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AN ECOPHYSIOLOGICAL STUDY IN THE FIELD LAYER OF ASH COPPICE

III INFLUENCE OF DIMINISHING LIGHT INTENSITY DURING GROWTH ON GEUM URBANUM AND CIRSIUM PALUSTRE

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SUMMARY

The adaptability of *Cirsium palustre*, a shade avoiding species, and *Geum urbanum*, a species avoiding exposed conditions in the ash coppice cycle, to a change from a high to a low light intensity was studied, in order to simulate the changes taking place in the light climate in a deciduous woodland in spring. Both the vegetative rosette phase and the generative phase were considered. In the rosette phase a rapid adaptation to the low light intensity took place in both species in a similar way. In the generative phase *Geum* adapted much better after the plants had been transferred from a high to a low light intensity. The dry weight increase of *Cirsium* ceased after the transfer, whereas *Geum* continued to grow. The leaf area ratio was much higher after the transfer, giving better assimilation in limiting light conditions. *Cirsium* when continuously grown in a low light intensity also had a high leaf area ratio, but the stems were too weak to support themselves, in contrast with *Geum*. So in the vegetative phase both species can be considered shade tolerant, but *Cirsium palustre* is not shade tolerant in the generative phase.

1. INTRODUCTION

In an earlier paper (PONS 1976) it has been shown that the woodland plant *Geum urbanum* L. experiences a relatively high light intensity during the spring light phase in the woodland. The plant takes advantage of this and realizes the greater part of its biomass increase in this period. However, from the middle of May till the middle of June the light intensity decreases from 65% to 3% of full daylight, which is due to the expansion of the tree foliage. During this period the plant is adapting to the lower light intensity. *Cirsium palustre* (L.) Scop., a biennial which establishes itself only after the coppice is felled, is not present in the woodland part of the coppice. The adaptation of *Cirsium* plants to a decline in light intensity could not be studied in the field.

Comparative experiments were carried out to study possible differences in response to a decline in light intensity during growth. The vegetative phase as well as the generative phase of the two species are dealt with, because this may be especially different in the case of rosette plants. So the experiments aim at an explanation of the processes that may take place after the canopy has closed in the ash coppice cycle.

2. MATERIALS AND METHODS

2.1. Plant material and growth conditions

Vegetative phase: The experiments with vegetative plants were carried out at the same time as the experiments described in PONS (1977). Some of the plants grown in full daylight were transferred to 4.6% on July 7, 1975. The decline in light intensity is a factor 20, comparable with the situation in the woodland. However, there the plants experience a gradual decline in light intensity from 65% to 3% daylight throughout one month. Moreover the temperature conditions in May/June are different from those in July. This experiment only shows the response of the two species to a decline in light intensity but it does not intend to give a real quantitative simulation of the light factor in the woodland.

Apart from this, other experiments were carried out in the greenhouse during the winter of 1974/75. High light intensities were obtained by additional lighting with HPL or TL lamps and low light intensities by a light shading of natural daylight. Daylength was kept uniform in both treatments at 16 hours a day.

Generative phase: *Cirsium palustre* is a biennial which needs vernalization during winter. In the spring of the second year of the coppice cycle the main axis sprouts and flowers are formed. *Geum urbanum* is a perennial, wintering as a rosette. In spring a number of stems sprout from the leaf axils (1 to 4 in this experiment), but stems can also be formed in the first year after germination. During summer the leaf rosette continues to grow, whereas new stems may be formed.

The generative phase of both species was obtained by sowing in the garden in the preceeding year. The plants formed rosettes and wintered. In the spring of the next year (the middle of March 1975) the plants were potted. The pots were distributed between two light treatments. The greater number was put at full daylight and the remaining part at 4,6%.

The measurements started late in April. Just before flowering, which for both species took place at the same time, some of the plants in full daylight were transferred to 4.6% (May 28). The plants remaining at full daylight were placed in bigger pots. The full daylight plants were watered twice dayly by means of an automatic irrigation system. The shade plants were watered once every day or every other day. Stems which inclined to fall over were supported (only *Cirsium* in low light intensity). The differences in temperature regime between the light treatments have been described by PONS (1977).

2.2. Growth analysis

Harvesting and growth analysis with vegetative plants was fundamentally the same as described by PONS (1977). Since we could not start with a homogenous group in the experiment with generative plants, the normal periodical harvest method could not be used. The indirect method of growth analysis was used as it was described earlier for *Geum urbanum* (PONS 1976). In this case also the complete root system could be harvested because it was in pots. During the experimental period six plants per species and treatment were measured and finally harvested (standard plants). On the day of measurement 7 or 8 plants of the same group covering the range in size of the standard plants were harvested. From the linear correlation between dry weight and stem length multiplied by the square of the stem diameter at the base, the dry weights of the standard plants were estimated at regular intervals. The accuracy obtained with this method was not very good, but appeared to be sufficient to estimate the course of the dry weight and leaf area increase. *Cirsium* has thick green winged stems in contrast with *Geum*. To get the total assimilating area, the area of the winged stem was added to the leaf area. This area was estimated by taking the circumference of the stem at the base and multiplying it by the stem length.

2.3. CO_2-exchange measurements

CO_2-exchange characteristics of the vegetative plants were measured with a URAS, using the same method as described by PONS (1977). The photosynthetic capacity of the individual leaves was measured with the $^{14}CO_2$-method as described by PONS (1976). The plants were taken to the growth room with a temperature of 20 °C and placed under the same lamps as used for the URAS-measurements. The light intensity was chosen at a level that light saturation of photosynthesis at normal CO_2-concentrations was obtained. 300 W/m^2 PhAR was used for the sun phenotypes and 100 W/m^2 for the shade phenotypes. The leaves of the transfer plants grown in the shade were measured at 100 W/m^2 and then removed, next the light intensity was increased to 300W/m^2 in order to measure the leaves numbers 2 to 4, which had grown in full daylight.

At the generative plants only the respiration rates were measured at regular intervals throughout the experimental period. The plants were placed in aluminium stovepipes adjusted to the plant height in a growth room at 20 °C. The technical details were the same as for the URAS-measurements on vegetative plants. The measurements were performed between 11 and 12 a.m. to make them comparable to one another, because a shift in respiration rate throughout a 24 hour period might be possible.

3. RESULTS AND DISCUSSION

3.1. Growth in the vegetative phase

Differences in growth rate between *Cirsium palustre* and *Geum urbanum* in different light intensities have already been described (PONS 1977). What happens with the growth rate after a transfer from full daylight to shade (4.6 %) can be seen in *fig. 1*. The relative growth rate (RGR) declined immediately after the transfer down to a new level similar for both species, but lower than for

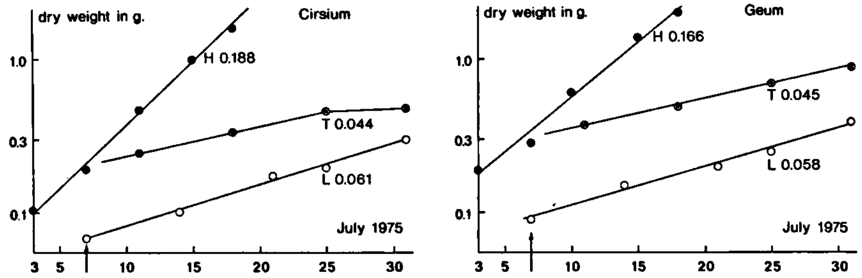

Fig. 1. Dry weights and relative growth rates of vegetative plants of *Cirsium palustre* and *Geum urbanum* in full daylight (H), 4.6% daylight (L) and after the transfer from full daylight to 4.6% (T). The moment of transfer is indicated by arrows.

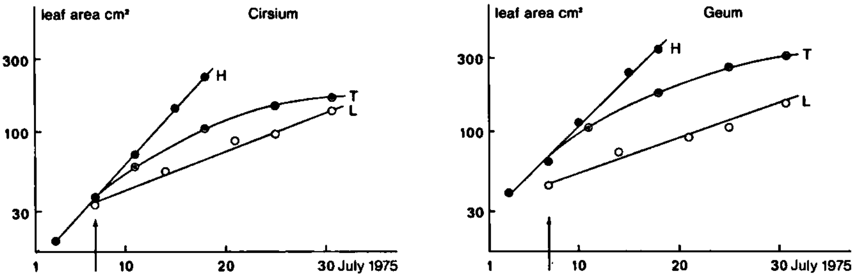

Fig. 2. The leaf area increase of vegetative plants of *Cirsium palustre* and *Geum urbanum* in full daylight (H), 4.6% daylight (L) and after the transfer (T). The moment of transfer indicated by arrows.

the control plants grown at that intensity. The day after the transfer the RGR might have been still somewhat lower because the intercept of both growth lines is somewhat before the moment of transfer. The latest harvest of *Cirsium* shows a decline of the growth rate.

The leaf area growth rate appeared to respond rather differently (*fig. 2*). In both species a gradual decline can be seen after the transfer. At first the leaf area expansion proceeded at a rather high rate, although leaf appearance was retarded instantaneously. This resulted in a gradual decline of the leaf area growth rate.

The leaves formed after the transfer had less dry weight per unit leaf area, resulting in a decline of the average specific leaf weight (SLW) towards the control value of the low light plants (*fig. 3*). Combined with an increase in the shoot/root ratio, this resulted in a rise in LAR (*fig. 4*). This is supposed to be important in adaptation to low light intensity. In the vegetative phase the two species reacted in a similar way. Although the SLW of the leaves of the control plants was not determined individually, it seems rather likely that there has been redistribution of dry matter from already fully expanded leaves, probably to young growing leaves. In the glasshouse experiments the SLW of the leaves was determined individually and after the transfer the fully expanded leaves

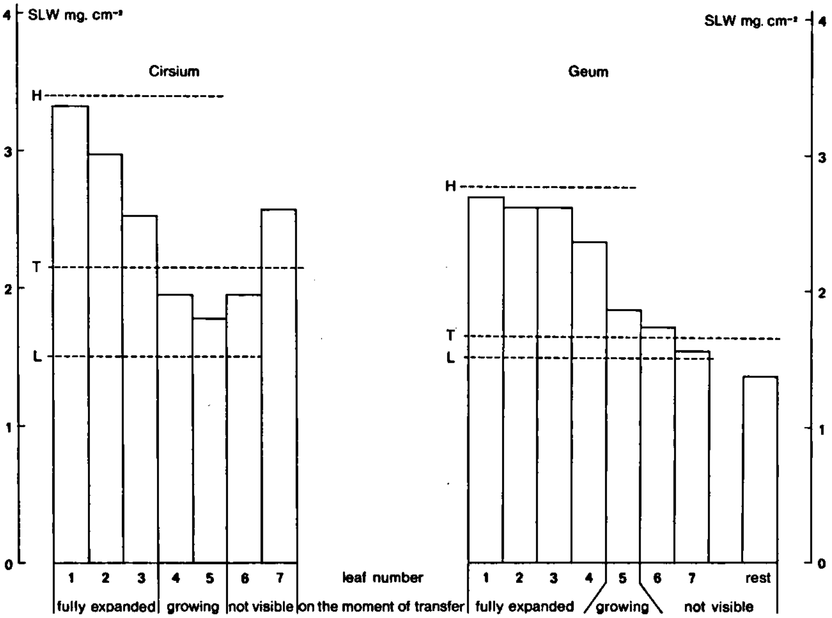

Fig. 3. The specific leaf weight (SLW) of the individual leaves of vegetative plants of the transfer group at the end of the experiment. The average SLW of the total leaf area of the full daylight plants at the moment of transfer (H), and of the transfer plants (T) and the 4.6 % daylight plants (L) at the end of the experiment indicated.

appeared to decrease in dry weight. But the SLW of these leaves remained higher than those developed in the shade (*table 1*). In the experiments the oldest leaves did not die as has been reported for white clover by McCree & Throughton (1966). Evans & Hughes (1961) changed light intensity from high to low and the reverse with *Impatiens parviflora*. They found an adaptation of LAR within a week. However, they did not use such big shifts in light

Table 1. The specific leaf weight (SLW) in mg.cm^{-2} of the individual leaves of *Geum urbanum* before and after the transfer (T) from a high (H) to a low (L) light intensity in the glass house.

	1	2	3	4	5	6	7	leaf number
H (t)	3.5	3.5	4.2	4.5	–	–	–	
H (e)	4.0	4.3	5.6	6.7	5.6	5.0	4.0	
T (e)	2.2	2.4	2.6	2.7	1.6	1.4	–	
L (e)	average 1.2				–	–	–	
treatment								

(t) on the moment of transfer.
(e) at the end of the experiment.

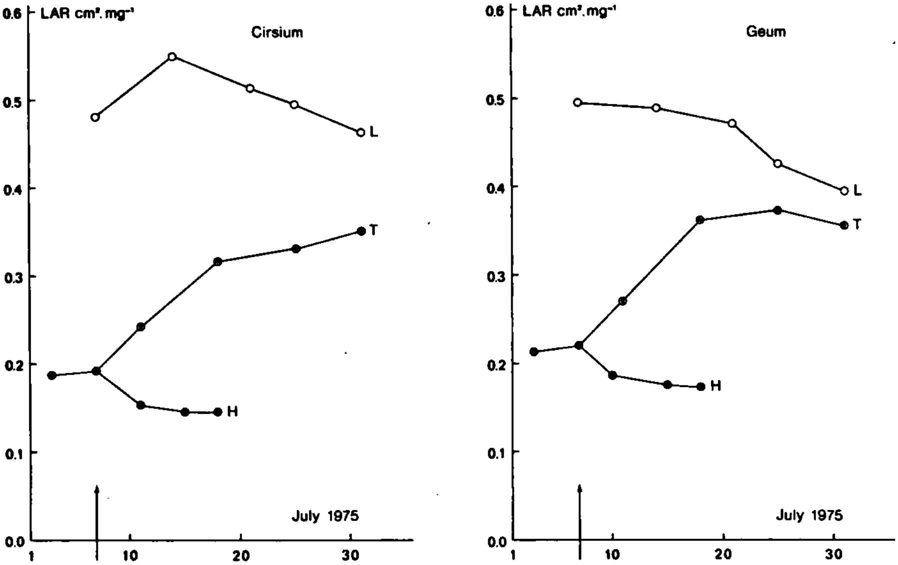

Fig. 4. The course of the leaf area ratio (LAR) of vegetative plants in full daylight (H), 4.6% daylight (L) and after the transfer (T). The moment of transfer is indicated by arrows.

intensity as were used here. Like in the present experiments, they found a lower RGR with plants transferred from a high to a low intensity than with control plants at a low intensity. The lower RGR (*fig. 1*) after transfer can be explained by the fact that the plants have a lower LAR. But the reason why their growth rate did not increase parallel to the subsequent increasing LAR is not clear.

3.2. Growth in the generative phase

The dry weight increase of the above ground and underground parts are shown in *fig. 5*. In full daylight the relative growth rate of the two species was about the same, although the size of the *Geum* plants was much smaller (less dry weight and a lower water content). The growth of the underground parts of *Cirsium* tended to slow down in June at the onset of flowering. In 4.6% daylight both species showed a very low rate of dry weight increase. The relative proportion of the underground part is greater in *Geum* than in *Cirsium*. However, more special differences appeared when the plants were transferred from full daylight to 4.6%. After this, *Geum* showed a gradual increase in dry weight of the above ground parts, but in *Cirsium* no net dry weight increase could be demonstrated. After the transfer the leaf area increase reacted in a way similar to the one in the vegetative phase (*fig. 6*). At first the leaf area continued to increase at the same rate, but afterwards it stopped (*Cirsium*) or continued at a lower rate (*Geum*). It is striking that especially in *Cirsium*, leaf areas hardly differed between the high and the low light intensity treatments. This is in

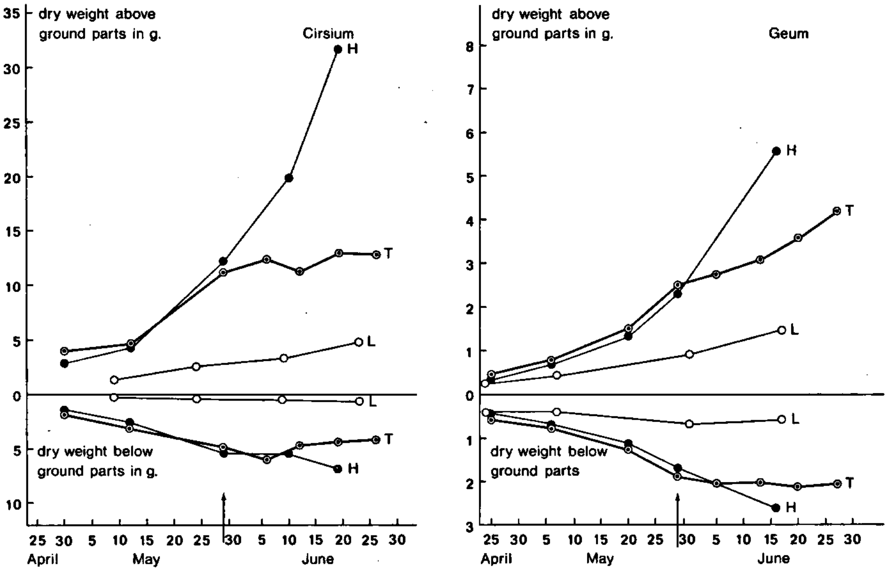

Fig. 5. The dry weight increase of generative plants of *Cirsium palustre* and *Geum urbanum* in full daylight (H), 4.6% daylight (L) and after the transfer from full daylight to 4.6% daylight (T). The moment of transfer indicated by arrows.

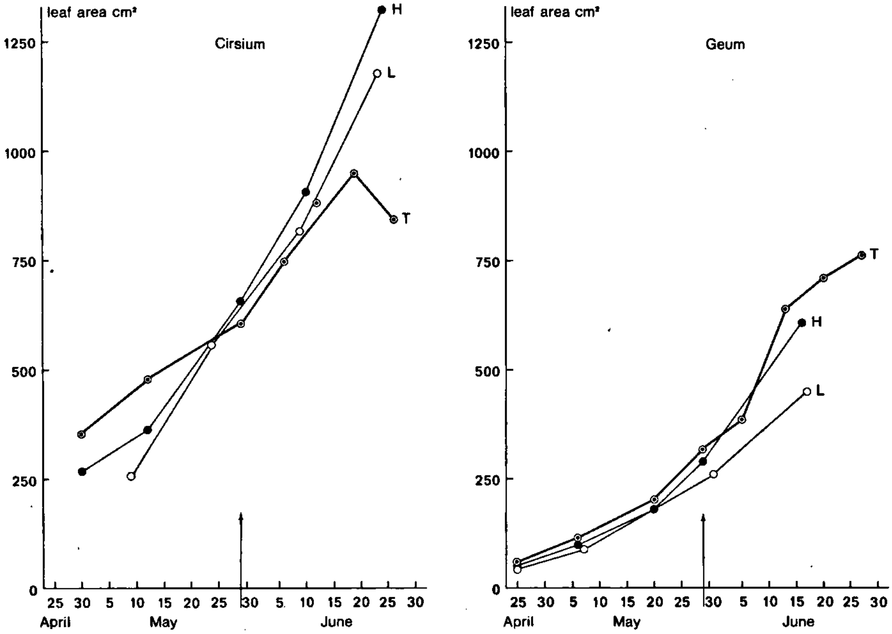

Fig. 6. The leaf area increase of generative plants of *Cirsium palustre* and *Geum urbanum* in the different light treatments (see *fig. 5*).

contrast with the vegetative phase, the plants in full daylight had a much higher leaf area growth rate (*fig. 2*). The effects described above were also reflected in the LAR (*fig. 7*). When both species were grown in a low light intensity, the LAR was relatively high (*Cirsium*) or became high (*Geum*). In full daylight the LAR was much lower. *Cirsium* showed a gradual decline during its development, but *Geum* showed a more or less constant level. When *Cirsium* was transferred just before flowering its LAR rose somewhat, but *Geum* was able to raise its LAR appreciably. There will be a morphological basis for this phenomenon. *Cirsium*, when continuously grown in 4.6% daylight, formed thin flat leaves and consequently had a high LAR (shade phenotype). In full daylight only the rosette leaves and the lower stem leaves had a considerable assimilation area, with the upper leaves being very small and spiny which resulted in a low LAR (sun phenotype). At the moment of transfer, the stems had reached about half there ultimate length and after the transfer stem growth proceeded in all treatments. As mentioned above, in full daylight the upper part of the stem had little assimilation area, only the winged stem with small spiny leaves and branches were formed. In 4.6% daylight, however, the upper part of the stem had thin flat leaves. After the plants had been transferred from full daylight to 4.6%, a shade type upper part of the stem could not be formed any more and a stem was formed with small leaves like in full daylight, but without branches. So in this stage of its development *Cirsium* had no possibility to increase its leaf area appreciably and the LAR only rose

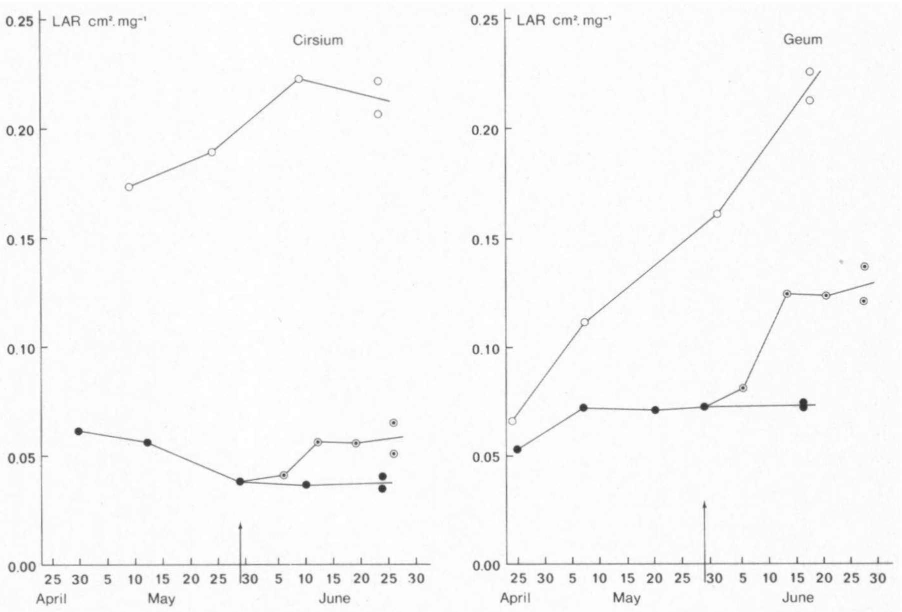

Fig. 7. The course of the leaf area ratio (LAR) of generative plants of *Cirsium palustre* and *Geum urbanum* in the different light treatments (see *fig. 5*).

slightly. Apparently the structure of the leaves was already determined to such an extent that shade leaves could not be formed any more (the transfer was just before flowering of the terminal bud). Moreover after the transfer all rosette leaves and lower stem leaves died, whereas at the plants that remained in full daylight, some 2 out of about 10 rosette leaves and all lower stem leaves persisted. In the low light intensity only those rosette leaves died which had been formed during the winter before the plants were potted.

After the transfer *Geum* continued to form new leaf area while the increase in dry weight slowed down, this resulted in an appreciable rise in LAR. The new leaves were lighter and the old leaves probably lost weight because of a sharp decline in average SLW. In contrast with *Cirsium*, *Geum* was able to form shade leaves after the transfer in the generative phase also. In all light treatments the leaf rosette of *Geum* continued to grow, while the oldest leaves died. Some of the lower stem leaves died in the high light intensity and transfer group. The fact that *Cirsium* had a small assimilation area at the time of the transfer and developed only a little green area afterwards, is likely to be the explanation for the complete check of dry weight increase after the transfer.

The ultimate stem length of *Geum* was about 60 cm in all light treatments (in the coppice about 75 cm). In 4.6% daylight the stems only sprouted in spring and did not branch. In the transfer group some plants developed young stems just before the transfer, afterwards no new stems were formed any more. In full daylight new stems were formed just before or during flowering of the first stems and afterwards as the old stems branched.

In all light treatments *Cirsium* reached a height of about 1.5 m (in the coppice up to 2 m). In 4.6% daylight the ultimate stem length was reached somewhat later than in full daylight. In the low light intensity and transfer group no branches were formed, but in full daylight many branches developed on the main axis. In low light intensity most *Cirsium* plants had to be supported in order to prevent them from falling over and breaking their stems. This was not the case in *Geum*. GRIME (1966) mentioned the "resistance" against etiolation as an important characteristic of shade tolerant woodland plants. Rapid attenuation in shade weakens the stem because of a lack of supporting tissue which causes the stem to collapse. In a dense short vegetation plants may benefit from this by rapidly reaching the light, but in a woodland it has no adaptive value and is even a disadvantage for the plant. In fact the few thistles starting to flower in the woodland all collapsed, as did other species of the felled area such as *Valeriana officinalis*.

The seed formation had just started at the termination of the experiment. But some plants which were allowed to grow somewhat further, showed that the seed production in full daylight was high in both species: however, both the low light intensity and the transfer treatment gave some seed production in *Geum*, but very little or none at all in *Cirsium*.

3.3. Photosynthesis and respiration

The course of the changing CO_2-exchange characteristics in the vegetative

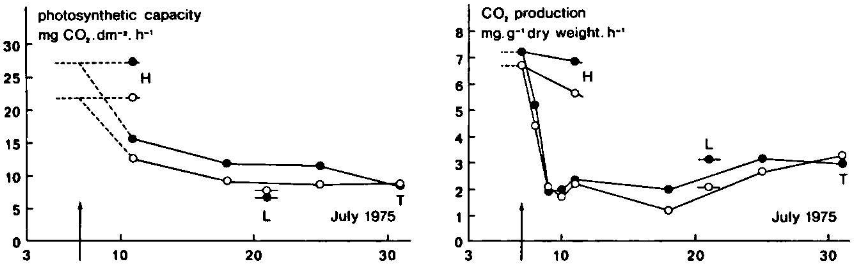

Fig. 8. The course of the photosynthetic capacity (a) and the respiration rate (b) at 20 °C after the transfer of vegetative plants from full daylight to 4.6%. ● *Cirsium palustre*; ○ *Geum urbanum*. The rates of plants continuously grown in full daylight (H) and 4.6% (L) are indicated.

phase after the transfer is shown in *fig. 8*. The respiration rate of the aboveground part of both species appeared to decline within two days to a new level, which was more or less similar to that of the control plants in the shade. The results agree rather well with those of McCree & Throughton (1966) who also demonstrated the greatest decline in respiration rate the first day after the transfer from a high to a low light intensity with white clover.

The photosynthetic capacity also appeared to decline after the transfer (*fig. 9*). This was not only caused by an increasing proportion of new leaves with a low capacity. The capacity of the leaves formed in full daylight also decreased, especially in *Cirsium*. This has also been found for *Geum* in the coppice (Pons 1976). In older leaves shaded in a growing crop, a similar decline has been

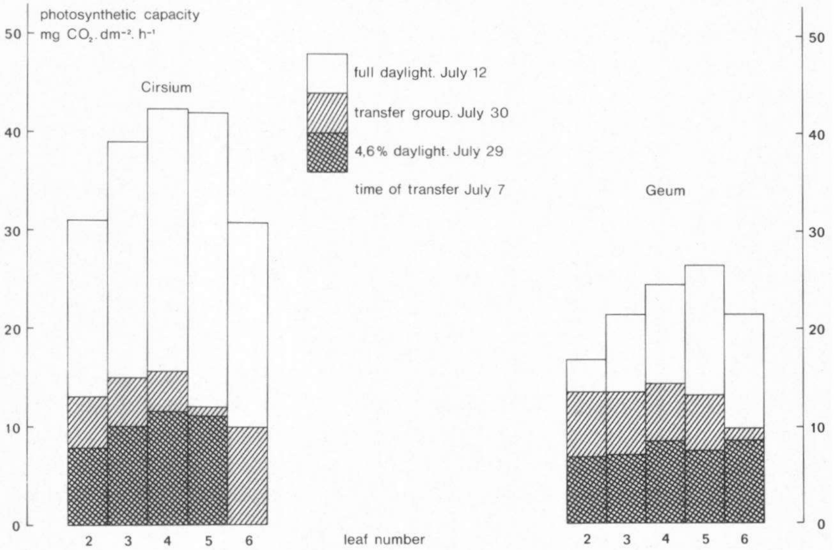

Fig. 9. The photosynthetic capacity of the individual leaves of vegetative plants in the different light treatments measured with the $^{14}CO_2$-method.

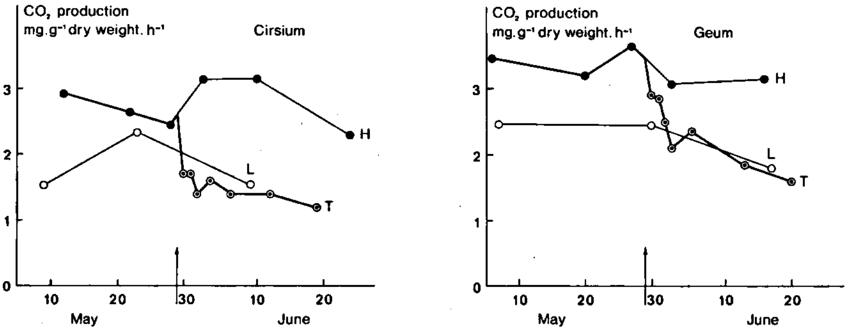

Fig. 10. The course of the respiration rate of generative plants of *Cirsium palustre* and *Geum urbanum* at 20°C in the different light treatments (symbols see *fig. 5*).

demonstrated (NAGARAJAH 1976). Possibly the carboxilation enzyme activity is lowered, causing the mesophyl resistance to increase, as TAYLOR & PEARCY (1976) showed for a number of woodland species in spring during the expansion of the tree foliage.

In the generative phase the respiration rate was measured at regular intervals (*fig. 10*). In general the respiration rates of *Geum* were somewhat higher than those of *Cirsium*. However, both species appeared to react in a similar way on a sudden decrease in light intensity. Directly after the transfer the respiration rates declined. These results are comparable with those obtained with vegetative plants (*fig. 7*). However, the values in full daylight were higher in vegetative plants than in generative plants expressed on a dry weight basis.

GRIME (1966) considers the respiration rate to be an important factor in the adaptation of shade tolerant and shade avoiding species. According to him the lower respiration rates of shade tolerant species should be regarded as an adaptation to the low light intensity in their habitat. Besides, he showed that shade avoiding species have a high respiration rate when grown in high light intensity, but he assumed that they maintain their high respiration rate when grown in a low light intensity. The present results and those of MCCREE & TROUGHTON (1966) show that this is not the case. It seems likely that the higher respiration rates of sun plants in high light intensity are the result of their higher growth rates. As soon as the growth rate declines as a consequence of shading the respiration rate will follow. There might be a difference in respiration rate between shade tolerant and shade avoiding species beneath their compensation point, as recent experiments of MAHMOUD & GRIME (1974) may indicate.

4. CONCLUSIONS

In the vegetative phase no differences appeared in these experiments which could explain the different behaviour of the two species in the ash coppice cycle. The growth rates are of the same order and the time of adaptation to the new light intensity after the transfer is rather similar. The sudden decline in light intensity in these experiments was even more extreme than the gradual lowering experienced by the plant in the coppice. Hence it cannot be expected that in the vegetative phase a decline in light intensity is more disadvantageous for *Cirsium palustre* than for *Geum urbanum*.

The generative plants of the two species reacted in a different way. Although *Geum* had a somewhat higher respiration rate before and after the transfer, this species adapted well to the lower light intensity by an increase of its LAR. *Cirsium*, however, did not manage to develop sufficient leaf area in this stage of its development in order to be able to compensate for the decline in light intensity and thus it was not well adapted to the new situation. When *Cirsium* was grown continuously in shade, it was well adapted with regard to its LAR, but the stems were too weak to avoid their falling over. So, although *Cirsium palustre* can be looked upon as shade tolerant in the vegetative phase, it is not in the generative phase.

In the vegetative phase as well as in the generative phase *Geum* grew well in full daylight with a good mineral and water supply. After coppicing this is not the case. Limitations in the root environment are likely to play a part in these exposed conditions. This phenomenon has also been described for some tropical crops (tea, coffe, cocoa) at a low nutrient level. At a high nutrient level the highest production was achieved in full daylight (MURRAY & NICHOLS 1966).

The fact that the respiration rate and the rate of photosynthesis react similarly in both species and that only differences in LAR and rigidity of the stem appeared, justifies the conclusion that differences in adaptation to shade in these plants are mainly morphological and less metabolical. This has also been concluded by GROEN (1973) in a comparative stydy with *Calendula officinalis* and *Impatiens parviflora*.

In the coppice there are two conditions in which *Cirsium palustre* experiences a decline in light intensity during its generative development. In the woodland phase of the coppice cycle some *Cirsium* plants may be present. In spring they begin to develop a stem rather slowly and they are shaded by the tree foliage rather early in their development. These plants have the typical shade phenotype and owing to their lack of rigidity they fall over in summer. In the third year of the coppice cycle quite a lot of rosettes may sprout in spring when the tree canopy has not yet closed. During that year the canopy closes and the *Cirsium* plants, having further developed, have the sun phenotype. They cannot adapt to the low light intensity and their growth ceases as shown in the present experiments.

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