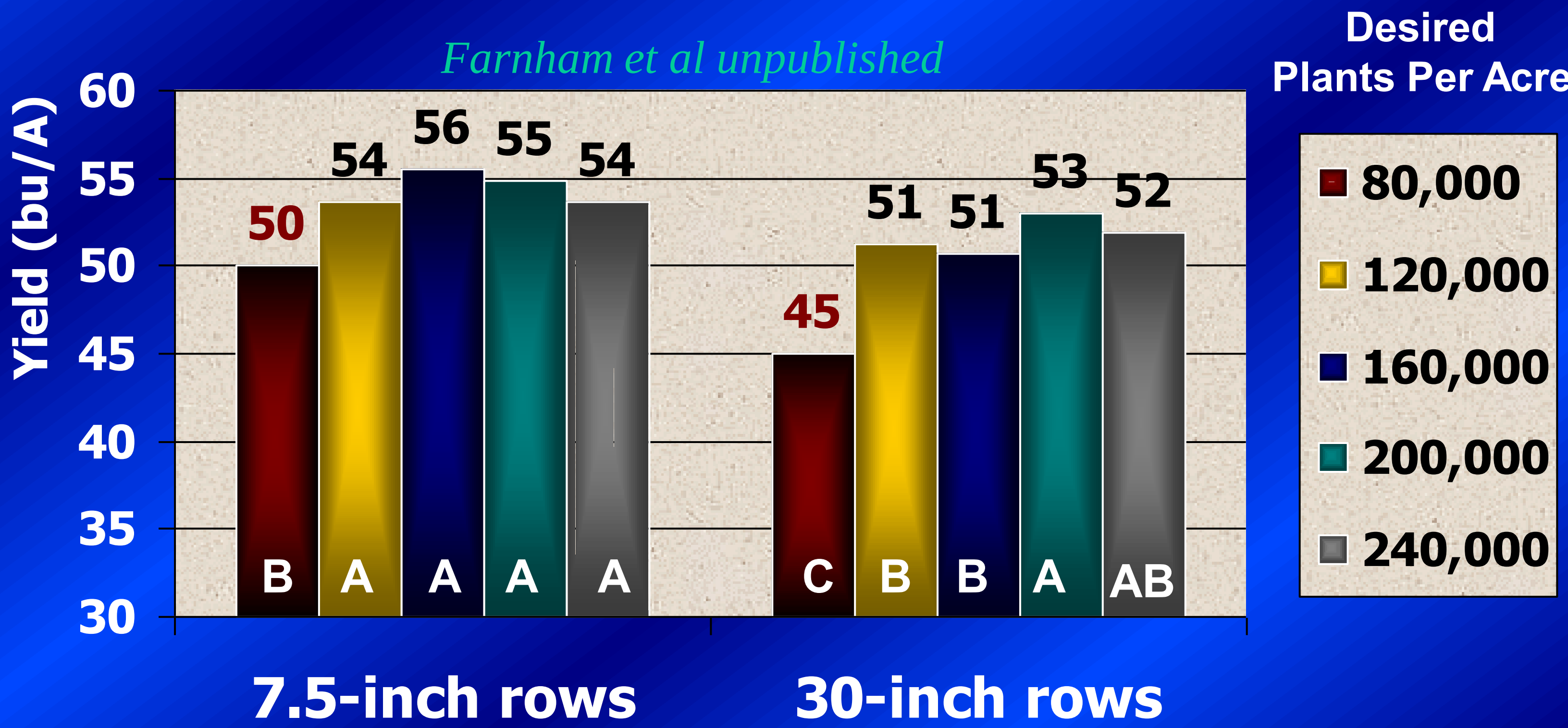

Canopy photosynthesis
and grain yield of soybeans...

As with maize, photosynthetic rates of the soybean canopy increase with LAI, and reach a maximum at LAI ≥ 4.0, which coincides with pod set and early seed fill.



from Christy and Williamson (1985)

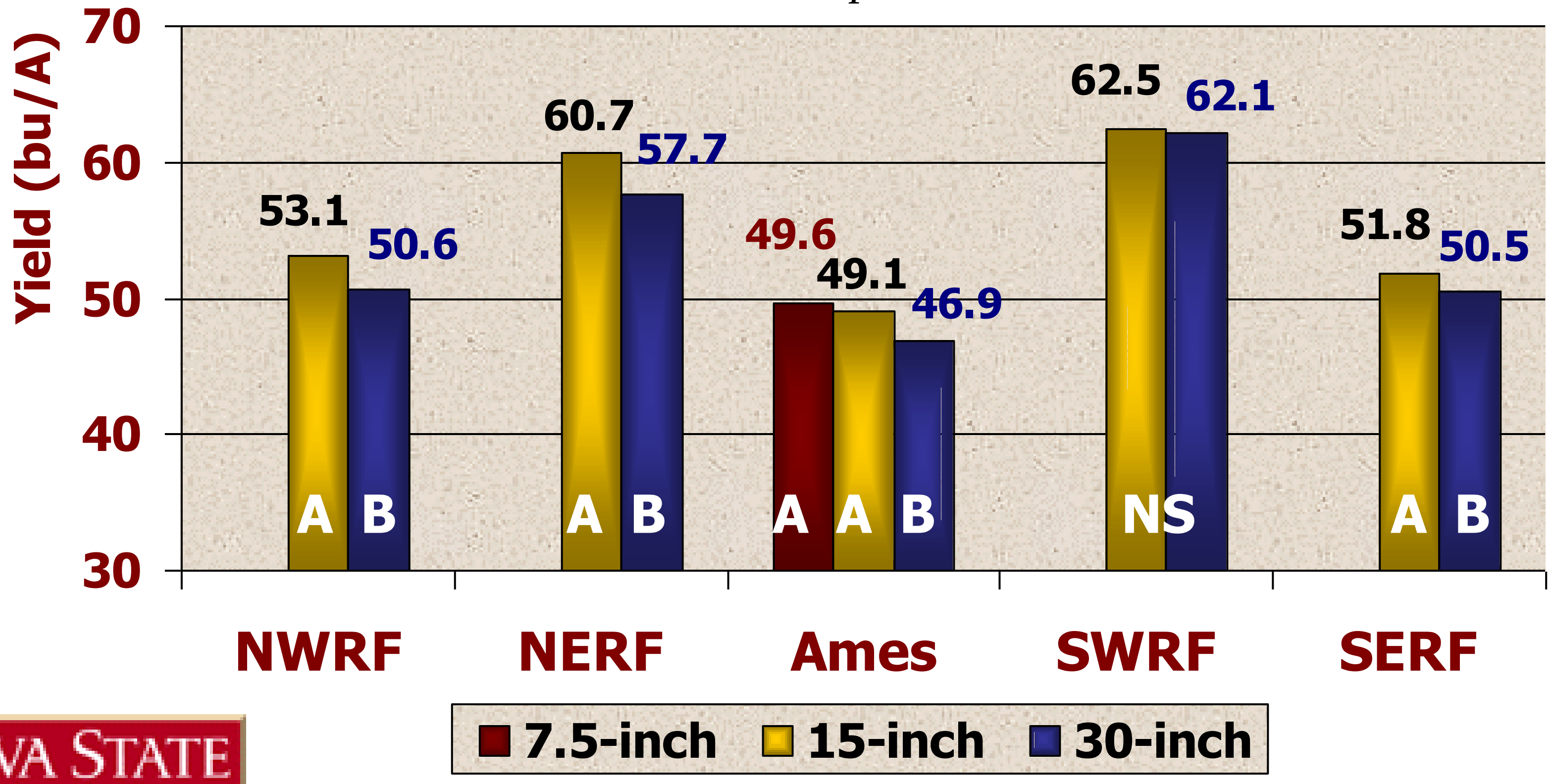
Row Spacing and Harvest Stand Effects on Soybean Yield (Ames, 1994-96)



Within a RS, yields with the same letter are similar (P = 0.05).
Esti. harvest PPA (x 1000) (7.5”: 116, 156, 178, 203, 251)
(30”: 80, 125, 143, 174, 205).

Row Spacing Effect on Soybean Yield
Five ISU Research Farms (1997-99)

Farnham et al unpublished



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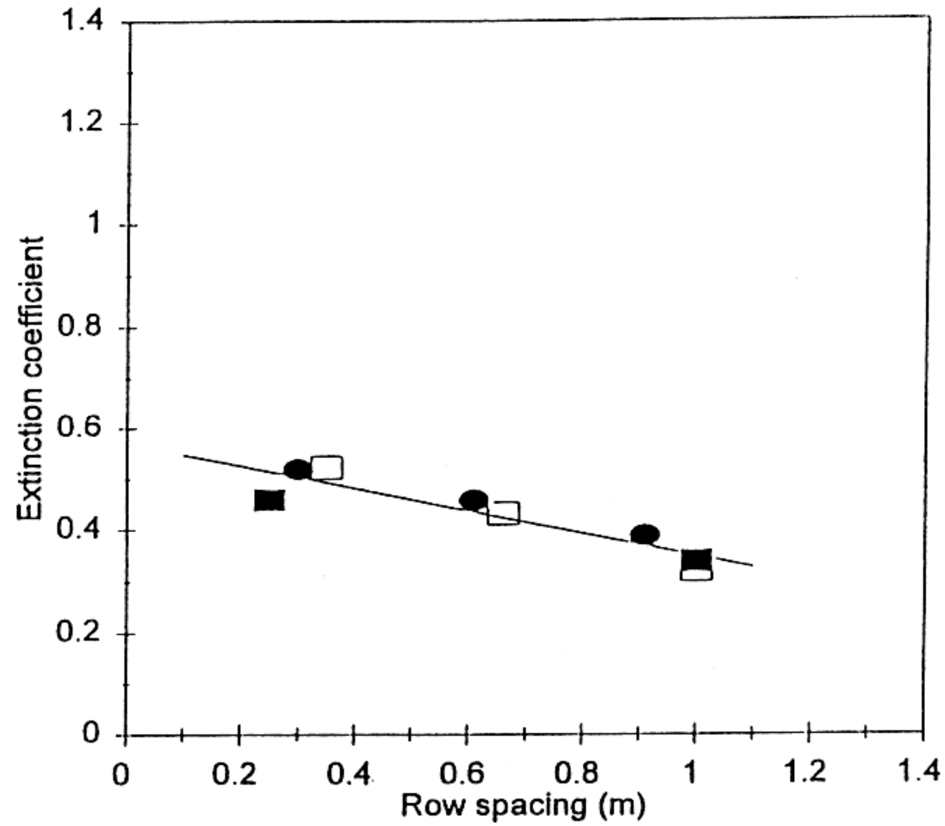
Each yield value represents an ave. of 8 adapted varieties. At a site, yields with same letter are statistically similar (P=0.05).

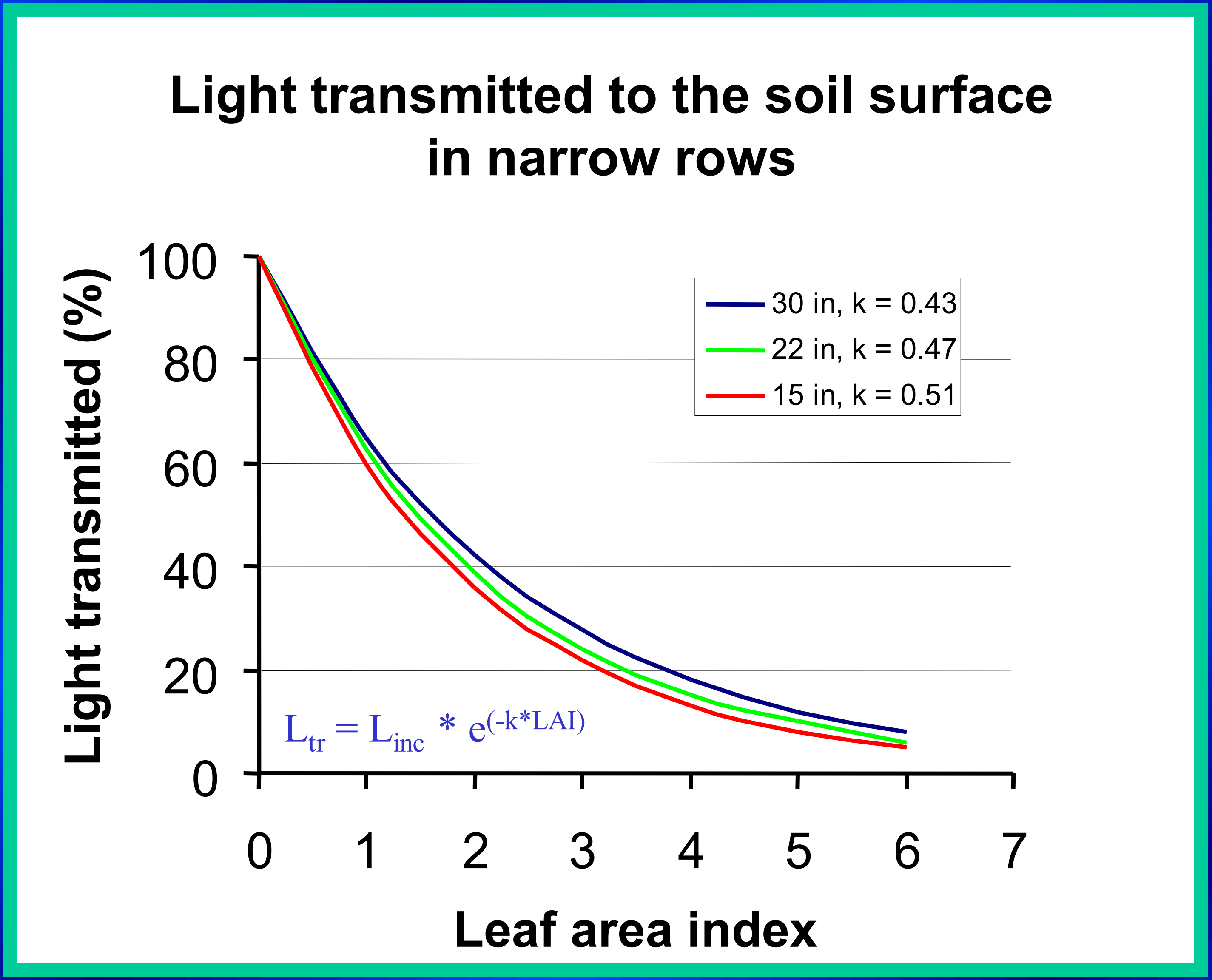
Many studies show a yield advantage for soybeans planted in narrow rows. Decreased row spacing can increase the efficiency of light interception.

Is efficiency of light interception limiting yield?

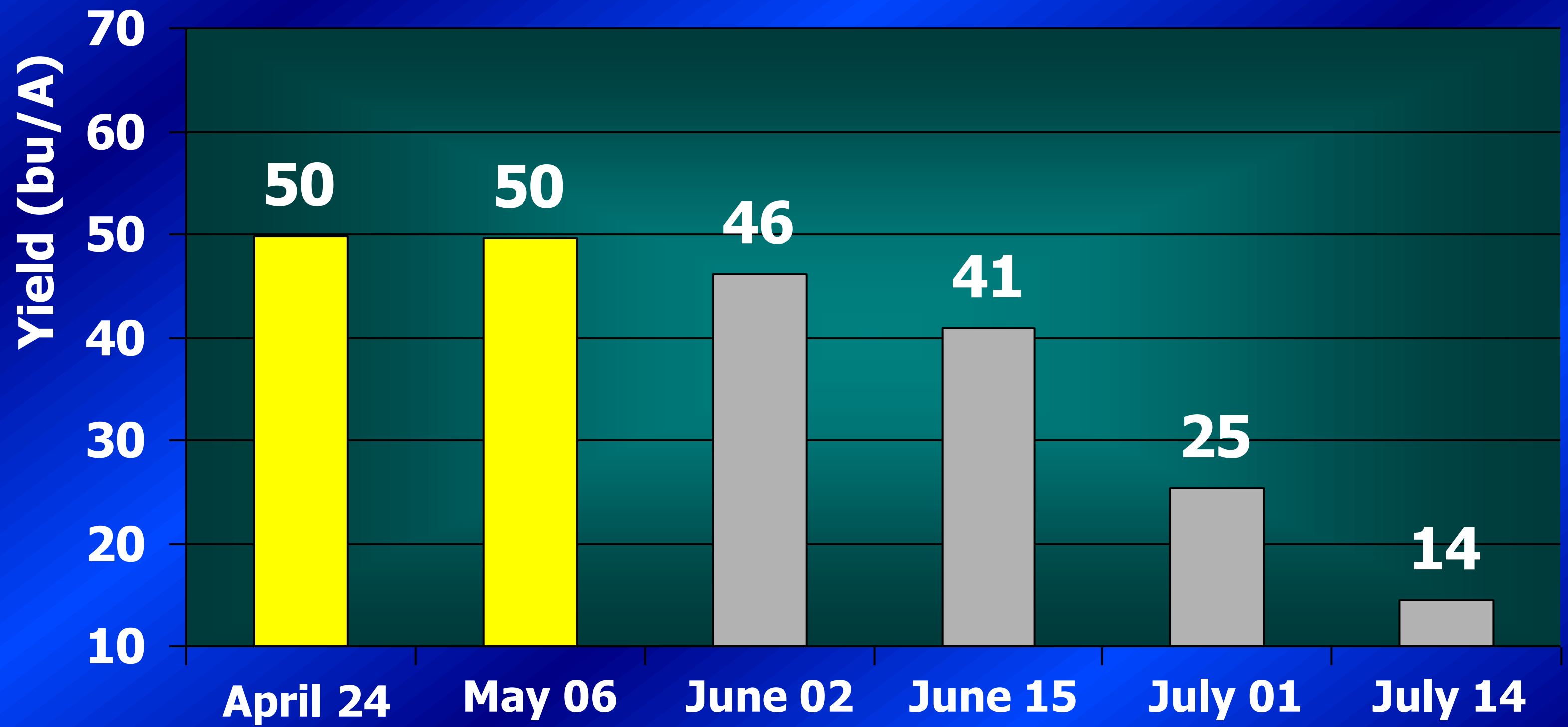


from Flenet et al. (1996)

Increasing LAI has a greater impact on light interception than does increasing the canopy extinction coefficient, *k*



Planting Date Effect on Soybean Yield
Southeast Research Farm (1995-97)



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Yield values represent an average of 6 adapted varieties.
Yellow yield bars are statistically similar to top yield (P=0.05).
Source: ISU Extension Soybean Mgmt. Research (Whigham/Lundvall)

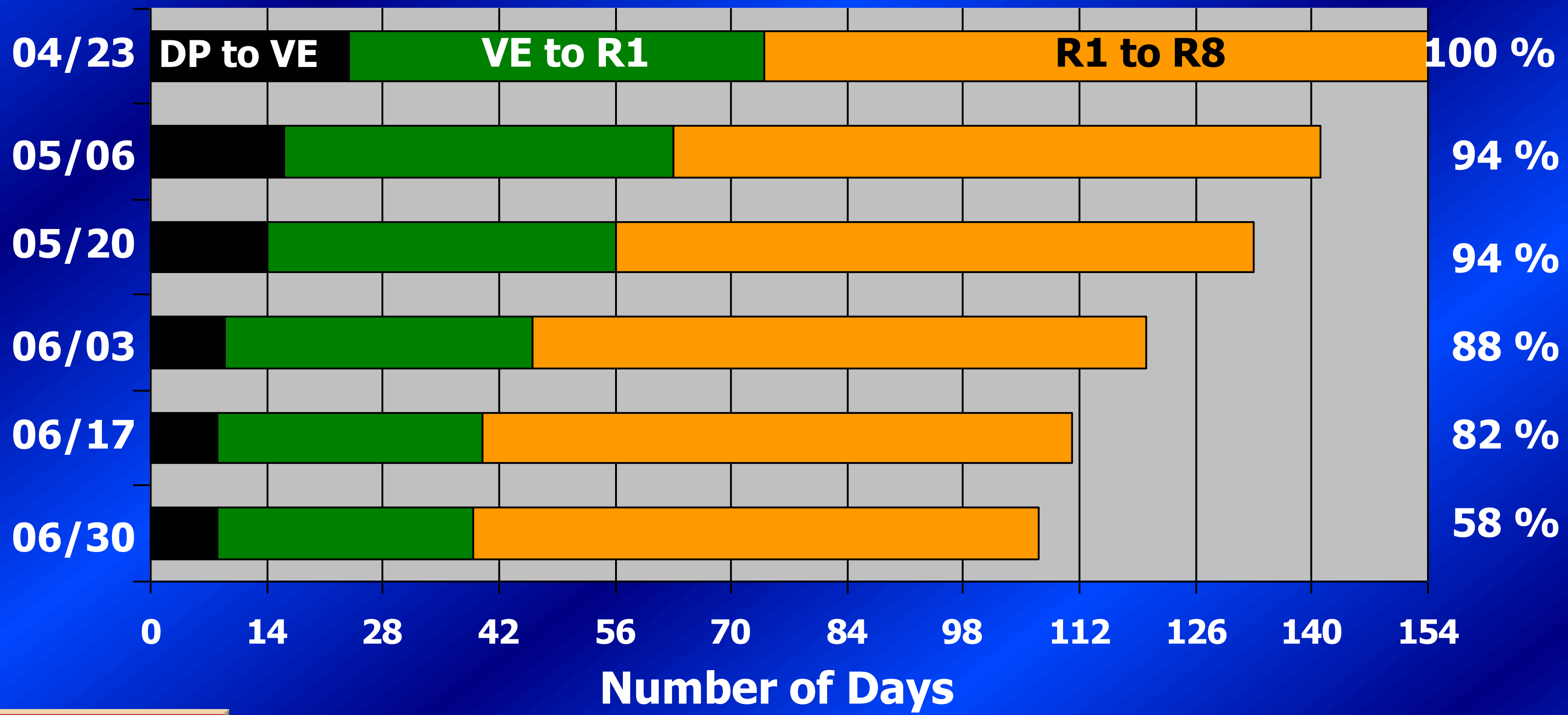
Effect of Planting Date (DOP) & Variety on Soybean Yield in Southern Iowa (1995-97)

Variety Relative Maturity	April 24	May 07	May 18	June 02	June 15	July 12	Variety Means	LSD (0.05)
	Average Planting Date							
	bushels/acre							
2.2	48.0	52.9*	50.7	48.5*	42.7*	22.3*	42.1	2.8
2.5	50.0	51.3	49.9	47.4*	43.8*	**23.4***	42.3	2.2
2.8	**53.1***	**53.9***	51.2*	**49.1***	44.1*	22.0*	**43.4***	2.2
3.2	53.0*	51.6	**51.8***	48.2*	**44.7***	18.9	42.7*	3.2
3.5	52.1*	52.2	50.4	48.2*	42.0	18.8	41.8	3.7
4.1	47.0	49.0	49.0	42.9	39.0	12.2	38.0	3.2
Date means	50.5a	**51.8**a	50.5a	47.4b	42.7c	19.6d	41.7	1.9
LSD (p=0.05)	2.6	1.5	1.2	2.4	2.2	2.0	0.8	
% of top DOP	97	100	97	92	82	38		

Within columns, yields followed by '*' are statistically similar to top yield for that date (designated by boldface type) (p=0.05).

Source: ISU Extension Soybean Mgmt. Research (Whigham/Lundvall)

Planting Date Effect on Development of a MG III (RM 3.2) Soybean Variety: Southern Iowa (1997)



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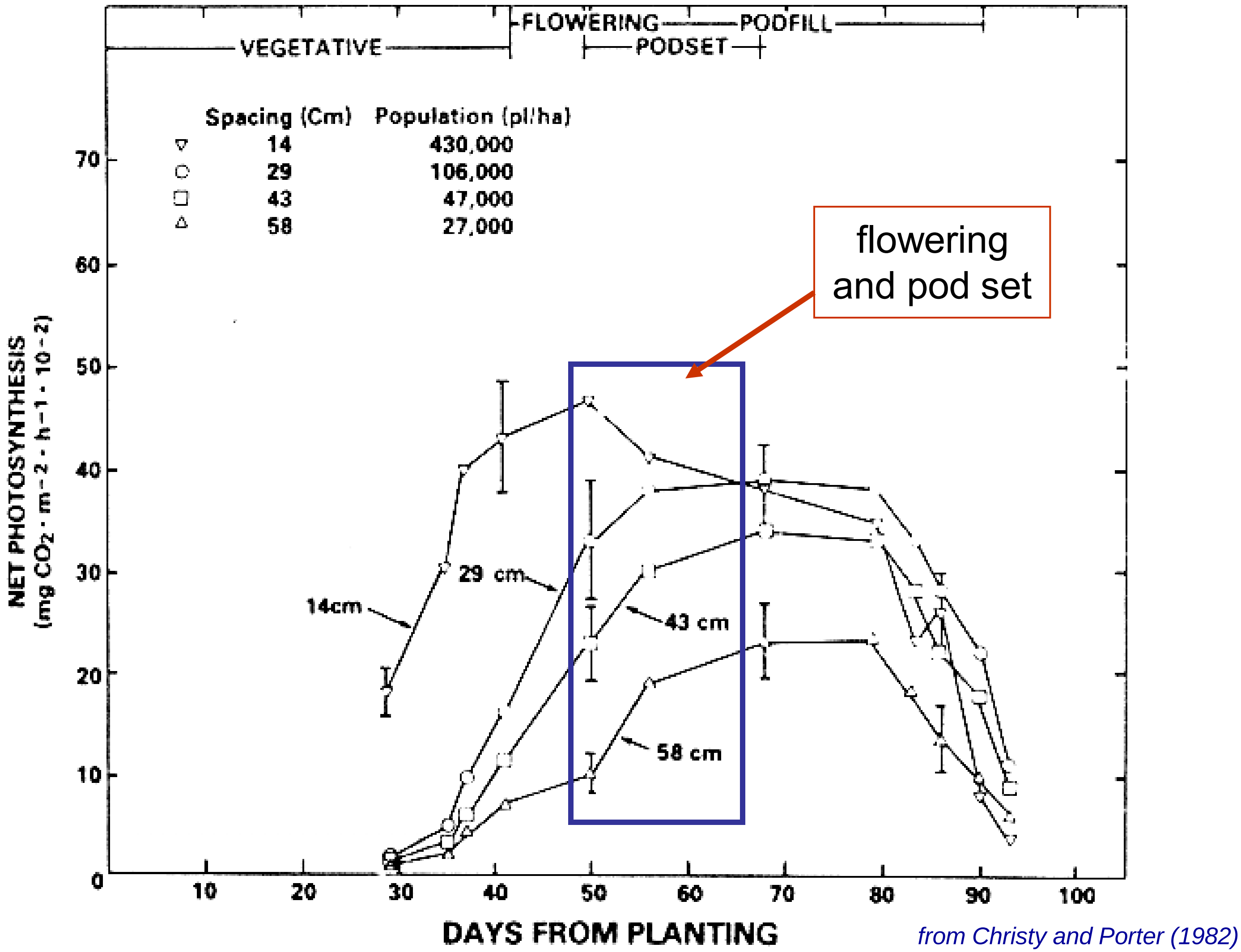
Percent figures are relative yield values by date. DP: planting date; VE: emergence; R1: flowering; R8: physiological maturity.
Source: ISU Extension Soybean Mgmt. Research (Whigham/Lundvall)

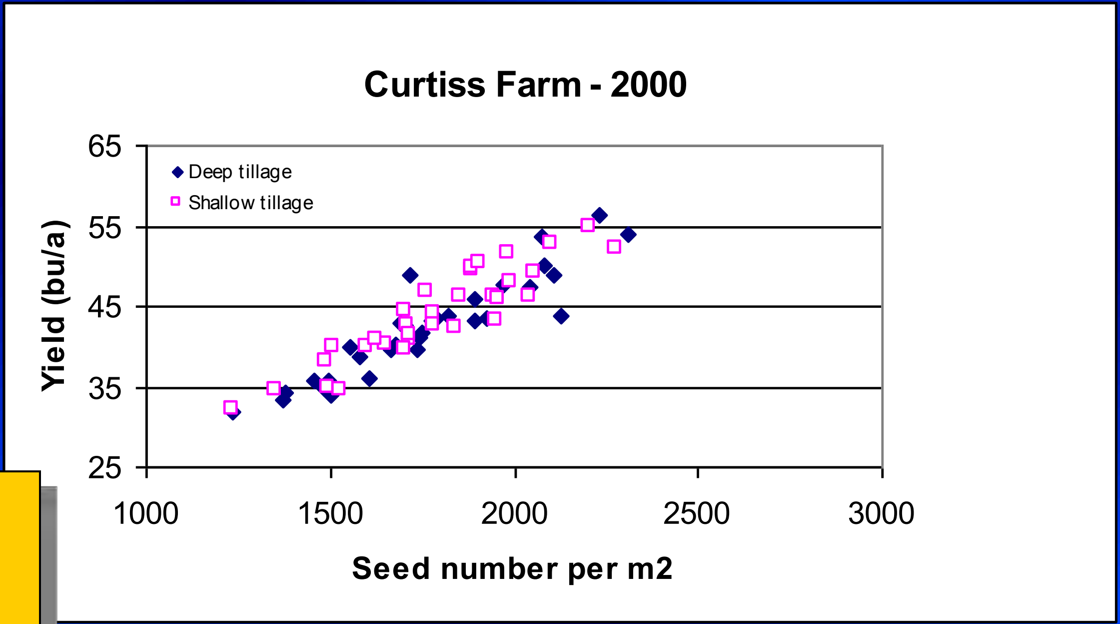
Early canopy closure… increases canopy photosynthesis during flowering and total seasonal photosynthesis



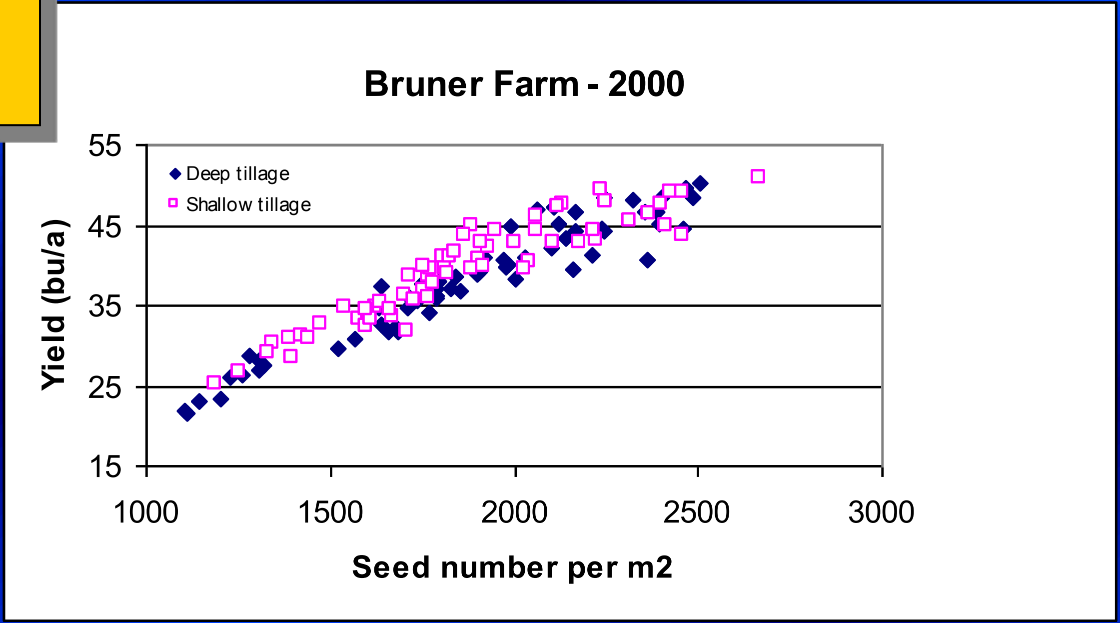
from Christy and Porter (1982)

Soybean Yields Project

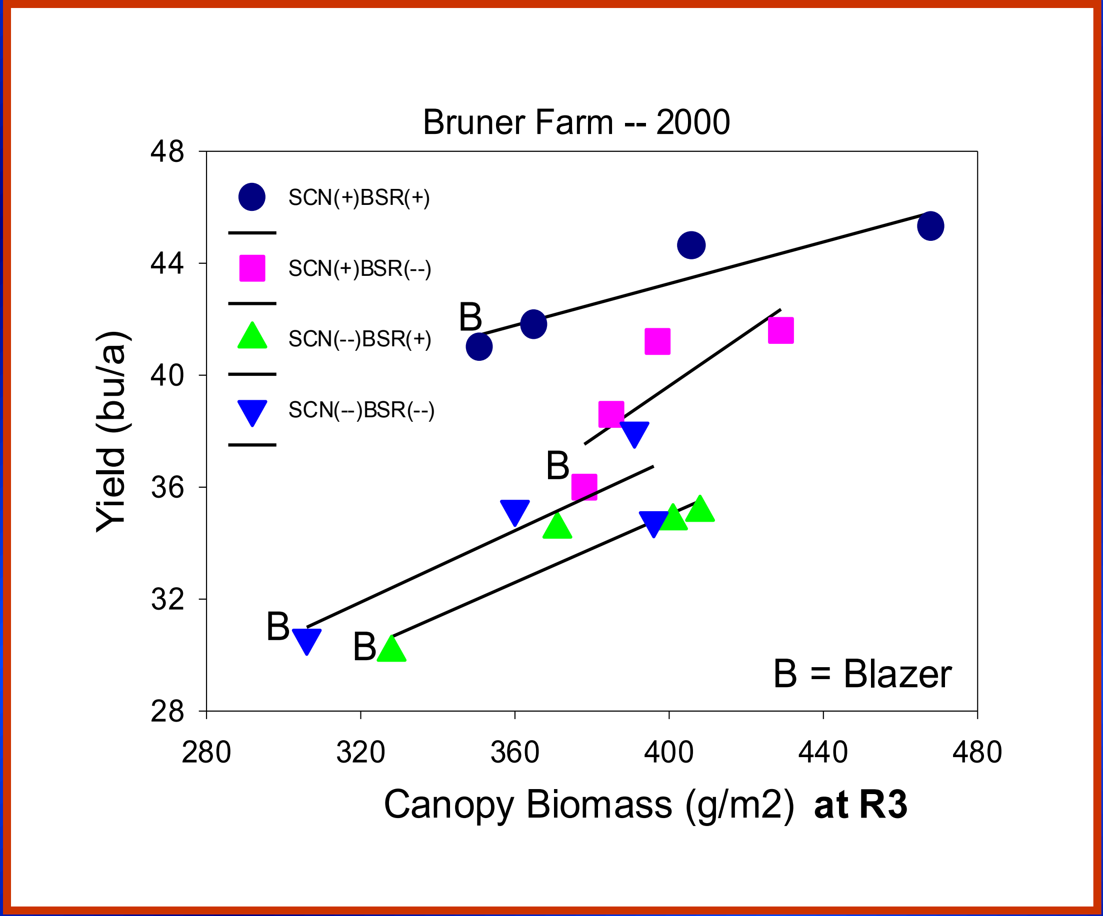
Iowa State University
University of Illinois
University of Wisconsin



Yield variation caused by water stress, pests and herbicides is closely correlated with variation in seed number per unit area



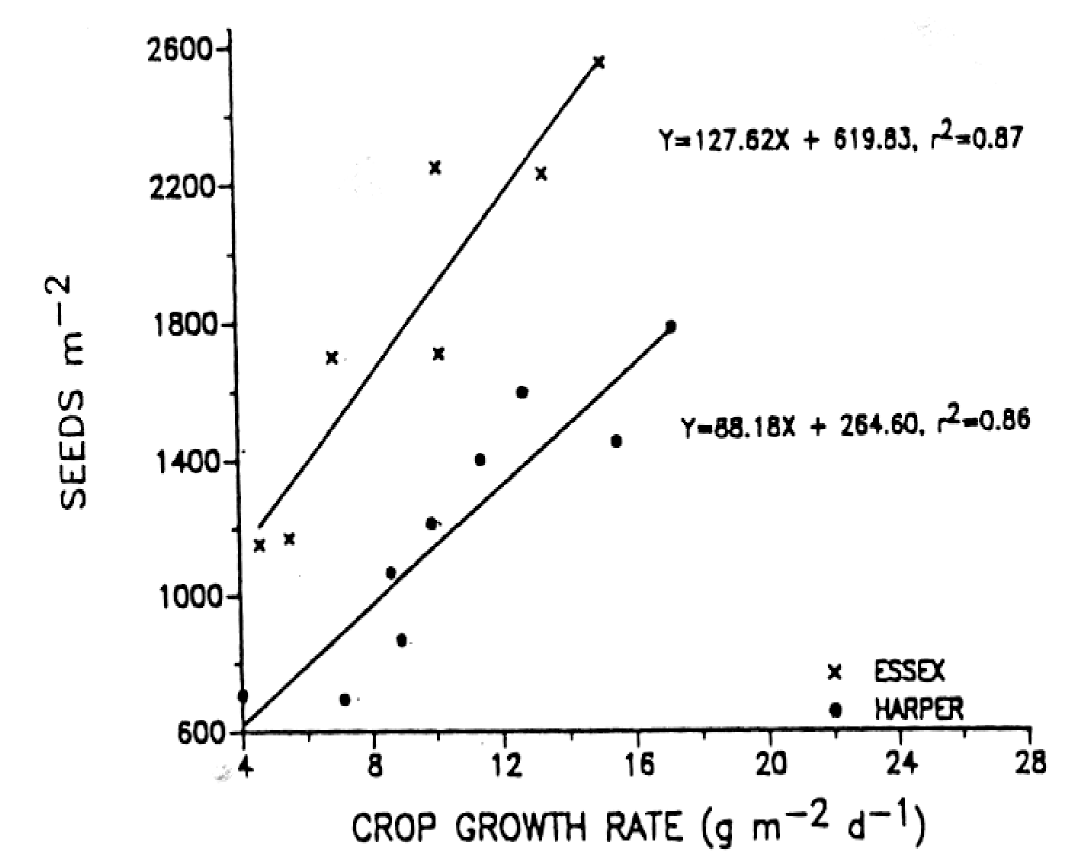
Higher yields were associated with greater biomass and faster canopy growth rates during pod set (R1-R3).



SCN(+) canopies had more biomass at R3 yielded more, despite the growth inhibition caused by Blazer.

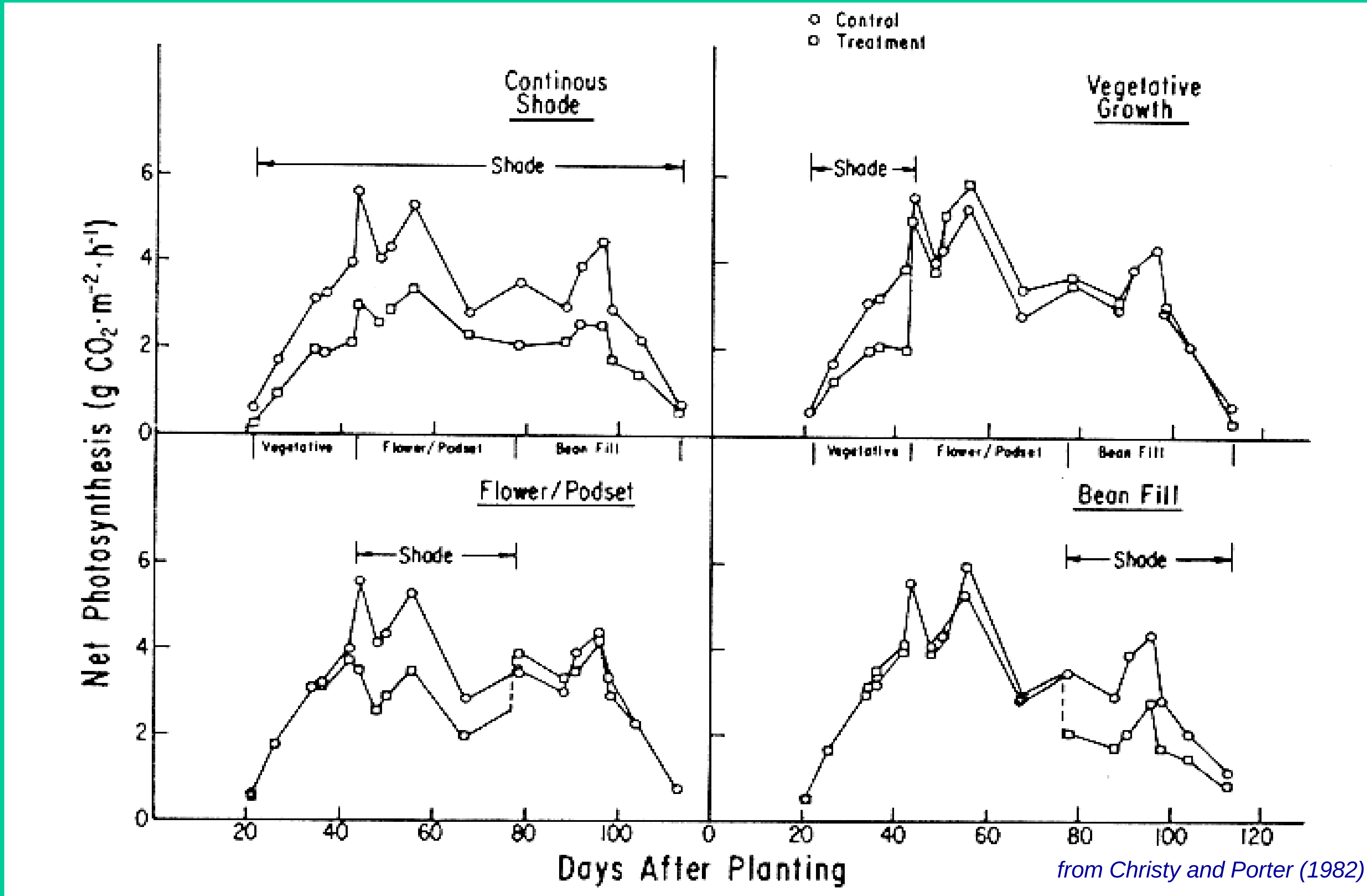
Seed number m^{-2} depends on the crop growth rate during flowering and pod set...

It is essential to establish the maximum crop growth rate by the time flowering occurs



from Egli and Yu (1991)

Shading studies reveal how canopy photosynthesis during flowering and pod filling determine seed number and size.



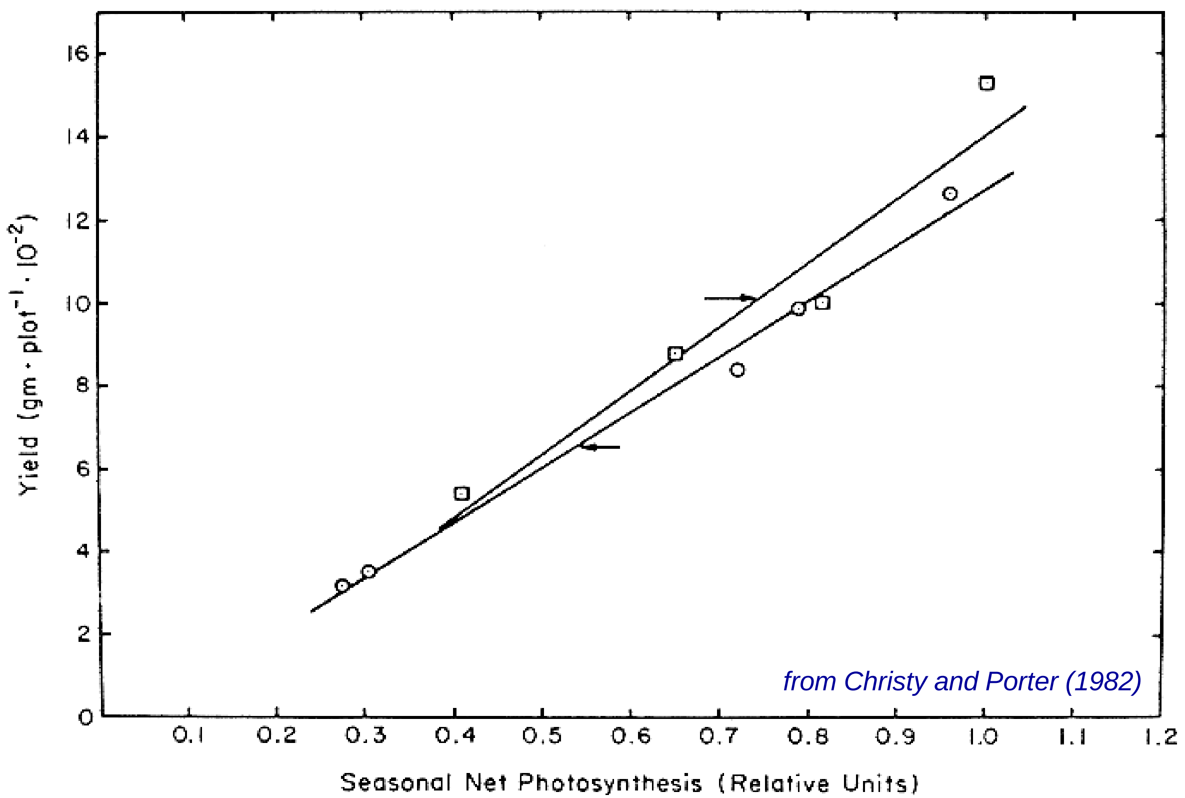
from Christy and Porter (1982)

Seed number per m^2 is the yield component most sensitive to a decrease in photosynthate supply. Yield losses occur when compensation is no longer possible.

Stage of Shade Treatment	Estimated Canopy Photosynthesis During Treatment Period				Yield Components		
	Vegetative	Flowering/ Podset	Bean fill	Total Season	Yield	Seed Number	Seed size
Vegetative	62	104	95	93	101	104	97
Flower/ Podset	97	65	98	84	83	77	107
Bean fill	109	106	63	88	74	78	96
Continuous	69	68	68	68	70	69	103

from Christy and Porter (1982)

Unlike maize, there is a very close relationship between seasonal canopy photosynthesis of the soybean canopy and grain yield



Summary...

- **Yield formation in soybean is source-limited. Efforts to increase seasonal canopy photosynthesis will likely return an increase in grain yield.**

- **Seeds m^{-2}, the primary determinant of yield, is closely coupled to the rate of crop growth during flowering and podset. Maximizing crop growth rate during this period is essential for maximum yield.**

Summary ...

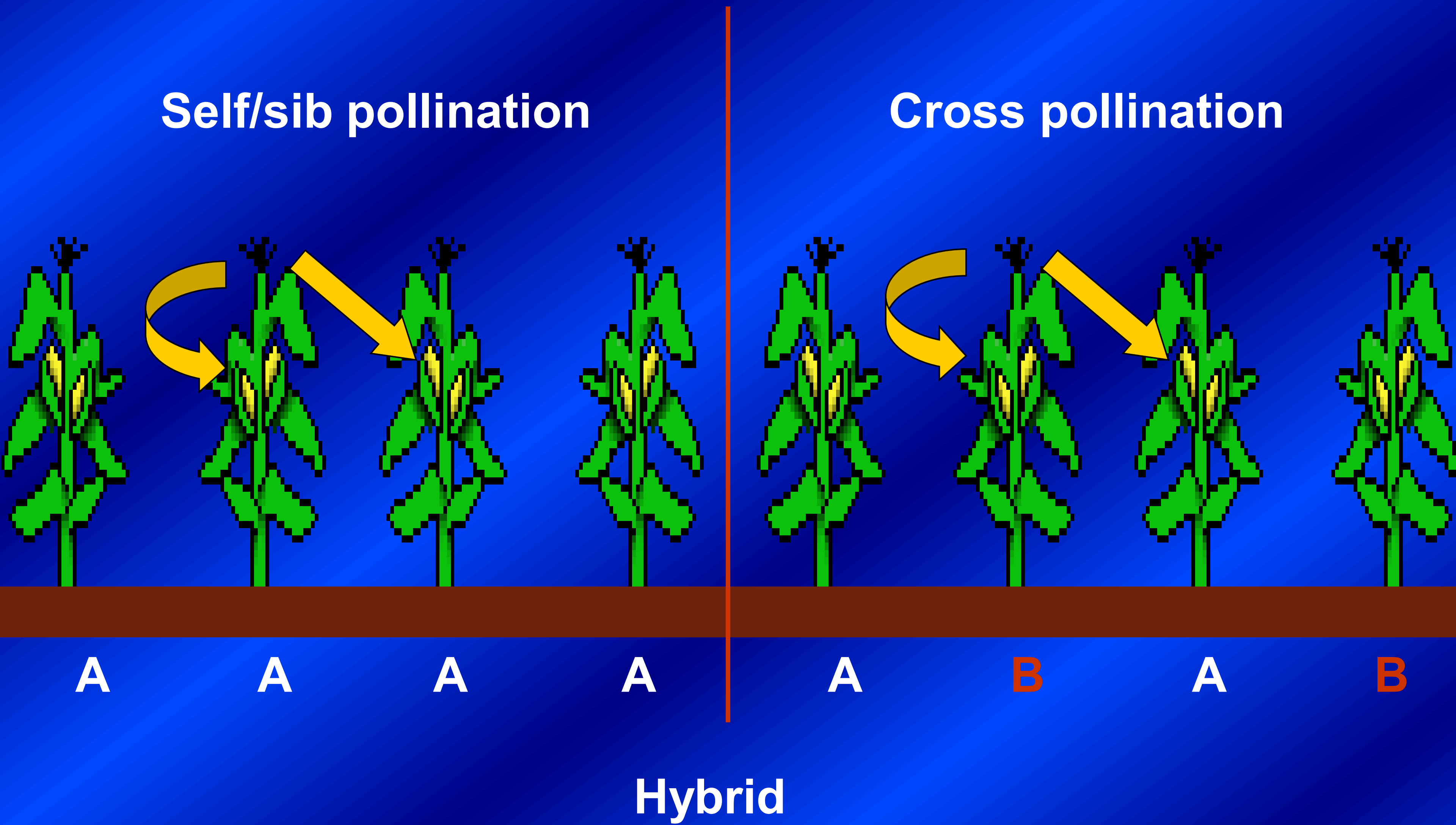
- **Optimum row spacing and plant population can improve light capturing efficiency of the soybean canopy. But providing optimum conditions for plant growth early in the season will likely have a much greater impact on seasonal canopy photosynthesis.**

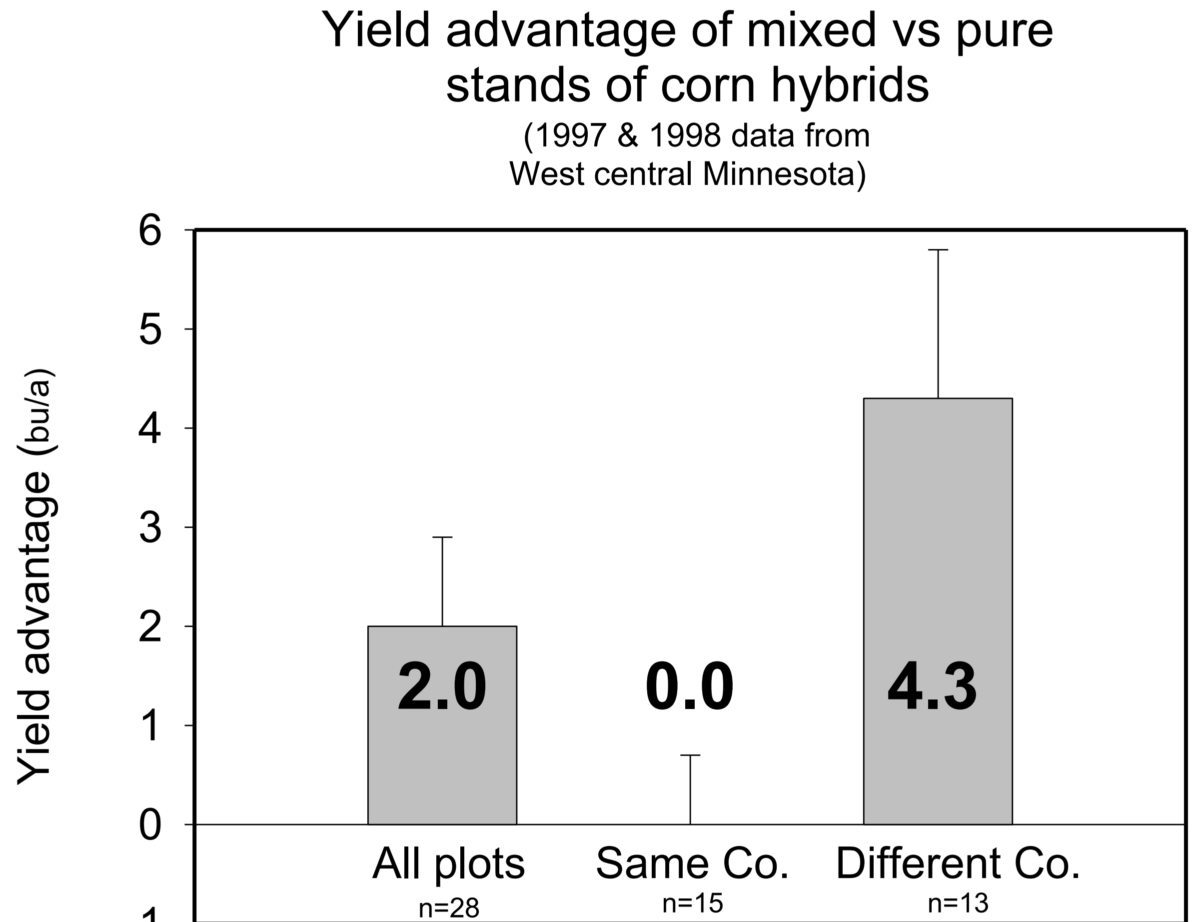
Managing for more efficient use of available photosynthate in maize

-- potential advantage of out-crossing hybrids


Spikelets
Anthers


Silks
Stalk
Ear shoot

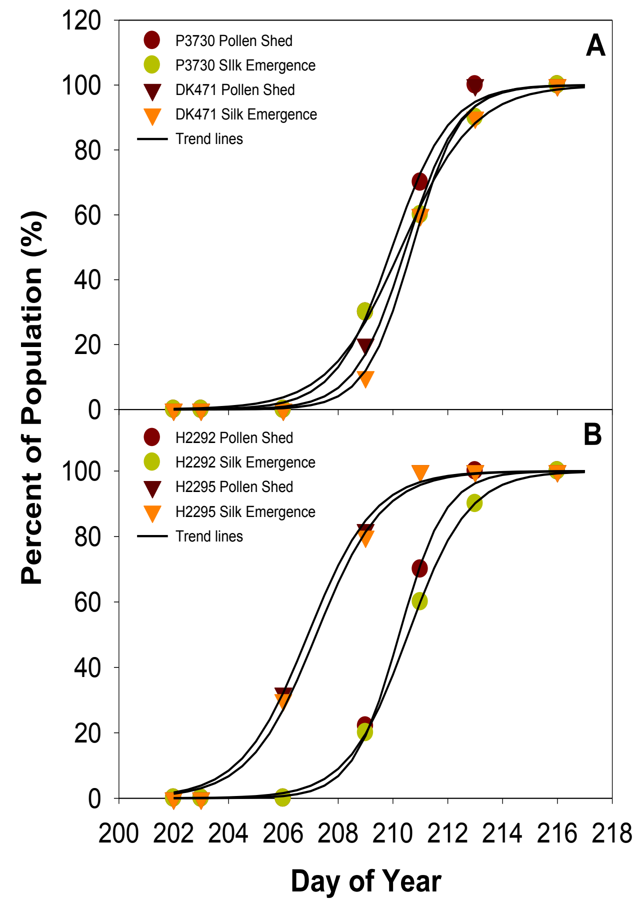

Self/sib pollination
Cross pollination
A
A
A
A
A
B
A
B
Hybrid



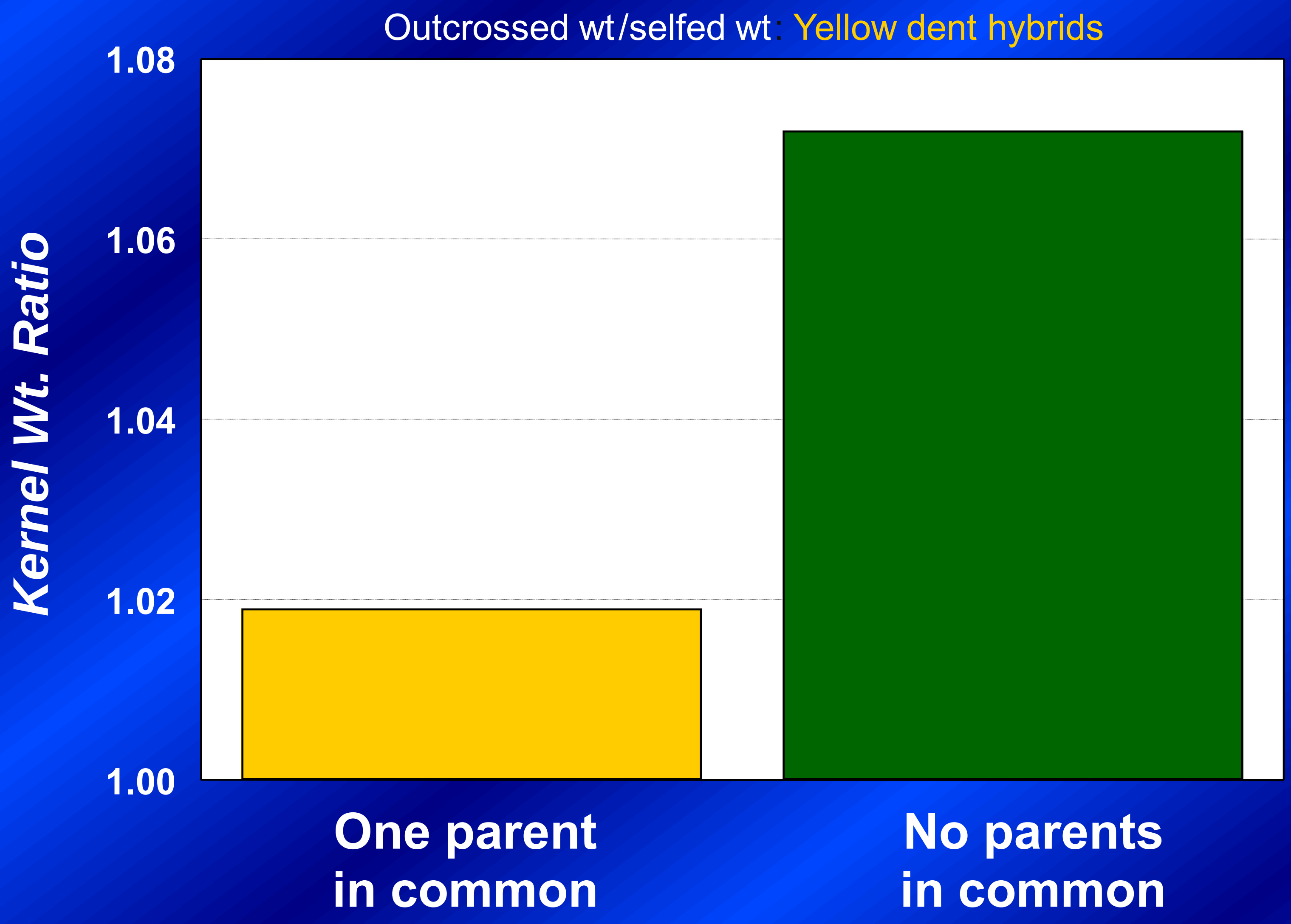
Yield: Ave = 165 bu/a, range = 130 - 217 bu/a
Plot size: Ave = 1.0 ac, range 0.4 - 2.6 ac.

Close synchrony in flowering between hybrids is required for effective cross pollination

Flowering dynamics in mixed stands of hybrids with excellent synchrony for cross-pollination (**A**) and poor synchrony for cross pollination (**B**).

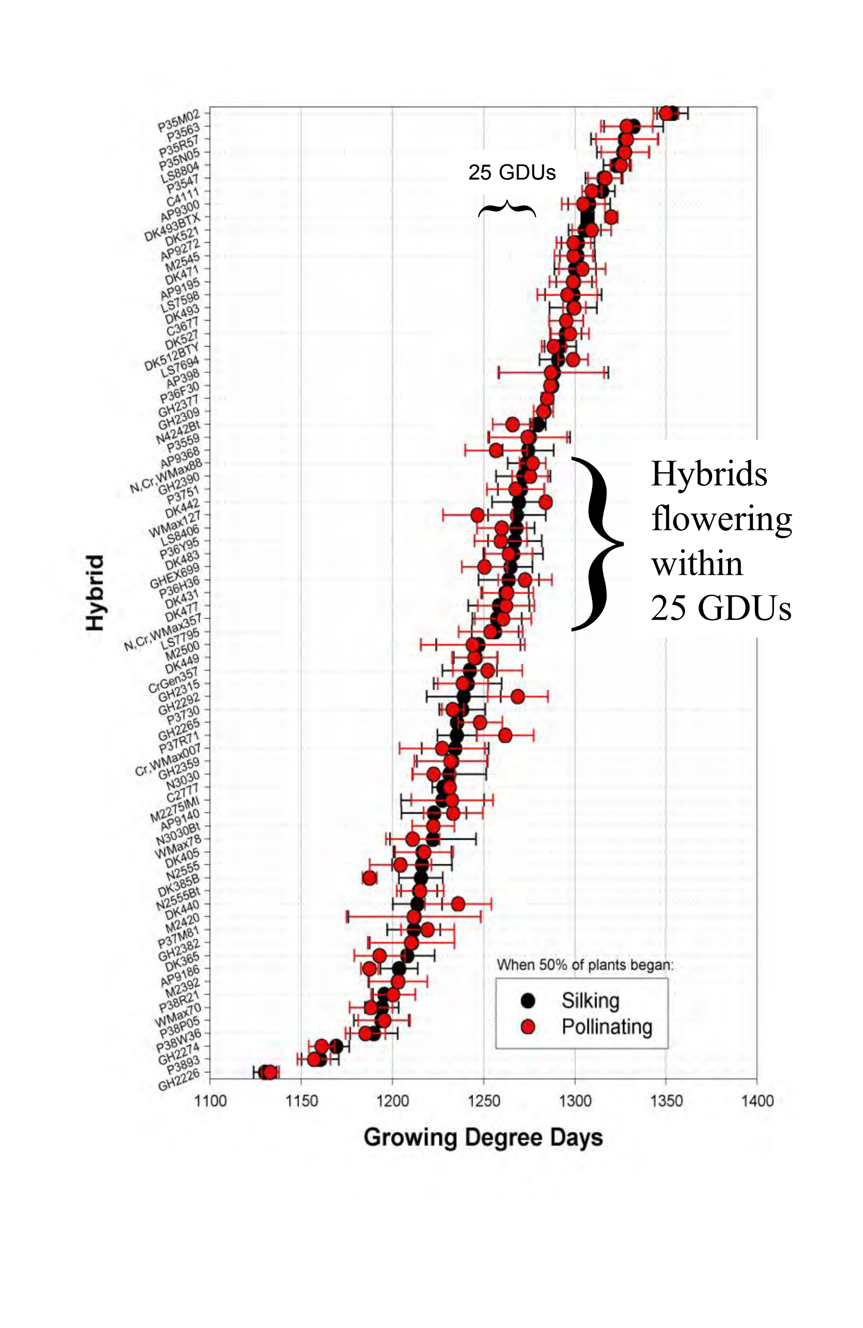


Outcrossing increases kernel weight



Comparison of GDU for silking and pollen shedding for 75 commercial hybrids available to growers in West-central Minnesota in 1998.

Hybrid pairs that flower within 25 GDUs have maximum potential for cross-pollination.



Conclusion

Out-crossing between maize hybrids can generate a ‘free’ yield advantage

Hybrids must be genetically unrelated and reach anthesis at the same time

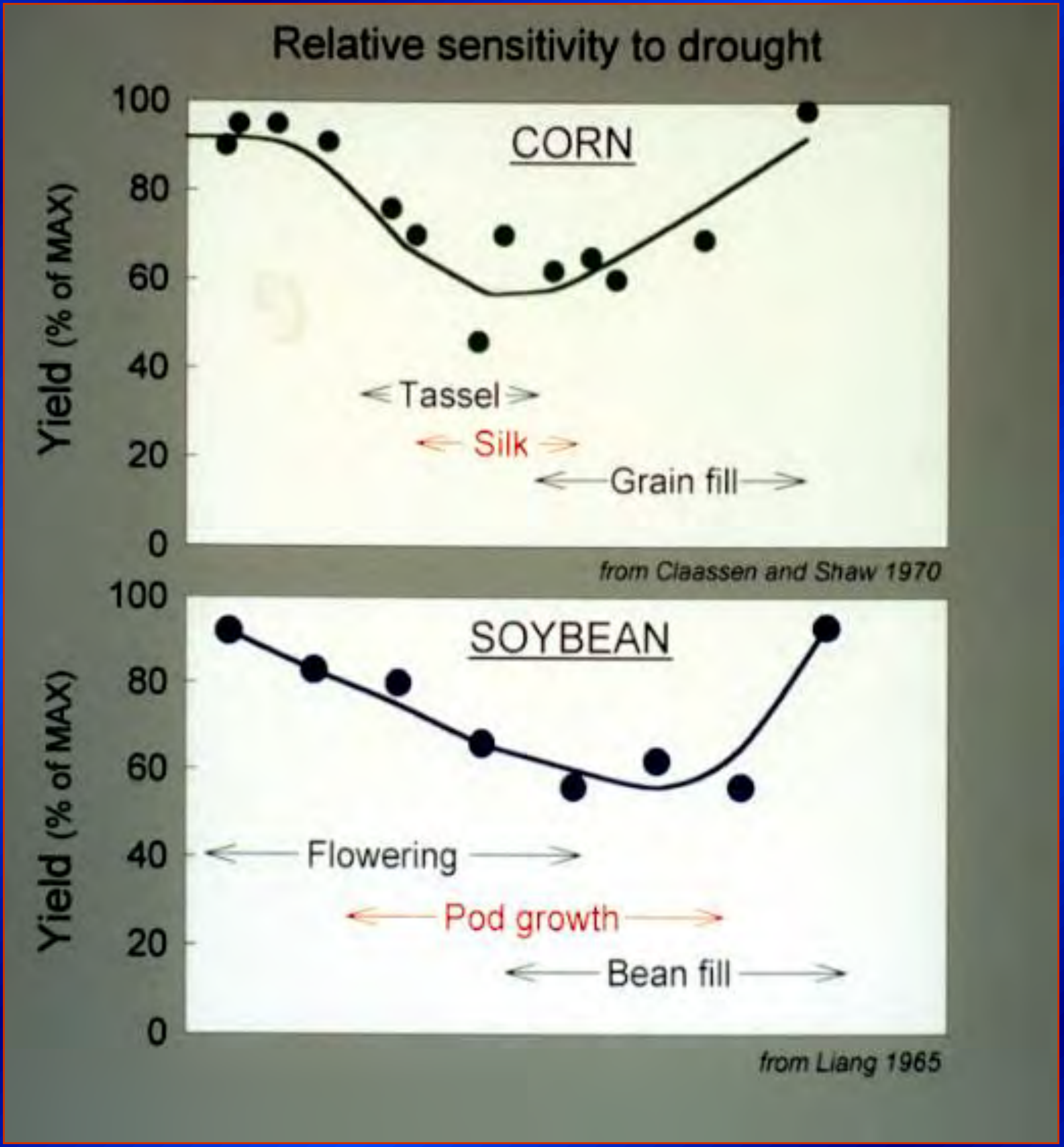
Reproductive Development

Physiology of seed formation under adverse environmental conditions

Reproductive development is highly vulnerable to water stress.

Stress during flowering decreases seed number.

Stress during seed filling results in smaller seeds.



Most important drought - induced problems to overcome:

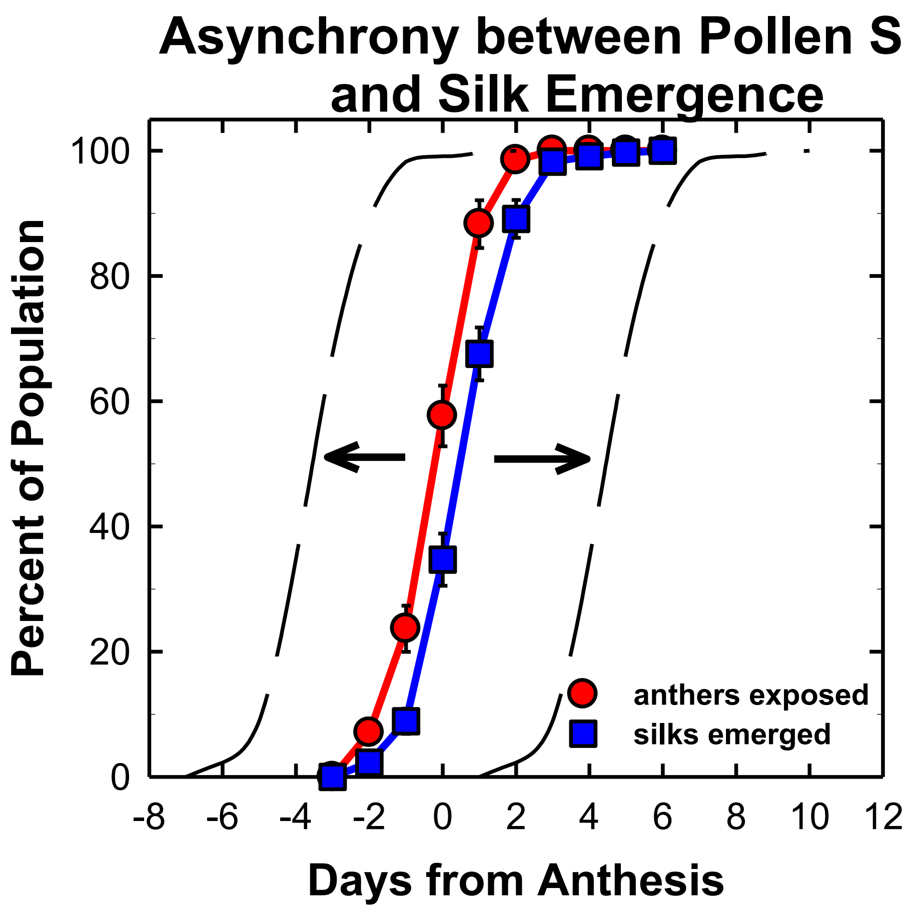
- Inhibition of pistillate rachis development
  - (asynchrony)
- Inhibition of zygote development
  - (abortion)

Maize genotypes selected for improved drought tolerance have a shorter anthesis-silking interval (ASI) and more rapid ear growth during drought

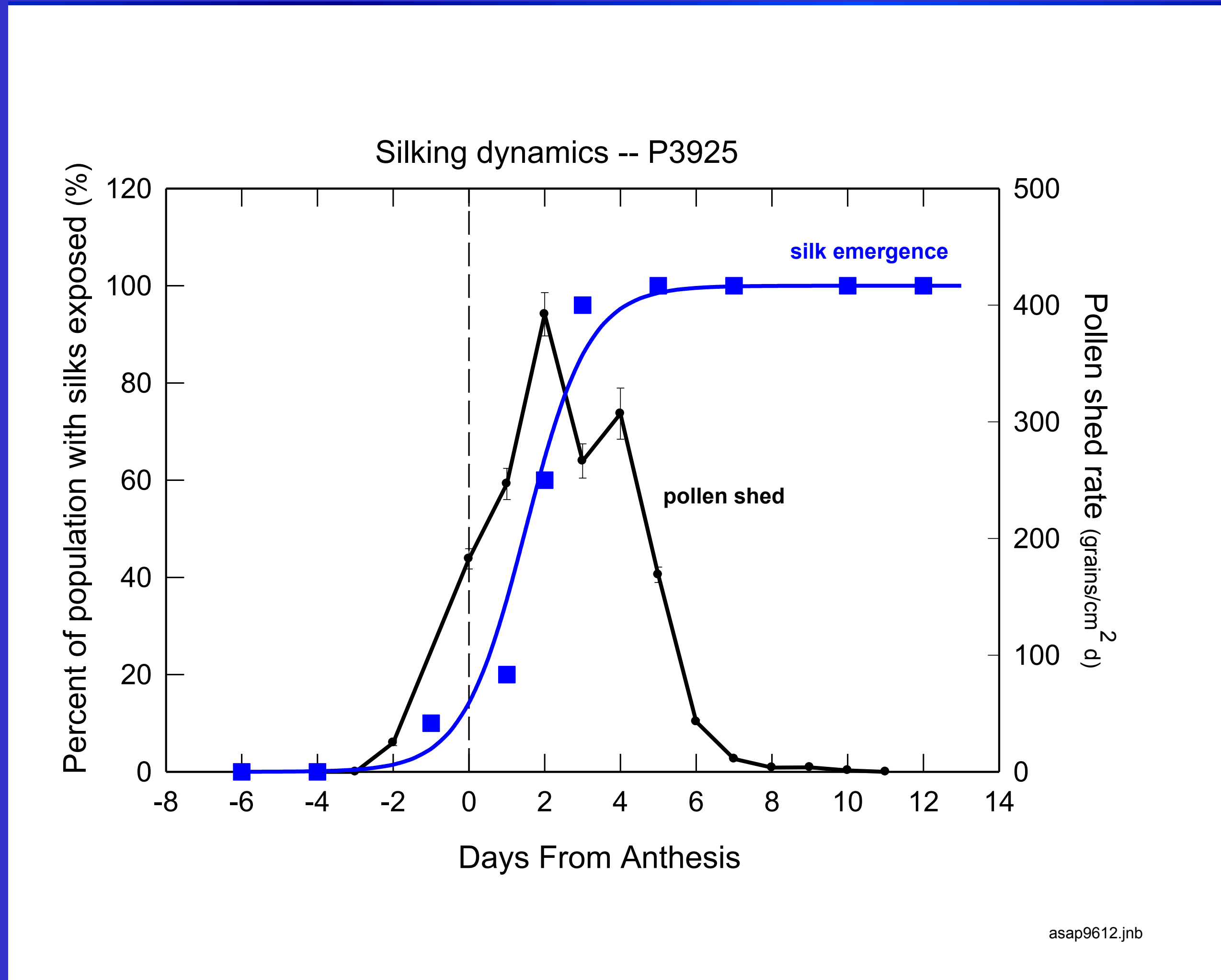
Table 1. Yield and associated traits for Cycle 0 and Cycle 8 of Tuxpeño sequía selected for a short ASI under severe drought conditions. Adopted from Edmeades *et al*. (1997).

Tuxpeño Sequía	Yield Droughted (t/ha)	Yield Well-watered (t/ha)	ASI Droughted (d)	EPP Droughted (no/no)	HI Droughted (t/t)
C0	1.75	7.48	6.4	0.73	0.12
C8	2.39	7.78	2.9	0.93	0.22

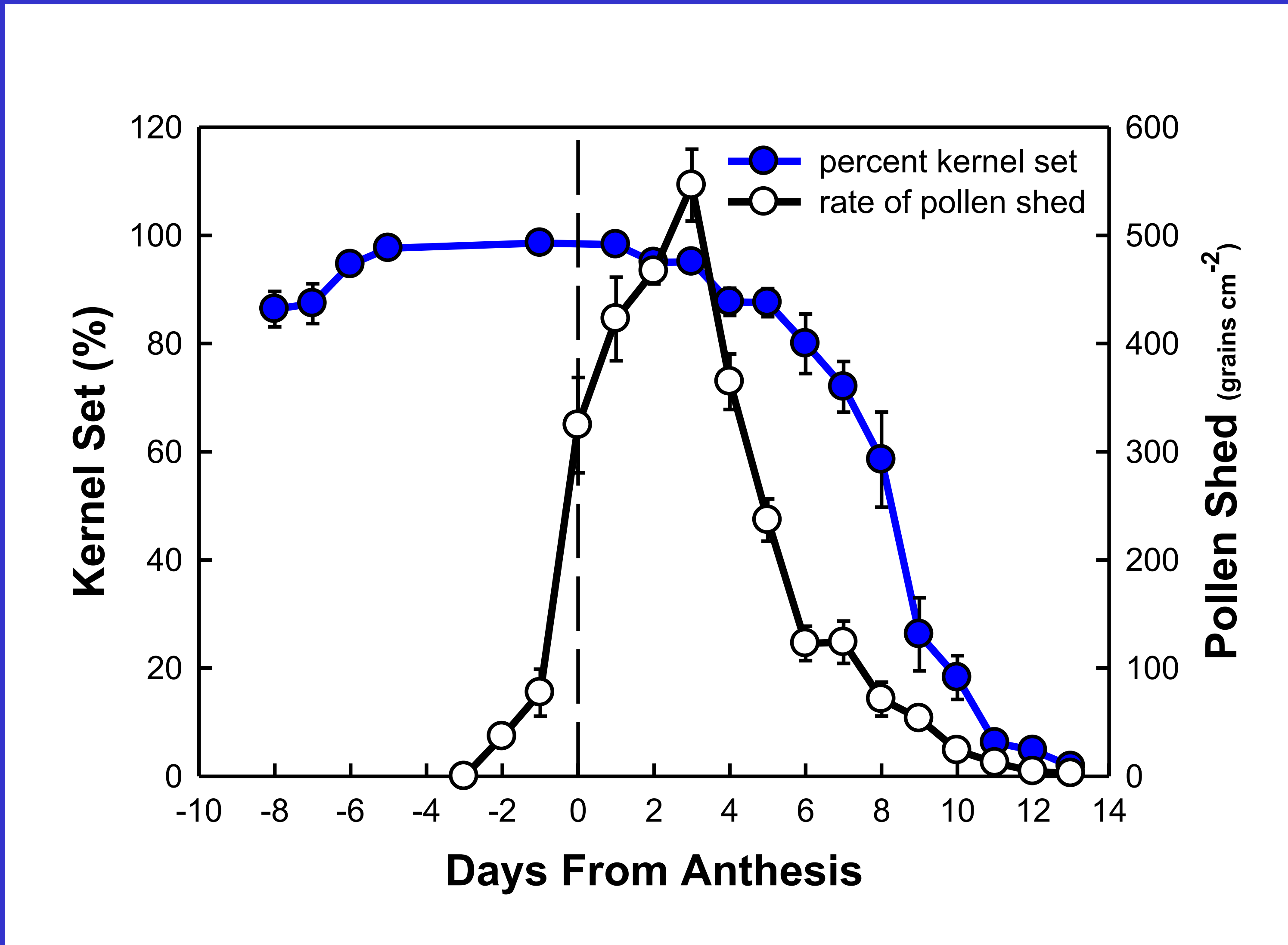
Ideally, all silks emerge when intensity of pollen shed is sufficient to ensure pollination



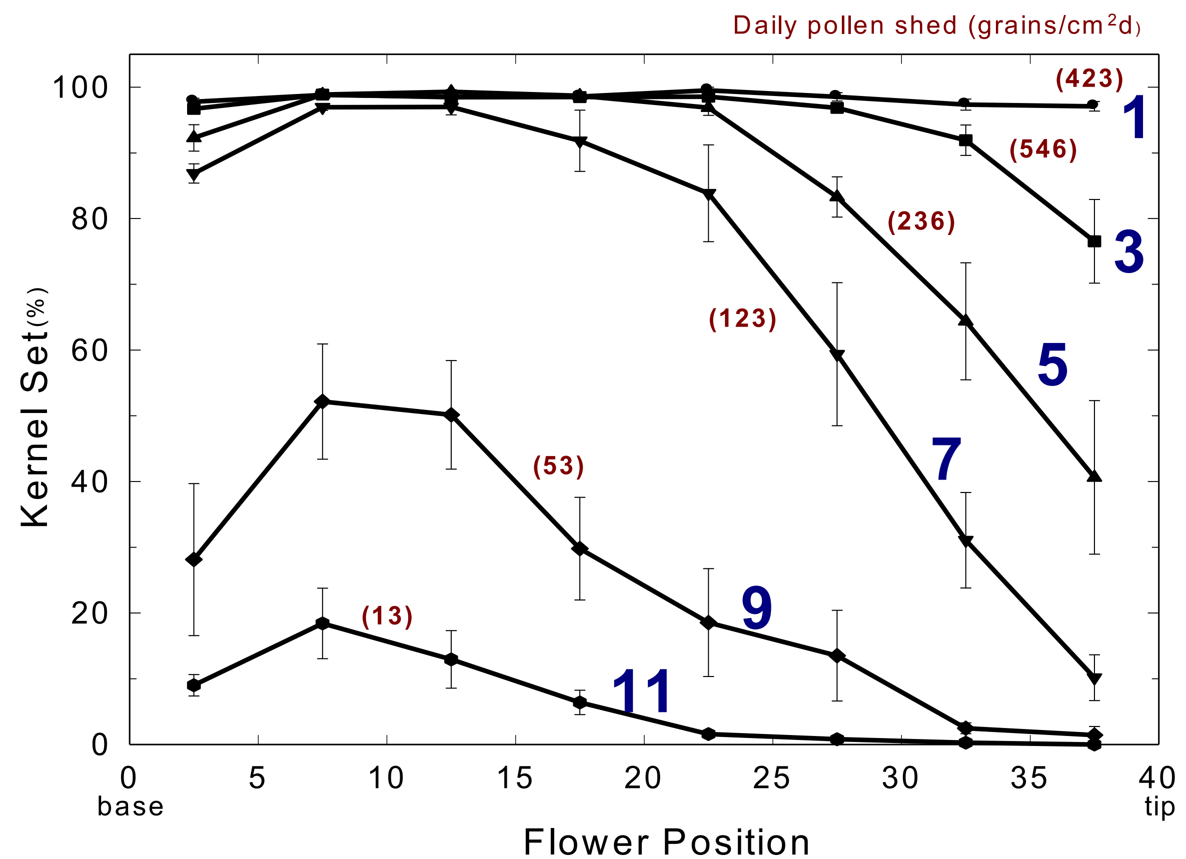
But many silks appear as pollen shed declines and may not be pollinated



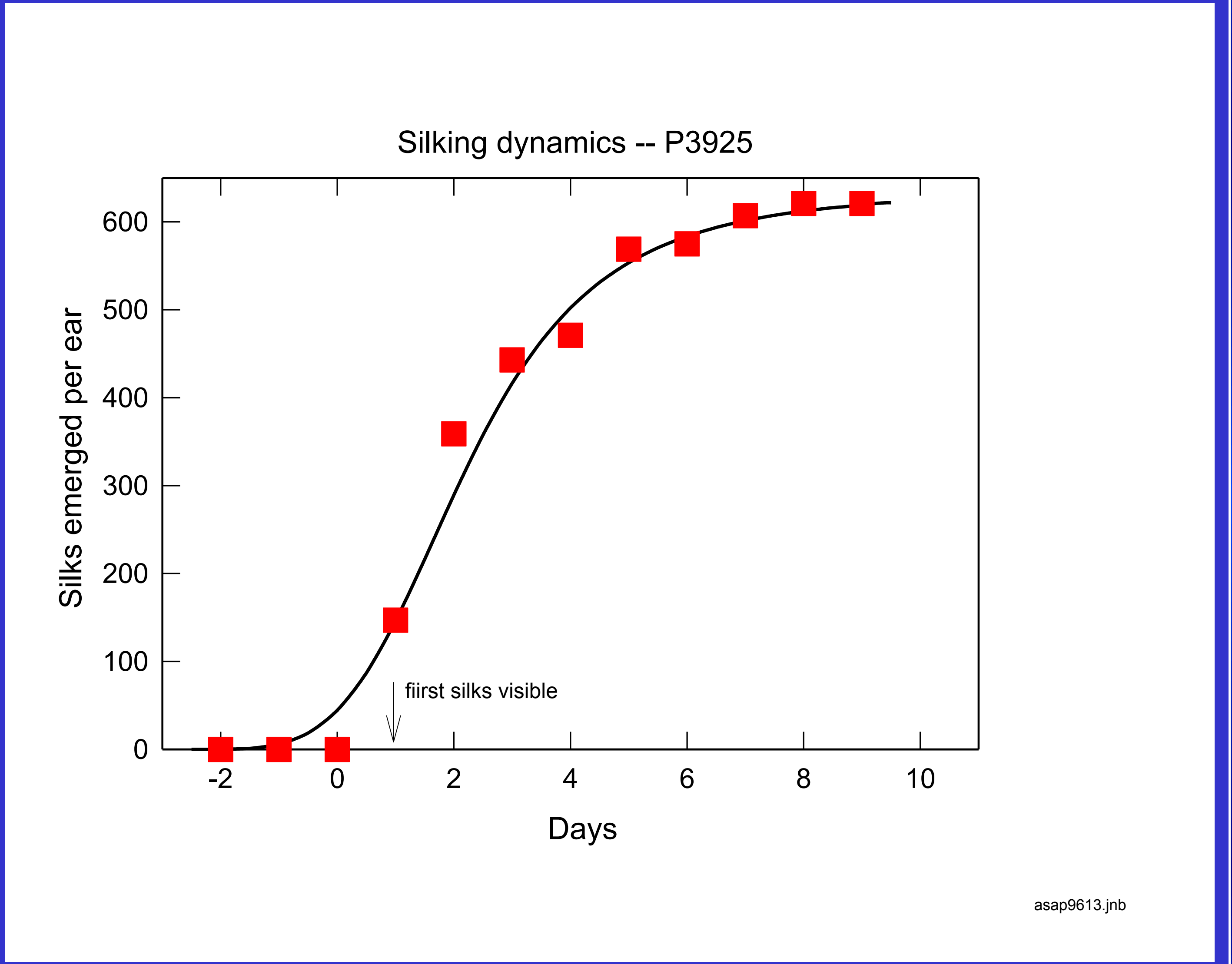
When does kernel set decrease due to lack of pollen?



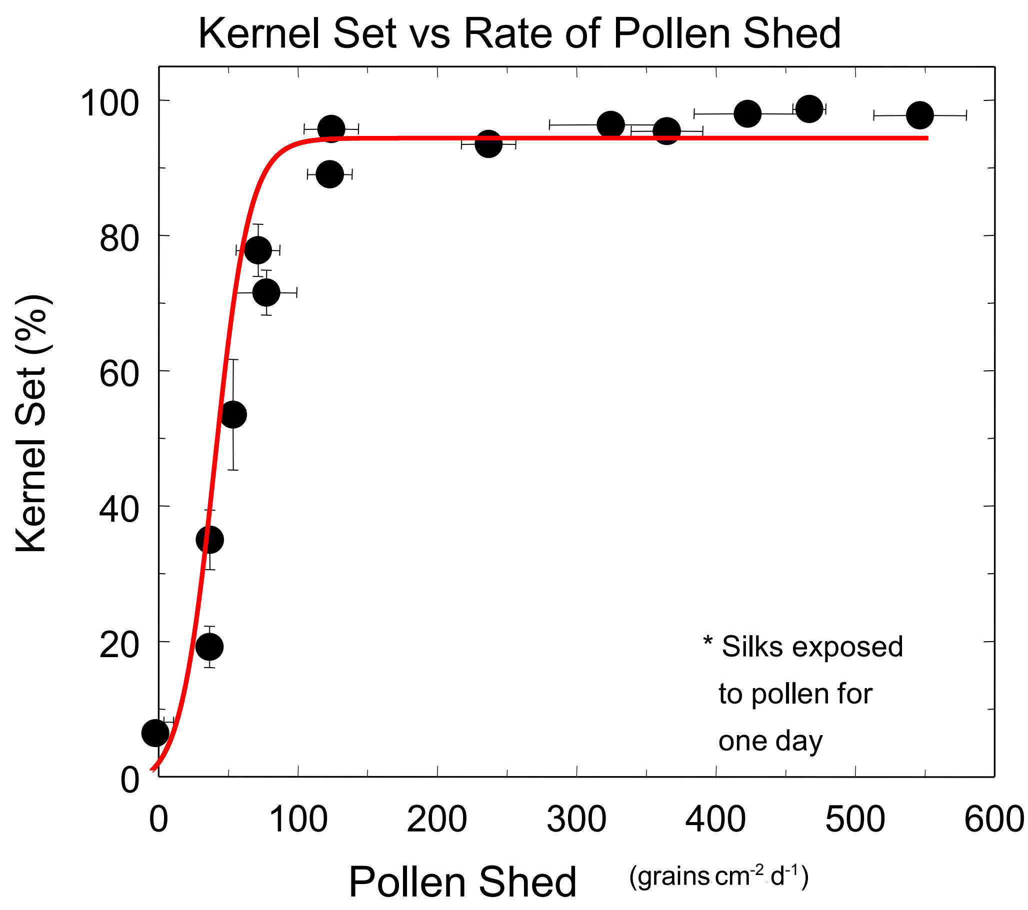
Pollen density was sufficient for perfect kernel set for ASI up to 7 days



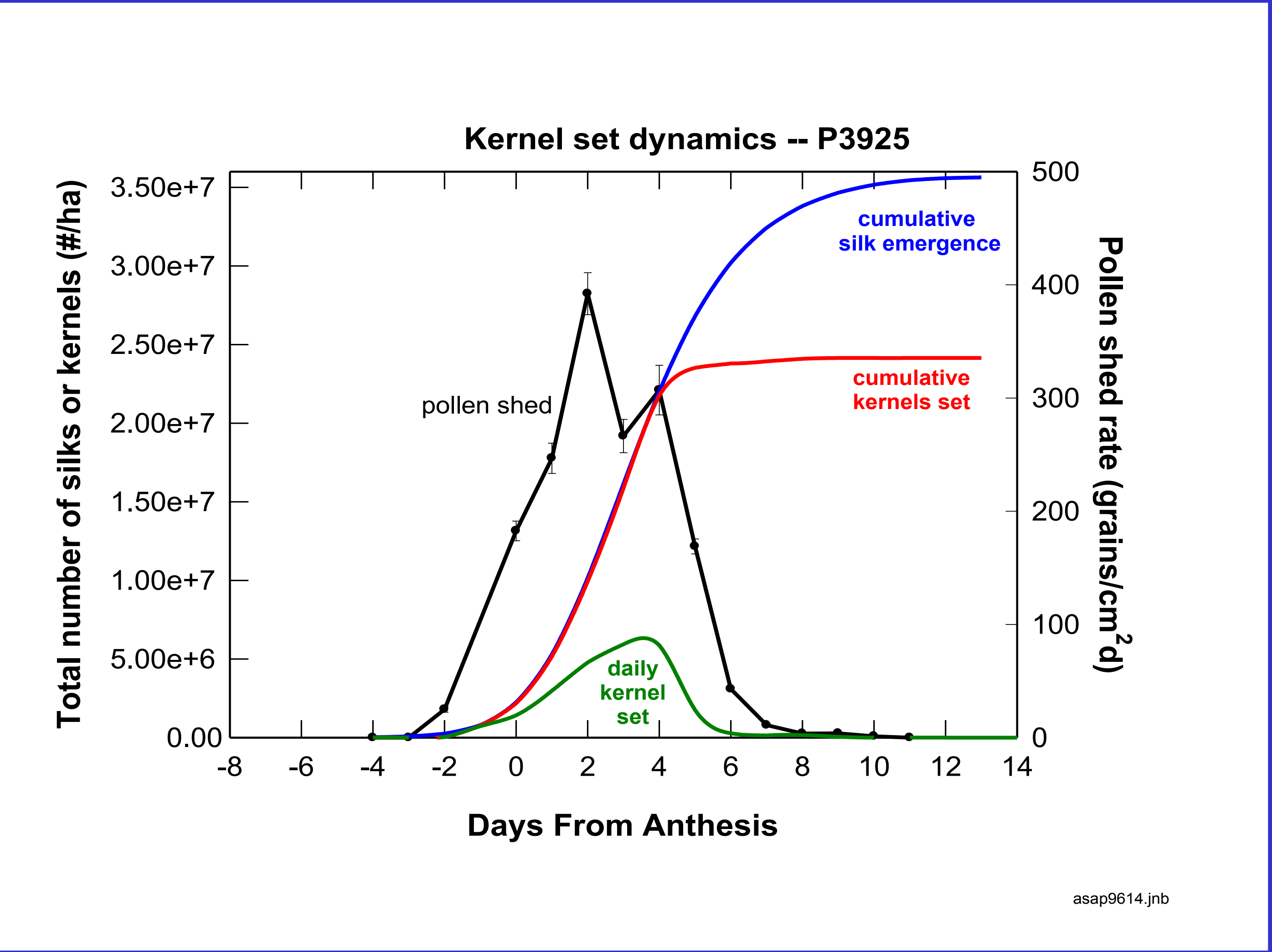
It can take up to 10 days for all silks to emerge…



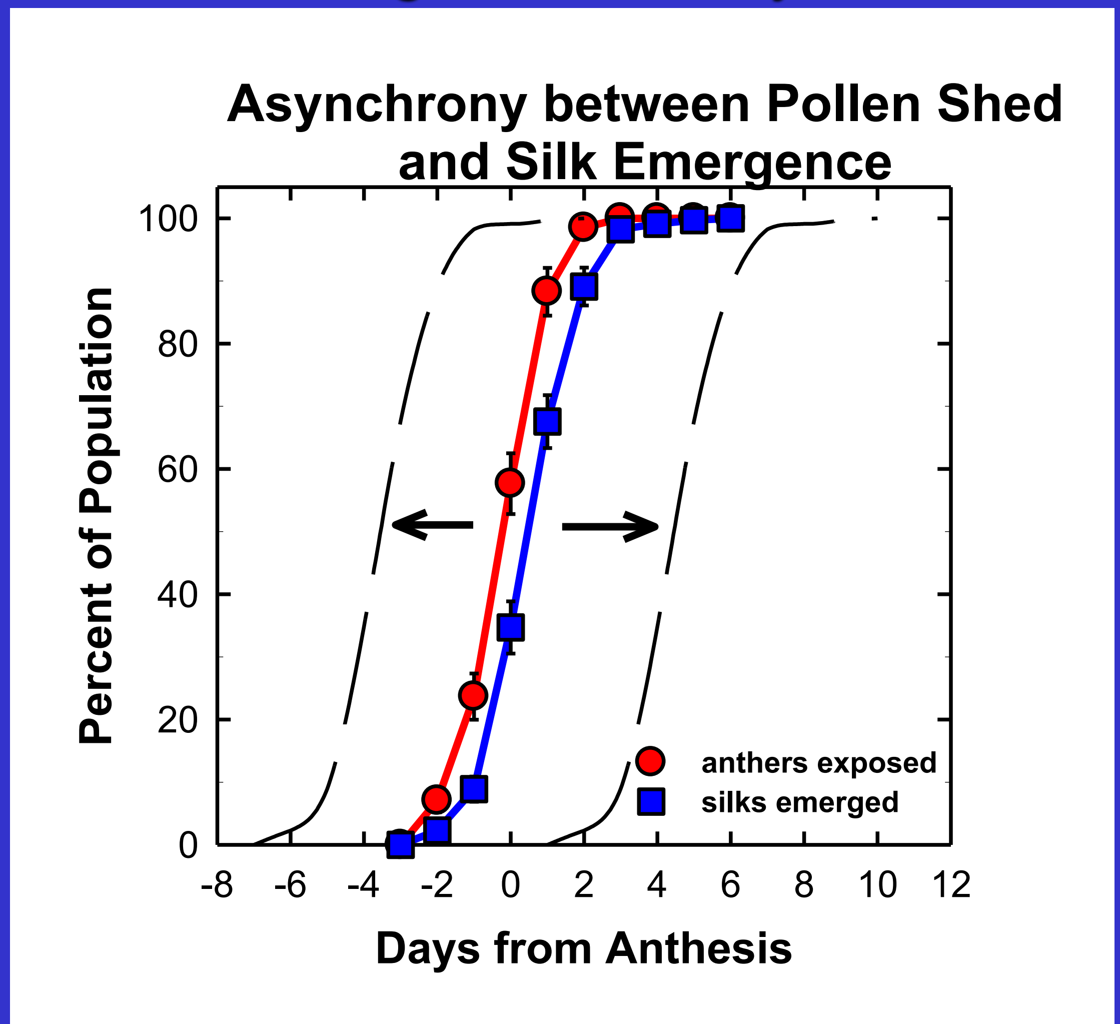
Pollen shed density < 100 gr/cm^2 d limits kernel set



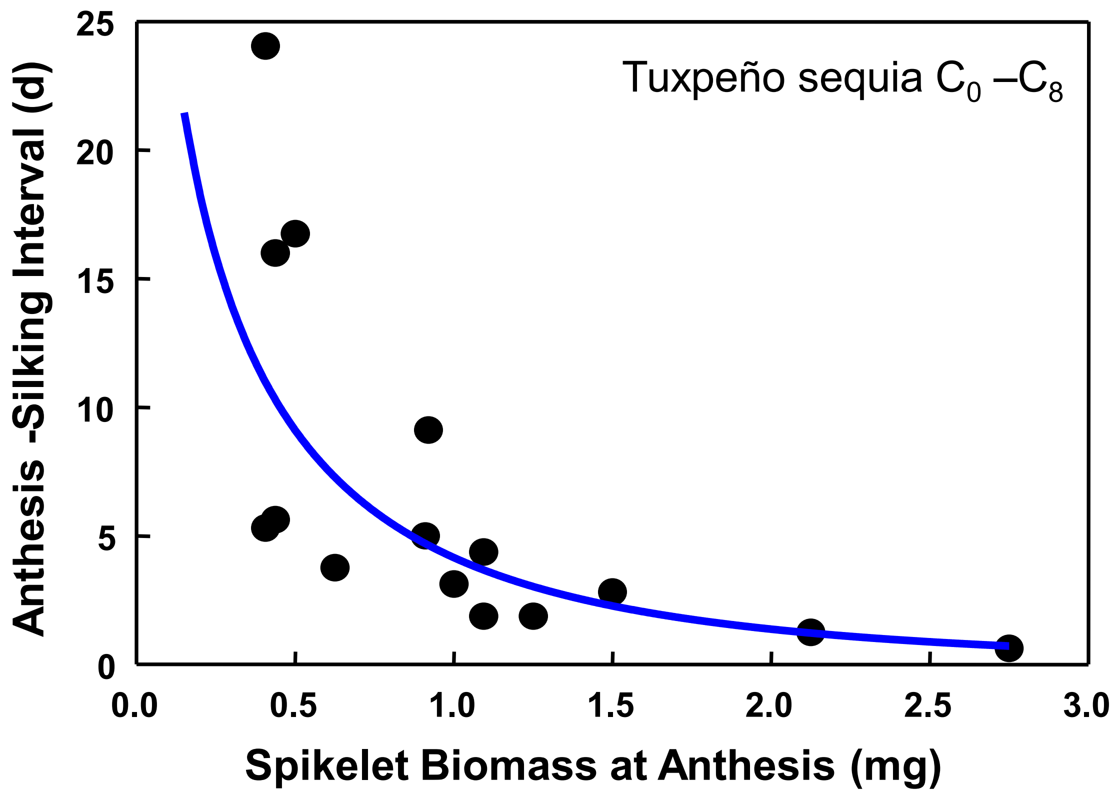
Using quantitative measures of pollen shed and silk, we can predict kernel set on a daily basis



Selection for silk emergence prior to pollen shed (protogyny) can improve pollination if silk emergence is delayed

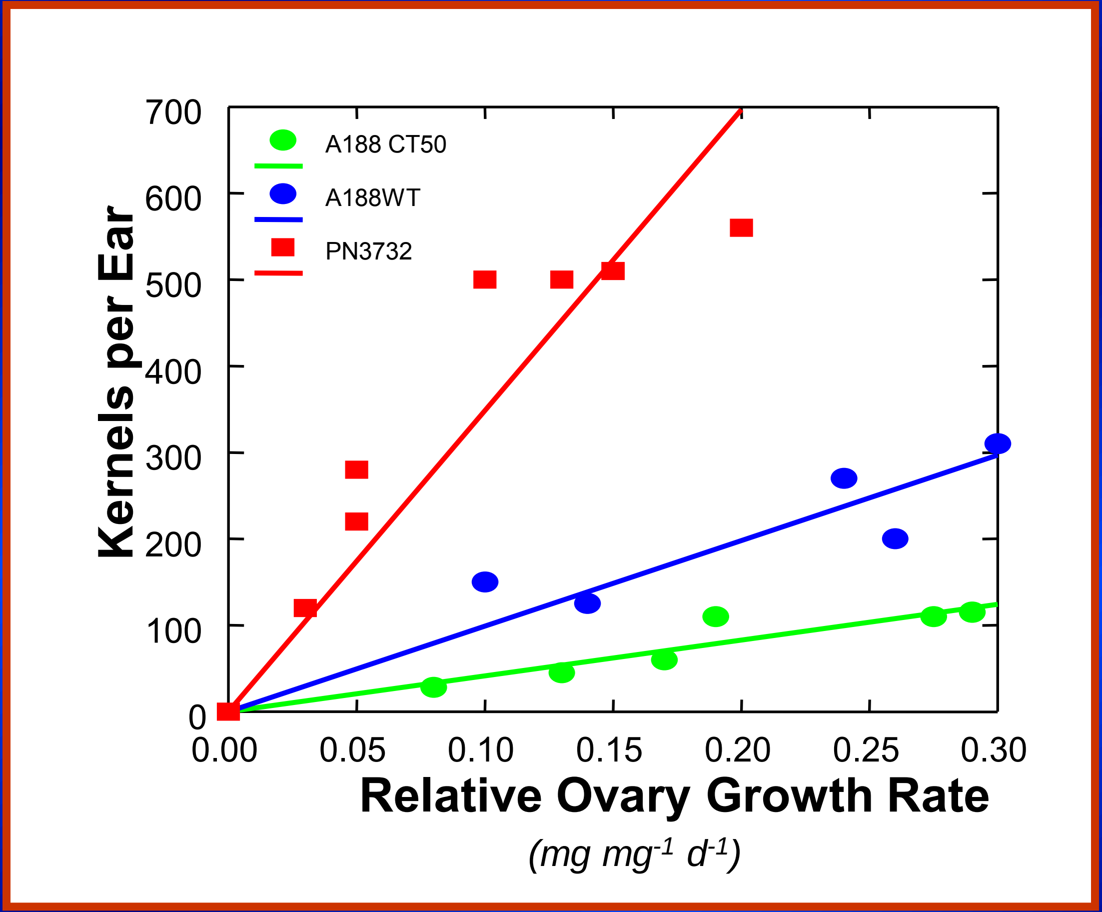


A shorter (or negative) anthesis-silking interval (ASI) reflects a rapid rate of ovary growth at anthesis

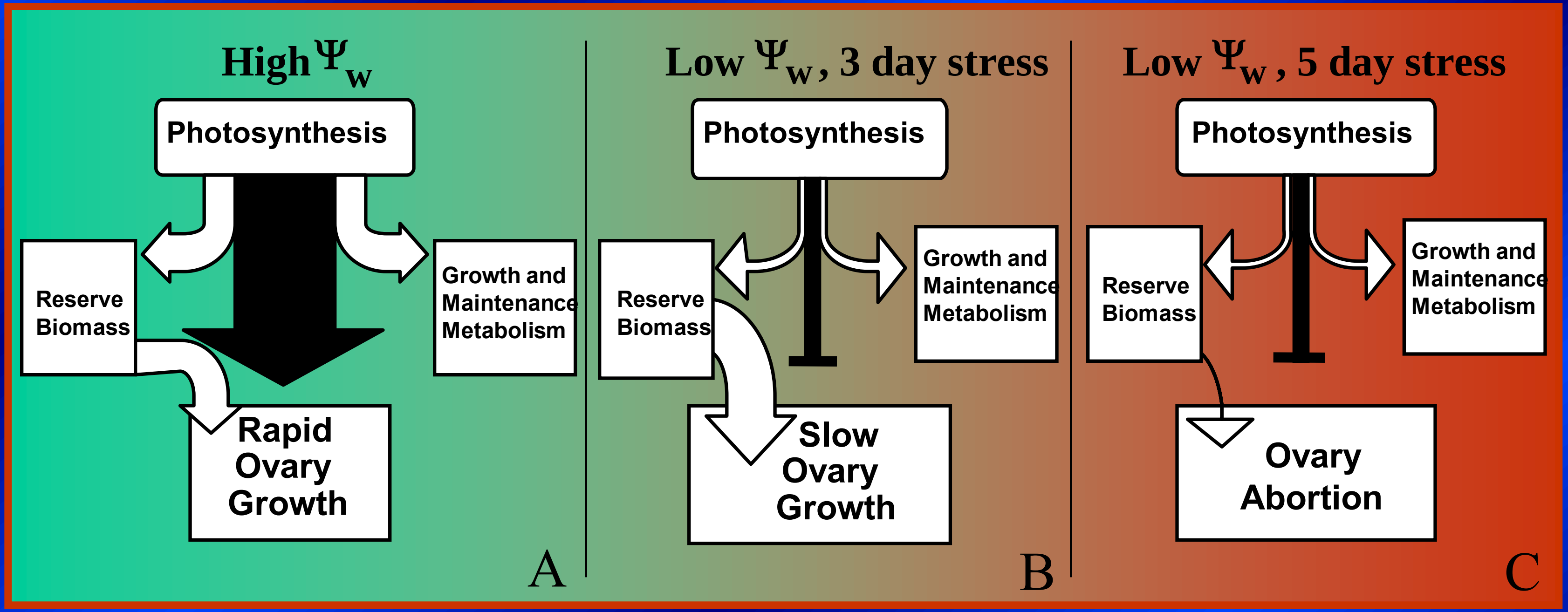


from Edmeades et al. 1993

Many drought stress experiments indicate kernel set in maize is closely correlated with ovary growth rate during anthesis



Ovary growth is closely coupled to the current supply of photosynthate…



Zinselmeier et al 1999

Possible ways to increase assimilate supply to the reproductive structures during drought

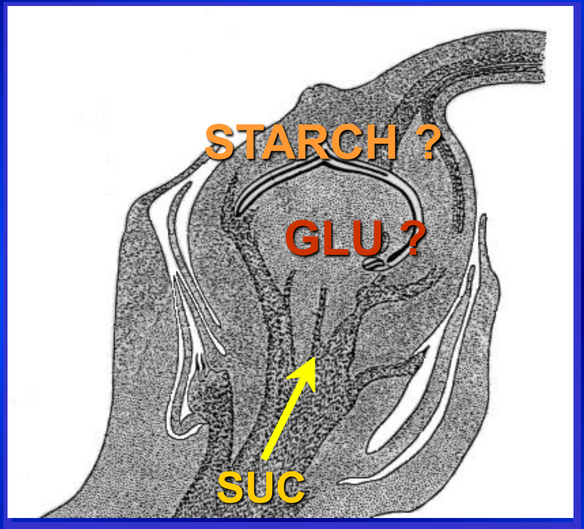
- Maintain photosynthetic rate at low water potential
- Increase contribution from temporary storage tissues
- Sustain metabolic activity within the ovaries at low water potential

Several physiological 'barriers' limit delivery of available sucrose to pistillate flowers during drought...

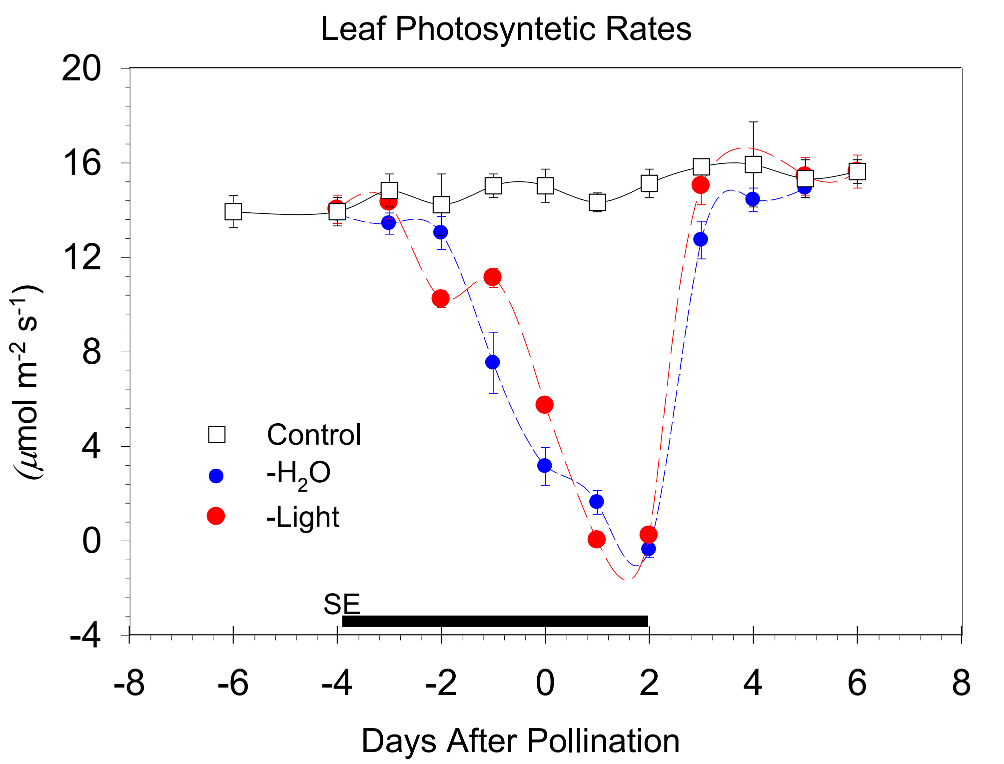
Competition with stronger sinks

Sugar storage as hexoses

Inhibition of sucrose metabolism at low ovary Ψw



How important is the supply of current photosynthate for kernel set?

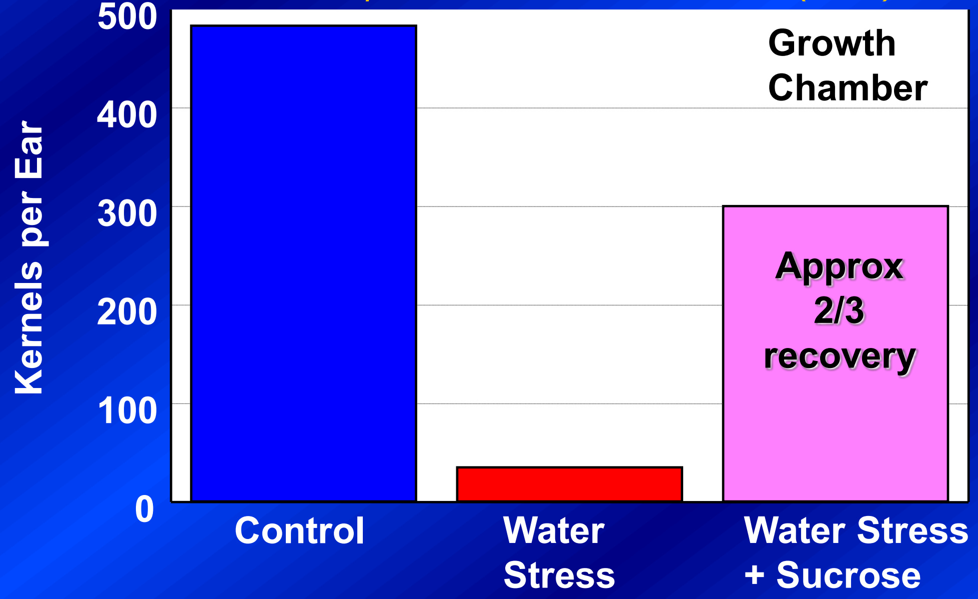


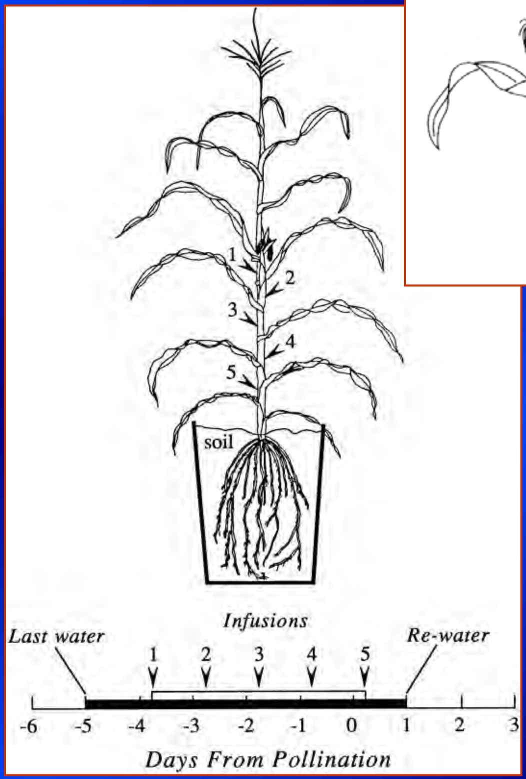
Inhibition of photosynthesis accounts for about 70% of the kernel loss caused by a water deficit during anthesis

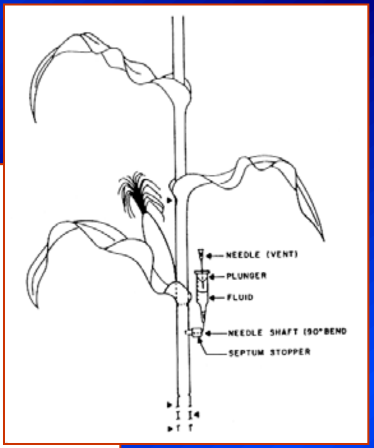
Treatment	n	Silk WP (MPa)	Kernel Number (gr/ear)
Control	5	-0.41 ± 0.03	598 ± 17
-Light	11	-0.40 ± 0.04	222 ± 72
-H_2O	8	-1.00 ± 0.02	15 ± 6

Supplying photosynthate (sucrose) via stem infusion recovers about 70% of the kernels that would have aborted in water stressed maize plants

adapted from Zinselmeier et al. (1995)

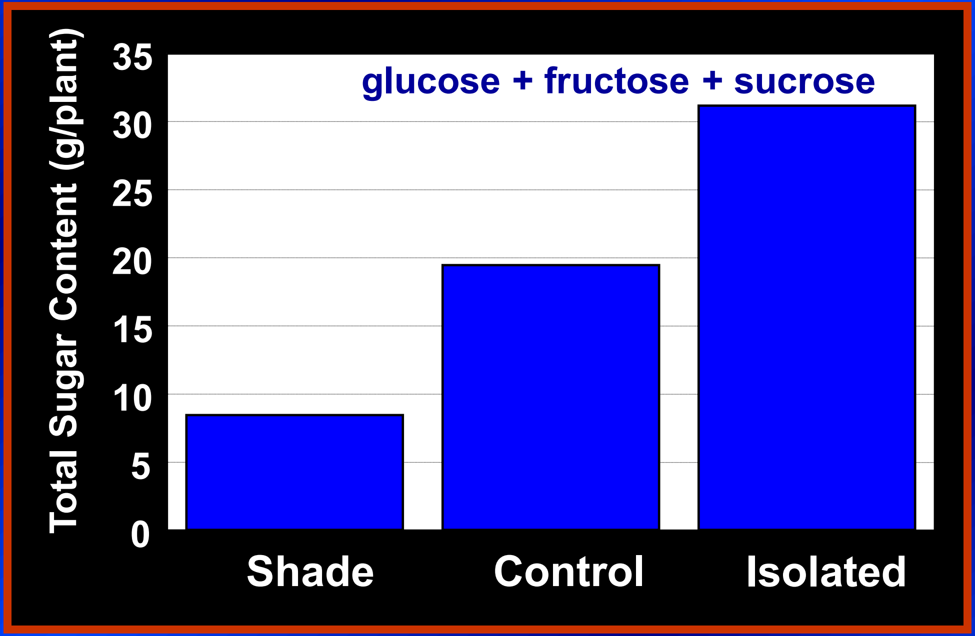


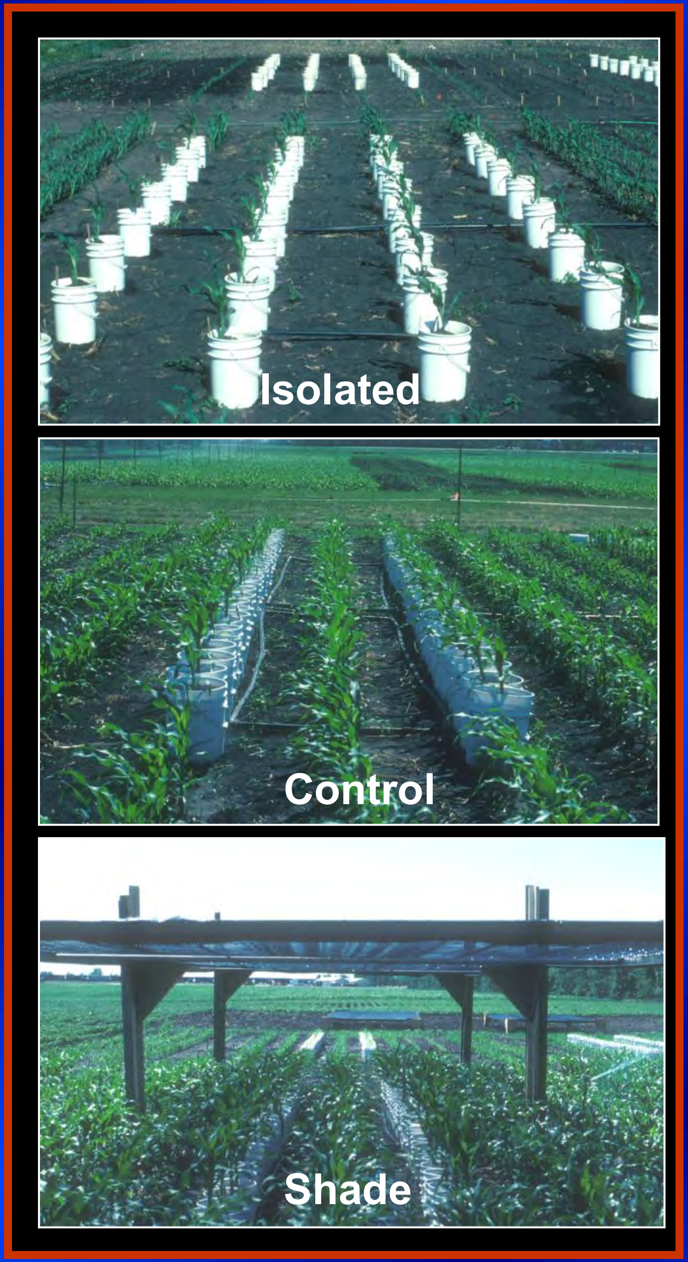




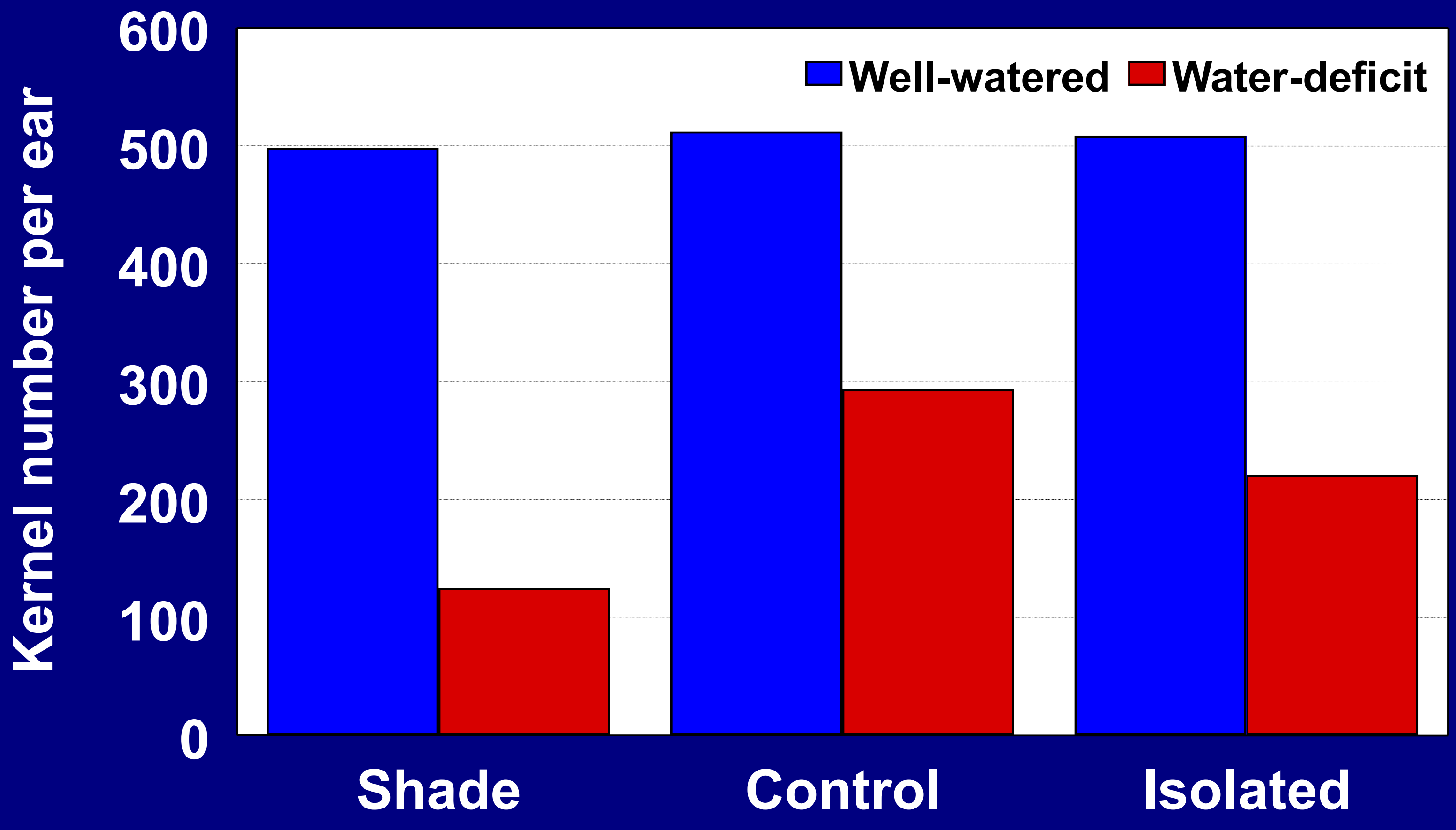
Boyle et al 1991

Levels of 'reserve sugars' in maize can be varied more than 4-fold by cultural practice

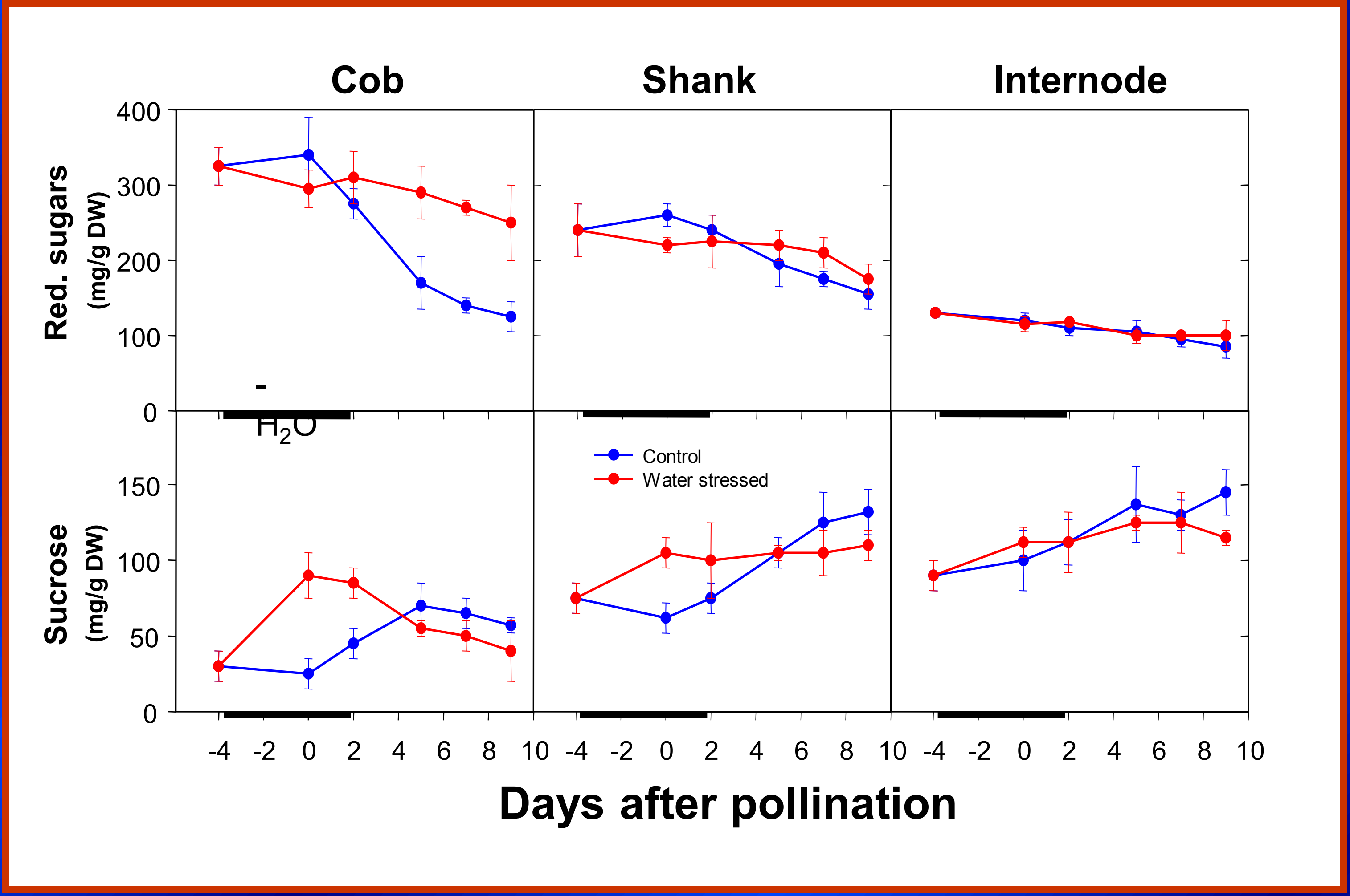




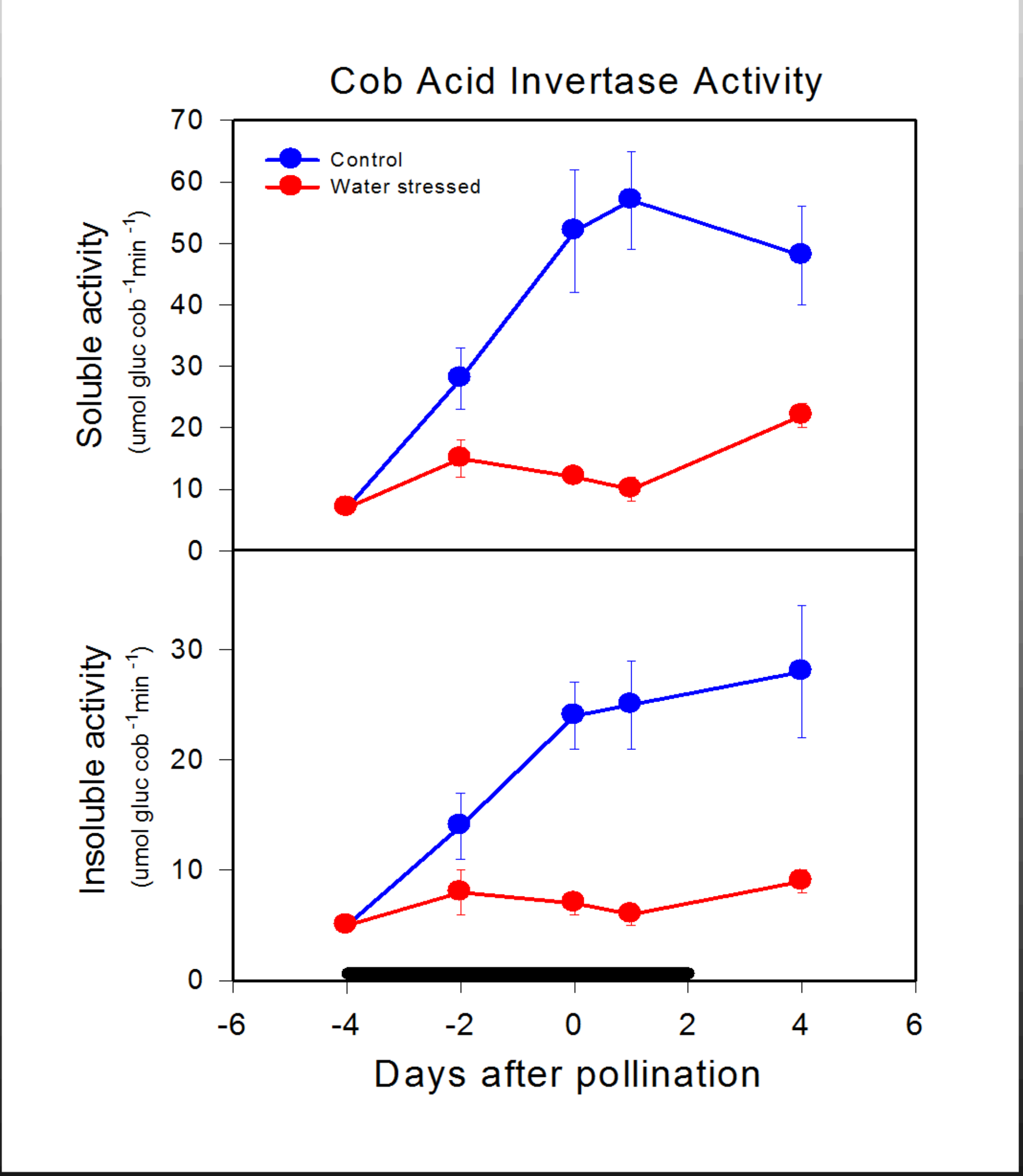
Increasing total plant sugar levels does not prevent kernel loss when a water deficit occurs during anthesis



Maize ‘storage structures’ do not export sucrose when photosynthesis is inhibited during anthesis



Drought inhibits acid invertase activity

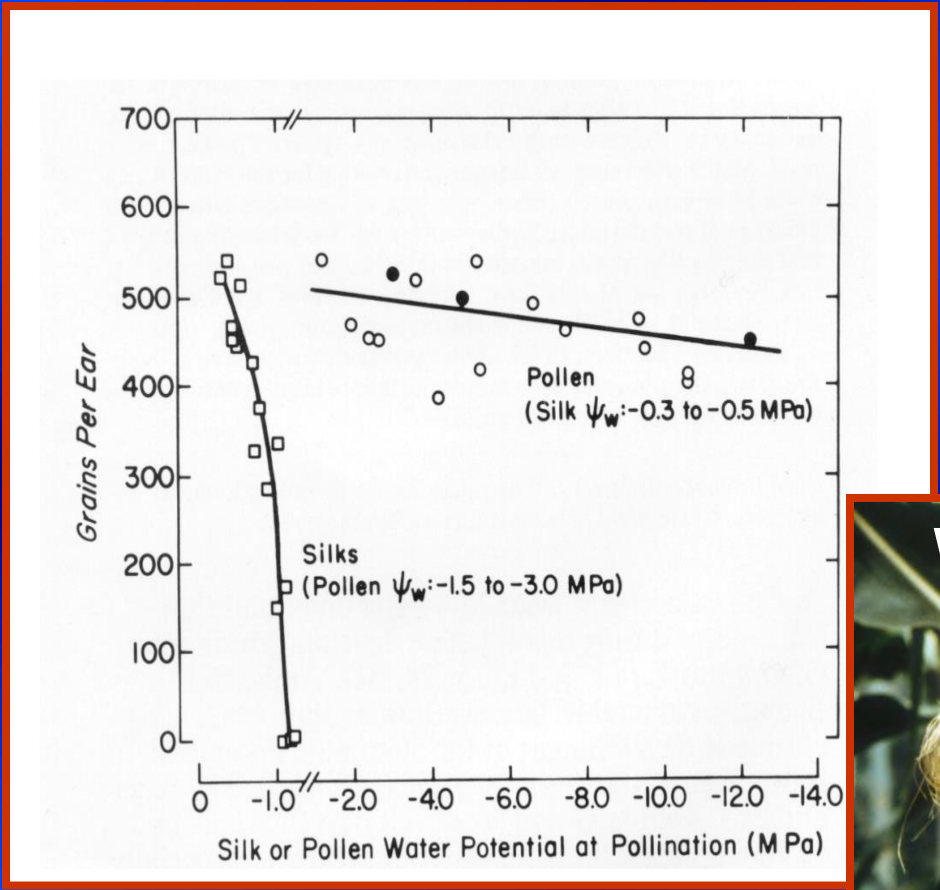


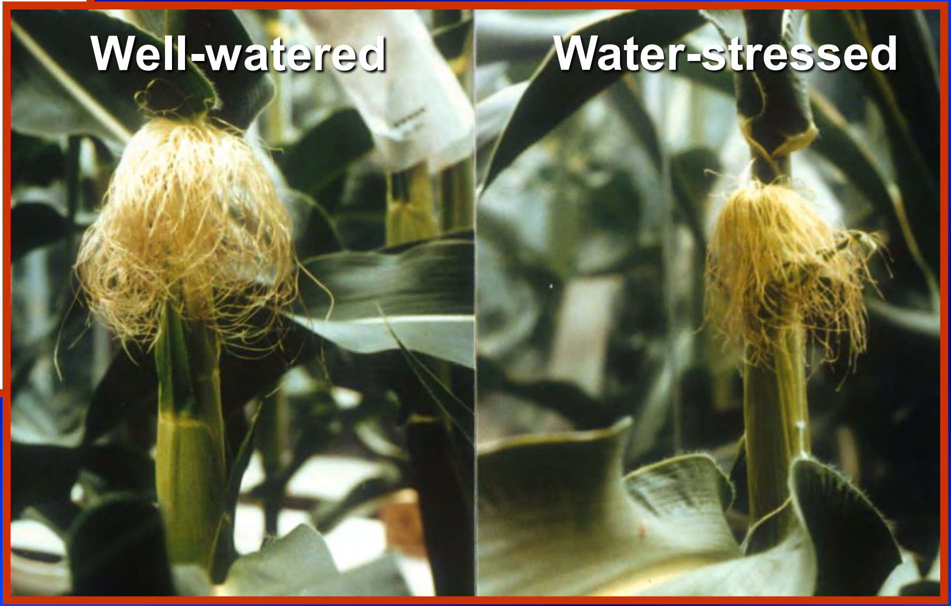
Zinselmeier unpublished

Limitations for altering the pattern of sucrose storage in stem, shank, and cob tissues

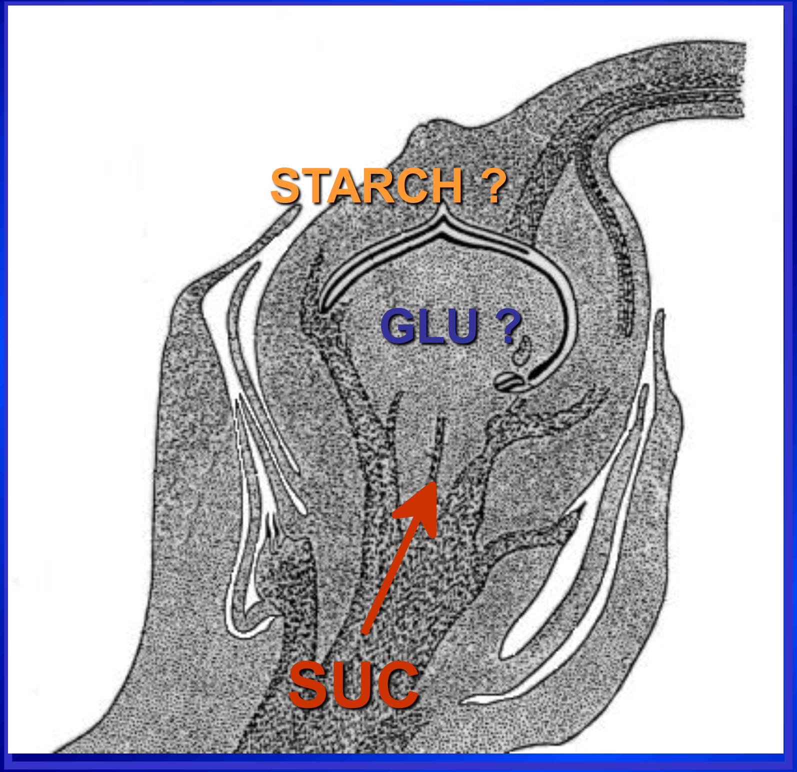
- Mechanisms of sucrose import/export not known
- Biochemistry of carbohydrate metabolism not fully characterized
- Tissue-specific promoters for stem, rachis, and pedicel are not yet available
- Sucrose accumulation is coupled to development

Kernel set depends on conditions within the pistillate flowers…

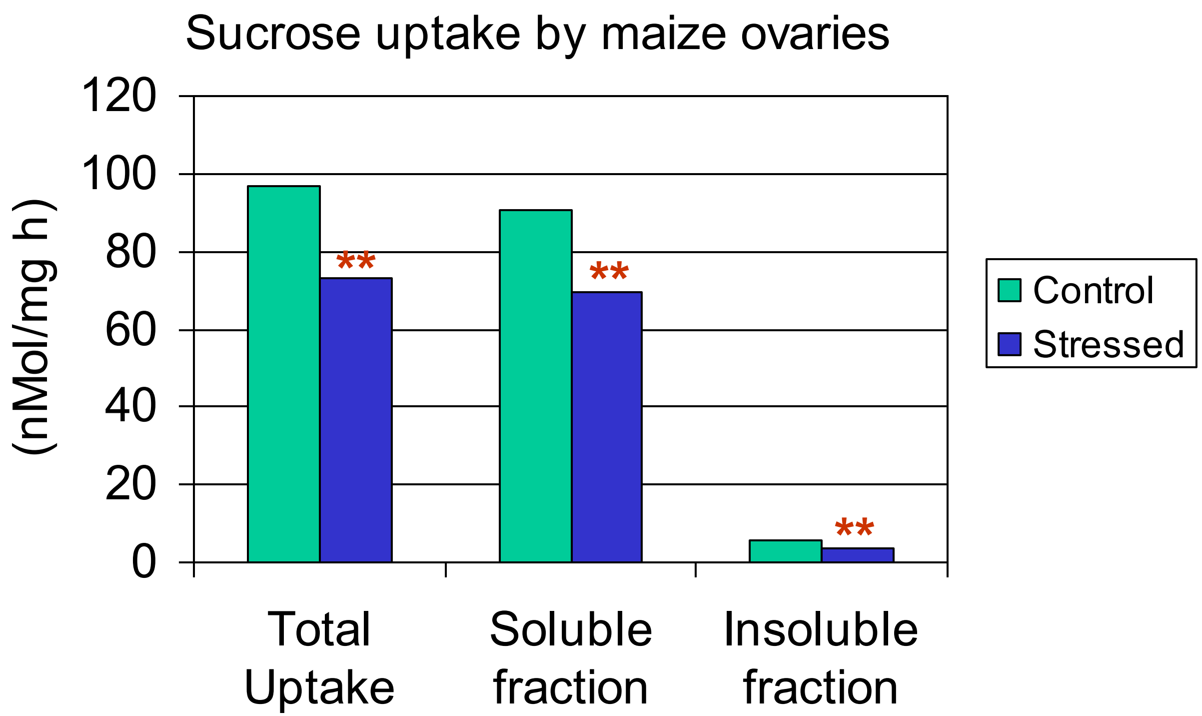




Does drought affect the capacity of maize ovaries to utilize photosynthate supplied by the plant?

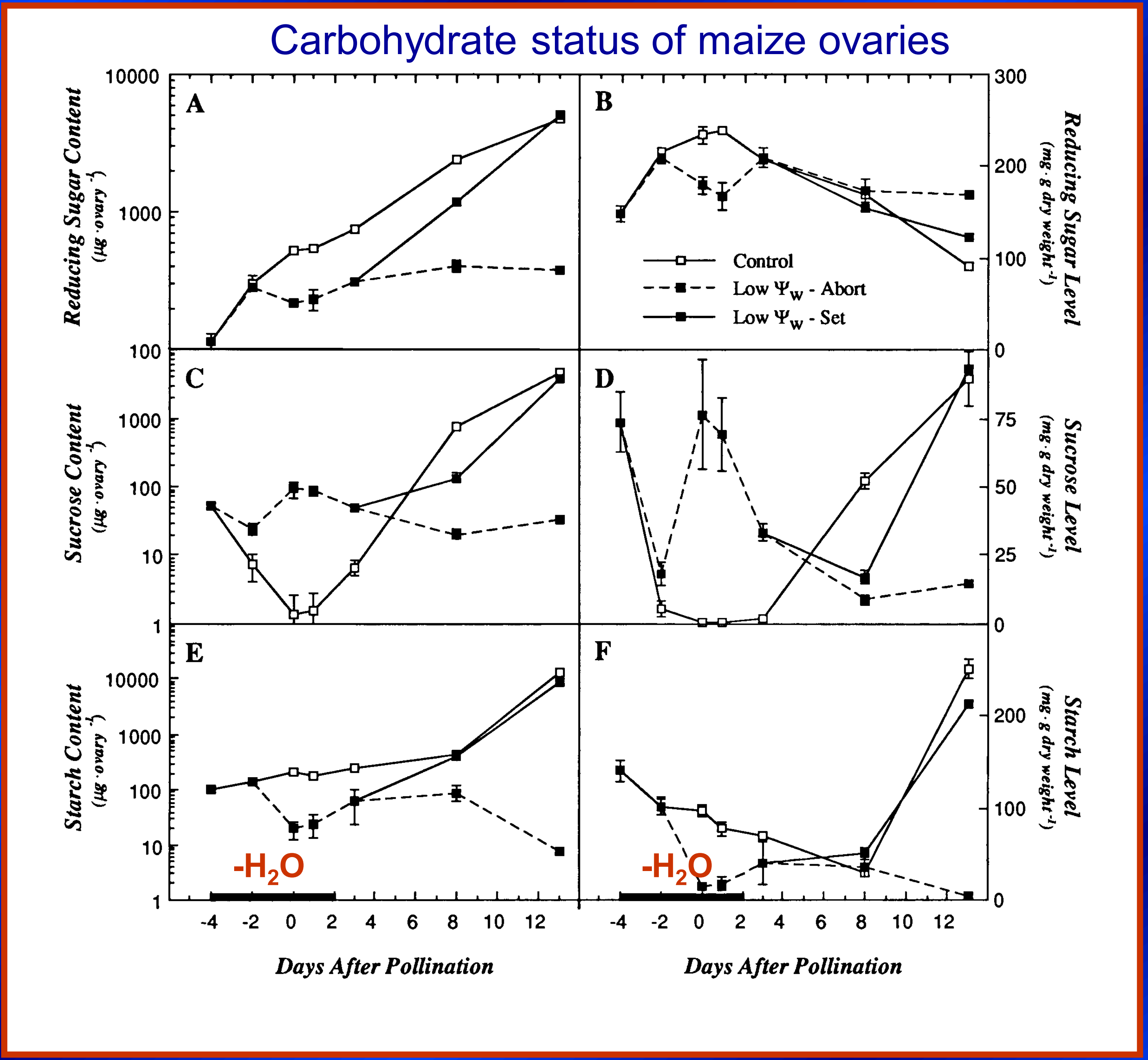


Water stress inhibits the uptake and metabolism of sucrose by maize ovaries

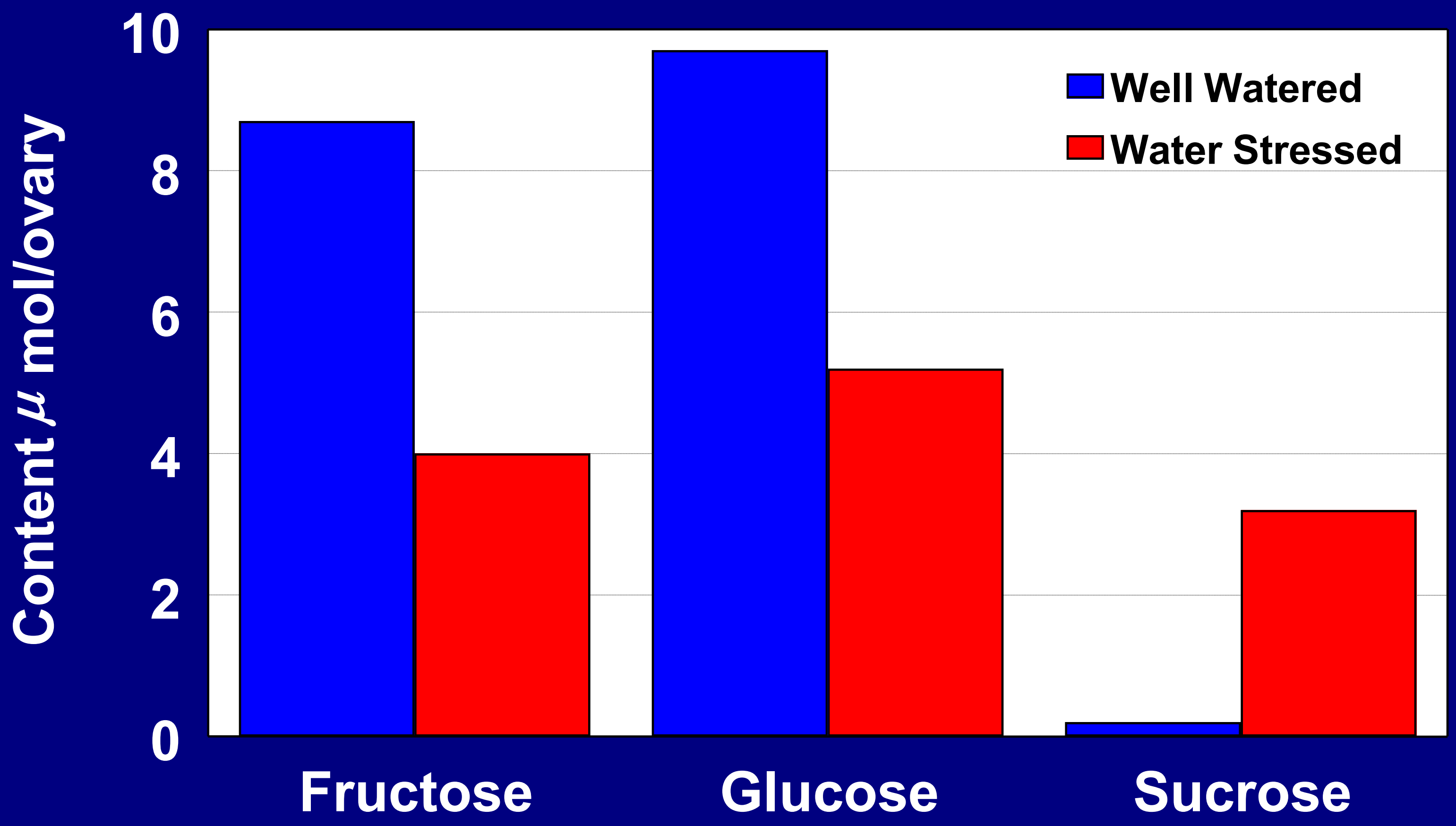


Ovaries were incubated in vitro in 250 mM sucrose, 25 mM glutamine for 2 h at 25 C.

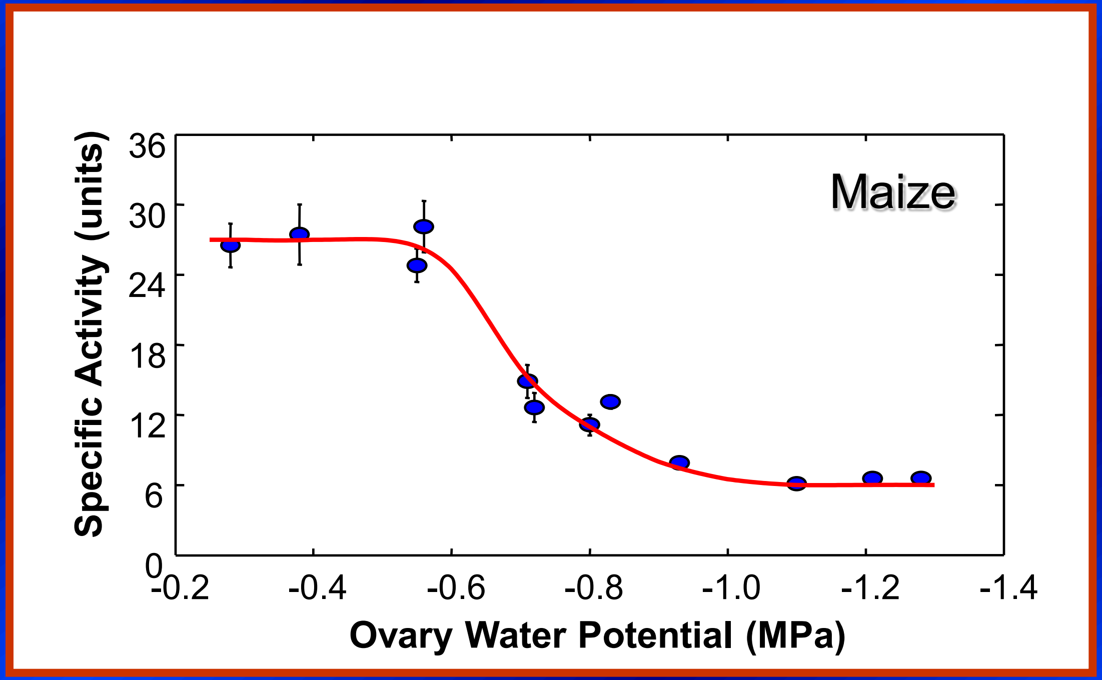
Water deficits alter the pattern of CHO use by maize ovaries



Water stress decreases the (glu+fru)/sucrose ratio in the apoplast of maize ovaries

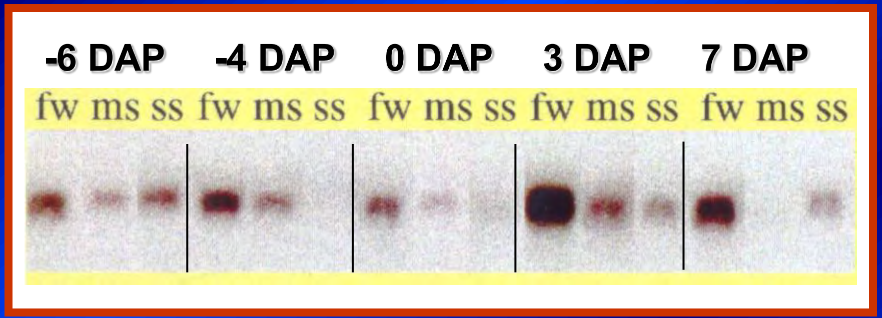


Invertase activity decreases at low ovary Ψw



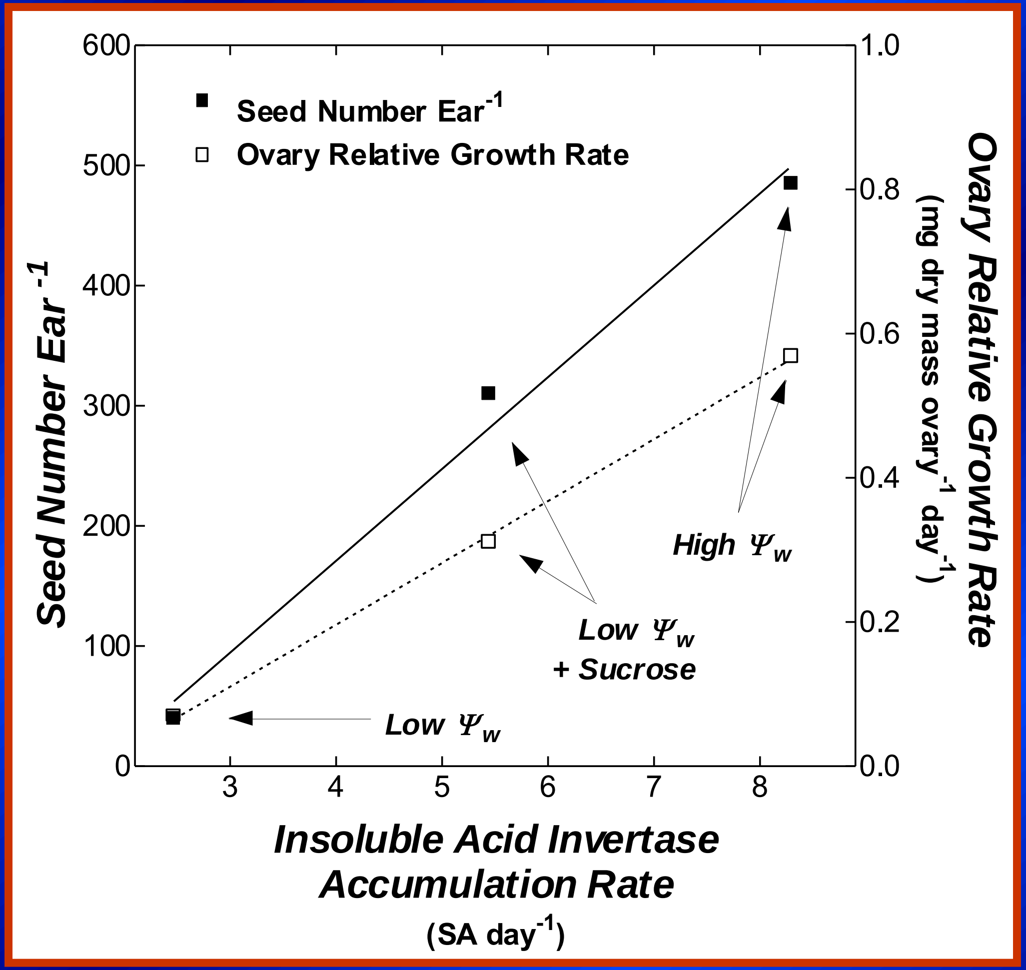
Results of Anderson et al. (2000) suggest invertase synthesis may be down-regulated in water-stressed ovaries

Relative abundance of Ivr2 mRNA



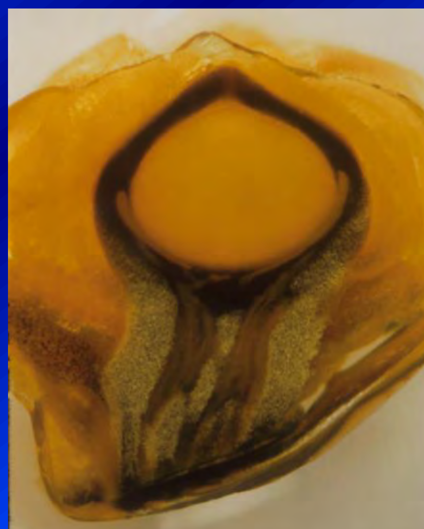
fw = fully watered, **ms** = medium stress, **ss** = severely stressed

The relative inhibition of insoluble invertase activity is correlated with the inhibition of ovary growth rate and subsequent kernel set



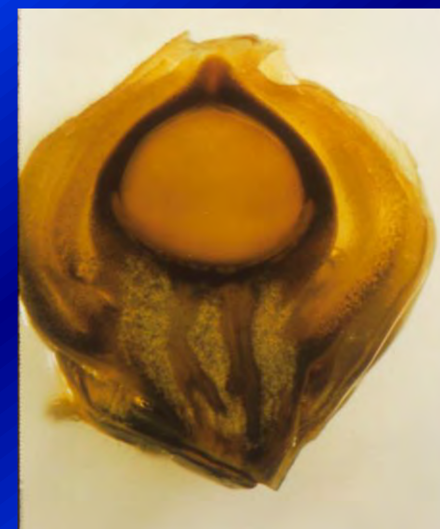
Zinselmeier et al 1999

Supplemental sucrose increases ovary starch content during drought



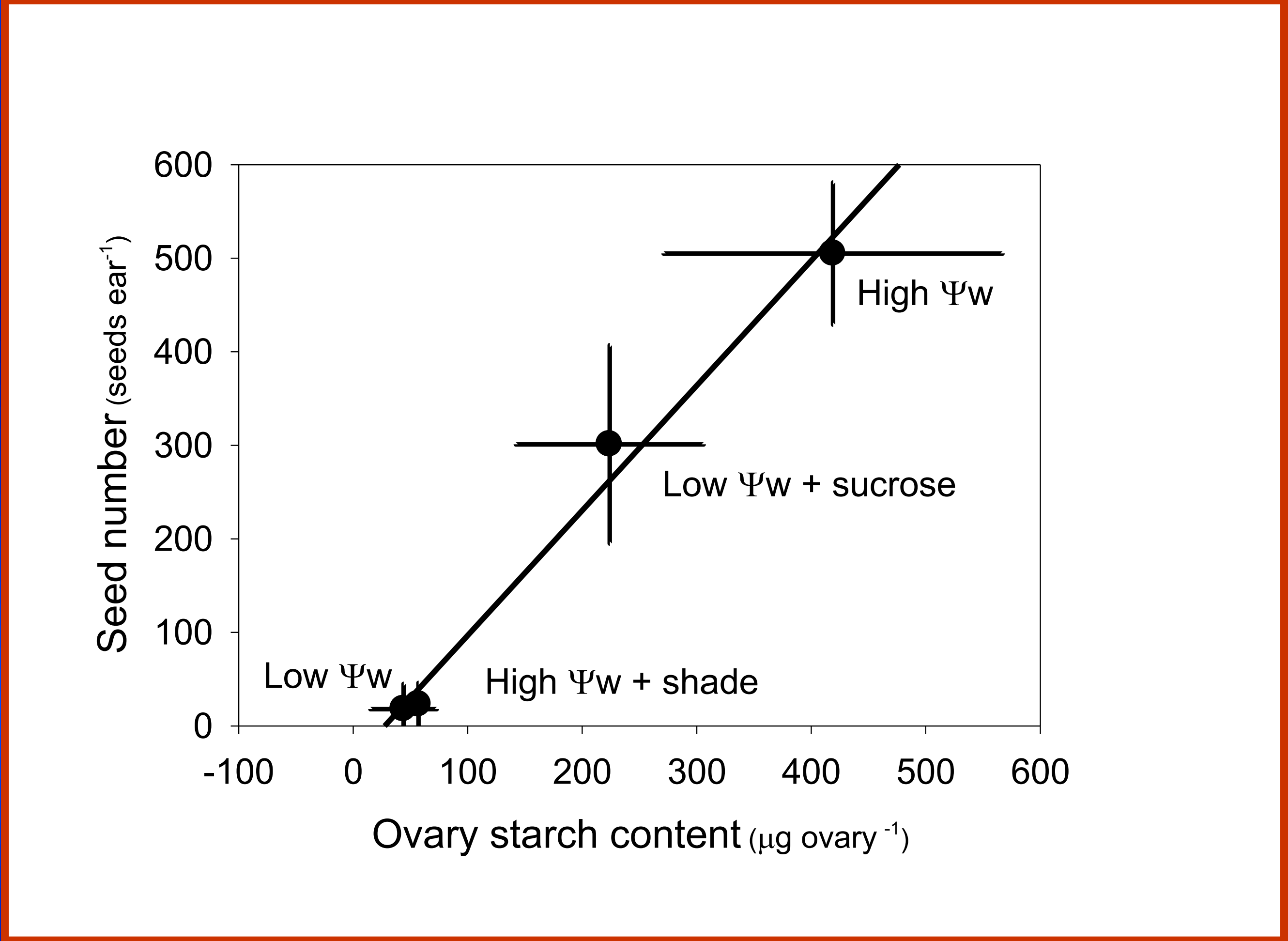
Control

$-H_2O$



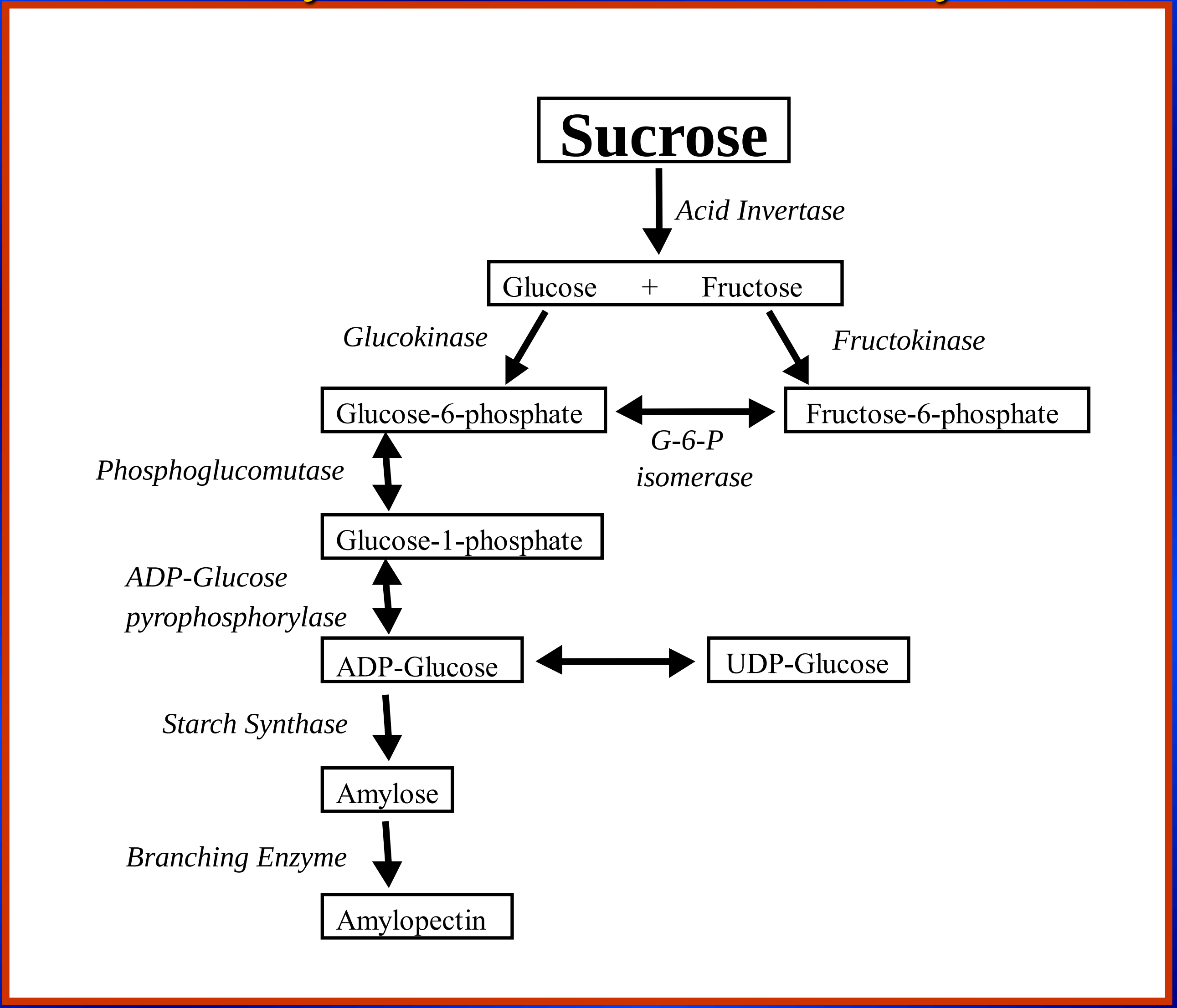
$-H_2O$
+ sucrose

Kernel set also is correlated with ovary starch content at anthesis



adapted from Zinselmeier et al 1999

Carbon flow to starch is limited by loss of invertase activity



Adapted from Zinselmeier et al 1999

Summary:

drought during anthesis of maize flowers…

- inhibits ovary growth
- decreases assimilate flux to the reproductive structures
- disrupts carbohydrate metabolism

Present → future: strategies to maintain maize zygote development during drought

Understand molecular control(s) of sucrose and starch accumulation in storage tissues prior to anthesis

Determine the molecular basis for inhibition of ovary acid invertase activity at low ovary Ψw

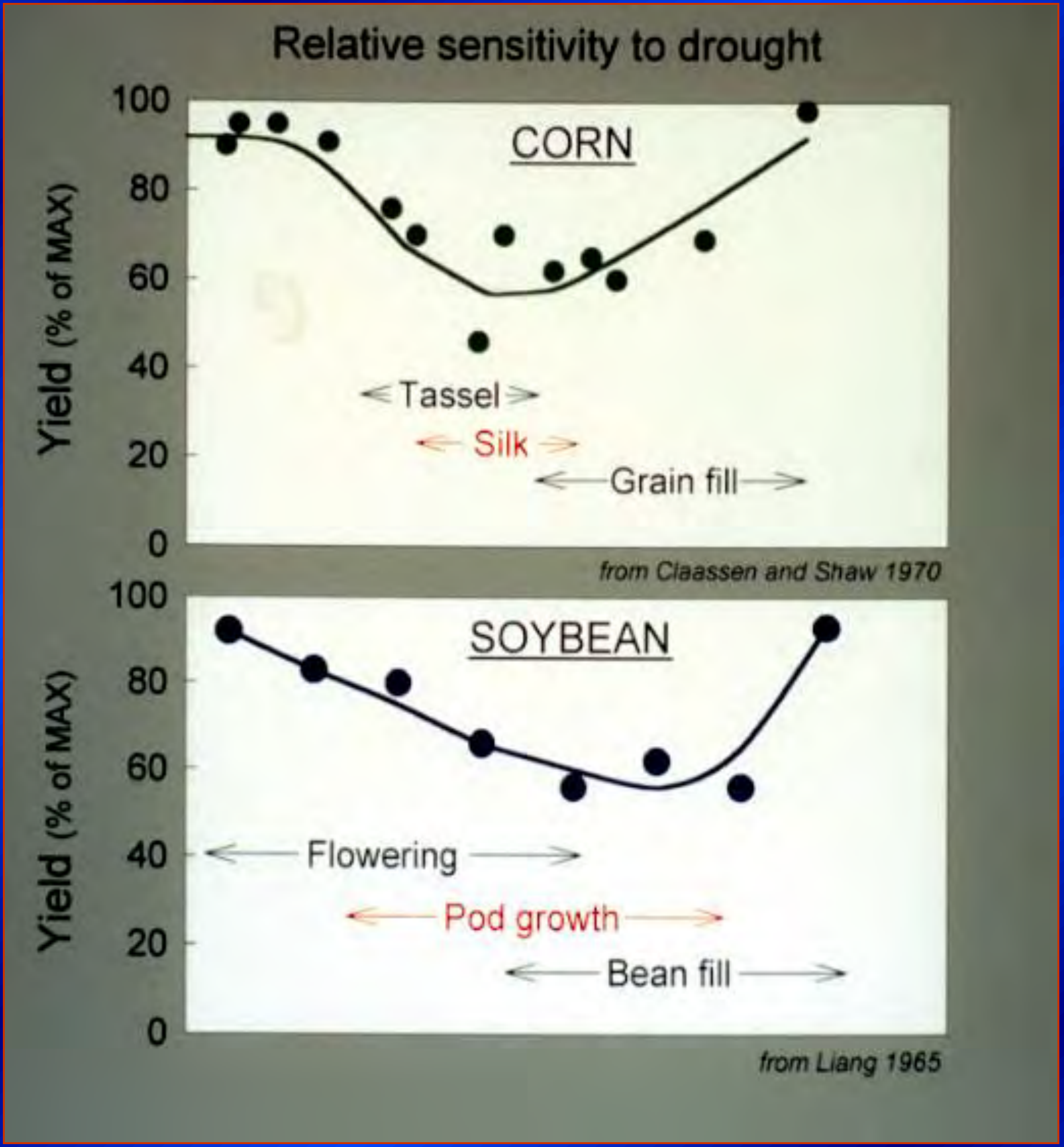
Identify genes whose expression is causally related to inhibition of ovary growth during drought

Seed Development

Drought Effects on Rate and Duration of Seed Filling

Yield loss due to water stress decreases as reproductive development progresses.

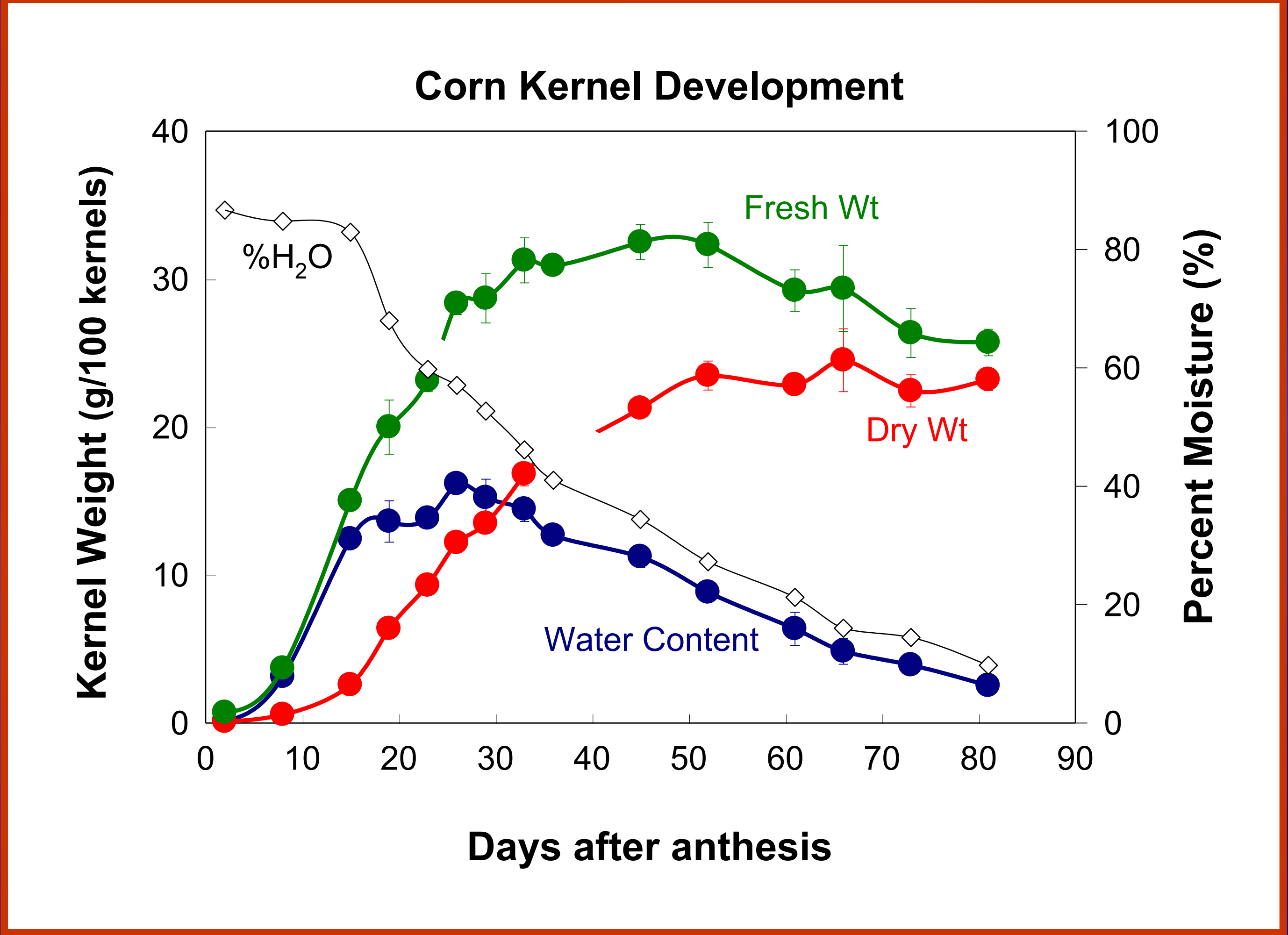
Stress during seed filling results in smaller seeds.



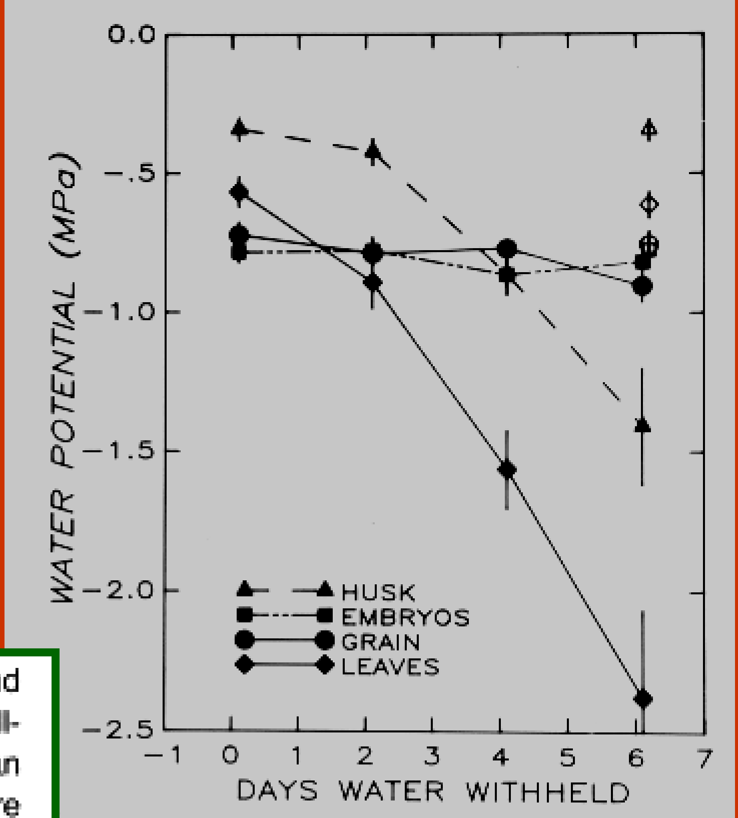
Possible explanations for smaller seeds produced under drought conditions

- Loss of concurrent assimilate supply
  - Accelerated leaf senescence, ‘stay-green’ types do better under dry conditions
- Decreased sink capacity
  - Fewer sites for storage product synthesis
  - Smaller cell volume.
- Inhibition of metabolism during desiccation
  - Drought accelerates seed desiccation?
  - Loss of metabolic competence at low moisture content

In maize, kernels achieve maximum volume early in development, and maximum dry weight during ‘terminal’ desiccation



A short – term water deficit during kernel filling has little impact on kernel growth rate, despite an apparent decrease in kernel water content.



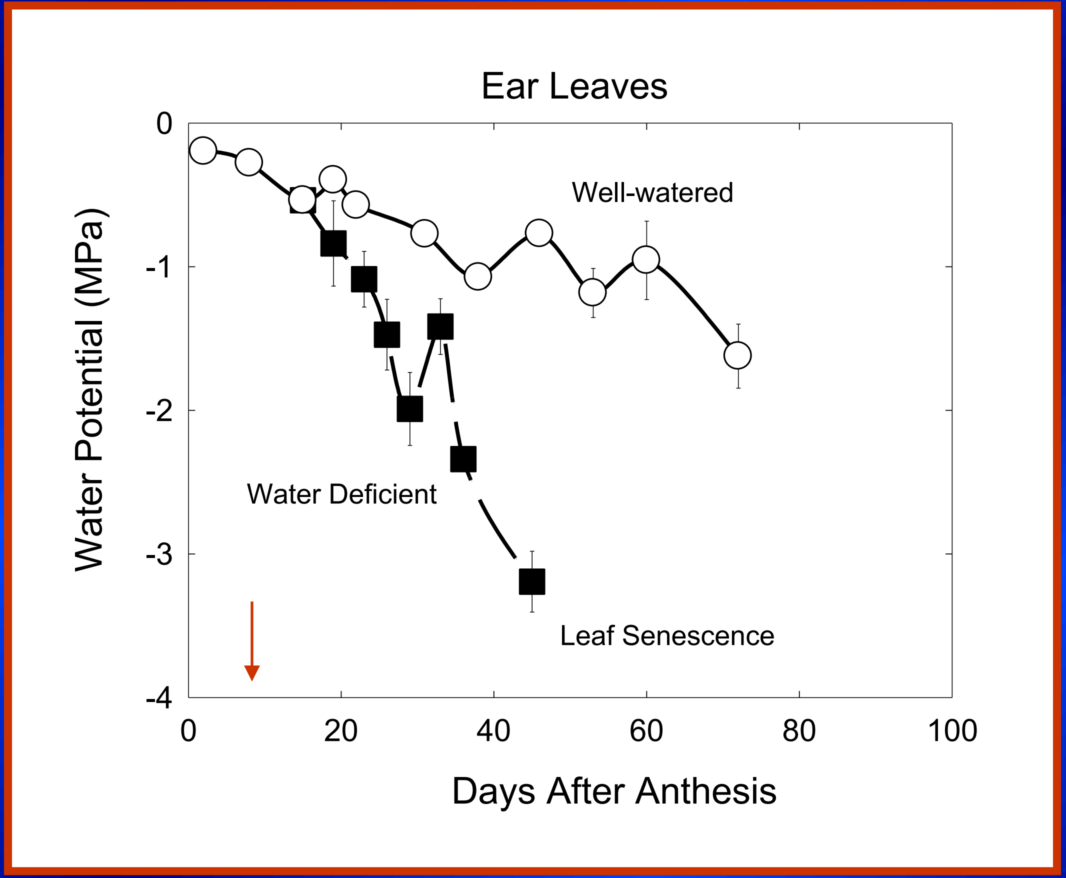
Fresh weight, dry weight, water content, percent moisture, and solute content (expressed in glucose equivalents) of grain from well-watered (+H_2O) and water-deficient (−H_2O) plants. Data are the mean of eight samples. Values in columns followed by the same letter are not significantly different ($P < 0.1$) by Tukey's HSD.

Treatment		Fresh Wt	Dry Wt	H_2O	% M	Solute Content
			mg/grain			*mg/grain*
+H_2O	Day 0	281.1 a	144.6 a	136.5 a	48.5 a	12.3 a
−H_2O	Day 6	284.2 a	167.2 b	117.1 b	41.2 b	13.0 a
+H_2O	Day 6	299.5 a	161.4 b	138.1 a	45.7 a	14.6 b

The change in kernel water status is not apparent from measurements of kernel Ψw

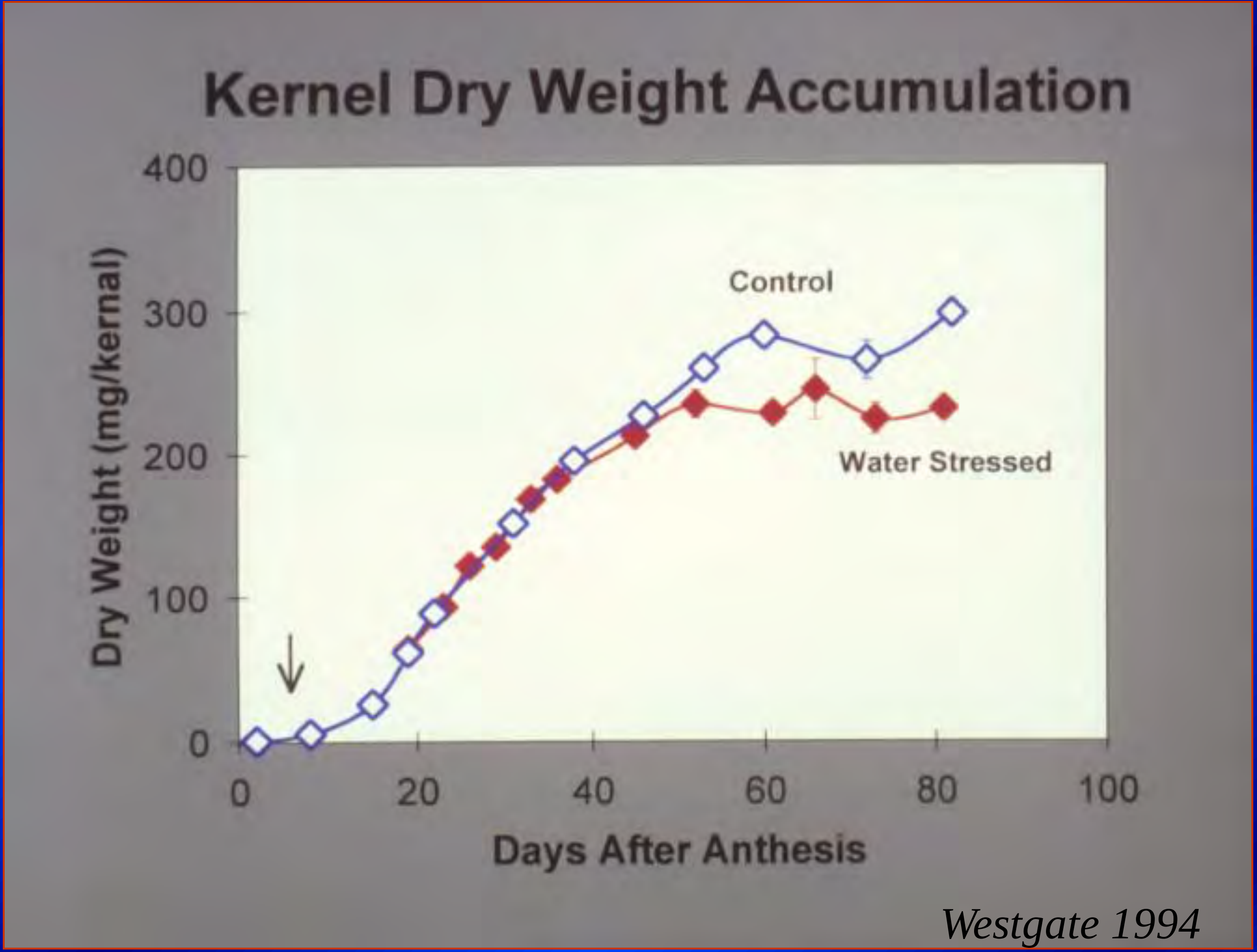
Westgate and Grant 1989

What factors limit kernel growth in maize plants exposed to drought after anthesis under field conditions?

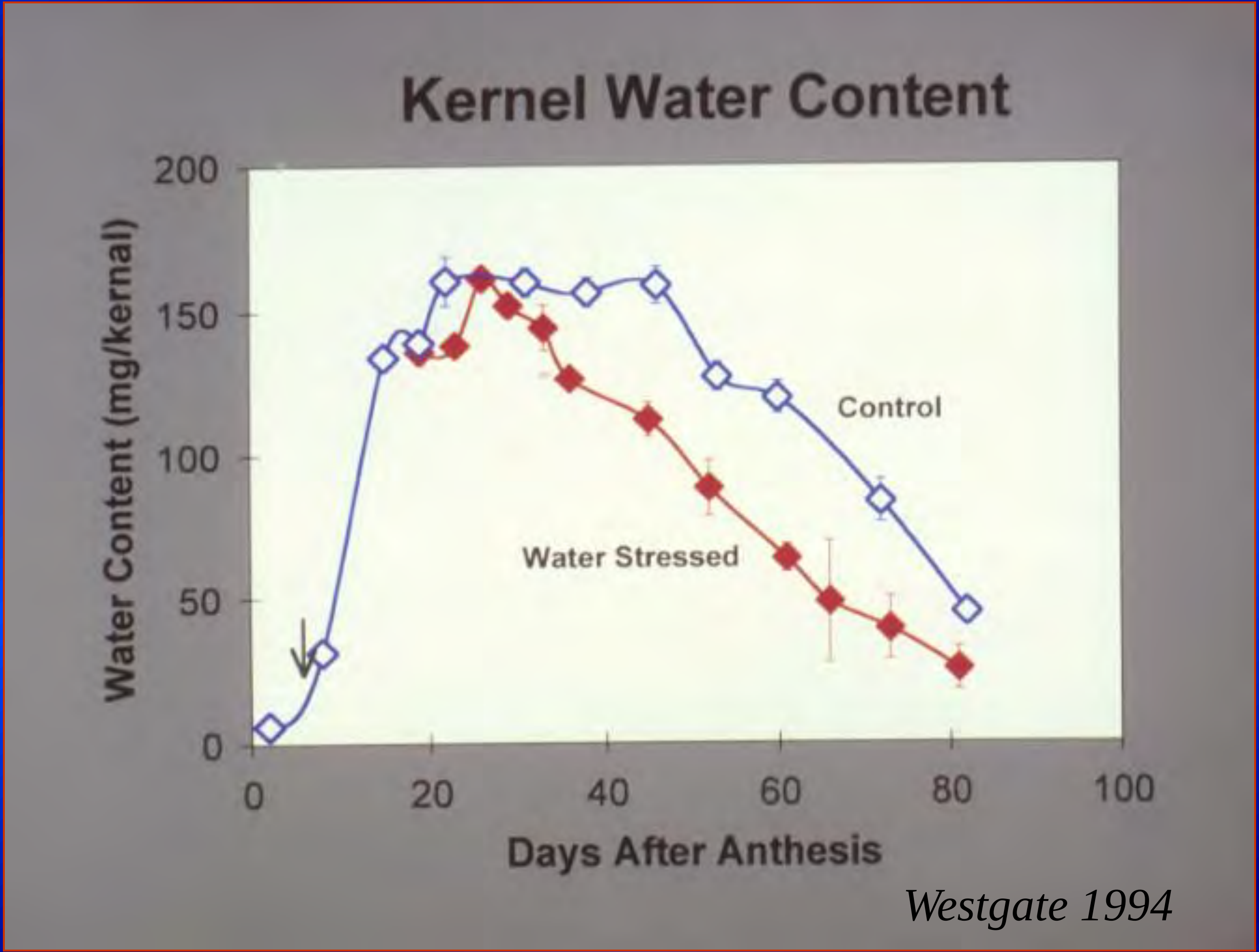


Westgate 1994

Kernels on water stressed plants continue to fill, but cease DM accumulation sooner



Kernels on water stressed plants begin to lose water sooner after anthesis



Westgate 1994

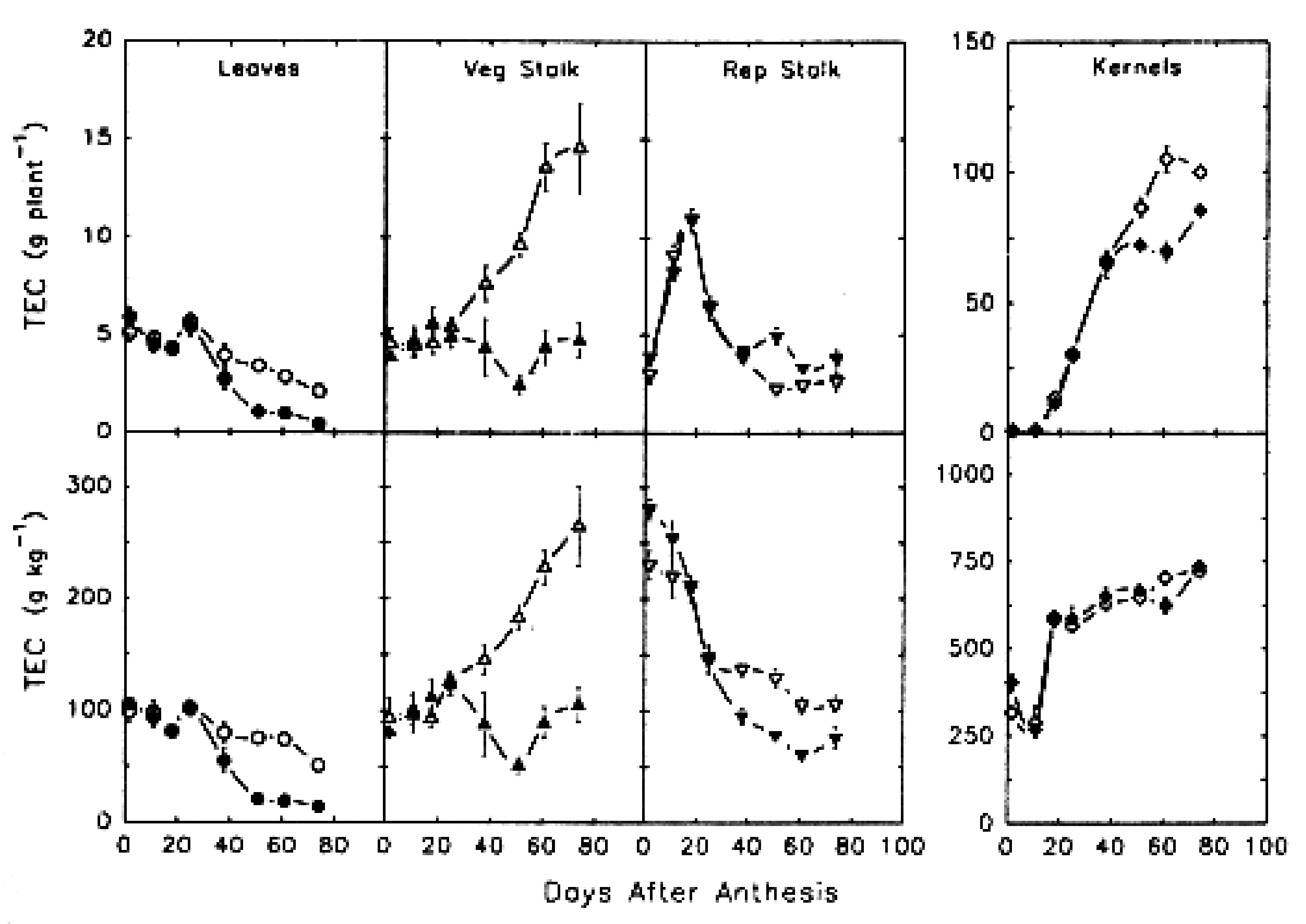
Water deficit during grain filling decreased kernel size by shortening the effective filling period (EFP)

Treatment	Rain	Irrig.	Grain Yield	Yield Components: kernel/ear	Yield Components: mg/kernel	Yield Components: HI
	(mm)		(Mg/ha)	(no.)		
WW	76	261	11.1a	580a	240a	0.50a
WD	76	37	9.1b	583a	195b	0.50a

Treatment	Final Dry Wt. Ker	Final Dry Wt. Emb	Growth Rate Ker	Growth Rate Emb	EFP Ker	EFP Emb
	(mg)		(mg/d)		(d)	
WW	297a	33a	6.1a	0.8a	46	43
WD	233b	28b	5.9a	0.7a	39	39

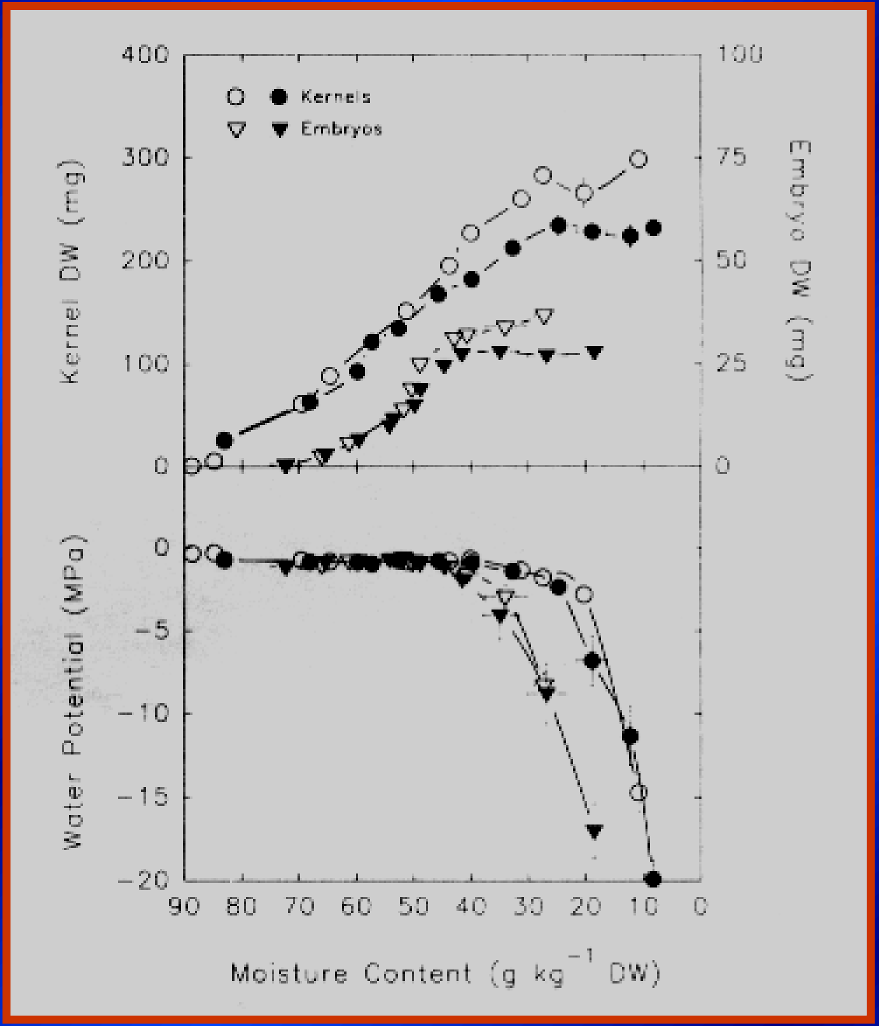
Ker = whole kernels, Emb = embryos

"Reserve" carbohydrate decreased in water stressed plants, but was not depleted from the stalk when kernel growth ceased.

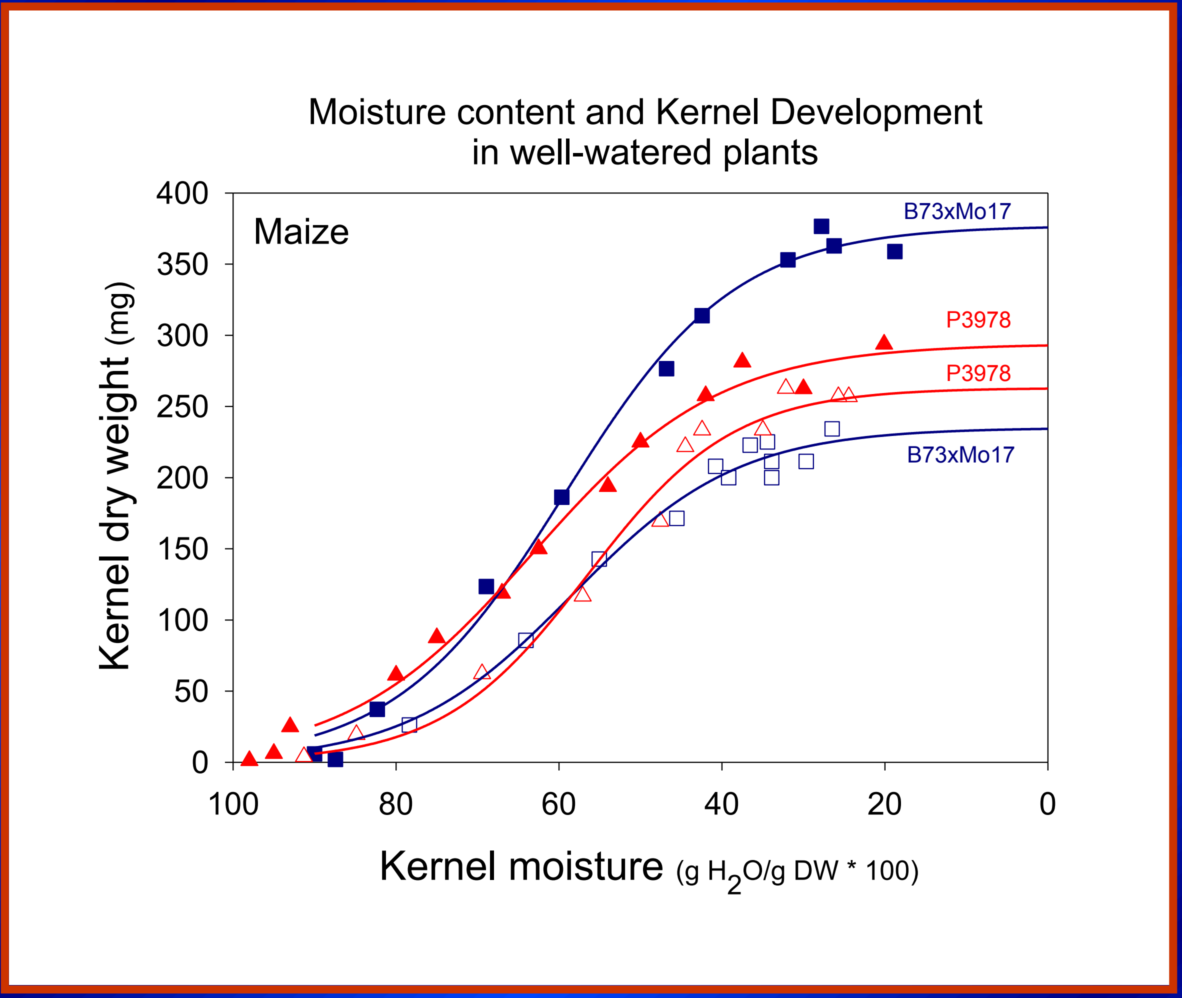


Severe water deficits during grain filling did not alter the relationships between moisture content and Ψw of the kernel or embryo.

Maize hybrid P3732

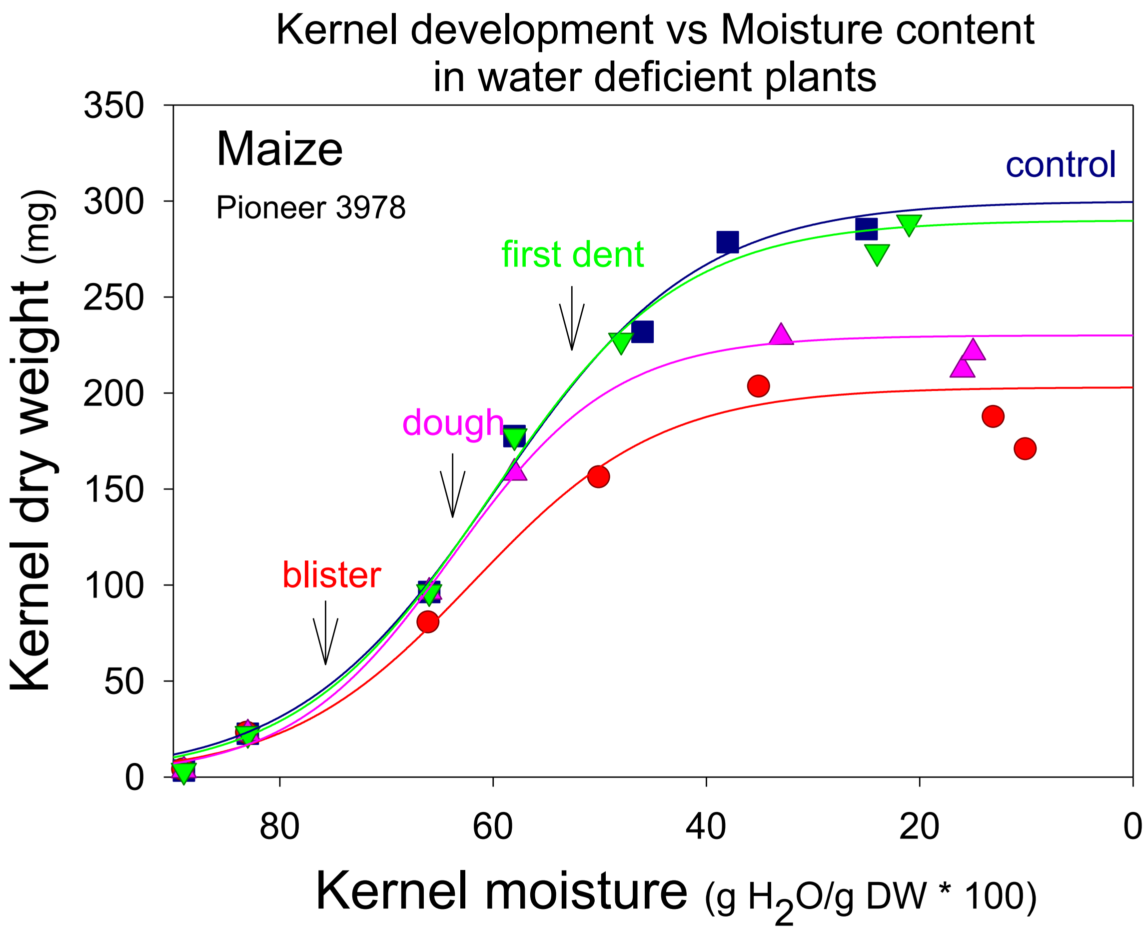


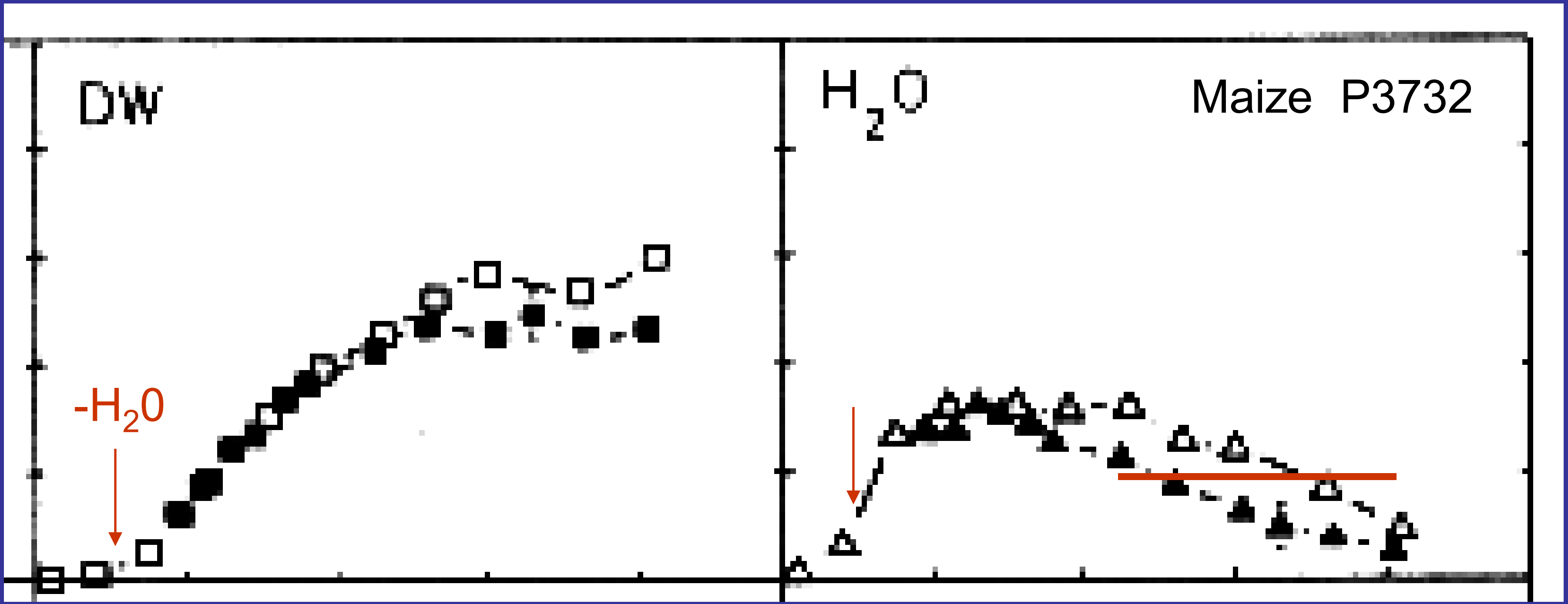
Dry matter accumulation in maize kernels continues until kernel moisture reaches about 30%.



adopted from Egli and TeKrony (1997), Westgate and Boyer (1986b)

Water stress during seed filling decreases final kernel weight, but does not affect the moisture content at which dry matter accumulation ceases.



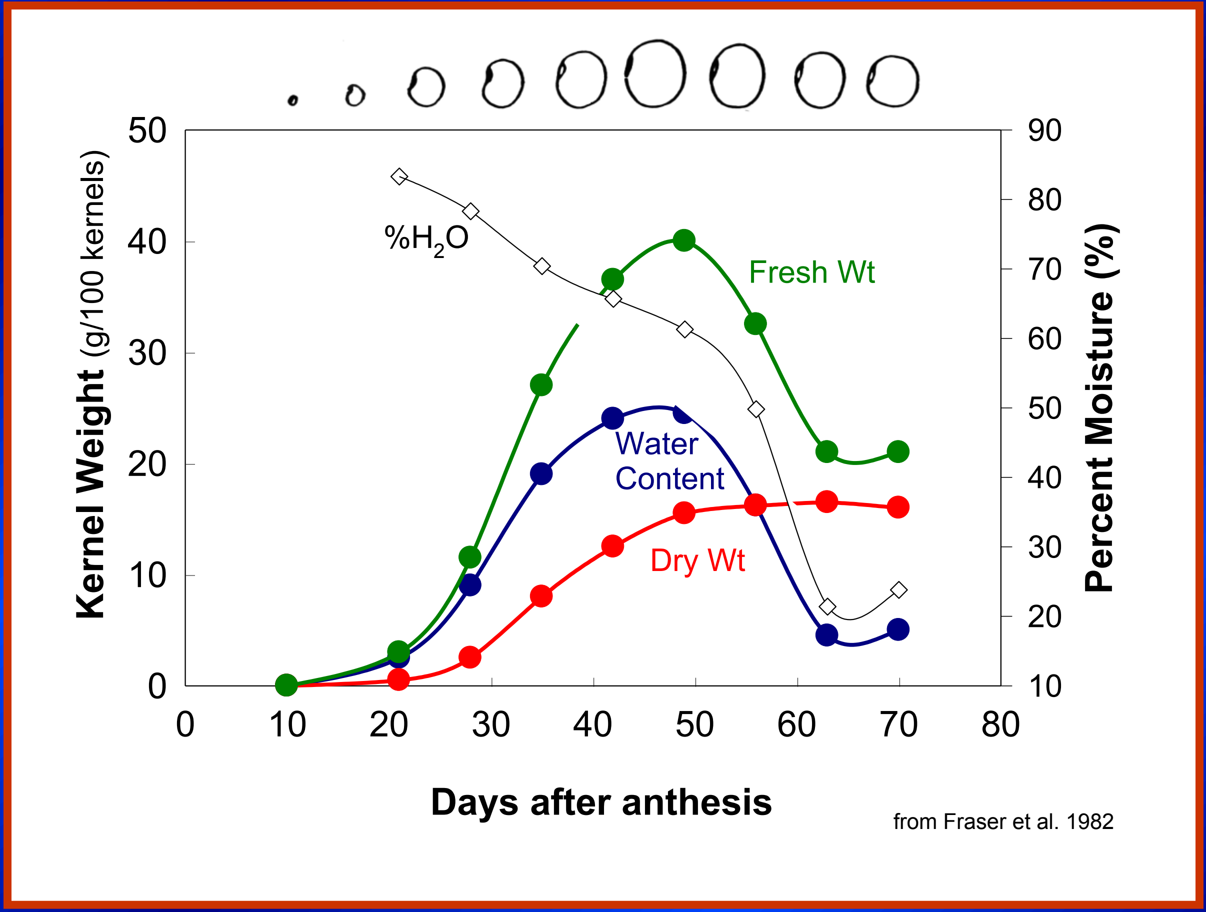


Days after anthesis

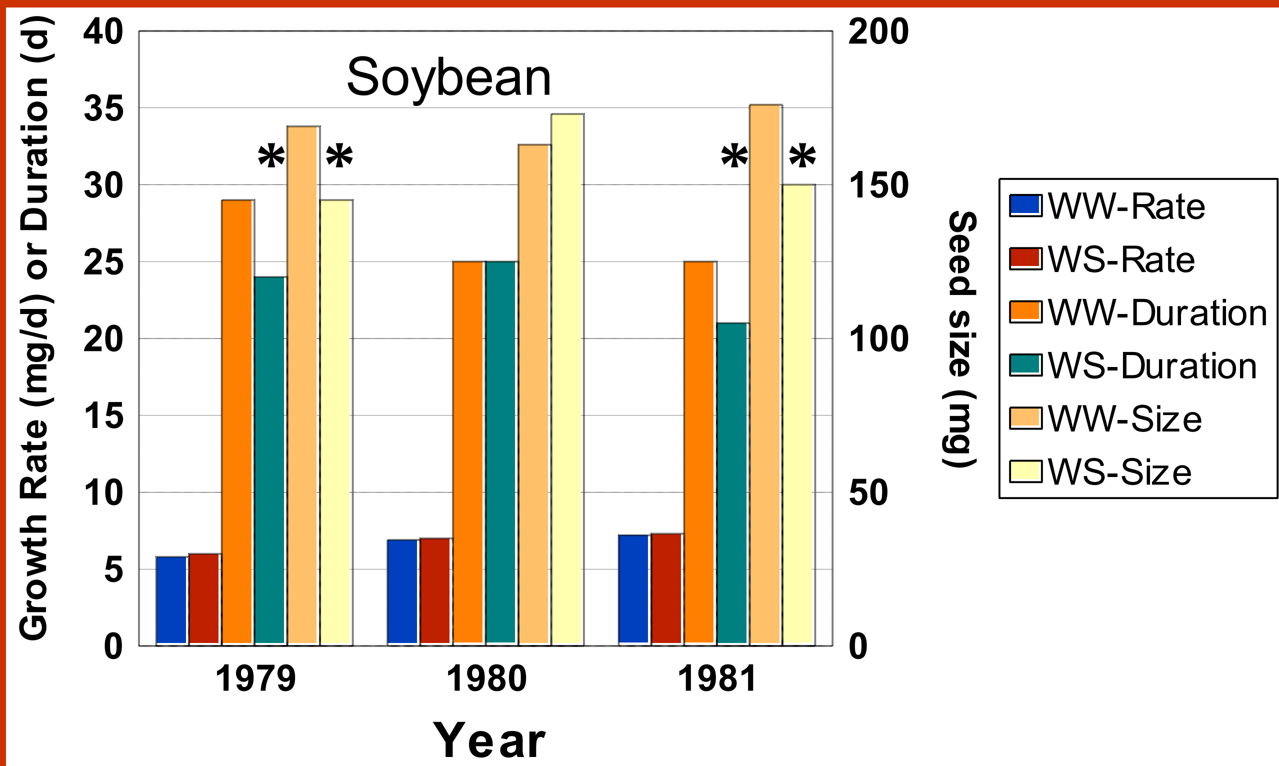
Kernels on droughted plants achieved less mass because they reached a minimum water content to support metabolism sooner after anthesis.

Selection for desiccation later during filling or greater water volume early in filling could allow greater kernel mass during drought.

For the soybean embryo, accumulation of final seed dry weight coincides closely with achieving maximum water content

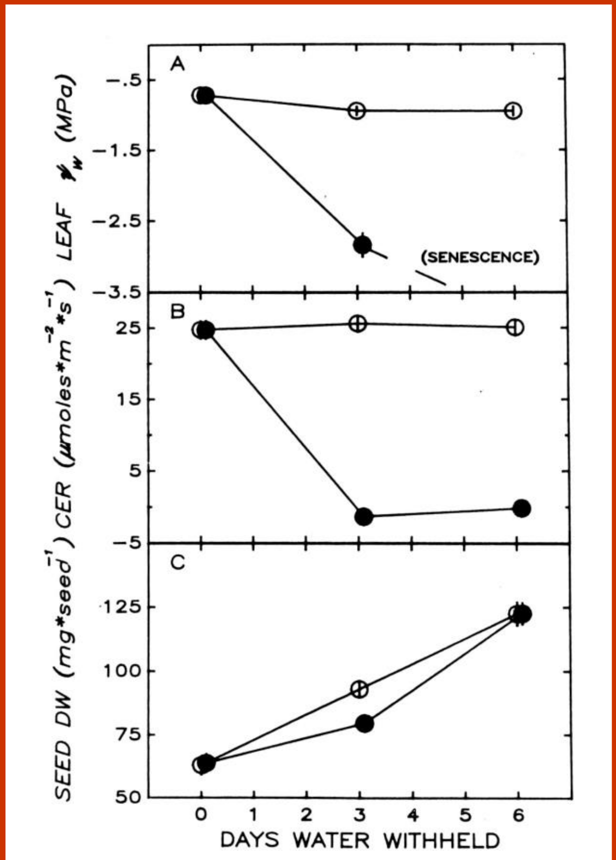


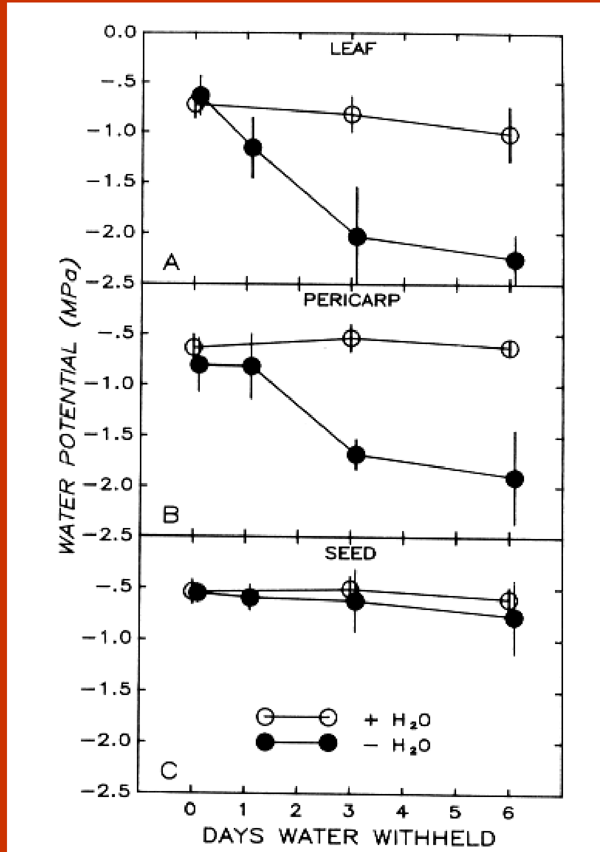
Water stress during seed filling shortens the duration of seed filling in soybean – resulting in production of smaller seeds



from Meckel et al. 1984

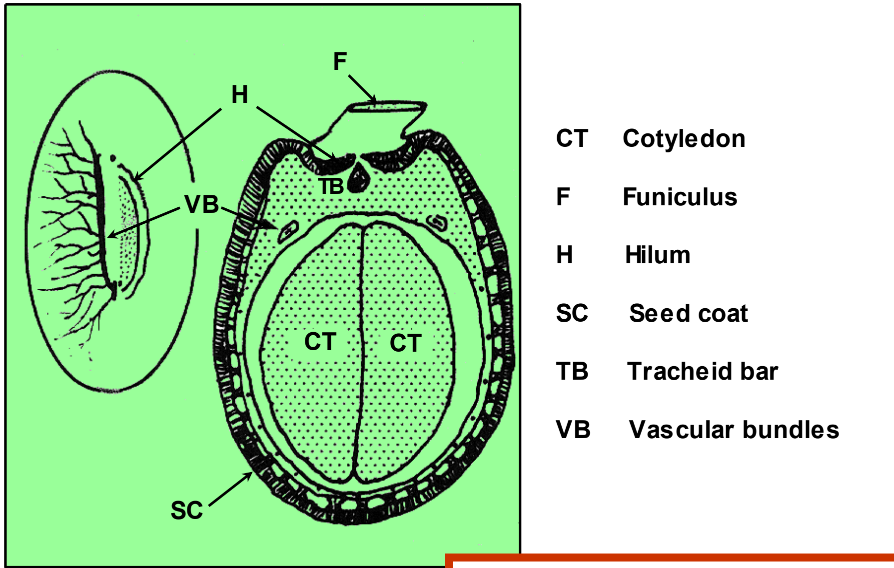
A short-term water deficit during filling severe enough to eliminate current photosynthate supply had little impact on rate of seed filling.



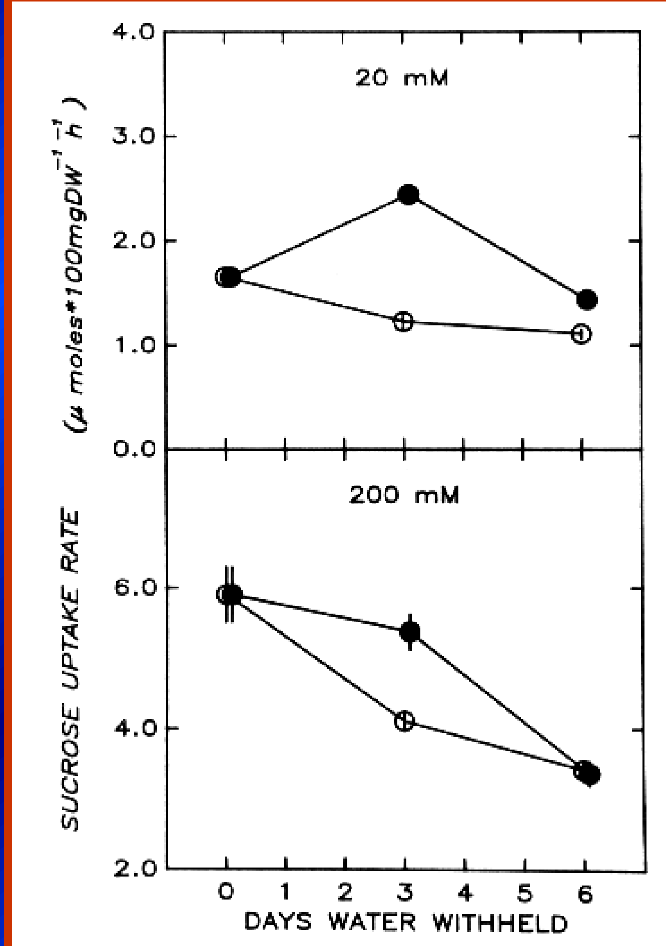


The apparent 'hydraulic isolation' of the embryo maintains a favorable water status to growth

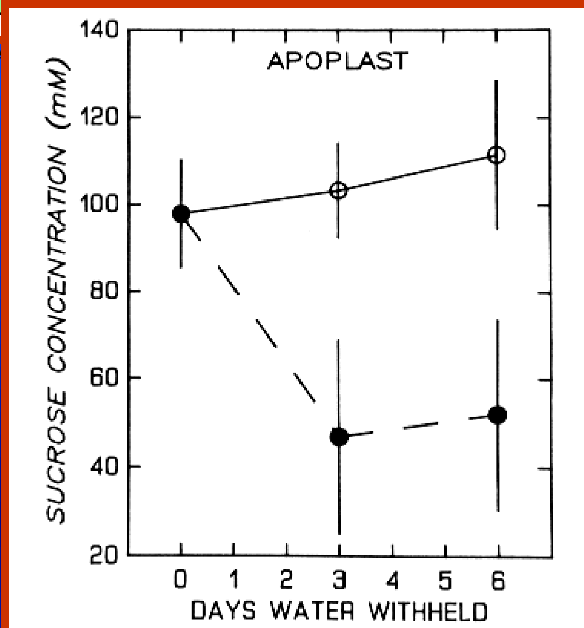
- Soybean embryo are supplied assimilates via the apoplasm



Anatomy of soybean seed attachme

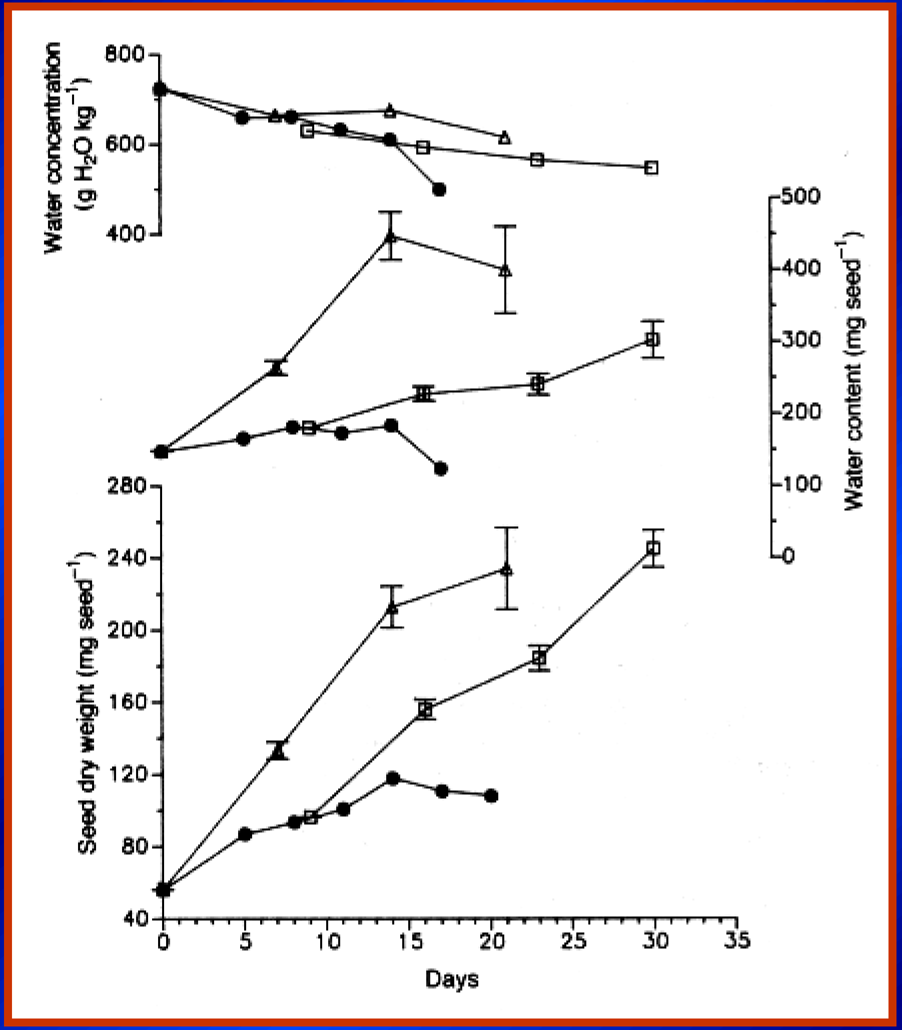


- Drought decreases sucrose concentration in the apoplasm around the embros



- Increased capacity for sucrose uptake partially compensates for lower sucrose concentrations

Soybean embryos grown in culture continue to accumulate dry matter as long as water content increases



adapted from Egli 1990

from Egli 1998

"Restraining" embryo expansion limits the dry matter that can accumulate

Limiting embryo volume decreases seed size, but not the relationship between seed moisture and the duration of filling.

Conclusions:

In embryos storing a large amount of protein in vacuoles, protein accumulation continues until maximum seed water volume is achieved.

eg. maize embryo, soybean embryo

In seeds storing starch, seed fill duration is determined by maximum cell volume established early in filling and by the onset of desiccation later in filling.

eg. maize kernel, wheat kernel

Unresolved issues – seed development

How do conditions early in seed filling regulate the duration of seed growth?

Under what conditions does lack of assimilate supply rather than seed water status limit the duration of seed filling?

How is seed composition maintained when seed growth rate and filling duration are altered by environmental conditions?

Many thanks to

Dale Farnham
Jon Lizaso
John Lundvall
Keith Whigham
Chris Zinselmeier

Thank you