Temporal dynamics of light and nitrogen vertical distributions in canopies of sunflower, kenaf and cynara

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ABSTRACT

To enhance eco-physiological and modelling studies, we quantified vertical distributions of light and nitrogen in canopies of three Mediterranean bio-energy crops: sunflower (*Helianthus annuus*), kenaf (*Hibiscus cannabinus*) and cynara (*Cynara cardunculus*). Field crops were grown with and without water stress in 2008 and 2009. Canopy vertical distributions of leaf area index (LAI), photosynthetically active radiation (PAR), specific leaf area (SLA), nitrogen concentration (N_{conc}) and specific leaf nitrogen (SLN) were assessed over time for each crop × year × water input combination. Light and nitrogen distributions were quantified by the Beer's law (exponential model) and extinction coefficients for light (K_L) and nitrogen (K_N) were calculated. Within a year, K_L did not change significantly over the studied period in all irrigated crops, but differences in K_L were significant between years (sunflower: 0.74 vs. 0.89; kenaf: 0.62 vs. 0.71; cynara: 0.77). K_L estimates were always lower (−48 to −65%) in water-stressed sunflower and kenaf crops because of the reduction in leaf angle. These results should be taken into account, when simulating water-limited biomass production. Vertical SLN distributions were found in canopies when LAI was >1.5 (40 from 51 cases). These distributions were significantly correlated with the cumulative LAI from the top ($r^2 = 0.75$–0.81; $P < 0.05$), providing parameters to upscale photosynthesis from leaf to canopy levels. Vertical SLN distributions followed species-specific patterns over the crop cycle and varied less compared to PAR distributions between years. Lastly, we observed strong associations between SLN and PAR distributions in irrigated sunflower and kenaf canopies ($r^2 > 0.66$; $P < 0.001$). However, observed SLN distributions were less steep than the distributions that would maximize canopy photosynthesis.

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1. Introduction

A sharp increase in energy production from biomass in the coming years (Tuck et al., 2006), requires that new energy crops (e.g. cynara) will be included in the cropping systems while the production area of other crops (e.g. sunflower) would need to be expanded. The global Scientific Committee on Problems of the Environment (SCOPE) announced that expansion of biofuel production on area basis must be achieved in the context of a 50% increase in food production by 2030 (Connor and Hernandez, 2009). This means that a sustainable increase in bioenergy production must come from greater productivity of existing arable land. Crop modelling is an appropriate way to explore such objectives by conducting scenario studies.

A prerequisite to model crop growth and productivity is an appropriate quantification of crop canopy dynamics (light penetration and nitrogen allocation) in response to management and environmental conditions. Vertical distributions of light and nitrogen in a crop canopy have been quantified by so-called extinction coefficients for light (K_L) and for nitrogen (K_N). In simple crop models such as LINTUL (van Ittersum et al., 2003), K_L is widely used to calculate light interception by the canopy and to predict biomass yields based on the light use efficiency concept. More detailed approaches, in which both K_L and K_N are used to scale up photosynthetic CO_2 fluxes from leaf to canopy levels (Leuning et al., 1995; de Pury and Farquhar, 1997), have been incorporated into crop growth simulation models such as GECROS (Yin and van Laar, 2005). However, research is needed to parameterize these models for new energy crops.

Even for well-known food crops such as wheat, little is known about the dynamic changes in K_L and K_N (Bertheloot et al., 2008), nor about the effects of drought on these changes (O'Connell et al., 2004). Without water stress, vertical distributions of light and nitrogen in a canopy were sufficiently described by assuming an exponential decline over canopy depth – the Beer's law (Hirose

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and Werger, 1987; Monsi and Saeki, 2005). In most studies, K_N was shown to be closely related to K_L, indicating that nitrogen allocation is driven to some extent, either directly or indirectly, by light distribution (e.g. Evans, 1993; Anten et al., 1995; Milroy et al., 2001; Pons et al., 2001; Bertheloot et al., 2008). Under water stress, the light and nitrogen distributions over canopy depth are more complicated because water stress affects not only appearance and elongation of leaves and uptake and partitioning of nitrogen, but also morphological aspects of leaf positioning, leaf angle and azimuth angle.

In this work, we aim to quantify extinction coefficients for light (K_L) and for nitrogen (K_N) for potential energy crops sunflower (*Helianthus annuus*), kenaf (*Hibiscus cannabinus*) and cynara (*Cynara cardunculus*), crops with contrasting leaf area distributions along the stem. Sunflower, kenaf and cynara were chosen for this study because (i) they have a great potential in terms of seed and biomass production in Mediterranean type climates (Geronikolou et al., 2005; Archontoulis et al., 2010a; Danalatos and Archontoulis, 2010; and references therein), including regions like southern Australia, South Africa, Southern California, and Chile (Estienne and Godard, 1970); and (ii) they cover a large range of bio-industrial applications (biodiesel for transport, pellets for heating, biomass for electricity production, bio-products for buildings, fibres; Karp and Shield, 2008).

Our specific research questions were (i) Can light and nitrogen distributions in canopies of sunflower, kenaf and cynara be accurately described by Beer's (exponential) formula? (ii) How do K_L and K_N depend on species, canopy development, water limitation, time of season and year? (iii) Which generalizations about values of K_L and/or K_N can be made that are suitable for implementation in models? and (iv) Can conservative associations between K_L and K_N be derived from this study? To investigate these questions, we studied three energy crops in the field under two irrigation regimes for two consecutive years in Greece.

2. Materials and methods

2.1. Growing conditions, species, management and climate

All experiments were carried out on a loamy fertile soil (Aquic xerofluvent; high ground water levels; Archontoulis et al., 2010a) in central Greece (Thessaly Plain, Karditsa, 39°25′N, 22°05′E, 107 m asl.) in 2008 and 2009. The crops, sunflower, kenaf and cynara, were grown in different sections of the same field in east–west rows (plot size: 184 m²). No attempt was made to include species into a common layout for practical reasons (irrigation application and inter-plot interference). Per crop, pests were controlled chemically and manually, while there were no obvious diseases. Sunflower and kenaf are fast growing summer crops (Figs. 1 and 2), while cynara is a perennial crop with annual cycles of 11 months each (for growth stages see Archontoulis et al., 2010b).

Table 1 provides an overview for the studied species and summarizes details such as growing conditions, management practices and water treatments. Per crop, the combination of two years × two irrigation rates resulted in four water treatments: T_1 = 2009, irrigated; T_2 = 2009, water stressed; T_3 = 2008, irrigated; T_4 = 2008, water stressed (Table 1). Irrigation was applied via a drip irrigation system. For the summer crops T_1 and T_3, the irrigation rate was based on class A-pan evaporation measurements (for site-specific calculations see Danalatos and Archontoulis, 2010) at weekly intervals (Fig. 2a and b). Water-stressed summer crops (T_2 and T_4) received one irrigation application during early growth. For cynara the water treatments were: 3–4 irrigation applications (T_1 and T_3) during the period of rapid increase in biomass (BBCH 55–65;

May–June) and no irrigation application (T_2 and T_4) as is common for cynara.

Full weather data were recorded hourly by an automatic meteorological station (DL2, Delta-T, UK) which was installed at the experimental site. The mean air temperature during summer was 25.9 °C for 2008 and 24.6 °C for 2009 (Fig. 1), close to the long-term average for this site of 25 °C. Precipitation during winter–spring season varied considerably between years: 103 and 295 mm for 2008 and 2009, respectively (Fig. 2c). Radiation is not a limiting factor in this region (summer period: 25 MJ m⁻² day⁻¹).

2.2. Sampling protocol

In sunflower and kenaf, first the fraction of intercepted photosynthetically active radiation (PAR) was measured, followed by sampling, and assessments of leaf area, dry weight and nitrogen (N) concentration. Measurements began when the canopy height was at least 25 cm; at the first sampling the canopy was not divided into layers. Later on, when plant height increased (Fig. 2d and e), the number of layers was increased progressively to three for sunflower and to five for the kenaf crop. These successive canopy layers had equal vertical thickness per crop (calculated based on plant height). PAR extinction was measured during vegetative stages for kenaf and during vegetative and flowering stages for sunflower. However, vertical N distribution in the canopy was measured throughout the crop cycle for both crops (Table 1).

In cynara PAR and N profiles were assessed separately at different periods (Table 1) for practical reasons. PAR penetration was measured at vegetative stages (BBCH 10–37; no layer defined) because later during reproductive growth, the canopy was too voluminous to allow us to perform accurate measurements (note LAI > 7). Vertical N distributions were undertaken during reproductive growth (BBCH 59–82; 4 layers of equal vertical thickness were defined) because at vegetative stages leaves formed a rosette. Periods of PAR and N measurements per species are provided in Table 1. Sampling frequency can be seen in Fig. 2.

2.3. Measurements

Fraction of PAR intercepted by the successive canopy layers was measured using a 1-m light sensor (Delta-T Devices, Cambridge, UK). We measured under clear skies to avoid poor quality of incident PAR (O'Connell et al., 2004) and around maximum sun height (11:30–13:30 h summer time; diffuse/total ≈ 0.2; radiation ≈ 1000 MJ m⁻² s⁻¹) when differences in leaf angle due to solar tracking – evident in sunflower and kenaf – would be minimal (Sassenrath-Cole, 1995). In each measurement, a reference light sensor was placed above the canopy to provide simultaneous readings of incident PAR. At the bottom height of the canopy layers defined beforehand, the 1-m light sensor was placed diagonally across two rows (in an X pattern) and 10 readings were taken at each depth in the canopy. Few measurements above the canopy were also taken to check the reference light sensor. Per sampling event (combination of crop species × year × water level × date), measurements were taken from two to four independent samples.

Early during the following morning, plant samples were taken (2 rows of 0.66 m long each = 1 m²) and green leaf lamina area (henceforth leaf area index, LAI) was determined per layer using a LI-COR area meter (LI-3000A, Nebraska, USA). Leaf samples (excluding petioles) were dried at 70 °C to constant weights and weighed. Then materials were analyzed for total nitrogen concentration on a mass basis (N_{conc}, g N kg⁻¹ dry weight) using the Kjeldahl method. When measuring light extinction and sampling for N profiles, the senesced leaves (>50% green surface area) were removed; this is in line with many reports (e.g. Connor et al., 1995; Hall et al., 1995). When the proportion of a partially senesced leaf (<50% of green