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Net CO_2 Exchange Rates and Diffusion Resistance of Leaves from Chicory Selections during Vegetative Growth

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Abstract. Net CO_2 exchange rates, stomatal and internal resistances for CO_2-transport were followed on fully expanded Witloof chicory leaves (*Cichorium intybus* L. cv. Foliosum) for several months during vegetative growth. Maximum net CO_2 exchange rate (P_{max}) stayed high with a sudden drastic drop at the end of the growing season largely due to an increase in internal diffusion resistance.

During an analogous growth period the H_2O vapour diffusion resistances of leaves for four selections were measured. The adaxial stomatal resistance was always higher than the abaxial one. Stomatal densities calculated for those selections showed higher values at the abaxial leaf side.

Witloof chicory is a biennal crop plant which is lifted at the end of the first growing season and then forced in the dark to produce large etiolated heads, known as chicons. Different chicory selections — adapted to different forcing periods — exist and can be separated by the time when their roots can be lifted in order to produce commercially high quality chicons. In practice selections can be classified into three main groups namely early, intermediate and late.

For Witloof production, especially with early and very-early selections, the degree of maturity at the moment of lifting the roots and before starting the forcing is of great importance. In order to get an idea of the degree of maturation, biochemical approaches have already been used (Roggen 1976, Jolivet and Fiala 1981).

The maturation process itself can be accelerated by vernalisation techniques for the harvested roots (Lips 1979). Although this is already practised by many farmers, research is to be continued, because the exact determination of the stage of maturity and of the changes during vernalisation still remains difficult (Lips 1982).

CO_2 exchange studies are commonly used to describe plant productivity and/or performance (Ceulemans *et al.* 1980). Variations in stomatal number

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between single plants (HUNT and CHRISTIE 1969), clones (CEULEMANS 1980), cultivars (ANDELIC *et al.* 1970, COLE and DOBRENZ 1970, MISKIN and RASMUSSON 1970, SAPRA *et al.* 1975) and species (TEARE *et al.* 1971, SHEARMAN and BEARD 1972) have been reported. Differences in leaf photosynthesis are widely discussed.

The results presented here are part of a project to evaluate if eventually the seasonal trend in CO_2 exchange behaviour of chicory leaves in the field may be used as an index for selection in terms of earliness and maturity period.

MATERIAL AND METHODS

The first year (1979) a comparative study of four Witloof chicory (*Cichorium intybus* L. cv. Foliosum) selections: "Hanssens vroeg"; "Zoom"; "Videna" and "Hanssens laat" — obtained by mass selection, except the French hybrid "Zoom" — was carried out at Steenhuffel (Belgium) on plants sown at the end of April and thinned at a density of about 25 plants/m^2.

After four months, fully-expanded and healthy leaves of plants chosen at random were measured. Stomatal density was defined by counting stomata under a microscope using colorless nail polish replica (MEIDNER and MANSFIELD 1968). Abaxial and adaxial surface stomata counts were made on the base, middle and tip portion of the leaves.

The stomatal resistance for H_2O vapour transport was measured weekly at saturating photon flux densities with an automatic porometer MKII (Delta-T Devices). Five plants were sampled at both leaf sides for each selection.

In 1980 the study was concentrated mainly on one selection, "Hanssens vroeg", sown at the same time, at the same place with the same plant density as in 1979.

Leaf net photosynthetic rates of that early maturing selection were measured at weekly intervals in the field.

Part of the leaf (20 cm^2) was enclosed in a ventilated plexiglass chamber (VERBAENEN 1980). Differences in CO_2-content between the incoming and outgoing air were measured with a portable, battery operated differential infrared gas analyser (BINOS I, Leybold Heraeus).

Assimilation chamber temperature was measured with a copper/constantan-thermocouple connected to a Comark electronic thermometer, and photosynthetically active radiation (PAR) at the upper part of the leaves was measured with a Lambda sensor in connection with a Li-18S quantum meter.

For obtaining net CO_2 exchange rates at different photon flux densities photon flux density (PFD) was reduced stepwise with cheese cloth.

The internal resistance for CO_2 transport was calculated according to HOLMGREN *et al.* (1965), using the electric analogue model. Boundary layer resistance to water vapour was determined using leaf model of blotting paper or empirical formulae dependent upon leaf dimensions and wind speed. Stomatal resistances (obtained by porometer) and boundary layer resistances to water vapour differences were converted to resistances to CO_2 transfer by multiplying by the molecular diffusion ratios (MONTEITH 1973).

TABLE 1
Mean stomatal resistances for H_2O vapour transport for the adaxial and abaxial leaf side ($s\,cm^{-1}$). Means given with standard deviation are calculated from eight measuring periods throughout the season

Selection	Stomatal resistance					
	adaxial			abaxial		
Hanssens vroeg	3.70	±	0.52	3.11	±	0.42
Zoom	3.73	±	0.67	2.87	±	0.43
Videna	3.79	±	1.22	3.51	±	1.24
Hanssens laat	3.74	±	0.76	2.99	±	0.44

Net CO_2 exchange rate-PFD curves were fitted using the method of least squares and the equation of a rectangular hyperbola:

$$Y = a + b/(X + c) \qquad \text{Bliss and James (1966)}\ .$$

Mean resistances and mean CO_2 exchange rates were calculated under saturated photon flux density values being above 300 μmol $m^{-2}\,s^{-1}$ for stomatal resistances and above 1200 μmol $m^{-2}\,s^{-1}$ for internal resistances and CO_2 exchange rates.

RESULTS AND DISCUSSION

Table 1 shows mean stomatal resistance for water vapour transport calculated for all our data, from 11 September to 8 November 1979, pooled. No statistical difference in stomatal resistance is found between the selections although "Hanssens vroeg", "Hanssens laat" and "Zoom" show a statistical significant higher stomatal resistance for the adaxial side than for the abaxial side.

This difference between the adaxial and abaxial leaf surface can also be found when looking at stomatal densities for the same selections as summarised in Table 2. Stomatal density is significantly higher (except for "Hanssens vroeg") in the abaxial than in the adaxial epidermis. The higher stomatal density at the abaxial leaf surface is generally found for most species, except for the *Gramineae* where there are more or less equal densities on both surfaces (PEMADASA 1979). Adaxial stomatal density values are statistically ($P = 0.05$) higher for "Hanssens vroeg" and "Hanssens laat" than for "Zoom" and "Videna".

Some authors were able to separate different cultivars or clones within one species on the basis of stomatal density: CEULEMANS (1980) observed differences in stomatal density for several poplar clones in building an ecological passport to predict productivity. SAPRA *et al.* (1975) determined differences in stomatal number and size and their relationship with varying ploidy levels for different cultivars of triticale, wheat and rye. We are able to separate the selections "Hanssens vroeg" and "Hanssens laat" from the other selections, "Zoom" and "Videna", but we are not able to suggest that stomatal

TABLE 2

Mean stomatal densities (number of stomata/mm²) given with standard deviation for both leaf sides, measured at 11 September

Selection	Stomatal density					
	adaxial			abaxial		
Hanssens vroeg	75.0	±	25.8	82.5	±	22.6
Zoom	53.8	±	11.4	79.1	±	22.8
Videna	58.1	±	14.9	87.3	±	30.3
Hanssens laat	79.4	±	11.7	98.3	±	18.2

density measurements could serve as an aid in chicory maturity classification. Possibly the stomatal density differences found, reflect differences in origin of the selections.

Fig. 1 shows some of the net CO_2 exchange rate — PFD curves obtained during the vegetative growth season. For practical reasons only the adaxial side of mature leaves for the selection "Hanssens vroeg" was measured. There is a great difference between the curve from 15 October and the others. Asymptotic net CO_2 exchange rate decreased from 500—540 $\mu g\ m^{-2}\ s^{-1}$ (September) to 115 $\mu g\ m^{-2}\ s^{-1}$ (15 October).

The relationship between net CO_2 exchange rate, adaxial stomatal and internal resistance for CO_2 transport is given in Fig. 2. At the beginning of

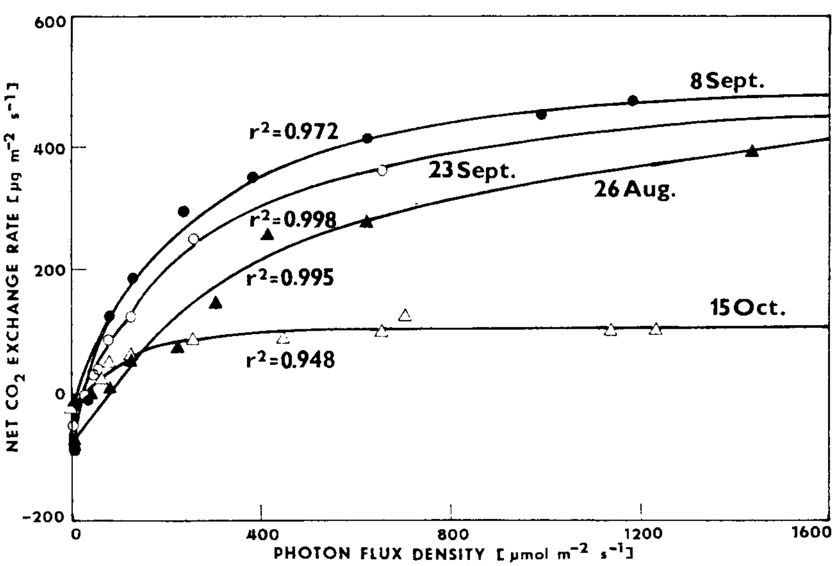

Fig. 1. Relationship between photon flux density and net CO_2 exchange rate of *Cichorium intybus* L. measured at 26 August, 8 and 23 September and 15 October for the selection "Hanssens vroeg".

October, net CO_2 exchange rate dropped suddenly while the internal resistance increased. The stomatal resistance increased only slightly, which means that the decrease in P_{max} may be caused mainly by a changed intracellular CO_2 transfer and/or carboxylation rate.

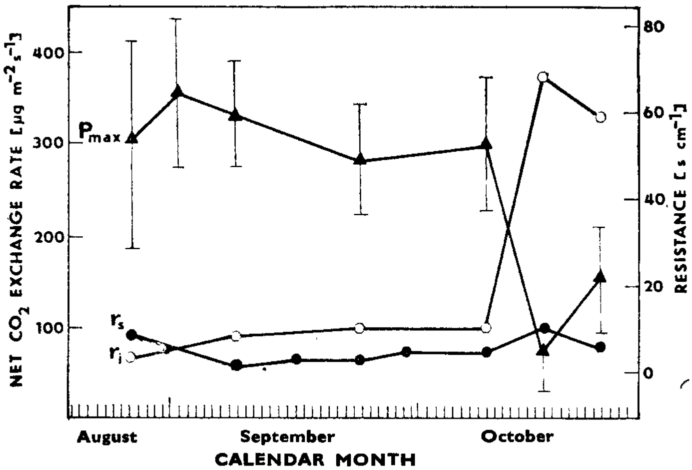

Fig. 2. Mean maximum CO_2 exchange rate (P_{max}), stomatal (r_s) and internal (r_i) resistance for CO_2. The adaxial leaf side of chicory plants was examined during the vegetative growth of the selection "Hanssens vroeg"; vertical bars are 95% confidence intervals.

Measurements on the later selection "Zoom" on 30 October gave the following results: a P_{max} of 498 $\mu g\ CO_2\ m^{-2}\ s^{-1}$; a stomatal resistance of 6.4 $s\ cm^{-1}$ and an internal resistance of 2.4 $s\ cm^{-1}$, suggesting a difference in photosynthetic behaviour between those two selections. Differences in maximum net CO_2 exchange rate for soybean cultivars belonging to different maturity groups were also found by GORDON *et al.* (1982). The differences in gas exchange behaviour between the early and late selection are possibly correlated with the root maturity stage since roots of the selection "Hanssens vroeg" were ready for forcing while those of the selection "Zoom" were not according to practical production standards.

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