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Is mutual shading a decisive factor for differences in overall canopy specific leaf area of winter wheat crops?

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ABSTRACT

In crop growth simulators, the daily increase of leaf area is often derived from the product of leaf mass increase and specific leaf area (SLA), while the SLA of already formed and expanded leaves is assumed as conserved. The SLA is influenced by many factors and remarkable efforts have been made to isolate the most important ones, aiming to obtain a robust empirical prediction. For a single leaf, SLA is negatively correlated to light intensity. Thus, mutual shading was discussed as a key factor for overall canopy SLA (cSLA) modeling. Our aim was to investigate whether cSLA is primarily a function of growth conditions or light environment.

Therefore, winter wheat (*Triticum aestivum L.* variety *Dekan*) was grown under different irrigation and nitrogen fertilization (N) treatments. Across all treatments, cSLA was positively correlated to LAI with an increase of approximately 15.8 $cm^2\,g^{-1}$ per LAI unit, but the relation was only significant for the phase after one node stage. The observed interaction between cSLA and LAI did not differ significantly between years and treatments. This impact of LAI was confirmed by an additional, independent and previously published dataset including different N treatments.

We also analyzed the influence of drought stress on SLA distribution within the canopy. Independently from the presence or absence of drought, the SLA increased from the top to the lower leaf-layers. Drought mainly reduced leaf area (L) in the higher leaf-layers, whereas SLA was reduced especially in the lower leaf-layers and the SLA of the flag leaves was not affected. Therefore, the lower cSLA under drought stress seems to be primarily an effect of differences in light environment within the canopy. The relevance for SLA modeling is discussed.

1. Introduction

The prediction of crop canopy dynamics resulting from growth and senescence processes is of high importance for plant growth modeling because it determines the fraction of intercepted radiation and has therefore a great impact on dry matter production rate and yield. In many crop growth models (CGM) the daily increase in leaf area is calculated by multiplying the amount of carbohydrate available to leaves by leaf blade area per unit blade mass, called specific leaf area (SLA); while the SLA of already formed and expanded leaves is assumed to be conserved (e.g. Ritchie and Otter, 1985; Marcelis et al., 1998; Asseng et al., 2003). López-Castañeda et al. (1995) found that variation in SLA was largely responsible for the variation in the net assimilation rate of barley and wheat, and a sufficiently accurate prediction of crop canopy is also essential for the calculation of evaporation and crop transpiration (Monteith, 1973). The canopy consists of individual leaves, which are differently affected by environmental conditions according to their position within the canopy. For a single leaf, radiation seems to be the dominating factor since it was observed that SLA of wheat declines at approximately 4 $cm^2\,g^{-1}$ per each mol quanta $m^{-2}\,day^{-1}$ increase in radiation at high temperature (Rawson et al., 1987). The light environment changes with leaf position, affecting leave size and SLA (Rawson et al., 1987) of individual leaves. Further influencing co-factors are genotype and sowing date (e.g. Rawson et al., 1987), temperature (Hotsonyame and Hunt, 1998), sink–source ratio, and CO_2 concentration (Marcelis et al., 1998).

Since CGMs often assume a monolayer canopy, the average canopy SLA (cSLA) is their target value. Thereby, the SLA of new formed leaf tissue is assumed to be constant (e.g. Singh et al., 2008) or a function of plant development stages (e.g. Ritchie and Otter, 1985; Marcelis et al., 1998; Asseng et al., 2003), whereas other environmental factors like temperature or light intensity are mostly not considered. For winter wheat the relation between cSLA and thermal time was reported to be weak (Van Delden et al., 2000), what indicates that variation of cSLA may be caused by other environmental factors than plant development.

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Stress factors like drought seem to have a large influence on cSLA, since water limited desert grasses showed markedly reduced cSLA (Fernández and Reynolds, 2000), and a reduced maximum SLA was found for durum wheat under drought conditions (Brisson and Casals, 2004). The decrease in cSLA due to water limited conditions has been observed not only for graminoids (e.g. Liu and Stützel, 2003), but always in conjunction with reduced leaf area development.

Leaves developed in shade are usually longer, thinner, and lower in specific leaf weight (Friend and Pomeroy, 1970; Woledge, 1997; Allard et al., 1991). Thus, Hotsonyame and Hunt (1998) suggested that mutual shading within the canopy should be taken into account for further understanding of cSLA. The importance of mutual shading is supported by Rawson et al. (1987), who noted that within canopies, the final rise in SLA with leaf age occurred earlier than in spaced plants. In contrast, the SLA of (mainly unshaded) flag leaves was mostly stable with leaf age. However, the consideration of these factors and their interaction within a mechanistic canopy architecture model would require a detailed and complex framework which would be difficult to parameterize. Therefore, SLA modeling remains difficult (Marcelis et al., 1998).

For a robust empiric estimation of cSLA, the main determining factors have to be identified. The objective of the presented study was to ascertain whether growth limiting stress factors have to be perceived as directly influencing SLA, or only indirectly influencing SLA through impacts on light environment. In order to answer this question, two contrasting hypotheses were postulated:

(i) Reduced leaf expansion directly reduces SLA of new formed leaf tissue, whenever environmental conditions have a greater depressive effect on leaf expansion rate than on photosynthesis (Tardieu et al., 1999); while the SLA of already formed and expanded leaves is conserved.
(ii) Since for a single leaf, photon flux density is negatively correlated to SLA (Rawson et al., 1987), cSLA is positively correlated to LAI via mutual shading. Therefore, a comparatively lower leaf expansion causes reduced shading of lower positioned leaves, and thus a reduced cSLA.

If the first hypothesis is true, it would be appropriate to model leaf expansion independently of the plant carbon budget (Tardieu et al., 1999), or at least to perceive stress conditions as an additional influencing factor on SLA. In contrast, if the latter hypothesis is true, mutual shading should be considered as an additional constitutive factor of cSLA modeling, but independently from stress conditions.

For analyzing the impact of LAI on SLA (and cSLA), data of winter wheat grown under different irrigation regimes and varying N supply were used.

Thereby leaf area and SLA distribution across specific leaf layers of wheat grown under different irrigation treatments were analyzed. Under drought conditions, a reduced SLA is primarily expected in the upper leaf layers (where radiation intensity is highest) if hypothesis (i), in lower positioned leaf layers (where shading is highest) if hypothesis (ii) is true.

2. Materials and methods

Two field experiments (E1, E2) conducted with the winter wheat variety *Dekan* were carried out in 2006 and 2010–11 on the Hohenschulen Experimental Farm of the University of Kiel, located in Northern Germany near Kiel. The sowing density was 220 (E1) and 300 seeds/m^2 (E2), with a row spacing of 12–13 cm. Nitrogen was split-applied at the beginning of spring growth, at the start of stem elongation, and at ear emergence. LAI and leaf dry matter were determined destructively at different development stages. During sampling, at least two edge rows were excluded to avoid boundary effects. Table 1 gives an overview of treatments, number of replications, as well as sampling areas and dates.

E1:

E1 was conducted in 2006 with four different N treatments (0, 80, 160, 240 kg N/ha) and four replications (except for early sampling dates before the first N application applied with two replicates).

E2:

Experiments E2 was conducted in a 380 m^2 rain-out-shelter with a mobile transparent house top, sheltered rainfall and ensuring controlled water supply for each parcel by an irrigation system.

Table 1
Experimental treatments, range of development stages (BBCH) when samples were taken, sample area, and number of replications (*n*).

Experiment	Harvest year	Treatment	*n*	Sample area	Sampling dates	BBCH
E1	2006	N1: 0 kg N/ha, N2: 80 kg N/ha (40/40/0), N3:160 kg N/ha (80/40/40), N4:240 kg N/ha (80/80/80)	4	0.25 m^2	11/28/2005, 03/27, 04/24/, 04/05/, 05/11, 05/18, 05/30, 06/18,	25–59
E2a	2010	W0, W1, W2	4	0.25 m^2	04/28, 05/26, 06/15	31–69
E2a	2011	W0, W1, W2	4	0.25 m^2	04/27, 05/17, 06/08, 06/21	31–75
E2b	2010	W0, W2	4	Seven plants	06/15	59–69
BOUWING	1983	N[a]: 115,175,275 kg N/ha Row space: 25 cm Seeds per m^2: 317	8	0.5	2/7, 2/28, 3/28, 4/18, 5/9, 5/24, 6/13, 7/4, 7/18	21–87
BOUWING	1984	N[a]: 100,200,260 kg N/ha Row space: 25 cm Seeds per m^2: 345	8	0.5	2/13, 3/12, 4/2, 4/24, 5/7, 5/28, 6/18, 7/2, 7/16, 8/6	12~80
EEST	1983	N[a]: 94, 154, 254 kg N/ha Row space: 15 cm Seeds per m^2: 317	8	0.5	5/11, 5/25, 6/15, 7/6, 7/20	22~83
EEST	1984	N[a]: 136, 186, 186(!) kg N/ha Row space: 15 cm Seeds per m^2: 317	8	0.5	2/15, 3/14, 4/4, 4/25, 5/9, 5/29, 6/20, 7/4, 7/18, 8/8	21~83
PAGV	1983	N[a]: 140, 240, 300 kg N/ha Row space: 12.5 cm Seeds per m^2: 300	8	0.5	2/8, 3/1, 3/29, 4/19, 5/10, 5/24, 6/14, 7/5, 7/19	22~83
PAGV	1984	N[a]: 120, 200, 300 kg N/ha Row space: 12.5 cm Seeds per m^2: 325	8	0.5	4/3, 4/24, 5/8 5/28, 6/19, 7/3, 7/17, 8/8	14~83

[a] Includes measured mineral nitrogen in spring (0–100 cm).