Crop water use efficiency, can we improve it further by manipulating soil drying signal?

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Abstract

Water use efficiency (WUE), if defined as the transpiration efficiency, is known as a conservative parameter (e.g. the difference between C_3, and C_4 plants) and largely a function of stomatal opening that determines CO_2 concentration gradient. Soil drying leads to partially closed stomata (a better WUE) but also a reduced biomass accumulation as a trade-off. Irrigated plants tend to open their stomata fully and some narrowing of stomatal aperture from full may reduce water loss without much effect on photosynthesis. This is possible when part of the plant root system is irrigated while the rest part is left drying. A root 'drying' signal is then transported to the shoots where shoot physiology is regulated. If a partial rootzone irrigation is applied on crops, plant water consumption can be improved.

If we define the WUE as the water productivity, it should be a function of biomass accumulation, harvest index and the total amount of irrigation. Our field experiments presented a case that WUE may be enhanced through an improved harvest index. Harvest index has been shown as a variable factor in cases where whole plant senescence of rice and wheat is unfavourably delayed. Such delayed senescence can delay the remobilisation of pre-stored carbon reserves in the straw and results in lower harvest index. A controlled soil drying at grain filling time can enhance whole plant senescence and therefore improve the remobilisation of pre-stored carbon reserve.

Media summary

Crop water use efficiency can be improved by either an enhancement in transpiration efficiency or an improvement of water productivity through an increased harvest index.

Key Words

Water use efficiency, partial rootzone irrigation, harvest index, grain filling, soil drying signal.

Can the transpiration efficiency be improved?

Water use efficiency (WUE), if defined as the carbon assimilated over the water transpired, is known as a conservative parameter (e.g. the difference between C_3, and C_4 plants). Conventional view states that biomass production is closely coupled with the amount of water used and thus WUE is largely a function of stomatal opening. Is there any way to increase WUE without substantially reducing the total carbon assimilated? Theoretically this is possible. Irrigated plants tend to open their stomata fully, a luxury state possibly keeping the leaves cool? Some narrowing of stomatal aperture from full opening may cut down water loss without much effect on photosynthesis. This is because photosynthetic rate responds to stomatal opening in a saturation pattern while transpiration in a linear pattern (Fig. 1). If stomata are partially closed, we may expect WUE to be improved.

Partial rootzone irrigation (PRI) is designed exactly for such a purpose. In this irrigation method, part of the plant root system is irrigated while the rest part is left drying. A root 'drying' signal, mainly abscisic acid (ABA), is produced in the roots of the soil in the drying zone. This ABA is then transported to the shoots where shoot physiology (mainly stomatal opening and leaf expansion rate) would be regulated. Root-sourced ABA may be termed as a stress signal since its strength increases with the progress of a drought, which helps plants to detect the available amount of water in the soil and regulate water loss accordingly.

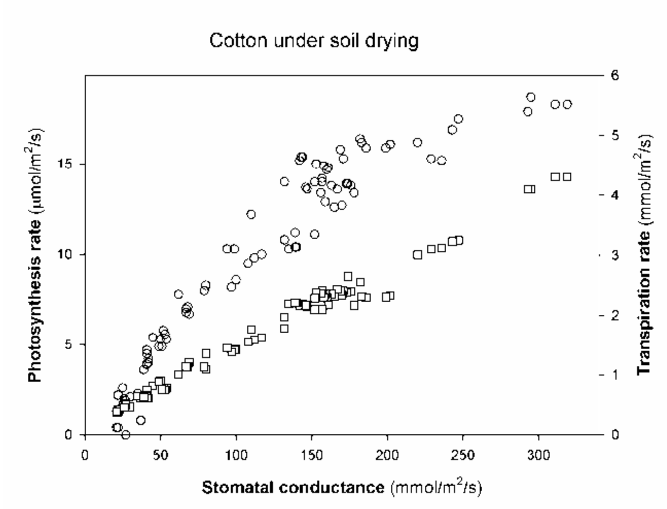

Fig. 1 Cotton photosynthesis (○) and transpiration (□) rates as a function of stomatal conductance. While photosynthesis shows a saturation pattern when stomatal conductance is increased, the transpiration rate is linearly regulated by the stomatal conductance if measured as the boundary resistance-free function.

We have applied PRI extensively to many plants, including crops and fruit trees that were either pot-grown or field-cultivated (Table 1). Plants could be kept hydrated (no visible leaf water deficit) with only part of the root system in wet soil. The biomass, or specifically the economic yield, could still be largely maintained along with substantial reduction of irrigated water. We observed such results for field-grown maize (50% less irrigation for 11% reduction of yield) (Kang et al. 2000, 2002), pear trees (10-18% less irrigation for same yield) (Kang et al. 2003bc), peach trees (35-40% less irrigation for comparable yield) (Gong et al. 2005) and other crops such as wheat, water melon and pepper (unpublished). More interestingly, in an experiment with field-grown cotton (Tang et al. 2005), we managed to save 30% of the irrigated water with only less than 5% reduction in seedcotton yield. In addition, the lint quality was enhanced because PRI led to earlier flowering (a result of better controlled vegetative growth) and better developed fibers before frost.

Table 1. Crops that have been reported with partial rootzone irrigation. Irrigated water can be saved by 10-50% with or without significant reduction of yield.

Species	*Irrigation saved(%)*	*Yield reduced (%)*	*References*
Maize	50	11	Kang et al. 2000 *Agricultural Water Management,* 45, 267-274. Kang et al. 2002 *Field Crops Research* 77, 31-41.
Pear	10-18	No	Kang et al. 2003 *Journal of Hydrology* 280, 192-206.
Peach	35-40	No	Gong et al. 2005 *Hydrological Processes* 19, 2575-2590.
Grapevine	30	No	Loveys et al. 1998 *The Australian Grapegrower and Winemaker* 404a, 108-113.
Grapevine	30	No	Gu et al. 2000 *Research Notes*, #000702, California Agricultural Technology Institute
Tomato	30	No	Zegbe et al. 2004 *Agricultural Water Management* 68, 195–206Wagdy et al. 2004 *Journal of Experimental Botany,* 55(407): 2353-2363.
Cotton	30	<5	Tang et al. 2005 *Field Crops Research* 94, 214-223. Du et al. 2006 *Agricultural Water Management* 84, 41-52.

Can the water productivity be improved by an enhancement of harvest index?

High WUE has been conventionally known as a trade-off for lower biomass production. Can we increase WUE without much reduction of yield? It has been well known that grain yield, a large proportion of the total biomass, shows a negative parabolic relationship with the amount of irrigation. This suggests that when water supply is sufficient, excessive vegetative growth may lead to less root activity, unhealthy canopy structure and a lower harvest index. That means that high biomass production, supported by high water supply, will not lead to high WUE if defined as the grain production per unit amount of water irrigated. Therefore the goal is to increase WUE under limited water supply and increase harvest index. Our recent research has shown that in many situations, grain yield can be improved while reducing the amount of water applied to the crop (Yang *et*

삭제됨: amount
삭제됨: more than optimum
삭제됨: overgrowth of
삭제됨: organs
삭제됨: the
삭제됨: it is
삭제됨: key aspect
삭제됨: the
삭제됨: the
삭제됨: is to
삭제됨: the
삭제됨: , if the biomass production is limited by the water availability
삭제됨: In deed
삭제됨: o
삭제됨: with actually less irrigations

al., 2000, 2001c, 2002b), mainly via improved harvest index which has been shown as the key component to improve WUE of yield (*e.g.* Ehdaie and Waines, 1993).

Remobilization of pre-stored carbon, the variable fraction in grain filling

Grain filling is the final stage of growth in cereals where fertilized ovaries develop into caryopses. At this stage, about 40 to 50 percent of total biomass is deposited into the grains. Monocarpic plants such as rice and wheat need the initiation of whole plant senescence so that stored carbohydrates in stems and leaf sheaths can be remobilised and transferred to their grains. Normally in these crops, pre-stored food contributes 1/4 - 1/3 to the final weight of a grain. Delayed whole plant senescence, leading to poorly filled grains and unused carbohydrate in straws, is a new problem increasingly recognized in rice and wheat production in recent years. A slow grain filling is always associated with the delayed whole plant senescence. Although farmers can choose cultivars of early-maturation, there are still some situations that have made the delayed senescence a serious problem that needs attention:

A). Heavy use of nitrogen fertilizers is well known to lead to a delayed senescence and in worst cases canopy lodging. This is possibly related to the intensive nature of today's agriculture: using less arable land to feed increasingly more people.

B). Selection of lodging-resistant cultivars to cope with the lodging problem has led to another problem in some cases, *i.e.* stems are short and strong but stored carbohydrate is poorly used because the plants may stay "green" for too long, particularly in some cases with short-grain rice cultivars.

C). Introduction of hybrid rice has been a fantastic success in China. Utilization of heterosis, *e.g.* a hybrid between the two subspecies (or ecotypes) of rice, the Japonica and Indica rices, has however also met the problem of delayed senescence. Grains are poorly filled or un-filled (Yuan 1996). Such hybrid genotypes seem too vigorous in terms of keeping "young".

We may define cases described above as unfavourably delayed senescence, which means that no gain is obtainable from the extended grain-filling period. We should however, distinguish this situation, from that in favourable conditions, in which early senescence should be avoided because it reduces the photosynthesis during the grain-filling period and therefore reduces grain weight (*e.g.* Zhang *et al.*, 1998).

A controlled soil drying promotes the whole plant senescence at grain filling

Our recent experience with field-grown wheat has found that a soil drying during the grain-filling period can enhance early senescence (Zhang *et al.*, 1998). While the grain filling period was shortened by 10 days (from 41 to 31 days) in unwatered (during this period) plots, a faster rate of grain-filling and enhanced mobilization of stored carbohydrate minimized the effect on yield. It seems possible that a controlled soil drying during the later stages of grain-filling may promote whole plant senescence, leading to increased re-translocation of pre-stored carbon reserve in the stem and sheath.

A controlled soil-drying means that crops should not be soil-dried to a degree that over-night rehydration cannot be completed and photosynthesis is too severely inhibited. It should be stressed that the soil drying should be at the later stage of grain filling because early development of embryos (at the rapid cell division stage), *i.e.* the "grain-setting" stage, is very susceptible to water deficit (Boyle *et al.*, 1991).

With the highly lodging-resistant rice cultivars, our results (Yang *et al.*, 2001c) showed that if a water deficit during grain filling of rice is controlled properly so that plant can rehydrate overnight, photosynthesis should not be severely inhibited. A benefit from such a water deficit is that it can enhance plant senescence and lead to a fast and better remobilisation of pre-stored carbon from vegetative tissues to the grains (Table 1). The early senescence induced by water deficit does not necessarily reduce grain yield even when plants are grown under normal N conditions. Furthermore, in cases where plant senescence is unfavourably delayed such as by heavy use of nitrogen, the gain from the enhanced remobilisation and accelerated grain filling rate may outweigh the loss of photosynthesis and shortened grain-filling period and increase the grain yield and harvest index.

Table 2. Remobilisation of pre-stored assimilates in straws of rice subjected to various N and soil moisture treatments. The two cultivars used are highly lodging-resistant, i.e. staying green when grains are mature. NN and HN indicate normal and high levels of nitrogen application at heading time. WW and WS are well-watered and water-deficit treatments during the grain filling. Values are means of 20 plants. Letters indicate statistical significance at $P_{0.05}$ within the same cultivar. NSC stands for nonstructural carbohydrate in straws.

삭제됨: .
삭제됨: This improvement
삭제됨: aims at the
삭제됨: that has been
삭제됨: in many situations
삭제됨: aspect
삭제됨: the
삭제됨: y
삭제됨: s
삭제됨: sis
삭제됨: In
삭제됨: as the grains during one month or so period.
삭제됨: Field crops such as wheat and rice usually have a total growing season for four to five months. Apparently,
삭제됨: food in their
삭제됨: which leads
삭제됨: is
삭제됨: food
삭제됨: in it
삭제됨: of some
삭제됨: unfavorably delayed
삭제됨: it
삭제됨: of
삭제됨: working in the
삭제됨: field for water-saving culture
삭제됨: greatly cause an
삭제됨: We have found that the
삭제됨: but
삭제됨: a less left-ove ... [1]
삭제됨: at the later
삭제됨: stage
삭제됨: the
삭제됨: which may
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Cultivars	Water deficit treatment	Nitrogen applied	Remobilised C reserve %	Contribution to grain %	NSC Residue mg g^{-1} DW	Total dry matter g m^{-2}	Harvest index
Wuyujing 3	WW	NN	47.5 c	14.4 c	142.3 b	1707.2 a	0.47 c
	WW	HN	24.5 d	7.6 d	218.5 a	1741.2 a	0.41 d
	WS	NN	74.6 a	28.5 a	64.5 d	1537.9 b	0.52 a
	WS	HN	61.2 b	21.5 b	103.5 c	1716.6 a	0.50 b
Yangdao 6	WW	NN	58.9 b	11.3 c	97.8 b	1788.0 a	0.51 c
	WW	HN	46.3 c	5.3 d	151.6 a	1743.6 a	0.47 d
	WS	NN	82.7 a	27.8 a	41.2 d	1578.8 b	0.56 a
	WS	HN	65.9 b	17.9 b	85.3 c	1768.3 a	0.53 b

When senescence is unfavourably delayed, rice will show a prolonged and slow grain filling, *e.g.* under high N condition (Fig. 1). Controlled soil drying increases the grain-filling rate and shortens the grain-filling period. The increased rate and shortened period are especially remarkable at high N condition (Figs. 1C and 1D). Our results (Yang *et al.*, 2001a) with lodging-resistant cultivars also showed that the final grain weight was not significantly different between well-watered and water-stressed treatments when normal amount of N was applied. However, it was significantly increased under water-stressed plus high N treatment, implying that the gain from accelerated grain-filling rate outweighed the possible loss of photosynthesis as a result of a shortened grain-filling period when subjected to water stress during grain filling.

삭제됨: the

삭제됨: well watered

Similar results were also obtained with hybrid rice which shows very strong heterosis but a slow grain filling as a result of delayed whole plant senescence (Yang *et al.*, 2002b). The stronger the heterosis, *e.g.* the hybrid between japonica and indica subspecies, the higher the harvest index can be improved by a controlled soil drying at the grain filling stage. The grain filling process and rate of the hybrid cultivars were substantially enhanced by the controlled soil drying. The grain yield was actually improved, rather than reduced, by the moderate soil drying the grain filling stage in cases where heterosis is very strong, e.g. the japonica and indica hybrids.

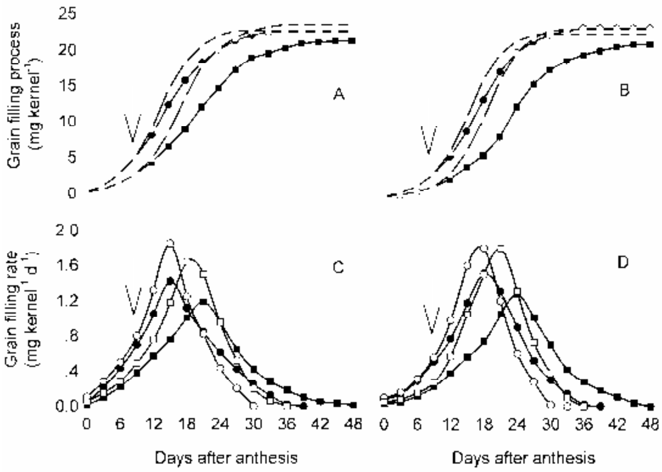

Fig. 2 Grain filling process (A and B) and grain filling rate (C and D) of the japonica cultivar Wuyujing 3 (A and C) and indica cultivar Yangdao 6 (B and D) subjected to various nitrogen and soil moisture treatments. The treatments are: normal N (NN) +well watered (WW) (●), NN + water stressed (WS) (O), high N (HN) + WW (■), and HN + WS (□). Grain filling rate was calculated according to Richards equation. Arrows in the figure indicate the start of withholding water. Vertical bars in the figure A and B represent ± SE of the mean (n=2) where these exceed the size of the symbol.

Heterosis of hybrid rice is usually a function of the genetic relations of the two parents. Hybrids from japonica and indica rice show stronger heterosis and also tend staying green longer in later grain filling than the indica/indica rice. When the whole plant stays green, its non-structural carbon (NSC), mainly the starch, in the culm also stays high for long. We found that concentration of NSC in the culm and sheath during grain filling was very different between indica/indica and japonica/indica hybrid(s) under WW treatments. NSC in the culm and sheath of the two japonica/indica hybrids showed a "V" shape pattern, i.e. initially decreasing from 7 to 21 days after anthesis, but increasing thereafter. NSC concentrations at maturity for both japonica/indica hybrids were nearly the same as at anthesis. For the indica/indica hybrid, NSC in the culm and sheath decreased sharply from 7 to 32 days after anthesis and slowly thereafter. Water deficits substantially reduced NSC in the culm and sheath of all three hybrids. The more severe the water deficit, the more the NSC was reduced. Under MD and SD treatments the patterns of the NSC were similar for both indica/indica and japonica/indica hybrid(s).

Wheat grain yield is more vulnerable to shortened grain filling period than rice. As shown with wheat under reduced irrigation, gain size can be greatly reduced by the less irrigation at this period (Zhang *et al.*, 1998). However, in cases where high N and very strong lodging-resistant cultivars (Yang *et al.*, 2000), moderate soil drying at later grain filling enhances the harvest index substantially with an improved WUE, if defined as the grain yield over the irrigated amount. Soil drying at grain filling stage can greatly shorten the filling period and reduce the gain size and yield. However, in cases where staying green is a problem as a result of heavy use of nitrogen, the moderate soil drying may not necessarily reduce the grain yield of wheat. An extra benefit from such practice is that less water may be required for wheat irrigation under this situation.

Conclusion

We have provided data showing that plant transpiration efficiency may be improved if the luxury stomatal opening can restricted. Such effect can be achieved if a partial rootzone wetting is feasible. We have demonstrated that crop water productivity can be improved further if the harvest index can be enhanced. There are cases where whole plant senescence is unfavourably delayed and harvest index is low. A controlled soil drying at the later grain filling stage can greatly promote grain filling rate and lead to a much enhanced harvest index. In cases where senescence is severely delayed, the gain from a better utilization of pre-stored food actually outweighed the possible loss due to a shortened grain filling period.

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a less left-over of food in straws were achieved