*Acta Bot. Neerl.* 26(1), February 1977, p· 29–42.

# AN ECOPHYSIOLOGICAL STUDY IN THE FIELD LAYER OF ASH COPPICE
# II EXPERIMENTS WITH GEUM URBANUM AND CIRSIUM PALUSTRE IN DIFFERENT LIGHT INTENSITIES

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## SUMMARY

The influence of different light intensities on the vegetative growth and $CO_2$-exchange characteristics of *Cirsium palustre* and *Geum urbanum* were studied in order to give a possible explanation for the different behaviour of the two species in the ash coppice cycle. The shade avoiding species *C. palustre* showed shade tolerant characteristics, whereas the species which avoids exposed conditions, *G. urbanum*, grew well in full daylight. Although there were some minor differences between the two species, the influence of light intensity on vegetative growth gives no sufficient explanation for the observed phenomena in the coppice cycle.

## 1. INTRODUCTION

In the field layer of ash coppice quantitative shifts take place in the populations of different species of higher plants in response to regular coppicing (PONS 1976). In order to give a physiological explanation for this phenomenon, experiments were carried out with two species, which were selected because of their opposite behaviour in the coppice cycle. *Geum urbanum* L. shows a shade tolerant and light avoiding behaviour, whereas *Cirsium palustre* (L.) Scop. behaves quite contrarily. Since the light factor was assumed to be important we started to pay attention to this factor.

The leaf canopy of the tree layer not only diminishes the light intensity but also alters its spectral composition on the woodland floor (STOUTJESDIJK 1972, GOODFELLOW & BARKHAM 1974). Next to changes in light intensity, changes in spectral composition might have additional influence on vegetative growth as FITTER & ASHMORE (1974) showed for two *Veronica* species, but only the light intensity factor is considered in the present experiments.

Different species respond differently to shading. Shade avoiding species often cannot develop a high leaf area ratio in order to compensate for the lower assimilation per unit leaf area in low light intensity, in contrast with shade tolerant species (BLACKMAN & WILSON 1951). Moreover, it is often stated that shade tolerant species do not show an increase in growth rate above a certain level of light intensity, or even show a reduction in growth rate at high light intensities (BLACKMAN & WILSON 1951, EVANS & HUGHES 1961, Huxley 1967, GRIME & JEFFREY 1965).

Shade and sun phenotypes of one genotype are known to have different $CO_2$-exchange characteristics (Prioul 1971, Groen 1973, Grahl & Wild 1972). The sun phenotype has a high photosynthetic capacity and a high respiration rate, in the shade phenotype rates are considerably lower. Some shade tolerant genotypes, however, are stated to lack the ability to develop a higher photosynthetic capacity in higher light intensities (Björkman & Holmgren 1963 and 1966, Gauhl 1976, Willmot & Moore 1973). The present paper deals with the question to what extent differences in reaction on light intensity during growth in the vegetative phase of the two species can explain their different behaviour in the coppice cycle.

## 2. MATERIALS AND METHODS

*The shade screens.* The different levels of light intensity were obtained by using various layers of black plastic shade screen. The screens were stretched over a metal frame and the roofs of the cages were additionally covered with transparent plastic in order to prevent the raindrops from damaging the weak shade plants. The plants in the open were unprotected. In this way five different light intensities were obtained by 0, 1, 2, 3 and 4 layers of shade screen, giving 100%, 32%, 13%, 4,6% and 1.2% of daylight respectively. Apart from diminishing the light intensity, this method of shading also causes a decrease of wind speed and a change in temperature conditions (*table 1*) (Wassink 1968).

*Light intensity measurements.* The average radiation during the experimental period of 3 to 31 July 1975 was 1780 J/cm².d. (The experimental plot was only a few hundred metres from the meteorological station at De Bilt). In the middle part of the period radiation was somewhat less than at the beginning and at the end. Some trees shaded the plot in the morning till about 9 o'clock, so that the radiation in the 100% daylight treatment was about 10% less than the measured radiation in De Bilt. The average light intensity during the light period at the 100% plot was about 125 W/m² PhAR (16 hour light period, 45% of total radiation and 10% decrease by shading of surrounding trees). The relative light intensities in the cages were measured in overcast weather with two PhAR-corrected Si-photocells, recorded at the 100% plot and in one of the cages at the same time.

Table 1. Average temperatures of hourly observations from 9 till 15 July 1975. The rise in temperature in full daylight is caused by higher maxima during daytime (average air temperature "De Bilt" 18.8 °C).

| | 100% | 32% | 13% | 4.6% | 1.2% | daylight |
|---|---|---|---|---|---|---|
| air temp. | 19.5 | 19 | 19 | 19 | 19 | °C |
| soil temp. | 20 | 19 | 18 | 18 | 18 | °C |

*Plant material.* In the experiments with the vegetative phase of the two selected species, *Geum urbanum* L. and *Cirsium palustre* (L.), Scop seed was used that was collected in the coppice or in the garden from plants originating from the coppice. The seeds of *Cirsium* gave no problems in germination, but dormancy in *Geum* had to be broken by stratification throughout the winter in pots with soil.

Sowing took place in 32% daylight in the end of May. In the second leaf stage at June 18 the plants were potted in clay pots and distributed over the different light treatments, where the pots were placed in the soil. Since in the three highest light intensities the plants became bigger than in the lowest ones, bigger pots were used (13 cm ∅; 9 cm ∅). Sieved sandy garden soil was used mixed with sand to which NPK fertilizer was added.

The plants with the highest growth rates received additional fertilizer during the experiment (100% and 32%). All plants were watered every day, twice (100% and 32%) or once (13%, 4.6% and 1.2%) by means of an automatic irrigation system.

The procedure described above accounts for the outdoor experiment in July 1975. In 1974 also an outdoor experiment was performed next to experiments in a glasshouse and a growthroom. The treatments used were essentially the same and the results were similar and are sometimes referred to.

*Growth analysis.* In the 1974 experiments there appeared to be a relatively long period of exponential growth of these species in the vegetative phase. The frequency of harvests in the 1975 experiment was chosen so that in every light treatment five harvests of five plants each were completed within this period. So fast growing plants were harvested more frequently than slowly growing plants. Only the last harvest of the 13% daylight treatment appeared to deviate considerably from exponential growth and was excluded from calculation. The average relative growth rate (RGR) was calculated by taking the linear regression of ln plant dry weight on time in days. The regression coefficient represents the average RGR per day.

*$CO_2$-exchange measurements.* The $CO_2$-exchange characteristics were measured with an URAS wich was mounted as described earlier (PONS 1976). However, in this case it was adapted to measurements with intact plants. In the vegetative phase both species are rosette plants, so the whole above ground part of the plant can easily be mounted in a gas exchange chamber with all leaves receiving about the same light intensity. All plants were measured at about the 6th leaf stage, except the plants grown at 1.2% daylight (they did not reach this stage). There is no mutual shading at this stage.

## 3. RESULTS AND DISCUSSION

### 3.1. Morphological aspects

Light intensity during growth had a distinct effect on the morphology of the

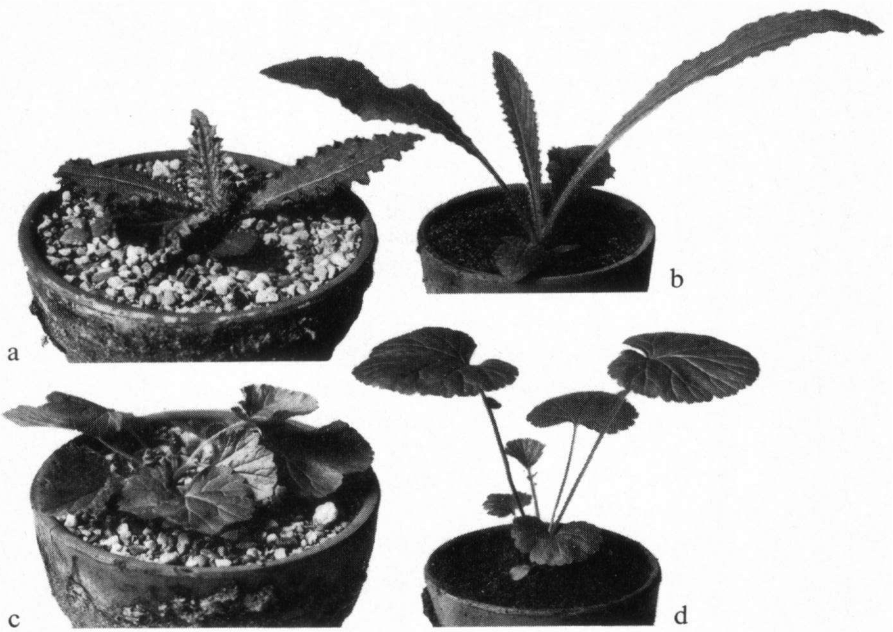


Fig. 1. Photographs of sun and shade phenotypes on the moment of measurement of photosynthesis (about the 6th leaf stage). a. *Cirsium*, full daylight; b. *Cirsium*, 4.6% daylight. c. *Geum*, full daylight; d. *Geum* 4.6% daylight.

two species (*fig. 1*). The petiole of *Geum* was short and nearly horizontal in high light intensity, the lower the light intensity the longer and more perpendicular the petiole. *Cirsium* showed more of less the same phenomenon, but there was no clear distinction between petiole and lamina. The fully expanded leaf in both species had its maximum area in the 32% day light treatment (*fig. 2*). Leaf expansion proved to be inhibited at the highest light intensity. With *Impatiens parviflora*, a shade tolerant species, GROEN (1973) found the maximum mature leaf area at 12% daylight; FRIEND (1966) found the same for wheat at 4 cal/cm$^2$.h. But PIETERS (1974) found with poplar the maximum mature leaf area at the highest light intensity used (40 W/m$^2$). MILTHORPE & NEWTON (1963) found the same for *Cucumis* up to 105 cal/cm$^2$.d, at a high nutrient level, but an optimum at a lower intensity at a low nutrient level. So it is possible that this effect is caused by limitations in the rooting medium.

*Cirsium* showed apical dominance in the rosette at all light intensities during the experiment except in full daylight, where axillary rosettes were formed. *Geum* showed a gradual decrease of apical dominance in the rosette from a low to a high light intensity. At 1.2% and 4.6% daylight no axillary rosettes were formed but in the three highest intensities they appeared and developed stems towards the end of the experiment. The rate of leaf appearance is the same for both species at the lowest light intensities (*table 2*) correlated with apical

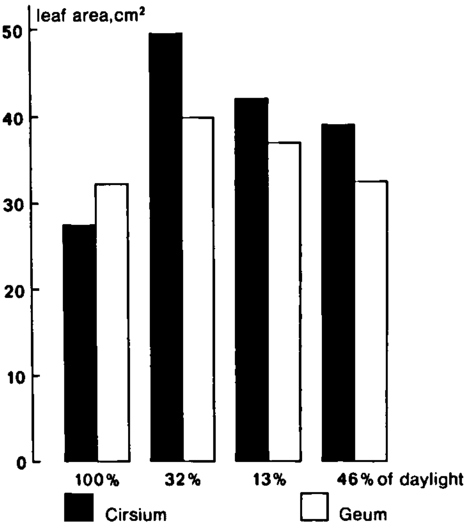


Fig. 2. The mature leaf area of the 4th leaf in different light intensities at the end of the experiment (the plants in 1.2% daylight had not yet a fully expanded 4th leaf).

Table 2. Rate of leaf appearance of the primary rosette (number of leaves per day).

| | 100% | 32% | 13% | 4.6% | 1.2% | daylight |
|---|---|---|---|---|---|---|
| *Geum* | 0.17 | 0.18 | 0.13 | 0.08 | 0.02 | |
| *Cirsium* | 0.43 | 0.30 | 0.15 | 0.08 | 0.02 | |

dominance which is also the same for both species. But at higher light intensities *Cirsium* reached a higher rate than *Geum*, correlated with a stronger apical dominance of *Cirsium* at these intensities.

The anatomy of the leaf clearly reacts on the light intensity in most species. Low light intensity produces shade leaves and high light intensity the more xeromorphic sun leaves. These two species showed the differences as normally described in literature, but not to the same extent (*table* 3). The stomata

Table 3. Some leaf characteristics of the just fully expanded 4th leaf of plants grown in a growth room at 20 °C and two different light intensities.

| | | 100 W.m$^2$ | | 5 W.m$^2$ | |
|---|---|---|---|---|---|
| | | *Geum* | *Cirsium* | *Geum* | *Cirsium* |
| stomata density | adax. | 35 | 60 | 4 | 2 |
| number.mm$^{-2}$ | abax. | 139 | 244 | 97 | 97 |
| leaf thickness mm | | 0.16 | 0.45 | 0.08 | 0.21 |
| SLW mg.cm$^{-2}$ | | 3.8 | 4.3 | 1.3 | 1.5 |
| % dry matter | | 24.9 | 8.6 | 15.8 | 5.9 |

density in *Cirsium* increased with increasing light intensity during growth somewhat more than in *Geum*, especially at the adaxial surface. Leaf thickness also increased with increasing light intensity, which was mainly due to the increase in thickness of the palisade parenchyma layer. *Geum* had one layer of palisade parenchyma cells at all light intensities, whereas *Cirsium* had more cell layers at the higher intensities. At 13% daylight two layers and at 100% three layers were produced. This agrees with the study of JACKSON (1967), who found that the shade tolerant species which he included, did only form one layer of palisade parenchyma cells in the sun leaves, whereas the intolerant species mostly formed two layers.

The water content of the *Cirsium* leaves is much higher, so that its leaves are thicker at the same SLW than those of *Geum*. The meaning of this phenomenon is not quite clear. GROEN (1973) also found a higher leaf water content in the shade avoiding *Calendula officinalis* than in the shade tolerant *Impatiens parviflora*. Some kind of water storage functioning as a mechanism to avoid water stress may play a part.

### 3.2. Distribution of dry matter

Light intensity during growth had a distinct influence on the distribution of dry matter between roots, petioles plus stem and laminae (*fig. 3*). The normally reported phenomenon of an increasing shoot/root ratio with decreasing light intensity during growth was found in both species (BROUWER 1966). But the leaf weight ratio (LWR) reacted differently. The LWR of *Geum* was independent of light intensity; the petioles plus stem accounted for an increasing part of the total weight with decreasing light intensity. In *Cirsium* the LWR rose with decreasing light intensity; the petioles plus stem accounted for a smaller part of the total weight and the increase with decreasing light intensity was not as much as the decrease in root weight.

With increasing light intensity during growth the SLW also increased in both species (*table 4*). Naturally this is due to the increase in leaf thickness

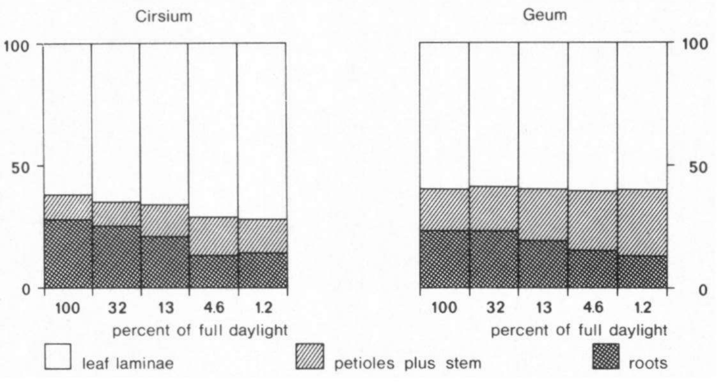


Fig. 3. The dry matter distribution between leaf laminae, petioles with short stem and roots in different light intensities.

Table 4. Specific leaf weight (SLW $mg.cm^{-2}$), leaf area ratio (LAR $cm^2.mg^{-1}$) and percent dry matter of above ground parts in the 1975 outdoor experiment.

| | 100% | 32% | 13% | 4.6% | 1.2% | daylight |
|---|---|---|---|---|---|---|
| SLW | 3.2 | 2.2 | 1.7 | 1.4 | 1.2 | *Geum* |
| | 3.9 | 2.5 | 2.0 | 1.4 | 1.5 | *Cirsium* |
| LAR | 0.19 | 0.27 | 0.36 | 0.46 | 0.52 | *Geum* |
| | 0.17 | 0.27 | 0.34 | 0.50 | 0.48 | *Cirsium* |
| % dr.m. | 19.4 | 16.5 | 15.3 | 13.2 | 11.7 | *Geum* |
| | 8.13 | 6.73 | 6.48 | 5.53 | 6.22 | *Cirsium* |

mentioned above. However, the SLW increased more than the leaf thickness. There is more dry matter per unit leaf area as well as per unit leaf volume. The latter appears in the increase in dry matter percentage (*table 4*). At the lowest intensity *Cirsium* showed a behaviour somewhat deviating from the prevailing trend in this experiment. This low intensity was not used in the other experiments, so it is not clear whether this phenomenon is reproducible or not.

Especially in *Geum* the light intensity had little or no effect on dry matter deposited in the laminae, but influenced SLW. This causes great differences in LAR. According to BLACKMAN & WILSON (1951), species reacting with a rise in LAR at lower light intensities are shade tolerant. A typical shade intolerant species such as *Helianthus annuus* does not develop a high LAR in shade. Both our species showed more or less the same rise in LAR with decreasing light intensity and can thus be regarded as shade tolerant to the same level in the vegetative phase on a morphological basis. The values for LAR found in *Geum* are even higher than those found by Blackman & Wilson in the same species.

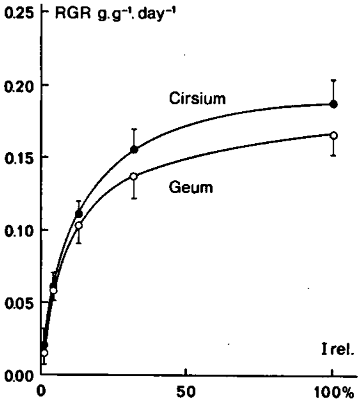


Fig. 4. The average relative growth rate (RGR) of *Geum* and *Cirsium* in different light intensities.

### 3.3. Growth rates

Although at every light intensity the relative growth rate of *Cirsium* was higher, the average RGR of the two species did not differ much (*fig. 4*). At 1.2%, 4.6% and 13% daylight this difference was not significant, but at 32% and 100% it was. In the 1974 glasshouse experiments the difference was of the same order and significant at the low light intensities too. The relation between RGR and light intensity resembles those found normally (BROUWER 1973). Some authors working with shade tolerant species, describe a decline or saturation type response of RGR above a certain level of light intensity (EVANS & HUGHES 1961 for *Impatiens parviflora*, BLACKMAN & WILSON 1951 for *Geum urbanum* and *Solanum dulcamara* and HUXLEY 1967 for *Coffea*). This phenomenon was not found for *Geum* in the present experiment. But in the 1974 outdoor experiment it was observed that the 32% and 100% daylight treatment gave the same RGR of 0,12 g/g.d. Other growth factors may have been suboptimal in 1974, especially with regard to the water factor. Plants in 100% daylight suffered more from water shortage than plants in 32%, which probably resulted in a further decline of growth rate at 100% than at 32%. Growth rates of *Cirsium* did not decrease as much. Possibly there were also limitations in the rooting medium depressing the growth rates of *Geum urbanum* in the experiments of BLACKMAN & WILSON (1951). They found a maximum RGR for *Geum* of 0.06 g/g.d at about 50% daylight a value very much lower than the recorded 0.17 in this experiment at 100% daylight. Much higher relative growth rates are recorded in other species: McDOWALL (1972) found 0.24 g/g.d for wheat, RAJAN et al. (1973) 0.29 for *Helianthus* and LUDLOW & WILSON (1970) about 0.4 for various tropical grasses in the first three weeks of growth. GRIME & HUNT (1975) also included *Geum urbanum* in their group of species of which the RGR was determined in growth rooms at a light intensity more or less corresponding to the 32% daylight treatment in this

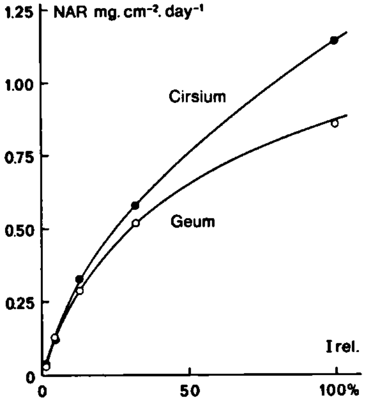


Fig. 5. The average net assimilation rate (NAR) of *Geum* and *Cirsium* in different light intensities.

experiment. They also found a period of constant exponential growth but of a somewhat lower rate (0.104 g/g.d against 0.137 in the present experiment).

The average net assimilation rate (NAR), calculated from RGR and LAR, revealed greater differences between the two species (*fig. 5*). *Cirsium* showed a stronger increase in NAR with increasing light intensity than *Geum*. In low light intensity there are no differences, but in full daylight the difference was considerable. These results will be discussed below when the photosynthesis characteristics are shown.

There need not be big differences in light compensation point for growth between shade tolerant and shade avoiding species as MAHMOUD & GRIME (1974) demonstrated in a comparative experiment. In the present experiment this also seems to be true for the two species. However, BJÖRKMAN (1973) mentioned a big difference; his heliophyte *Atriplex patula* was not able to grow at a light intensity prevailing in the habitat of the rainforest species *Alocasia macrorhiza*.

### 3.4. Ontogenetic drift

Although we have assumed a constant RGR and dry matter distribution up to a dry weight of 1 or 2 gram, there is a tendency to a minor decrease in RGR towards the end of the experiment, especially in the 100% and 32% daylight treatment (*fig. 6*). Since at the lower light intensities there is no such a decline, the phenomenon could be caused by an increase in mutual shading in the rosette, interference of pot size, or changing dry matter distribution. The last mentioned possibility can easily be checked. LAR decreases apreciably in the 100% daylight treatment but not in 32% (*fig. 7*). This decrease can be attributed to a rise in SLW, whereas distribution over the organs remains more or less constant. Some of the lower light intensity treatments also show a decline in LAR in the course of time, but no effect on RGR. A decline of LAR in the course of vegetative growth is a normally reported phenomenon (LUDLOW & WILSON 1971; EVANS & HUGHES 1961; FRIEND 1966). But when the RGR remains constant, as MCDOWALL (1972) reported for wheat also, this means that NAR rises, even under limiting light conditions.

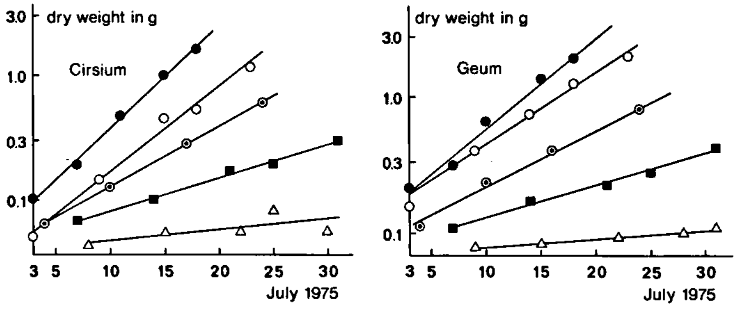


Fig. 6. The linear relationship of ln dry weight with time in ● 100%; ○ 32%; ⊙ 13%; ■ 4.6%; △ 1.2% of daylight.

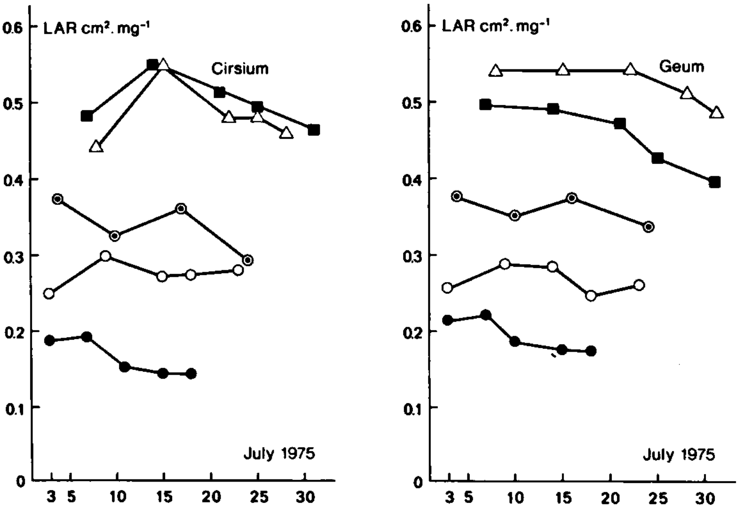
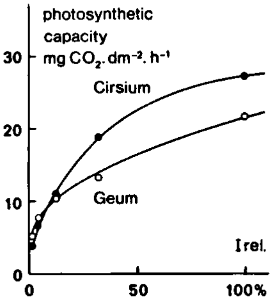


Fig. 7. The course of the leaf area ratio (LAR) during the experiment (symbols as in *fig. 6*).

### 3.5. $CO_2$-exchange characteristics

Photosynthesis of rosettes grown at different light intensities was measured. In both species the photosynthetic capacity was higher with higher light intensity during growth, which is a normally reported phenomenon. However, there appeared to be some quantitative differences between the two species. In high light intensities the photosynthetic capacity of *Geum* was not as high as that of *Cirsium* (*fig. 8*). At 13% daylight they were more or less the same, but in the lowest intensities *Geum* has a higher capacity. As is shown above, *Cirsium* had a multilayered palisade parenchyma in the higher light intensities. This is thus correlated with a higher photosynthetic capacity in this species. Pieters (1960) found a correlation of photosynthetic capacity with mesophyl thickness and Holmgren (1968) with SLW. In these species there is also a cor-



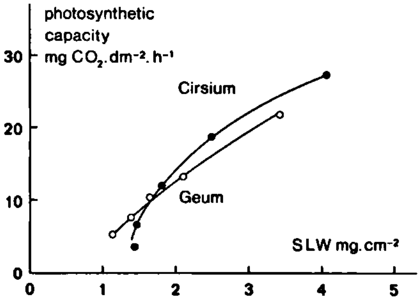


Fig. 8. Photosynthetic capacity of intact rosettes in relation to light intensity during growth.
Fig. 9. The relation of photosynthetic capacity with specific leaf weight (SLW).

relation with SLW (*fig. 9*). Among the different phenotypes of one species this holds true for thickness also, but not when the two species are compared. *Cirsium* has a much thicker leaf at the same SLW than *Geum* has. WILSON & COOPER (1969) found a negative correlation of mesophyl cell size with photosynthetic capacity. Not only the thickness of the mesophyl is important but also its structure. BJÖRKMAN (1968), HOLMGREN (1968) and CROOKSTON et al. (1975) showed that shading causes a rise in diffusion resistances: viz. stomatal resistance as a result of declining stomata density and/or dimensions and mesophyl resistance by a decrease in surface of mesophyl cells per unit leaf area. They also found a decline in activity of the carboxylation enzyme ribulose diphosphate carboxylase, which is considered to be another cause of this rise in mesophyl resistance. Apart from this WILD et al. (1973) found a lower content of the components of the electron transport chain in low light intensity.

The observed differences in photosynthetic capacity between *Cirsium* and *Geum* agree with the higher NAR of *Cirsium* in high light intensity. *Cirsium* is capable of using the periods of full sunlight more efficiently than *Geum*, which results in a higher overall assimilation.

In the spring light phase of the woodland, *Geum* uses its ability to develop a high photosynthetic capacity (PONS 1976). The values that were found in the field in the beginning of May were about the same as those found in this experiment in the full daylight treatment. Under a fully developed leaf canopy in about 3% daylight, the observed capacity of 7–8 mg $CO_2/dm^2.h$ is somewhat higher than the value interpolated between 4.6% and 1.2% daylight. Although the ability to develop a high photosynthetic capacity appears to be of adaptive significance for a woodland plant, some authors found that there are woodland plants which lack this ability. For instance, ecotypes from shade habitats of *Solidago virgaurea* (BJÖRKMAN & HOLMGREN 1963) of *Solanum dulcamara* (GAUHL 1976) and of *Silence dioica* (WILLMOT & MOORE 1973). *Geum rivale* from shaded habitats reached the same photosynthetic capacity in high light intensity of about 20 mg $CO_2/dm^2.h$ as *Geum urbanum* in the present experiments (BJÖRKMAN & HOLMGREN 1966).

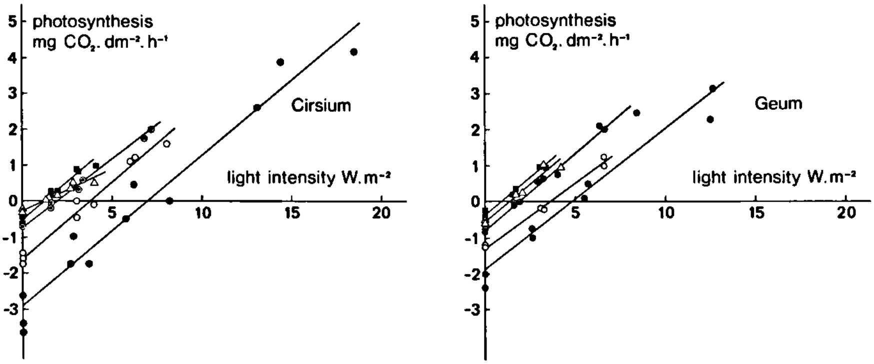


Fig. 10. The light limited part of the photosynthesis-light curves of the different phenotypes of *Cirsium* and *Geum* grown in ● 100%; ○ 32%; ⊙ 13%; ■ 4.6%; △ 1.2% of full daylight.

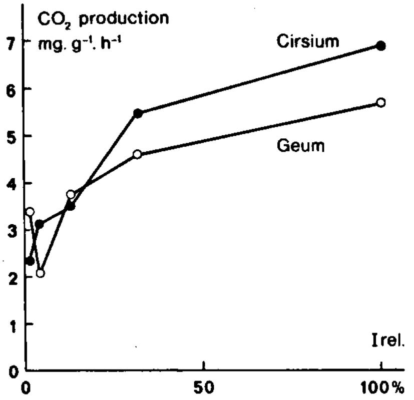


Fig. 11. The respiration rates of the above ground parts of *Cirsium* and *Geum* in relation to light intensity during growth.

The initial slope of the photosynthesis light curve is the same for both species in all light intensities except in the lowest one of *Cirsium* (*fig. 10*). Decreasing photochemical efficiency in low light intensity of plants grown in a high intensity has not been found as in *Solidago virgaurea* (BJÖRKMAN & HOLMGREN 1963) and *Acer pseudoplatanus* (WASSINK et al. 1956).

Apart from photosynthesis, also the respiration rate is influenced by the light intensity during growth (*fig. 11*). There is some correlation of growth rate with respiration rate: *Cirsium* having higher growth and respiration rates in the higher intensities, but in the lower ones the respiration rates only decline to about half this value in hardly growing plants at 1.2% daylight.

## 4. CONCLUSIONS

It is found that there are some differences between the two species with regard to the light intensity factor, which may be of importance for the behaviour of the plants in the coppice cycle. The first thing is that *Cirsium palustre* has a higher growth rate in high light intensities as a result of a higher photosynthetic capacity, which gives a higher assimilation than in *Geum urbanum*. Perhaps *Cirsium* gains advantage out of this but the differences are not so great that the almost complete failure of *Geum* after coppicing can be explained. In the experiments *Geum* grew well in full daylight but in the felled area it shows very poor growth. So the conclusion is that apart from the light intensity there are other factors that inhibit the growth of *Geum* after coppicing, probably factors in the root environment.

In the lower intensities there also are some differences between the two species. *Geum* develops longer petioles through which the LWR is not higher in shade and *Geum* has a higher photosynthetic capacity, which may be of value to exploit the frequent occurring sunflecks beneath the tree canopy (PONS 1976). At the lowest light intensity *Cirsium* showed deviating characteristics. Between 4.6% and 1.2% daylight the SLW does not decrease further, whereas the photosynthetic capacity continues to decline. Although photochemical efficiency in limiting light intensities declines too this does not result in a stronger decline in growth rate than *Geum* shows. Perhaps differences in growth rate appear at intensities below the compensation point as MAHMOUD & GRIME (1974) showed for some grass species.

Relative light intensity in the ash coppice after a few years of growth is about 3% in summer and on the basis of the present experiments we may assume that *Cirsium* is capable of good vegetative growth under the tree canopy. Actually this happens occasionally when a rosette has established itself. So the limiting factor in shade is probably the establishment of this biennial from seed. The ability to develop a high photosynthetic capacity can be considered to be of adaptive value in these ash woods with a leaf canopy that expands late in spring. However, the rapid decline in light intensity afterwards must be dealth with. This is another factor that may affect the behaviour of the species in the coppice cycle and will be treated in a next paper.

## ACKNOWLEDGEMENT

The author is grateful for the interest and advice of Prof. R. Brouwer and for the skilful assistance of mr. J. J. M. van Doormalen. He also wishes to thank miss J. G. Hack, mr. N. Dogterom and mr. J. M. M. Engels, students in plant ecophysiology at the Utrecht University, for the preliminary experiments they have carried out.

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