IRRI
INTERNATIONAL RICE RESEARCH INSTITUTE

Centre de coopération internationale en recherche agronomique pour le development

CIRAD

Montpellier, France

Beyond tillering: yield slipping down the sink

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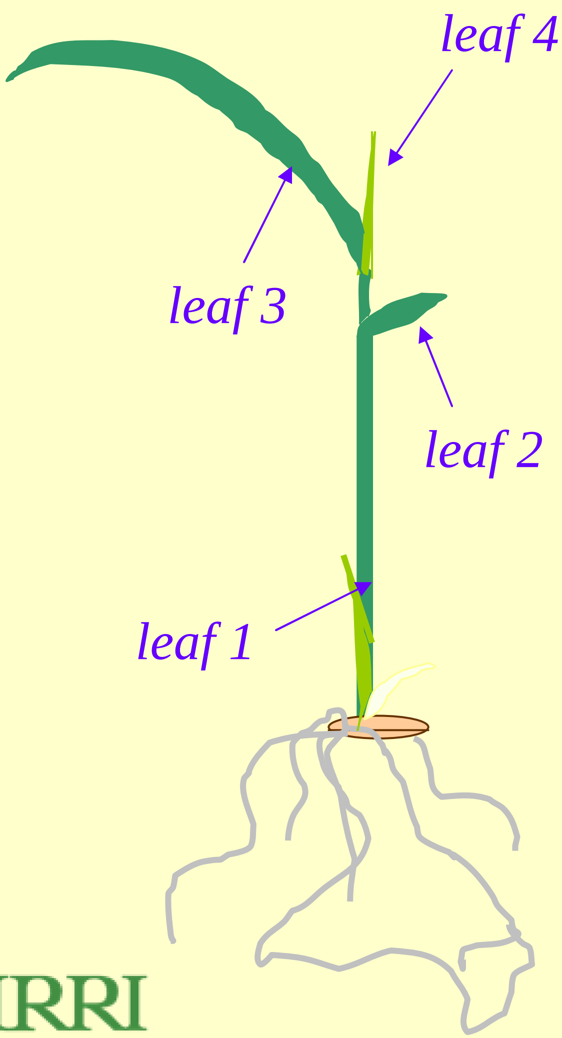
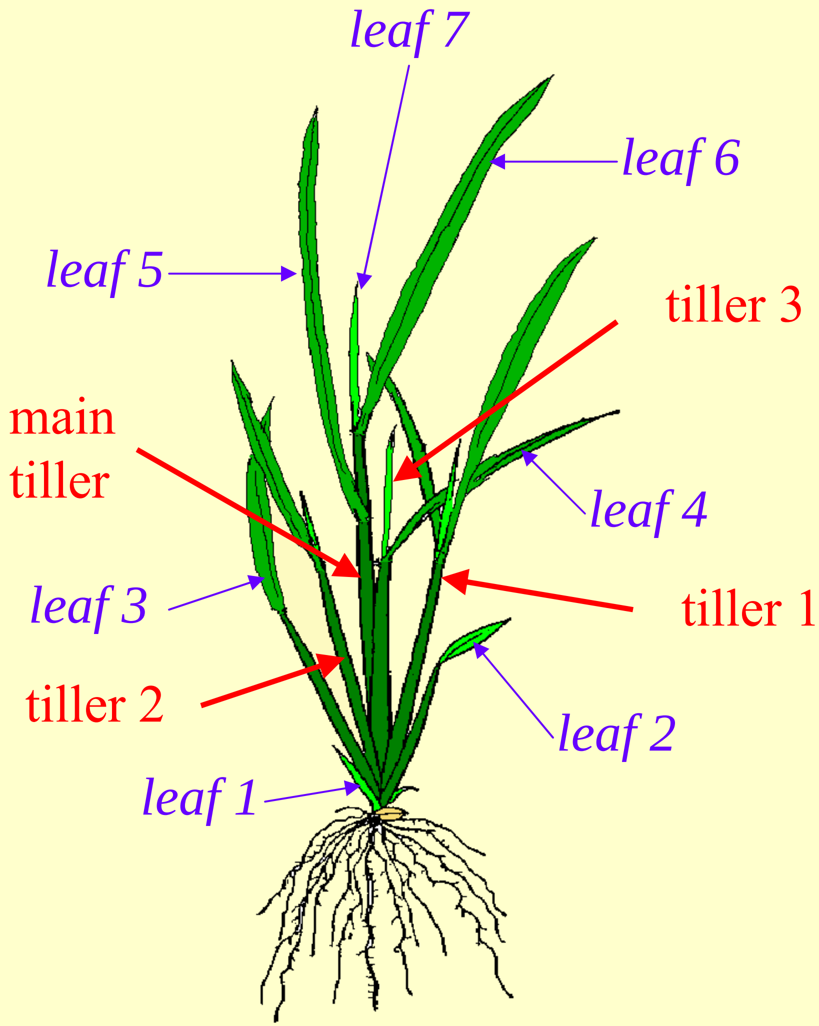
Thursday Seminar, IRRI, 3 December 2009

Leaf and tiller count





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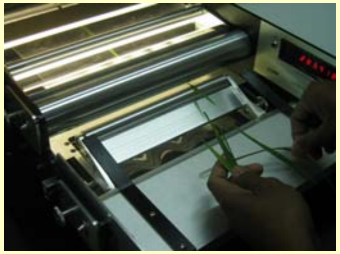
Outline

- Early tillering
- Rapid tillering
- Early cessation in tillering emergence
- Tillering plasticity at later stage
- Tillering and the unknown
- Compensation and selecting for yield components
- General conclusion

Early tillering: variability and role of buffer of SLA

Calculation of specific leaf area

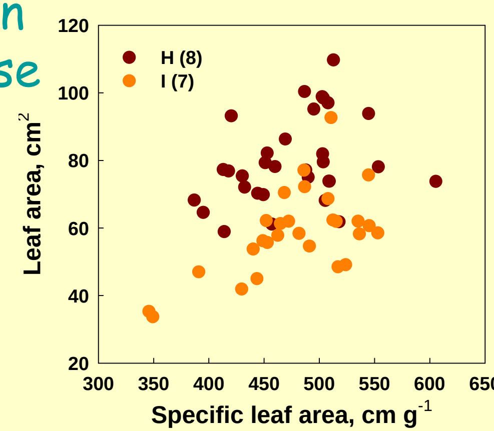


$$SLA = \frac{\text{leaf area}}{\text{leaf dry weight}}$$

The range of variation in SLA is not the cause of higher seedling vigor of hybrids

Higher SLA triggers higher leaf area and seedling vigor

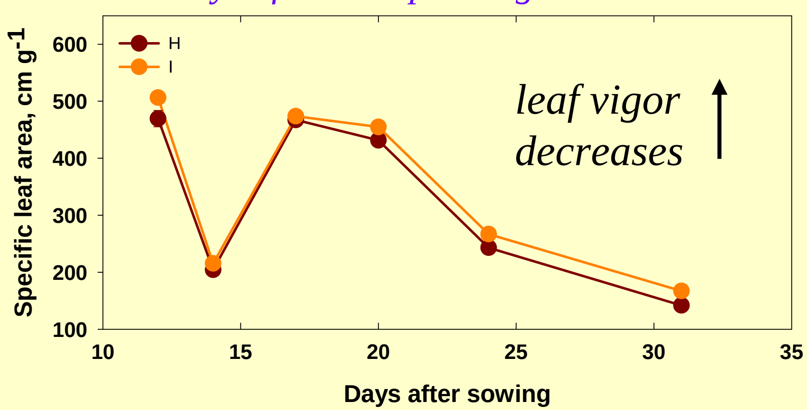
Transplanting, 8 hybrids, 7 inbreds



leaf vigor decreases →

High plasticity of SLA quantified right after transplanting:
a transient drop in SLA buffered the chock of transplanting

3 days after transplanting



There is room for improvement at early stage by growing seedlings with higher SLA (better weed competitiveness)

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Early tillering: seedling age at transplanting and leaf area growth

Farmers' practice:
- 20 to 30 days-old seedlings at transplanting
- 3000 to 10 000 seeds m^{-2} inside the nursery

IR72 in the main field,
shots taken 34 days after sowing for all 3 situations

Transplanting, hill spacing 20 x 20 cm

transplanted 7 days after sowing

transplanted 14 days after sowing

transplanted 21 days after sowing

Tillering and biomass were favored when transplanting young seedlings

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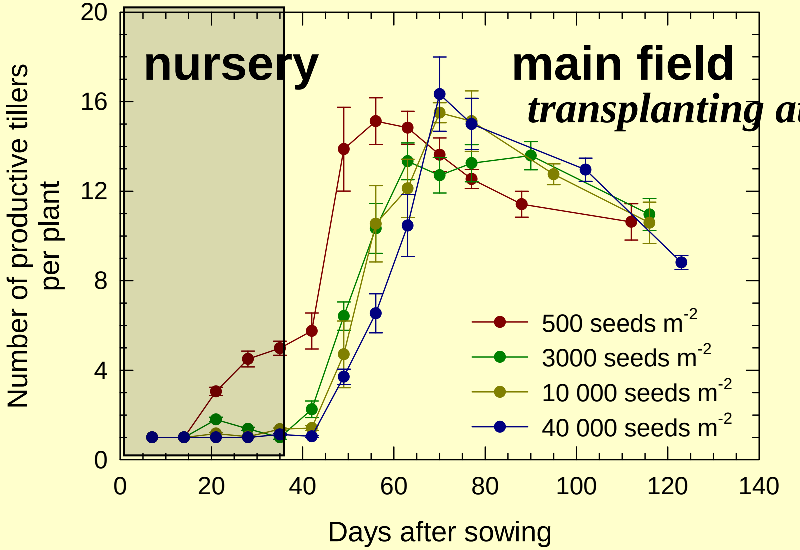
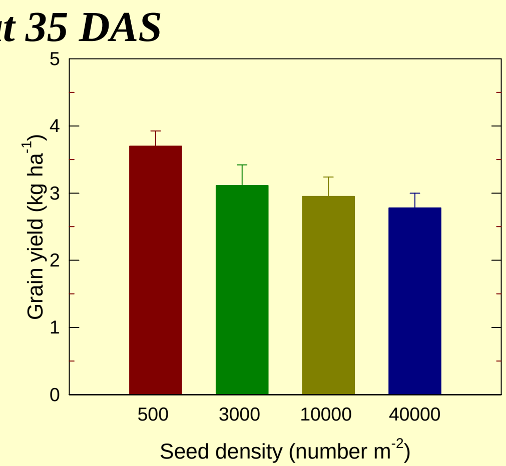
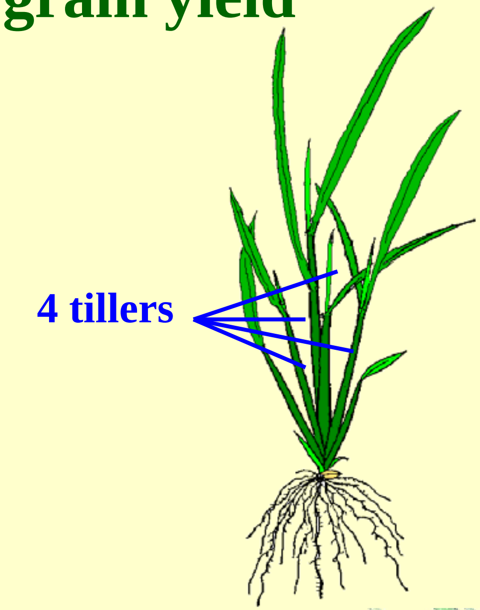
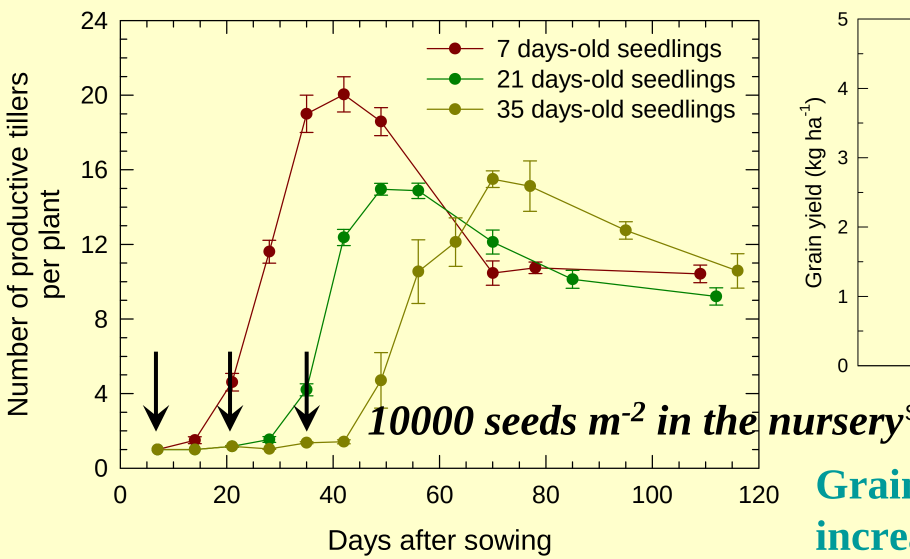
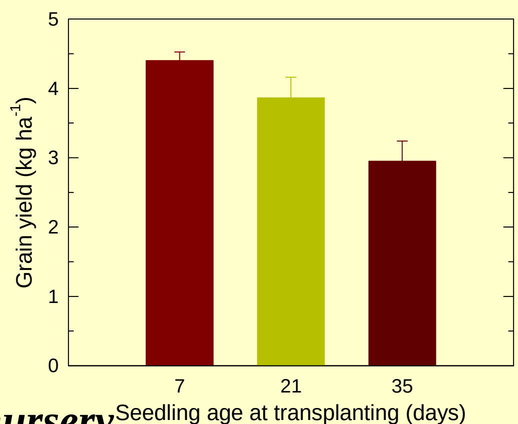
Early tillering: seedling age at transplanting and grain yield











- Tiller emergence resumed right after transplanting whatever the density and age

- Tiller emergence was delayed if extended growth duration or high density in the nursery

Grain yield was gradually reduced with respect to the increase in the age at transplanting or in the seed rate

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High seed density and extended stay in the nursery induced a delay in tiller emergence and a reduction in grain yield

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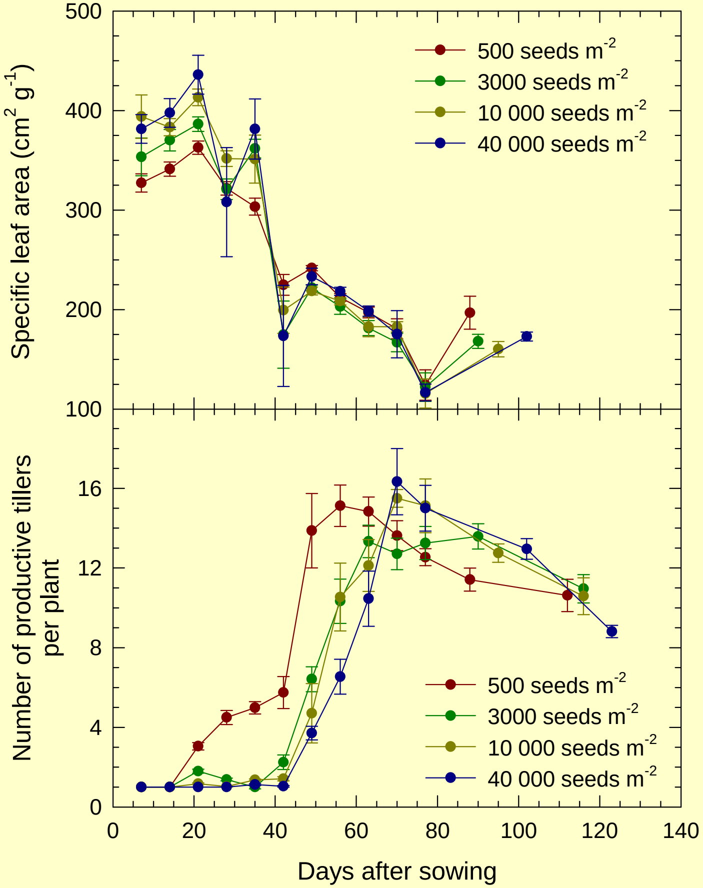
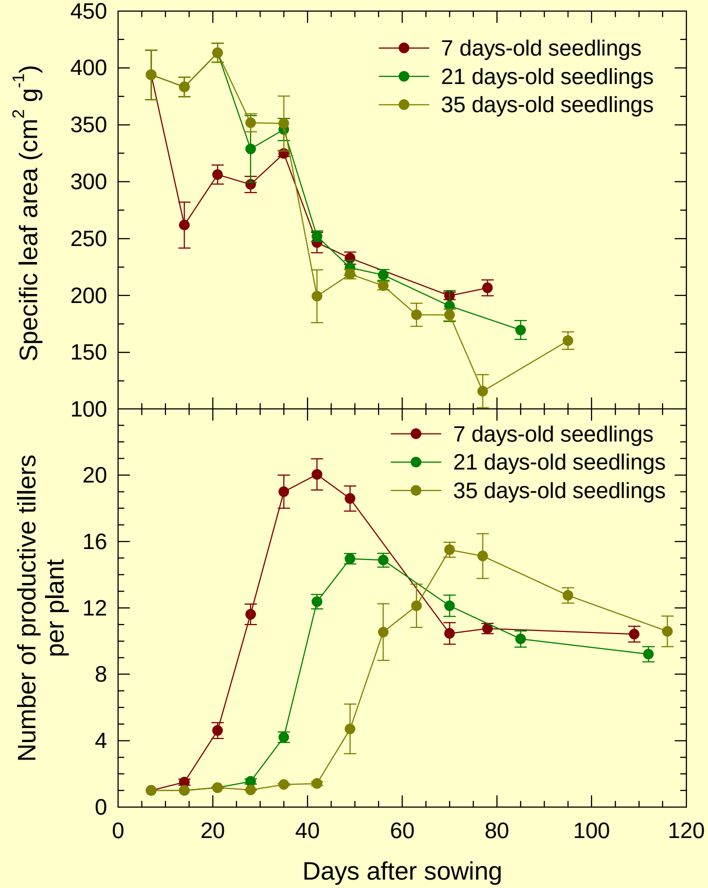
Early tillering: plasticity in SLA as a support of tillering

Transplanting 35-days old seedlings



SLA increased with the density in the nursery

Growing 10 000 seedlings m^{-2} in the nursery



SLA was maintained at a high value in case of an extended stay in the nursery

- SLA is highly responsive to plant competition at early stage which favored tiller production in the nursery and in the main field

- Tillering resumed at a high rate right after transplanting

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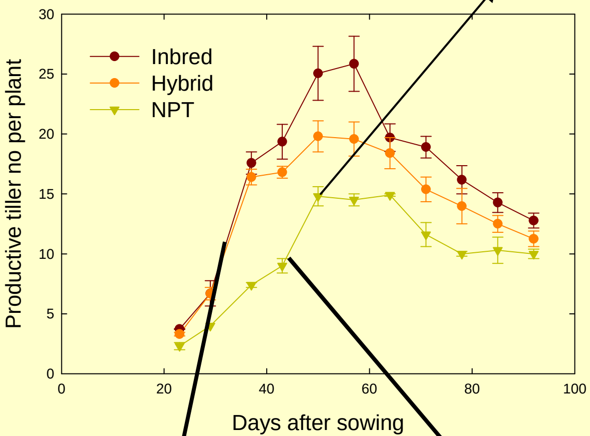
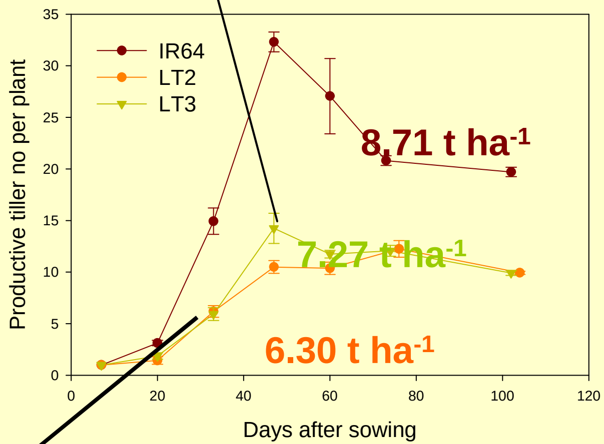
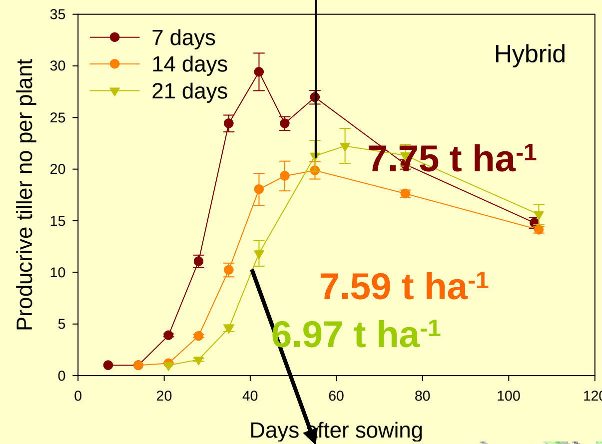
Rapid tillering: characteristic of the high-yielding genotypes

Synchrony in maximum tillering

Delayed maximum tillering







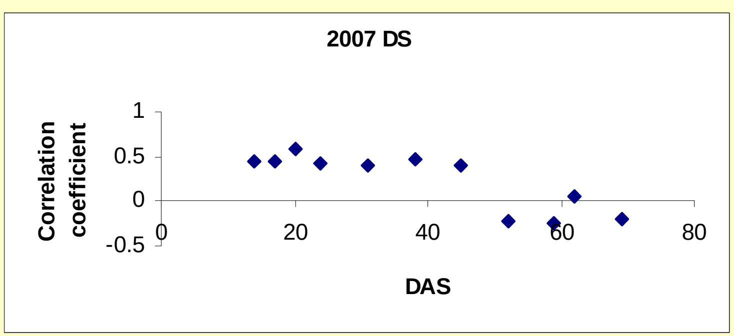
Lower tiller emergence rate

Lower tiller emergence rate

Early and rapid tillering is already a characteristic of hybrids and inbreds

NPT and LTG: low biomass accumulation because of reduced tillering capacity and more vigorous organs at early stage

Correlation of grain yield with leaf area index at early stage when comparing a range of hybrids and inbreds



Early tillering and leaf area closure are crucial for high biomass accumulation and high yield

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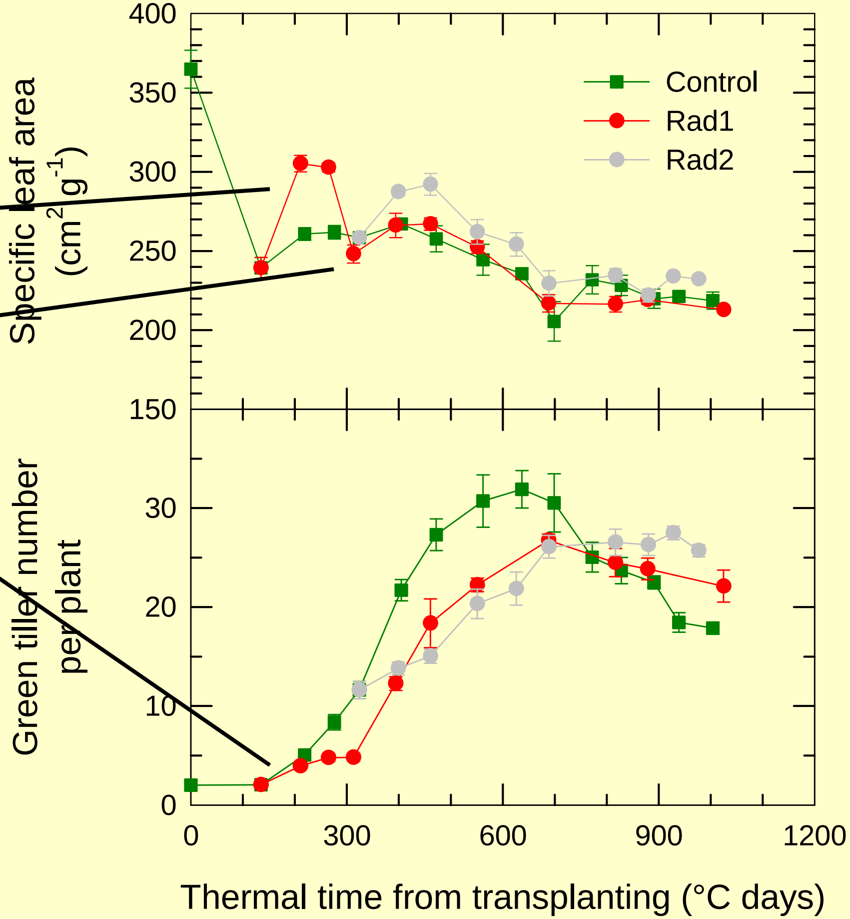
Rapid tillering: plasticity of SLA as a buffer to trigger tillering

Shading event (70%) were established for short periods of 9 days in Rad1 and Rad2

- SLA increased rapidly as a response to shading during the vegetative phase
- SLA was back to the control value as soon as the shading was removed at early stage
- Tiller production was maintained for a short period before being affected



Lower plasticity of SLA if a stress occurs around panicle initiation probably because of the competition between sinks

The high plasticity of SLA can sustain tiller production for a while at early stage. The plasticity of SLA is reduced at later stage

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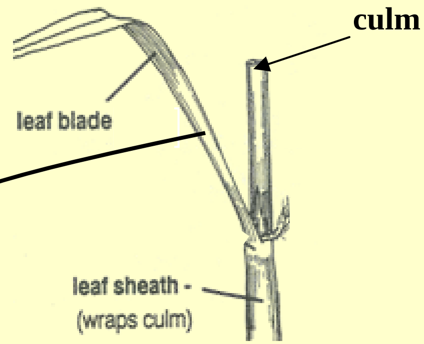
Early cessation of tillering: better sink regulation at early stage

Comparing partitioning coefficients of 3 hybrids and 3 inbreds of the same phenology

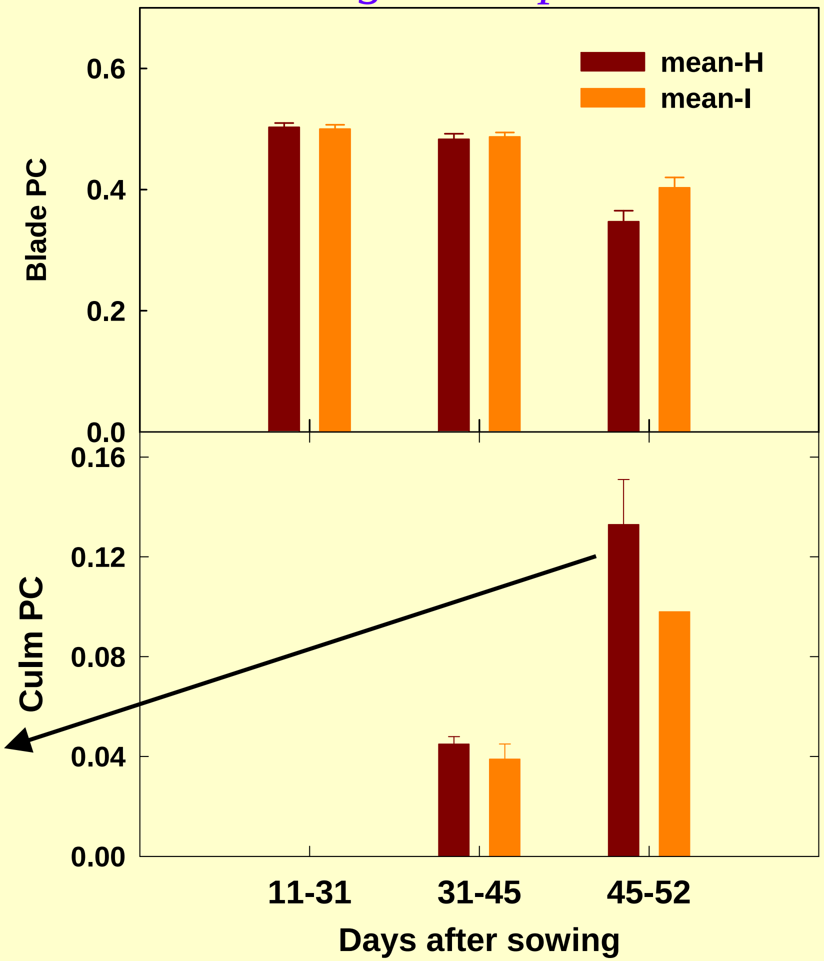


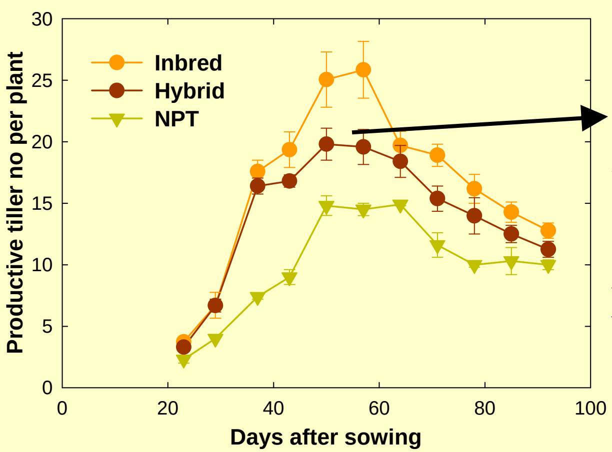
Calculation of blade partitioning coefficient:

$$\text{Blade PC} = \frac{\Delta dw_{\text{blade } 2\rightarrow 1} / \Delta time_{2\rightarrow 1}}{\Delta dw_{\text{shoot } 2\rightarrow 1} / \Delta time_{2\rightarrow 1}}$$

High correlation between stem vigor and reserves accumulation

vegetative phase





Hybrid:
earlier cessation in tiller emergence is associated with earlier partitioning in favor to culm

Earlier cessation in tiller emergence may generate an increase in reserves stored in the culm and remobilized during grain filling

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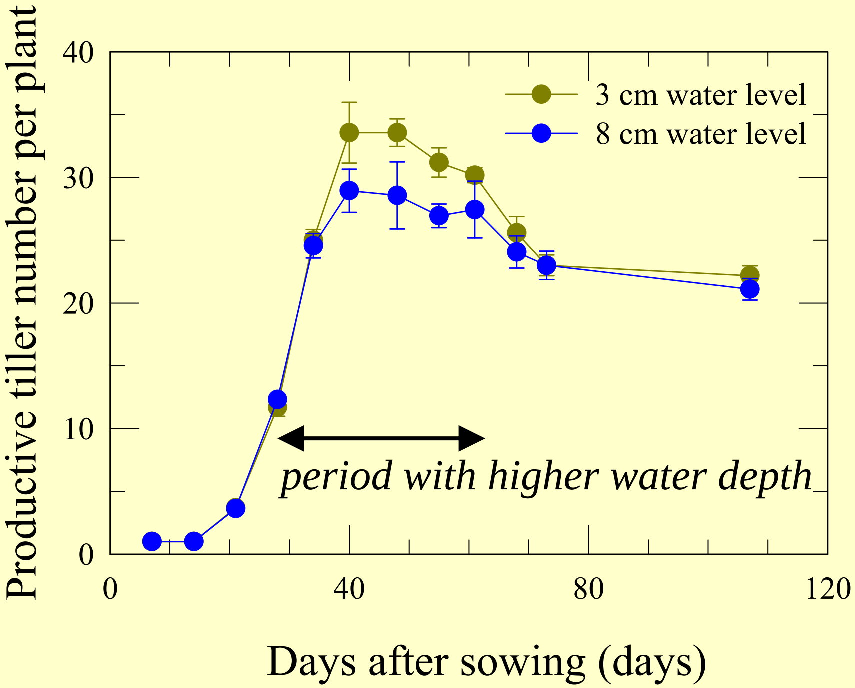
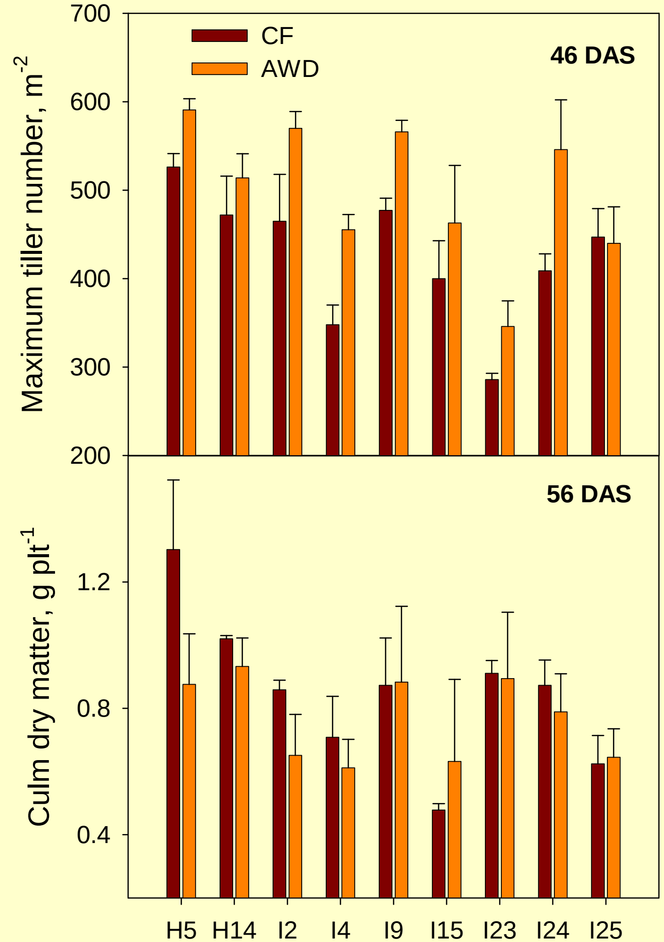
Early cessation of tillering: better sink regulation at early stage

Tiller emergence is affected by water depth: an increase in water depth at mid-tillering until booting stage triggers an earlier cessation of tiller emergence



In contrast, tiller emergence is extended under AWD management



and culm growth is delayed

Extended tiller emergence under AWD is associated with delayed culm growth and possibly less reserves storage

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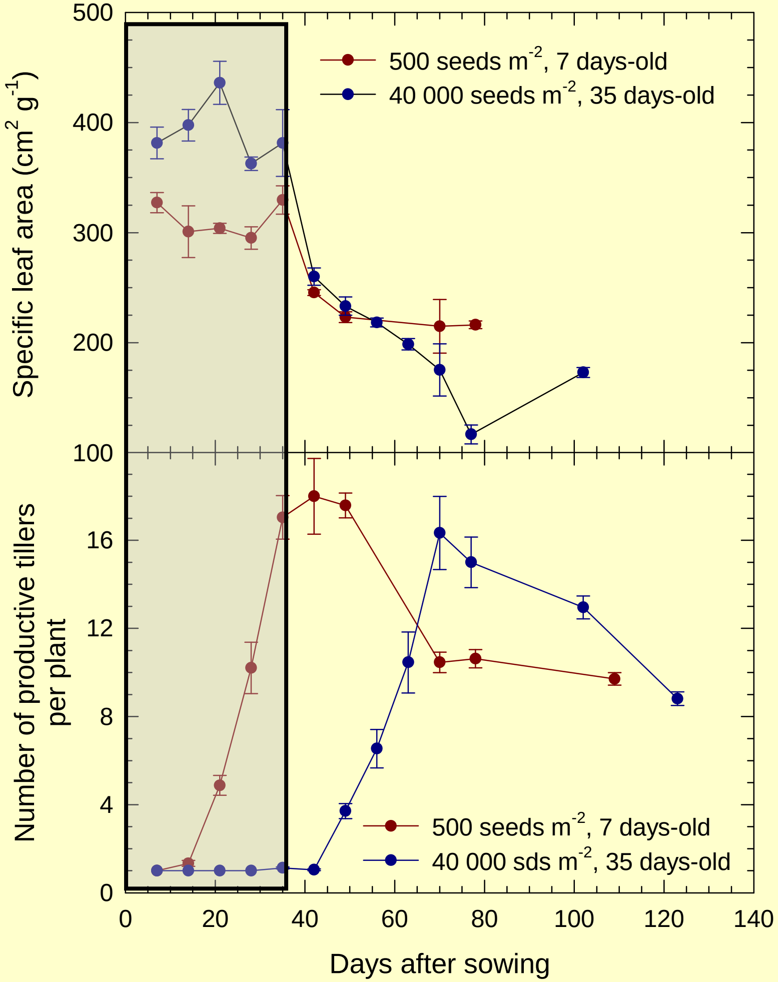
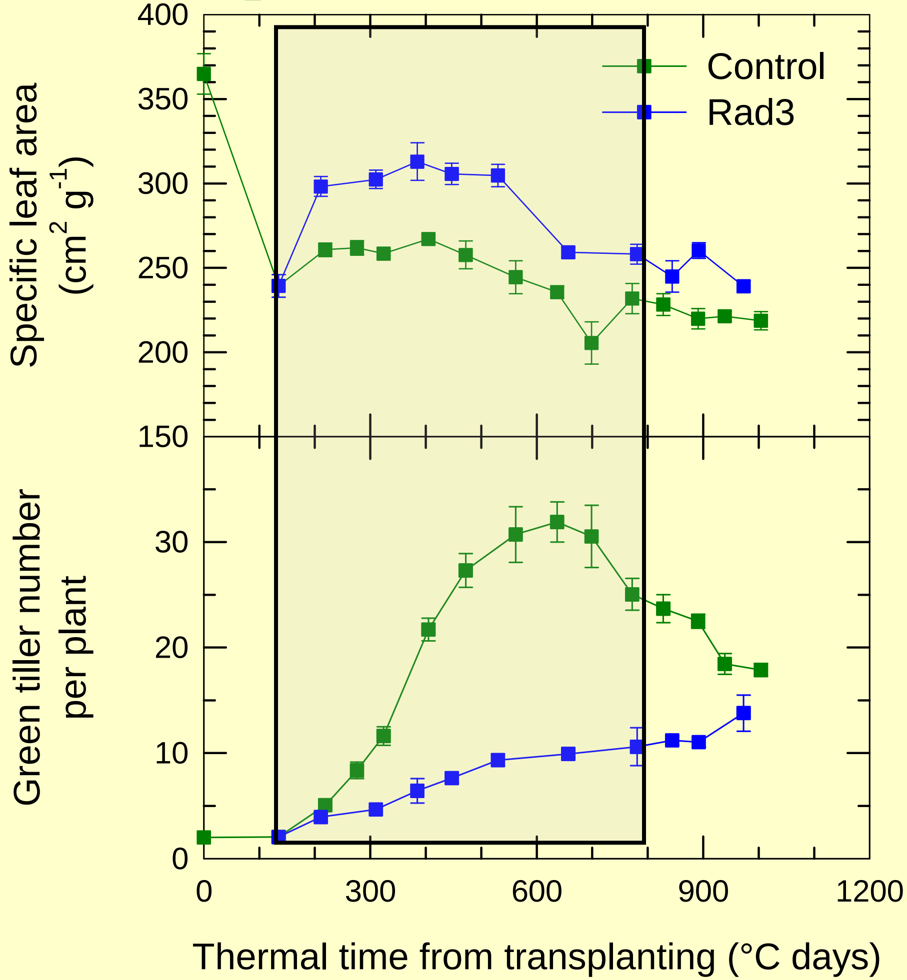
Tillering plasticity at later stage: associated with SLA plasticity…

…in response to high seedling density

Comparing dynamics of 7-days old and 35-days old seedlings



…in response to extended shading



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Production of tillers is favored to the detriment of organ vigor under limited access to radiation in the field

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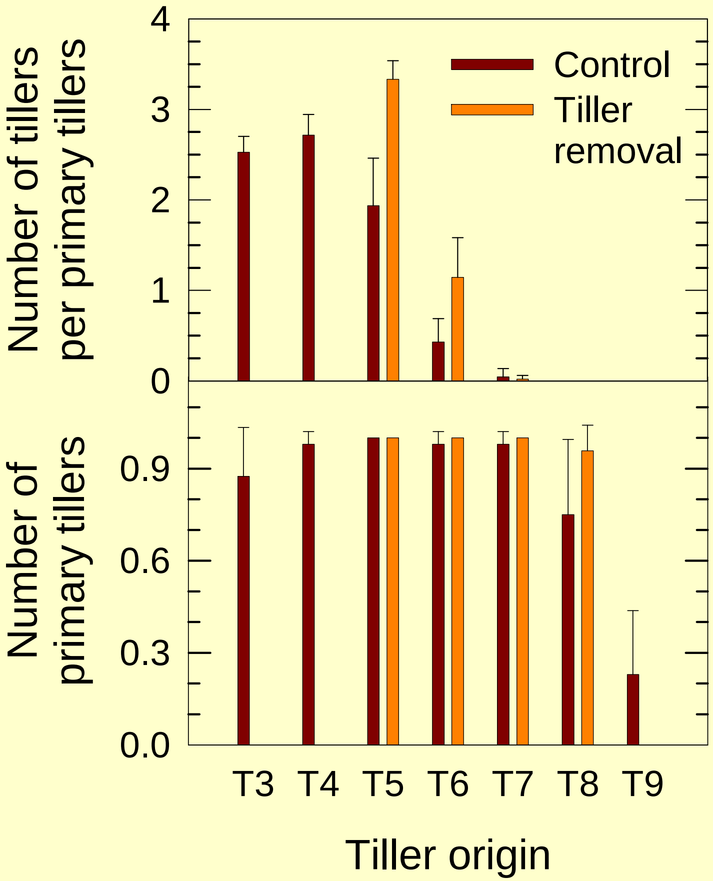
Tillering plasticity at later stage: emergence of extra tillers…

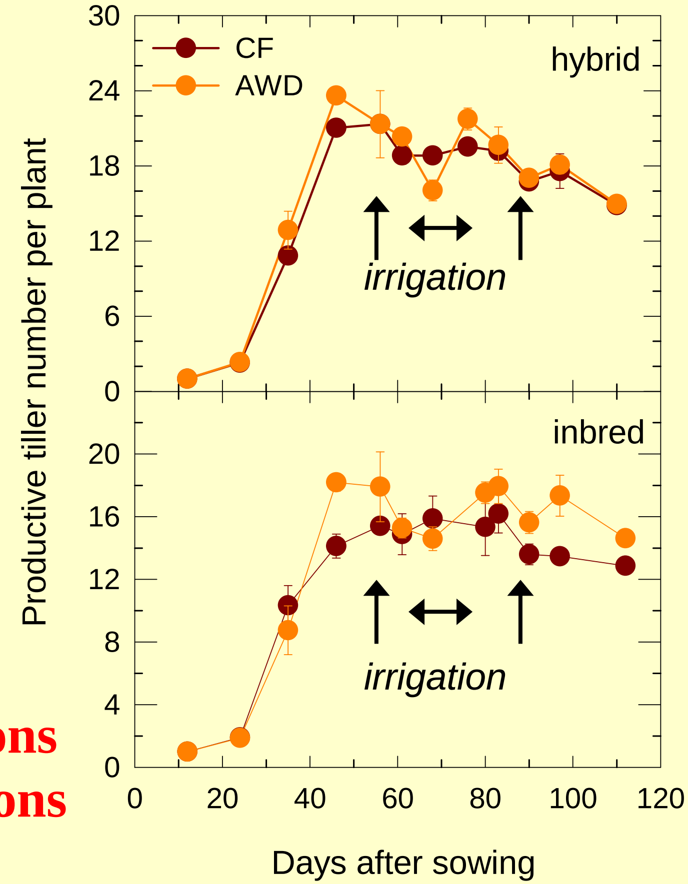
…in response to early tiller loss



Removal of primary tillers 3 and 4 at their emergence

Higher production of secondary and tertiary tillers attached to primary tillers 5 and 6

…in response to water drainage



Successive water drainage periods before and after flowering

Successive tiller loss in aerobic conditions and tiller emergence in flooded conditions

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Tillering plasticity at later stage: emergence of extra tillers…

…in response to heat

Initial panicle totally sterile at maturity because of heat

Panicles newly formed after flowering

Newly formed tillers attached to upper nodes of the mother tiller

…in response to pest injury

Newly formed tillers to overcome the loss of damaged tillers by stem borers

Table 3. Number of tillers in plants at 2 and 4 weeks after transplanting (WAT), treated with various methods of injury including 'real' stem borer damage (IRRI Greenhouse, 1992)

Treatment	Number of tillers* 2 WAT	4 WAT
Stem borer damage on main stem	4.3 a	12.5 a
Main stem cut	2.3 c	5.2 c
All leaves of main stem cut	3.2 b	8.5 b
Youngest leaf removed	3.0 b	5.2 c
Shaded main stem	3.1 b	10.8 ab
Control	3.3 b	11.8 ab

*Within a column, treatment means having a common letter are not significantly different by Duncan's multiple range test at $P = 5\%$ (N, 15 replications)

Rubia et al, 1996

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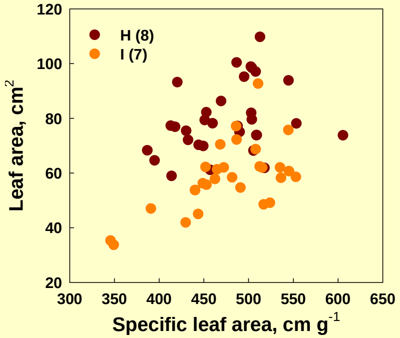
Tillering and the unknown: going for an earlier tillering?

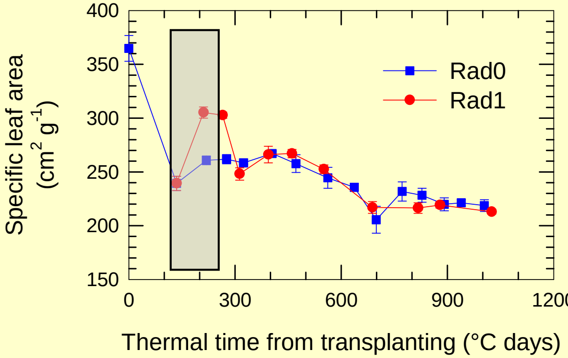
Transplanting, 8 hybrids, 7 inbreds

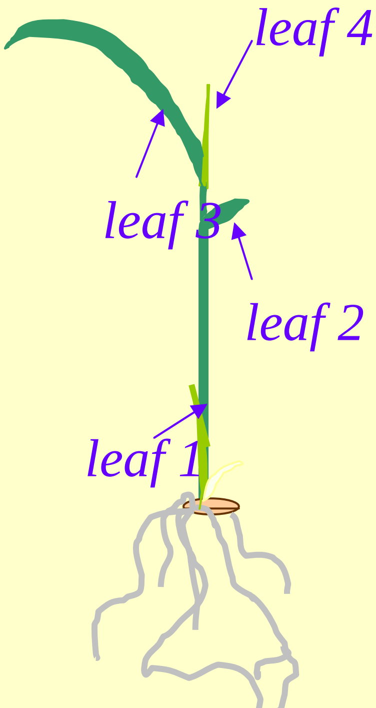


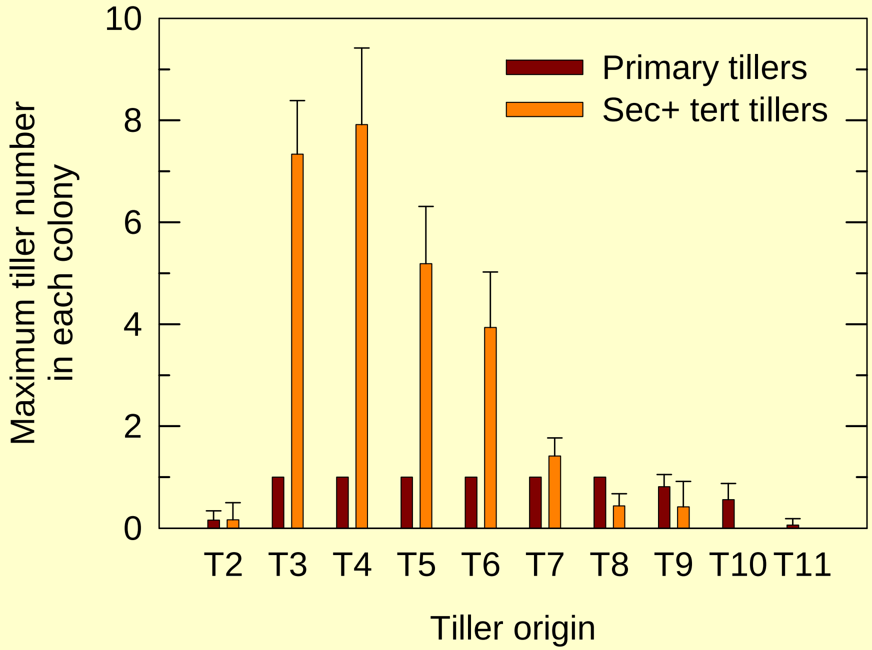
The higher SLA, the higher leaf area

There is still room to increase SLA

Shading in the field at early stage







The distribution of tillers per plant highlights that there is no production of tillers from the bud 2 of the main tiller

Can higher plant SLA trigger production of tillers from leaf 2?

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Can we breed for plants with primary tillers 2 ?

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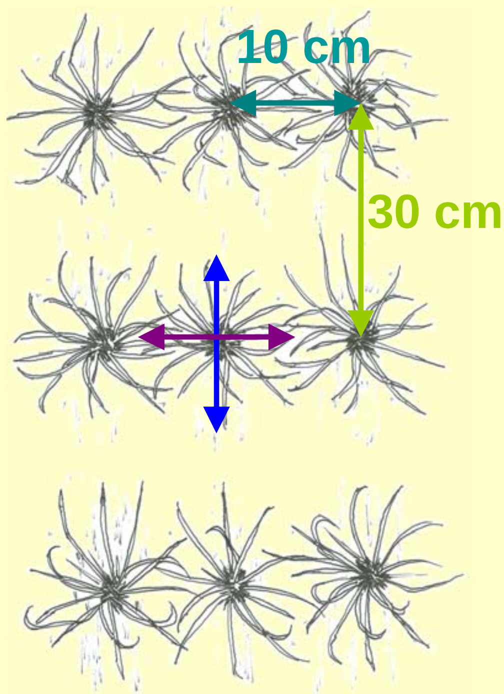
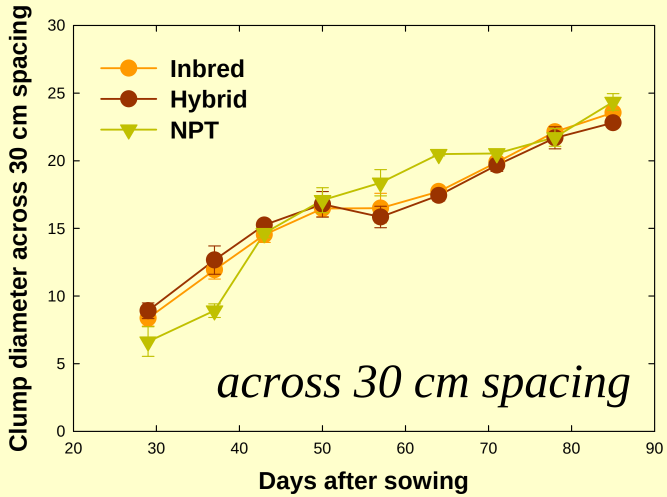
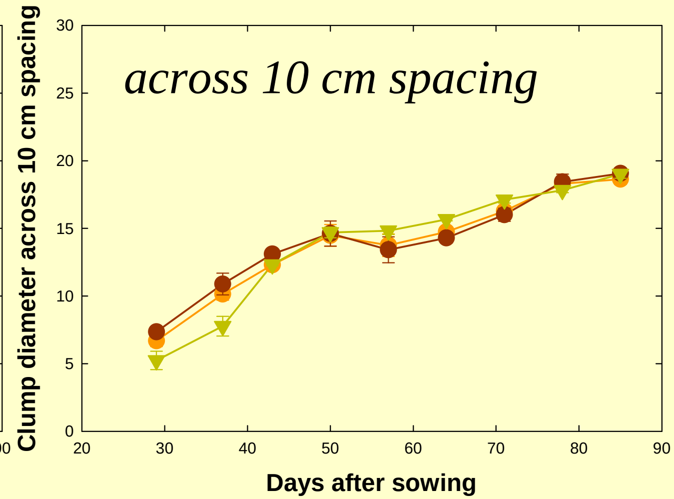
Tillering and the unknown: going for a more plastic architecture?



Is the plant able to adapt its tiller orientation according to access for light in the rice canopy?





- Same and weak sensitivity of hybrids and inbreds among 16 contrasted genotypes to intra-plant competition:
- No adaptation of IRRI hybrids/inbreds to direct-seeding
  - **All high-yielding genotypes were bred under transplanting**
  - **Minimal Genotypes x Establishment interaction**

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Can we breed for plants with plastic tiller orientation?

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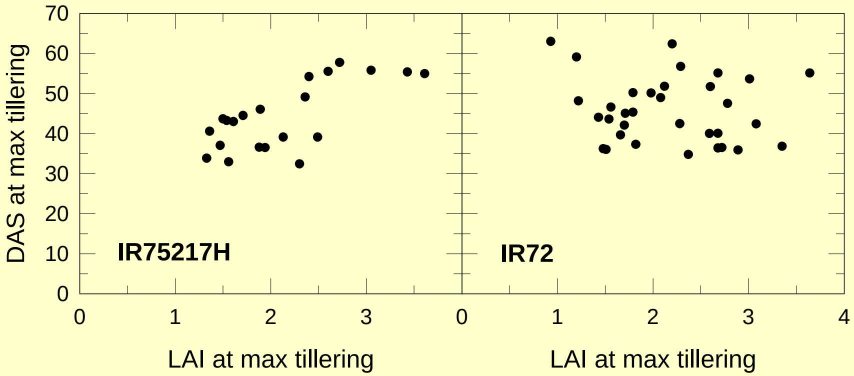
Tillering and the unknown: advancing the cessation in tillering?

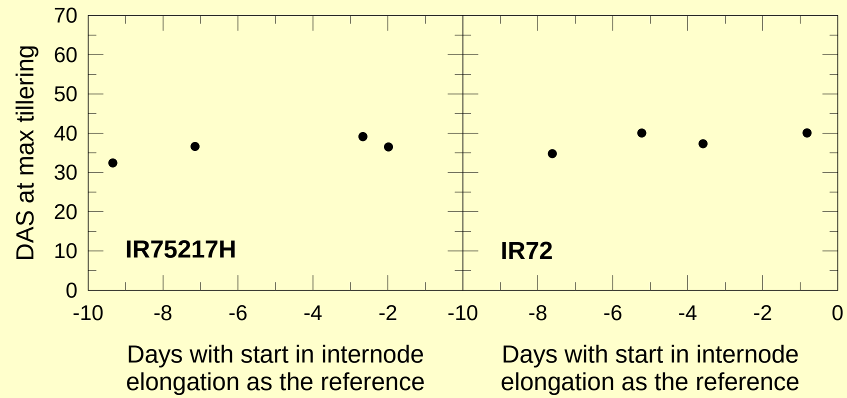
Gathering data from the wet and dry seasons, seedling age at transplanting of 7, 14 and 21 days, from contrasted water depth (3 to 10 cm) and plant densities (25 to 100 pl m^{-2})

No correlation between cessation of tillering and…

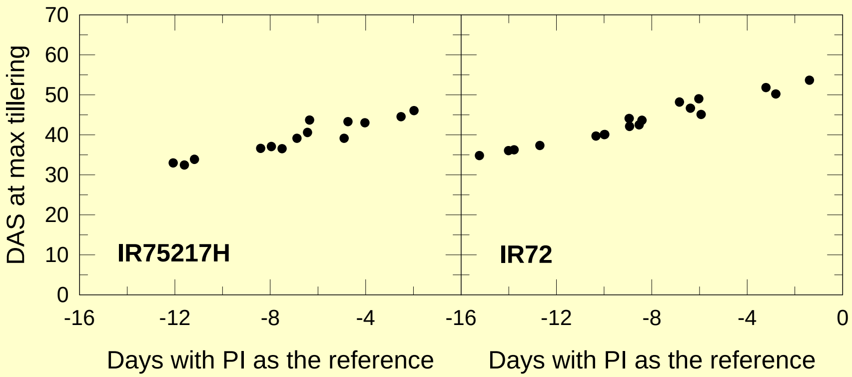
…the LAI value at maximum tillering



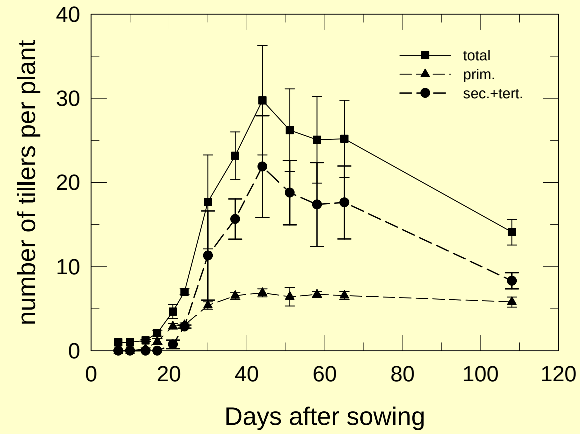
…the internode elongation starting date



…the time of panicle initiation



Cessation of emergence of secondary and tertiary tillers occurs later than that of primary tillers

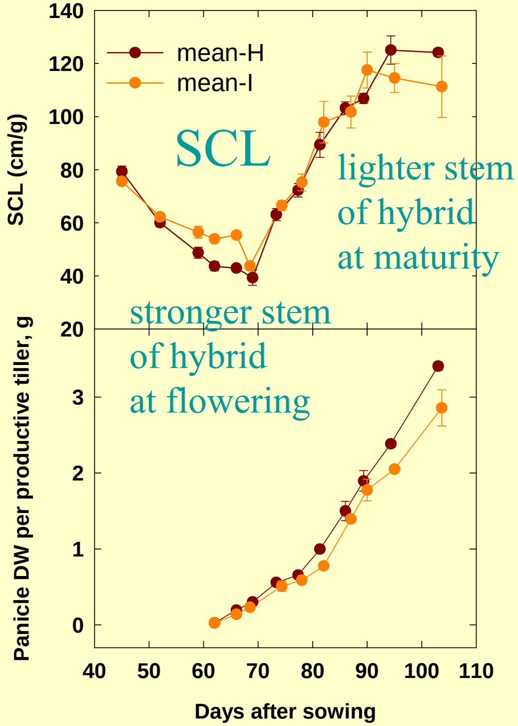


Predicting cessation of tillering with a mechanistic crop model?

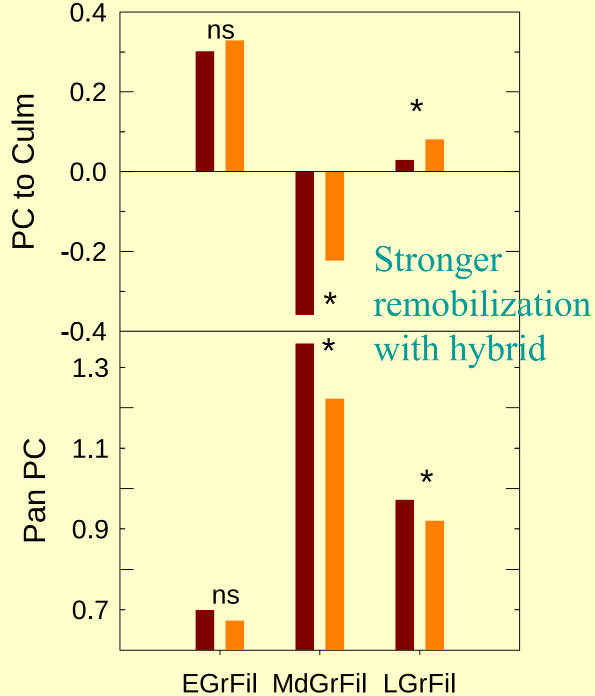
IRRI **Can an earlier cessation in tillering increase in grain yield?** CIRAD

Tillering and the unknown: accumulation or remobilization?

Tropical conditions: improving remobilization



Stronger stem and higher reserves storage



Stronger remobilization from culm to panicle

China: increasing biomass accumulation

Desire traits of *China's super rice:*

- 3-4 leaf tips above the panicle
- low position of the panicle
- erect tillers and leaves
- delayed leaf senescence
- moderate plant height

In subtropical conditions in China, the main objective is to increase biomass accumulation during grain filling

In tropical conditions, is sink regulation the main improvement to focus on?

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Tillering and the unknown: accumulation or remobilization?

Comparing the main traits supporting higher hybrid rice performance in the tropics in contrasted conditions: shoot biomass or harvest index (or sink strength index, SSI)?

Year/ Season		GY (t/ha)	ShDW m^{-2}	HI	SSI ($g\ cm\ g^{-1}$)
2007 DS	H (7)	11.03 a	2108 a	0.54 a	175 a
Transplanting	I (6)	9.48 b	1932 b	0.50 b	145 b
2006 DS	H (3)	8.45 a	1780 a	0.51 a	150 a
Staggered	I (3)	7.53 b	1634 a	0.45 b	102 b
2006 DS	H (2)	8.49 a	1587 a	0.55 a	156 a
AWD genotypes	I (3)	8.44 a	1611 a	0.52 b	133 b
2005 DS	H (2)	7.16 a	1959 a	0.45 a	114 a
Braodcasting	I (2)	5.94 b	1820 a	0.42 a	93 b
2004 WS	H (5)	5.93 a	1885 a	0.45 a	140 a
Wet season	I (7)	5.35 b	1748 b	0.42 b	117b

The partitioning efficiency (SSI) is significantly higher with hybrids in all the situations while the shoot biomass is higher only in 2 of the 5 situations

SSI at maturity can be used more acurately than harvest index to discriminate plants in their ability to partition biomass efficiently

In tropical conditions, sink regulation seems to play a major role in supporting higher hybrid performance

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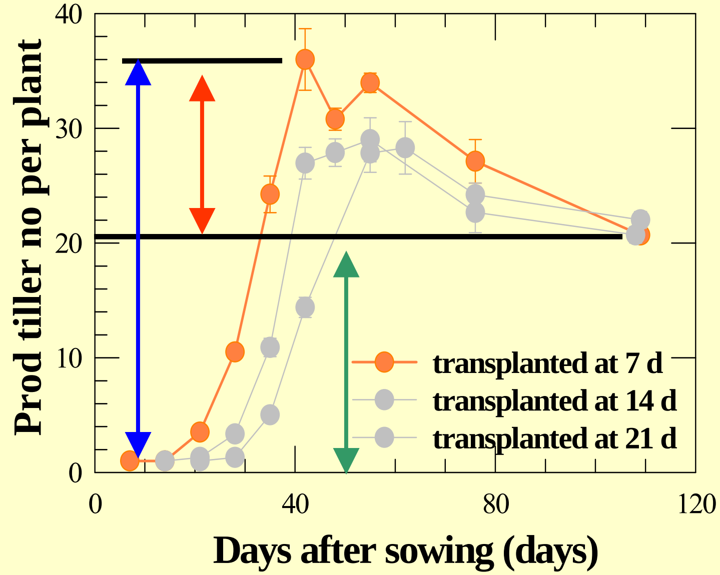
Tillering and the unknown: is a high tillering efficiency useful?

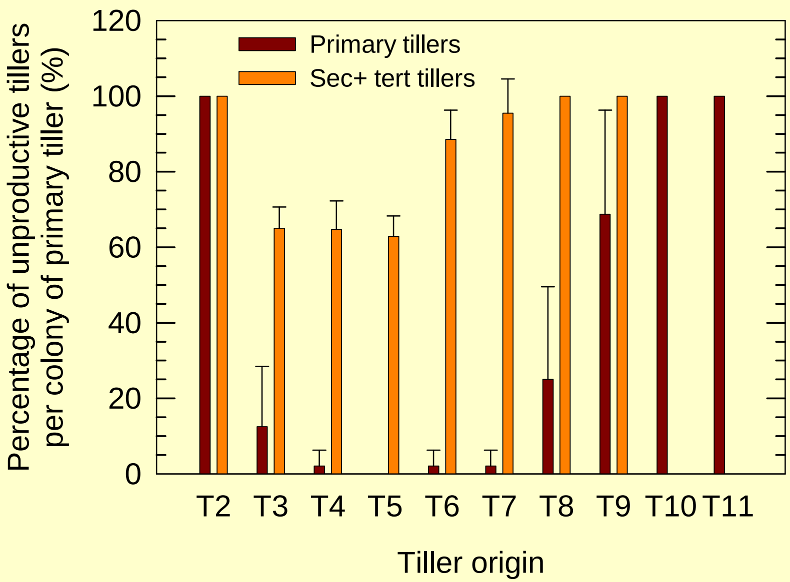
non-productive tillers

Tillering efficiency (TilE):

$$\text{TilE} = \frac{\text{productive tillers}}{\text{total tillers}}$$



Transplanting young seedlings is associated with higher tiller mortality because of higher maximum tillering

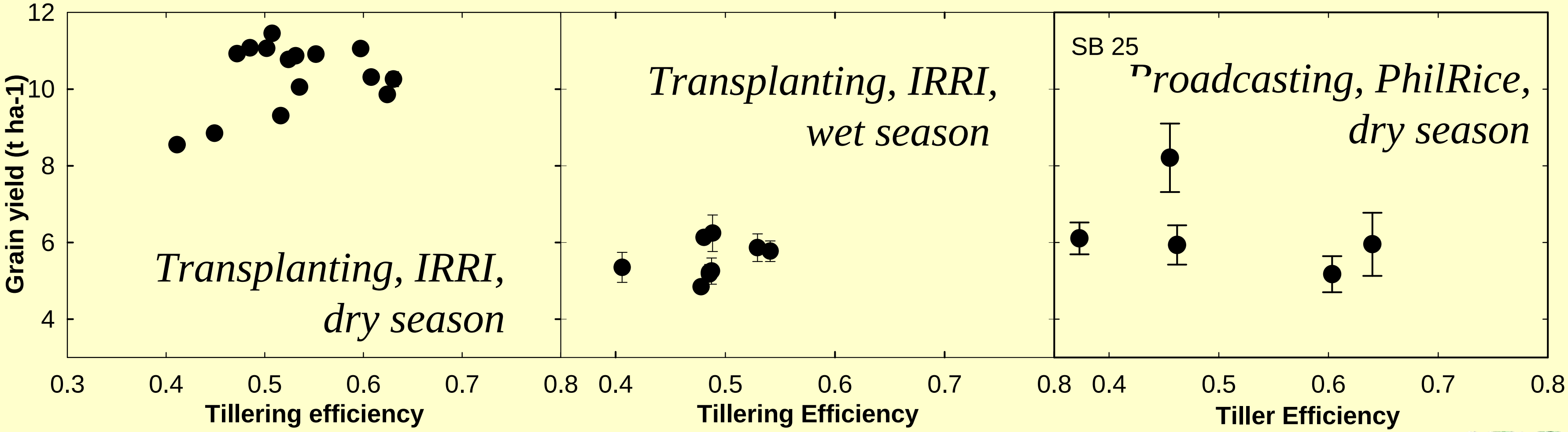


Tiller mortality concerns:

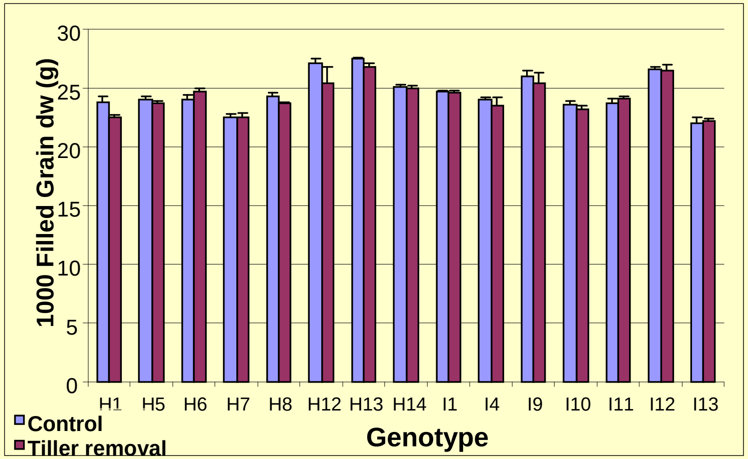
- young tillers, then low plant biomass
- small tillers, then low-competitive tillers for access to light with the taller tillers
- green tillers intercepting light inside the canopy for their own use

Is a low ratio of tiller efficiency correlated with lower grain yield?

Tillering and the unknown: is a high tillering efficiency useful?

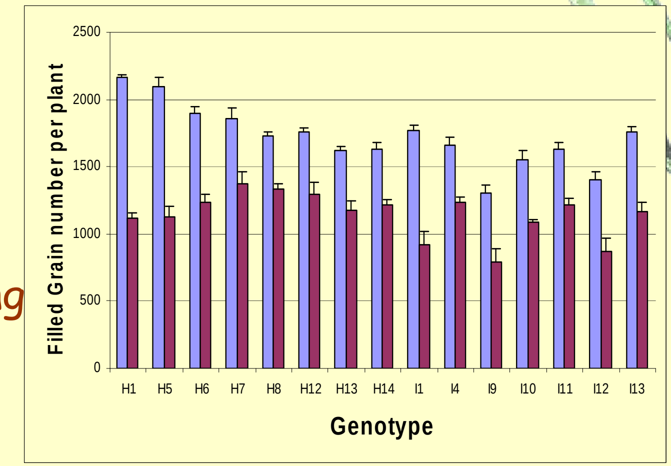


No positive correlation is observed between grain yield and TilE across genotypes



Manual removal of about 1/3 of the tillers per plant 11 days after panicle initiation

Grain size was not affected but a strong reduction in filled grain number per plant was reported



Are non-productive tillers useful to crop production by remobilizing substrates before getting senescent?

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Selecting for individual traits: dealing with the mutual benefit of opposite traits

Unproductive tillers
- ↗ higher light interception
- ↙ more efficient use of biomass

Plant height
- ↗ higher light interception
- ↙ more efficient use of biomass

Biomass remobilization
- ↗ higher grain filling
- ↙ higher tolerance to lodging

Leaf senescence
- ↗ higher biomass remobilization
- ↙ higher light interception

Unfilled spikelets
- ↗ higher sink allowance
- ↙ more efficient use of biomass

Grain filling duration
- ↗ higher biomass accumulation
- ↙ more harvested grains

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Selecting for yield components: high compensation phenomenon

Examples of measured field data and possible target components:

	IR72	NPT	HYB1	HYB2	Target 1	Target 2
Grain yield, t ha^{-1}	**8.5**	**8.2**	**10.1**	**9.7**	**12.0**	**11.9**
Total panicles/m^2	400	250	450	600	350	250
Total spikelets/pan.	100	150	80	65	150	200
% filled spikelets	85	80	74	67	80	80
1000 FiGrDW, g	22	24	26	21	25	26

High compensation between yield components (panicle number, grain number per panicle, grain size) indicates that many combinations can produce the same grain yield

Fixing a quantitative target for a single yield component should not be a strategy for increasing yield potential

In the objective of designing ideotypes for yield potential, it is needed to combine integrated approaches for complex traits with single-trait approaches for well-recognized traits of interest

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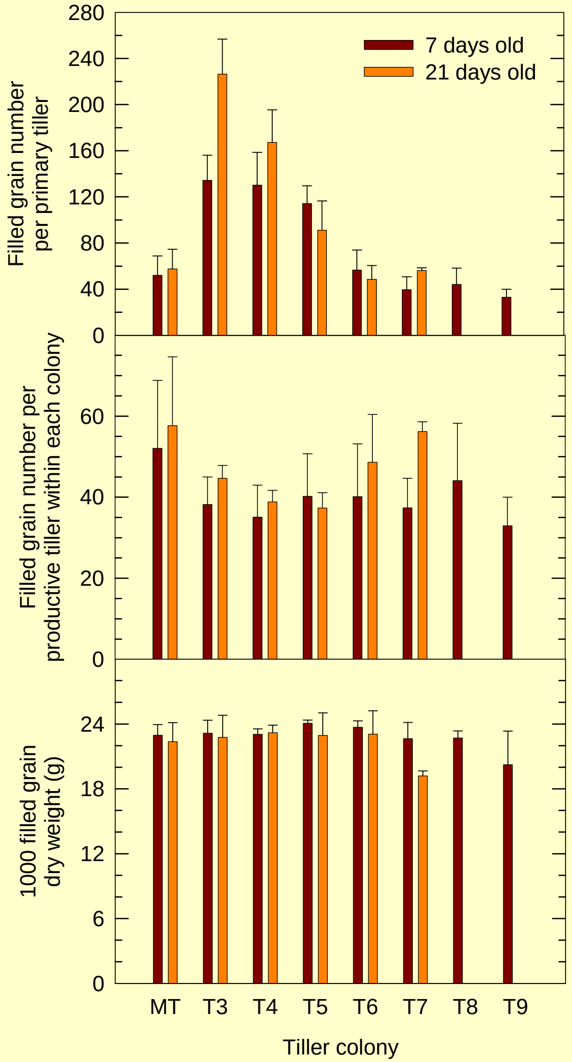
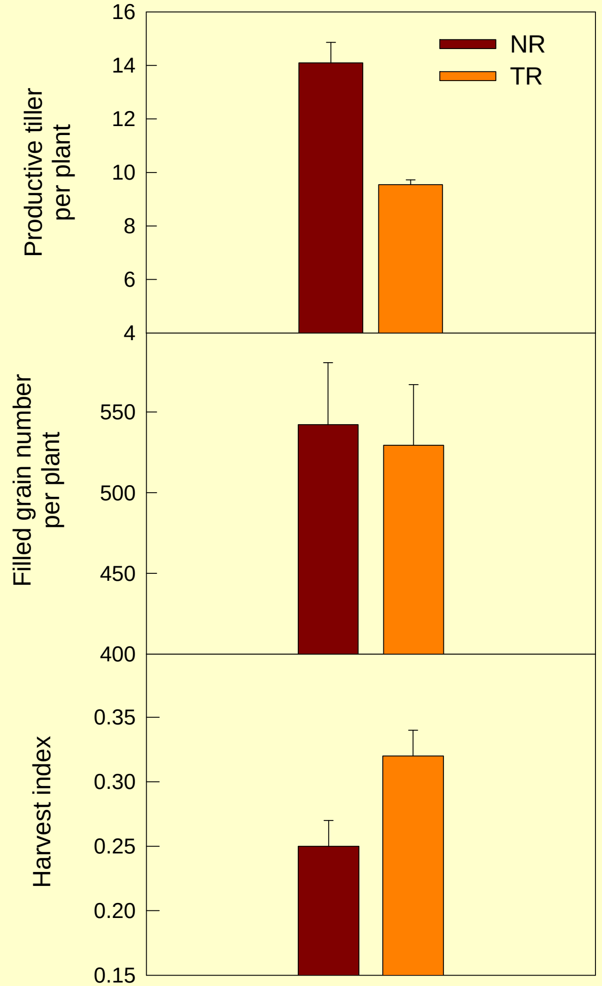
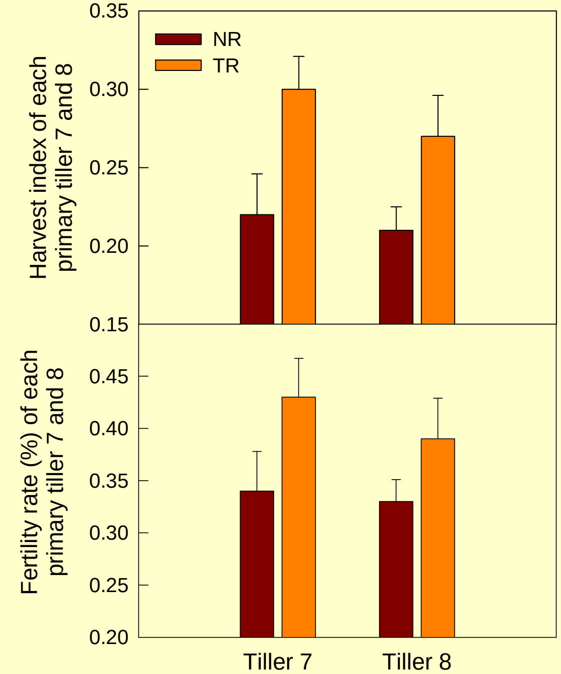
Selecting for yield components: high compensation at tiller level

Old seedlings transplanting and mechanical removal of early tillers reduced the productive tiller number but increased the number of filled grain per tiller







Mechanical removal of early tillers also increased ‘harvest index’ and fertility rate at the individual tiller level

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Outline

- **Early tillering**
- **Rapid tillering**
- **Early cessation in tillering emergence**
- **Tillering plasticity at later stage**
- **Tillering and the unknown**
- **Compensation and selecting for yield components**
- **General conclusion**

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General conclusion

- **Early and rapid tiller production as an essential plant trait for high yield**
  - through appropriate plant types (high-yielding hybrid rice and improved inbreds in contrast to NPT and LTG introgressed lines)
  - through appropriate crop management (direct-seeding, transplanting young seedlings)
  - opportunity to increase SLA at early stage (high plasticity under shading) and strong correlation reported between SLA and leaf area tend to indicate there is possibility to improve the early dynamics of tillers
  - some genes of interest (*Oshox* gene and *free lysin* gene, Inez Loedin et al, and *AtHOG1* gene, Prakash Kumar et al, University of Singapore) may promote earlier tillering and improved nutrition. This needs to be investigated

- **No architectural plasticity (tiller angle) was observed among high-yielding genotypes for adaptation to contrasting planting design and uneven plant distribution like under broadcasting**
  - it appears necessary to run breeding programs for direct-seeding: this is now the case under the CSISA project
  - this could be a strong justification to screen for plasticity in tiller angle within the gene bank accessions

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General conclusion

- **Earlier cessation in tillering as a potential trait to increase carbohydrate storage in culms and subsequent remobilization to during grain filling**
  - this is already observed with hybrid rice, compared to inbreds, and under continuous flooding compared to alternate and drying
  - the cessation in tillering could be associated with the initiation of new sinks that are observed about simultaneously, like the start in internode elongation, the development of the panicle and the storage of reserves. However, no correlation has been reported yet. More investigation is needed
  - it seems reasonable to investigate and look for a proof of concept if earlier cessation in tillering can trigger significant increase in carbohydrate storage. This can be done experimentally as cessation in tillering in cereals is sensitive to change in red/far-red ratio inside the canopy (Ballaré and Casal, 2000). This can also be investigated through simulation modelling via a mechanistic crop model
  - the strategy to breed for New Plant Types (IRRI) and Low Tiller Gene Genotypes (Japan) with the aim at reducing significantly the number of non-productive tillers could have been successful if it would have reduced the number of tillers through an earlier cessation in tillering rather than a reduction in tiller emergence rate

- **Non-productive tillers appear as an important trait of the rice crop in contributing to high yield**
  - no correlation between grain yield and tillering efficiency was reported when looking at many different situations (comparing genetic variability and also crop management practices)
  - non-productive tillers are the smallest ones, the youngest ones, so they are not that competitive against the productive tillers. They are also green which means they are photosynthetically active. They may intercept light that productive tillers cannot access to
  - non-productive tillers may be useful in contributing to high yield if a substantial amount of their biomass is remobilized towards the productive tillers. Remobilization from one tiller to another could be a high value trait for high yield. Such process should be investigated

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General conclusion

- **High plasticity of the rice crop is a remarkable trait to compensate against unexpected stress conditions**
  - SLA plays the role of a buffer and is rapidly modified at the plant level to enhance tillering and leaf area production, like in the case of reduction in access to radiation
  - new productive tillers are developed to overcome tiller loss due to stress damages like in the case of heat and pest injury
  - sink size and fertility rate are increased at individual tiller level to overcome the consequences of an earlier stress on tiller production
  - the rice crop may also be too sensitive to changes in growing conditions: initiation of new tillers under alternate wetting and drying conditions is not a desire trait. If the processes involved in the many responses of tiller plasticity to environmental conditions are different, then some could be blocked while the other would remain untouched

- **Improving the sink regulation to partition the shoot biomass even more efficiently seems to be the main option to increase grain yield of the C3 rice in tropical conditions**

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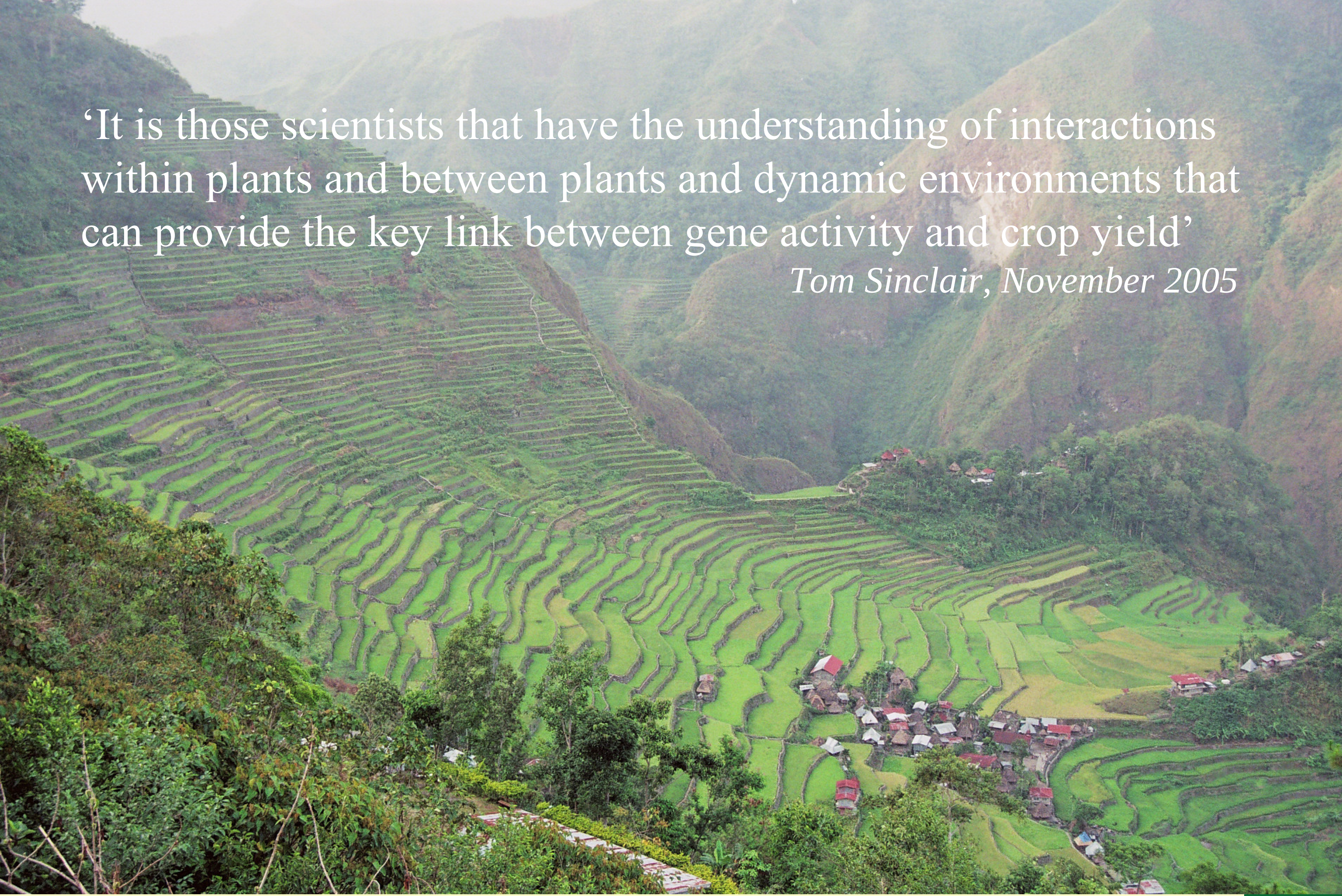

‘It is those scientists that have the understanding of interactions within plants and between plants and dynamic environments that can provide the key link between gene activity and crop yield’

Tom Sinclair, November 2005

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