Gas exchange of ears of cereals in response to carbon dioxide and light.

I. Relative contributions of parts of the ears of wheat, oat, and barley to the gas exchange of the whole organ

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Abstract. One cultivar each of spring wheat (Triticum aestivum L. cv. Arkas), oat (Avena sativa L. cv. Lorenz), and barley (Hordeum vulgare L. cv. Aramir) was chosen in order to study the relative contributions of individual bracts to the gas exchange of whole ears. The distribution and frequency of the stomata on the bracts were examined. Gas exchange was measured at normal atmospheric CO₂ (330 µbar) and at high CO₂ (2000 µbar) on intact ears and on ears from which glumes or lemmas and paleae (wheat and oat) or awns (barley) had been removed.

The relative contribution to the gas exchange of the whole organ is highest for the awns of barley ears. In wheat, the contribution of the glumes is slightly higher than that of the inner bracts before anthesis. Two weeks after anthesis the inner bracts contribute more than the glumes. This tendency of increasing importance of the inner bracts is also found in oat ears, but the relative amount of CO₂ uptake by the glumes is higher than in wheat. These changes during ontogeny result from the better supply of light to the inner bracts caused by opening of the ears' structures during grain filling, which in part compensates for the decreasing photosynthetic capacity.

The ratio of the photosynthesis rate at high CO₂ to that at normal CO₂ is lower for the glumes of oat and for the awns of barley ears than for the other bracts.

Key words: Avena (gas exchange, ear) – Grain filling – Hordeum (gas exchange, ear) – Inflorescence (cereal ear) – Photosynthesis (cereal ears) – Stoma-ta – Triticum (gas exchange, ear)

Introduction

Besides functioning as inflorescence and protectors of the growing grains, ears (together with the flag leaves) play a major role in the production of assimilates for grain filling. The contribution of the ear to grain filling varies, depending on species, cultivar, and ambient conditions (see the review in Evans et al. 1975), from 13% to 76%. It is higher in species with small flag leaves and/or awned ears and increases under water stress (Blum 1984). This may result from a greater availability of the assimilates produced by the bracts of the ears, because all parts of the ears are closely connected with the pericarp of the grains via the phloem (O'Brien et al. 1985). Ears are able to maintain a higher water potential even under water stress (Morgan 1977).

The smaller amount of photosynthetically active tissue in relation to heterotrophic tissue affects the photosynthetic activity of the ears. Tschakalova and Hoffmann (1976) give the following ratios for autotrophic/heterotrophic tissue in wheat: flag leaves, 1:2; glumes, 1:4.7; lemmas, 1:3.3; paleae, 1:5.5. If one takes the small amount of chlorenchyma into account, the photosynthetic activity of the bracts of the ears is comparable to that of leaves. The respiration rates, however, are much higher because of the larger amount of heterotrophic tissue.

The differences in the CO₂ response of the gas exchange between flag leaves and ears of wheat were discussed by Knoppik et al. (1986). In so far as these differences pertain to the rates of dissimilative respiration in the ears, they are well understood to be a consequence of the respiration in the grains and in the non-photosynthesizing tissues of the ears.
However, the fact that the maximum rates of photosynthesis at saturating CO₂ in relation to the rates at normal atmospheric CO₂ are much higher in ears than in leaves of wheat (Knoppik et al. 1986) was still unexplained. Flag leaves show steeper initial slopes of the A(p) curves (net photosynthesis rate versus intercellular partial pressure of CO₂) and are saturated at approx. 800 μbar CO₂ and approx. 1.8 times the rates of CO₂ uptake at normal CO₂, while ears reach maximum rates of approx. 2.5–3 times the rates at normal CO₂ not being CO₂-saturated below 1000 μbar. Stomata of the ears react less sensitively to changes in ambient CO₂ than do the stomata of flag leaves. This study addresses the questions, whether these characteristics are also to be found in ears of other species and whether they are a result of the arrangement (shading, competition for CO₂) or a specific property of the individual bracts. In addition, the role of the individual bracts for the gas exchange of the ear was of interest. For this purpose, parts of the ears were removed (inner or outer bracts or awns) and the remaining ears investigated.

Material and methods

Plant material. In the spring of 1985 seeds of spring wheat (Triticum aestivum L. cv. Arkas) were sown weekly in six series of ten pots with standard soil (Fruhstorfer Einheitserde). After germination they were thinned to three plants per pot in order to ensure uniform growth. In the spring of 1986 the barley (Hordeum vulgare L.) cultivar Aramir and the oat (Avena sativa L.) cultivar Lorenz were sown in the same way.

The plants were grown in a glasshouse under natural conditions of light, CO₂, temperature and humidity. They were watered daily and fertilized with standard fertilizer as required.

Explanation of the terms (for a simplified diagram see Radley 1981): Glumes are the lowermost two bracts in each spikelet (also called “outer bracts”). Each spikelet contains one (barley) or three to four (wheat, oat) fertile florets. Lemmas are the bracts below, paleae are the bracts above the growing grain in each floret. Awns are to be found on the lowest lemmas in the spikelets of oat and on the lemmas of the fertile florets of barley.

Treatments of plants. Wheat and oat were not treated, ear intact (N), the glumes removed (I) or the paleae, lemmas and grains removed (II). Extra treatment of wheat ears: glumes, paleae and lemmas removed; only the rachis was left. Barley was not treated, ear intact (N) or the awns removed (III).

Treatments were carried out on the afternoon before gas-exchange measurements so that the wound respiration could ease off, but no adaptation, e.g. to changed light conditions could begin.

After the end of the gas-exchange measurements the reference area of the ears (i.e. half of the area of an enveloping prism for wheat ears; for oat and barley the projective area measured by an areameter) was determined and the spikelets were counted. Chlorophyll content was determined according to Arnon (1949) for ears which were not used for the gas-exchange measurements (data not shown).

Gas-exchange measurements. Gas-exchange measurements started at the end of June with the beginning of ear emergence. Gas-exchange rates were determined in an open system as described in detail by Knoppik et al. (1986). The following is only a short summary.

The partial pressures of CO₂ and H₂O were adjusted and the gas flow determined upstream of the cuvettes. Wind velocities in the cuvettes were greater than 2 m s⁻¹ to prevent gradient build-up and to ensure that in case of leaks gas would evaporate in aliquot amounts only.

Air temperature was measured with Pt-100 resistances at two points in the cuvettes. Ear temperature was determined with a thermocouple calibrated under measurement conditions according to the procedure described by Ziegler-Jöns et al. (1986). Ear temperature was constant at 25°C ± 0.2 K. Vapour-pressure deficit of the measured objects was 15–20 mbar.

Photosynthesis and transpiration were determined with an infrared gas analyzer (BINOS; Leybold-Heraeus, Hanau, FRG) as the difference between the gas branched off upstream of the cuvettes and the gas leaving the cuvettes. After determining the H₂O partial pressure was adjusted to a value equivalent to that of the reference gas, so as to prevent any influence on the following measurement of CO₂ partial pressure. Gas-exchange rates were calculated according to Caemmerer and Farquhar (1981).

The measurements comprised CO₂ and H₂O-exchange rates in response to the CO₂ partial pressure at saturating photosynthetic photon flux density (PPFD) and in response to PPFD at saturating CO₂ (2000 μbar). All experiments were done in the same order and for the same period of time.

As a reference for the gas-exchange data the “standard ear” with an average number of spikelets (calculated from all measured ears of this species) was used. The area (projective area for oat and barley or half of the area of an enveloping prism for wheat) was used as a reference for the conductivity for CO₂ (Table 4).

Distribution of stomata. Colourless varnish was applied to the bracts and carefully removed after a drying period of 1 h. The stomata could be seen on the varnish and counted under the microscope. The size of the stomata was altered by this method, since the varnish contains acetone and dehydrates the bracts.

This procedure was used for all bracts of wheat and oats and for the awns, lemmas and paleae of barley, on both abaxial and adaxial sides. Distribution and number of stomata of some chosen areas and distances of the stomata from each other were determined.

Results

Characterisation of intact and treated ears

The wheat ears contained the lowest number of spikelets of all cultivars (16.2 spikelets on average with one pair of glumes and three to four lemmas and paleae each). After emergence, only the tips of the lemmas can be seen behind the glumes. During flowering and grain filling they open, and larger parts of paleae and lemmas become visible.

The ears of the oat cultivar (34.9 spikelets on average with one pair of glumes, two to three lem-