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AN ECOPHYSIOLOGICAL STUDY IN THE FIELD LAYER OF ASH COPPICE I FIELD MEASUREMENTS

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SUMMARY

Growth and CO_2-exchange were measured on two species in the field layer of ash coppice. Two independent methods for the measurements of photosynthesis were used: the $^{14}CO_2$-method and the URAS-method. Before coppicing the woodland plant *Geum urbanum* showed its adaptation to the deciduous woodland environment: a high rate of growth and photosynthesis in the spring light phase, and an adaptation to the shade conditions in summer. The first year after coppicing, *Geum* showed stunted growth and partly disappeared. *Cirsium palustre*, on the other hand, germinated after coppicing and demonstrated a high assimilation rate and rapid vegetative growth, which led to abundant blooming in the second year of the coppice cycle.

1. INTRODUCTION

Ash coppice has a well-developed field layer, which makes it very suitable for research into the changes taking place in the field layer throughout the coppice cycle. Originally the coppice was felled once every 6 to 8 years. At present, however, the felling is neglected more and more in our area. Partly it has grown too high for profitable felling and is neglected, some coppice has already been transferred into normal woodland, whereas the remaining part has a shorter coppice cycle, namely once every 3 to 4 years.

Up till now little attention has been paid to the changes taking place in the field layer during the coppice cycle. WESTHOFF & MÖRZER BRUYNS (1964) have only indicated rough outlines. Recent production studies of coppiced woodland of FORD & NEWBOULD (1970) in sweet chestnut coppice and of KESTEMONT (1974) in birch and willow coppice did not include the field layer.

In addition to major quantitative shifts occurring in the populations of the field layer, the morphology of the plant also changes as a response to regular coppicing. A number of phases can be distinguished in the coppice cycle:

1) After coppicing in winter there is a clear felled area with stools, where the perennial woodland plants will partly survive. In spring seeds of annual species germinate and rosettes of some perennial species start to grow. In the first year a mainly vegetative development takes place in the field layer and the ashes will grow up to a man's height; the tree canopy has not yet closed at all.

2) In the second year after coppicing the rosettes of the species of the felled area sprout and a mainly generative development starts. The woodland plants are still there, but they have declined considerably in number and vitality. The ashes will reach a height of about 3 m, but they do not yet have a closed canopy.
3) During the third year the ashes will form a closed canopy, the species of the felled area have declined considerably in number and vitality, whereas the woodland plants start to recover gradually.
4) In the following year a gradual recovery of the woodland field layer will take place. This development, however, is usually interrupted because there will be another coppicing after 3 to 4 years. But sometimes the development will proceed when the coppicing is neglected.

The purpose of the present investigation is to arrive at a physiological explanation of the succession from the vegetation of the felled area to the woodland herb layer and vice versa. One species out of every group was chosen as a representative: *Geum urbanum* L. as a woodland plant and *Cirsium palustre* (L.) Scop. as a species of the felled area.

According to the study of LUNDEGÅRDH (1921) with plants from open and shady habitats, great differences might occur in photosynthetic capacity of the woodland plants and the species of the felled area. However, some woodland plants are reported to have a high photosynthetic capacity during the spring light phase of temperate deciduous woodland (GORYSHINA 1972, SPARLING 1967, KOYAMA & KAWANO 1973 and TAYLOR & PEARCY 1976). The present paper deals with field measurements only.

2. MATERIALS AND METHODS

2.1 Site description

The coppice where the observations were carried out is a long stretched piece of land, running from the levee along the river Kromme Rijn near Wijk bij Duurstede into a backswamp. Only the part on the river levee soil is dealt with in the present investigation. The plot is divided lengthwise into two parts, one half was felled for the last time about 15 years ago and is now neglected, the other half is felled every 3 to 4 years. The vegetation belongs to the association Macrophorbio-Alnetum.

2.2 Micrometeorological measurements

In 1973 and 1974 the air temperature was recorded by means of shielded thermohygrographs; in 1975 this was carried out with a Grant miniature temperature recorder.

The relative light intensity in the woodland was measured with two silicium photocells adapted to measure photosynthetic active radiation (PhAR 400–700 nm) under a leaf canopy (TFDL-Wageningen). The reference cell was placed on a post over the leaf canopy, the other cell was used at the desired place in the coppice, where both cells were recorded at the same time. The measurements were only carried out in overcast and quiet weather.

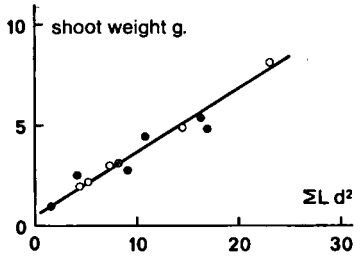


Fig. 1. Linear correlation of shoot weight and ΣLd^2 on August 15th. This was the last harvest in which the standard plants were included. L = stem length; d = smallest diameter at 4 cm height. ● Harvest plants; ○ Standard plants; ⊗ Standard plant shown in *figs.* 6 en 7.

2.3 Growth analysis

For the growth analysis in the field the indirect method was used (ONDOK 1971). A number of standard plants were protected against grazing by means of wire netting. Throughout the season measurements on these plants were carried out, while at the same time other plants were harvested (harvest plants). In *Geum urbanum* there appeared to be a linear relationship between shoot dry weight and $N.l^2$ before stem elongation (N = number of rosette leaves; l = length of the longest leaf with petiole). Later when the stems were there, between shoot dry weight and $\Sigma L.d^2$ (L = stem length; d = smallest stem diameter at about 4 cm height) *(fig. 1)*.

Roughly estimated, half of the root mass was lost in the heavy clay when harvesting. Therefore the weight of the excavated roots was multiplied by two. Moreover, there was no good correlation of rhizome weight with shoot weight, so the results for the underground parts are not very accurate.

2.4 CO_2-exchange measurements

Two independent methods were used. In the field a technique based on the uptake of $^{14}CO_2$ was employed. Next to this, leaves were taken to the laboratory where the CO_2-exchange characteristics were determined with an infrared gas analyser (URAS).

The field measurements with an air mixture containing $^{14}CO_2$ were carried out according to a system described by SHIMSHI (1969) and TIESZEN et al. (1974). The delivery system for air was comparable to that used by Tieszen, whereas the leaf chamber was used according to Shimshi. The incubation period was 30 sec with an air flow of 3 ot 4 l/h across a leaf area of about 1 cm^2. Dry air with a concentration of 265 ppm CO^2 was used; because of an error this concentration turned out to be rather low. The results are comparable with each other, but the maximum photosynthesis will be somewhat lower than it would have been with 330 ppm. The specific activity of the CO_2 in the air mixture was $1{,}66 \times 10^9$ dpm/mM.

The first measurements were always carried out at prevailing light conditions; later on shading at high light intensities (spring) or additional lighting at low light intensities (summer) was employed in order to acquire a complete photosynthesis-light curve. Fully expanded leaves, well exposed to the existing light intensity, were used for the measurements.

After exposure, the leaf disc was immediately punched and put into a counting vial with one ml soluene, so that the tissue was killed at once. In the laboratory the vial was heated at 65°C, thus causing the tissue to dissolve for the greater part. After that the solution was bleached in sunlight and after adding the counting liquid (Toluene PPO/POPOP) the sample was counted in a liquid scintillation counter with an efficiency of about 90%. Extraction of the leaf discs in alcohol showed results some 10% lower (cf. BRAVDO 1972), while the results were the same as those obtained with the in vial oxygen combustion method. The solution in soluene was preferred, especially because of the practical advantages: rapid inactivation of the leaf tissue after measurement in the field without any special equipment and further processing of the sample in the vial. CO_2 fixation rates were calculated according to the formula given by SHIMSHI (1969).

It was assumed that with this short incubation period, i.e. 45 sec at the utmost between the first contact with $^{14}CO_2$ and inactivation, the gross photosynthesis was more or less approximated. LUDWIG & CANVIN (1971) arrived at the conclusion that only after 30 to 45 sec the first measurable amount of $^{14}CO_2$ is excreted through photorespiration. TIESZEN et al. (1974) assume that their incubation period of 60 sec. lies somewhere in between the net and gross photosynthesis.

The URAS-measurements on detached leaves with their petioles in water (LARCHER 1963) were carried out in climatized gas-exchange chambers at a temperature of 20°C and a relative humidity of 80 to 90%. Philips HPI 400 W lamps were used with a water layer of 6 cm functioning as a heat filter. The measurements were performed in an open system with a fan in the chamber (LOUWERSE & VAN OORSCHOT 1969). Outside air was forced in through a barrel with some water in order to moisten the air and to level minor fluctuations in CO_2-concentration. The incoming air usually contained about 330 ppm CO_2 (measured with an URAS 2T); maximum depletion in the chamber was 20 to 25 ppm. When the rate of photosynthesis had reached a steady state at a light intensity which was assumed to be above saturation (about one hour) a complete photosynthesis-light curve was obtained by stepwise lowering the light intensity. From this curve the photosynthetic capacity and the light compensation point were read.

3. RESULTS

3.1 The microclimate

During the coppice cycle a great number of changes take place important to plant growth. Most of them are directly or indirectly related to changes in radiation, e.g.: radiation intensity, the red/far red ratio of the daylight, the temperature regime, air humidity, wind speed, water economy of the soil, rate of mineralization and soil compactness. The measurements, however, were restricted to the photosynthetic active radiation (PhAR) and the temperature regime.

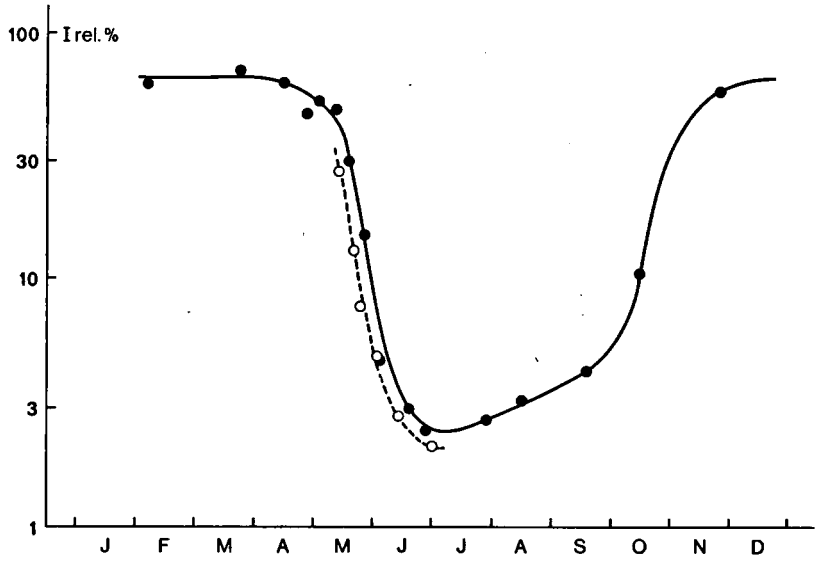


Fig. 2. The relative light intensity (PhAR 400–700 nm) throughout the year measured in overcast weather. ●——● 1974; ○- - - -○ 1975.

Light intensity

Throughout two seasons the relative transmission for PhAR in the neglected part of the coppice was measured *(fig. 2)*. In 1975 the foliage appeared earlier than in 1974. 4 phases can be distinguished which are of importance to the field layer:

1) the spring light phase, the period in early spring (until May) in which the trees are still leafless. Relative transmission is high, as is the absolute intensity in this time of the year.

2) the period of diminishing light intensity in May and June in which the leaf canopy expands.

3) the period of deep shade during summer under a closed leaf canopy, continuing until October.

4) the period throughout and after the leaf shedding in autumn and winter. The relative transmission rises, but the absolute intensity hardly increases, because of the strongly declining radiation in this time of the year (ANDERSON 1964). At first the felled area is exposed to full daylight, in the course of the year the light intensity decreases around the stools only. In the second year there is a strong spatial differentiation in the light climate, between the ashes the intensity is relatively high and underneath the stools it is low. In the course of the third year the tree canopy closes and a light climate is reached comparable to that of the neglected part of the coppice.

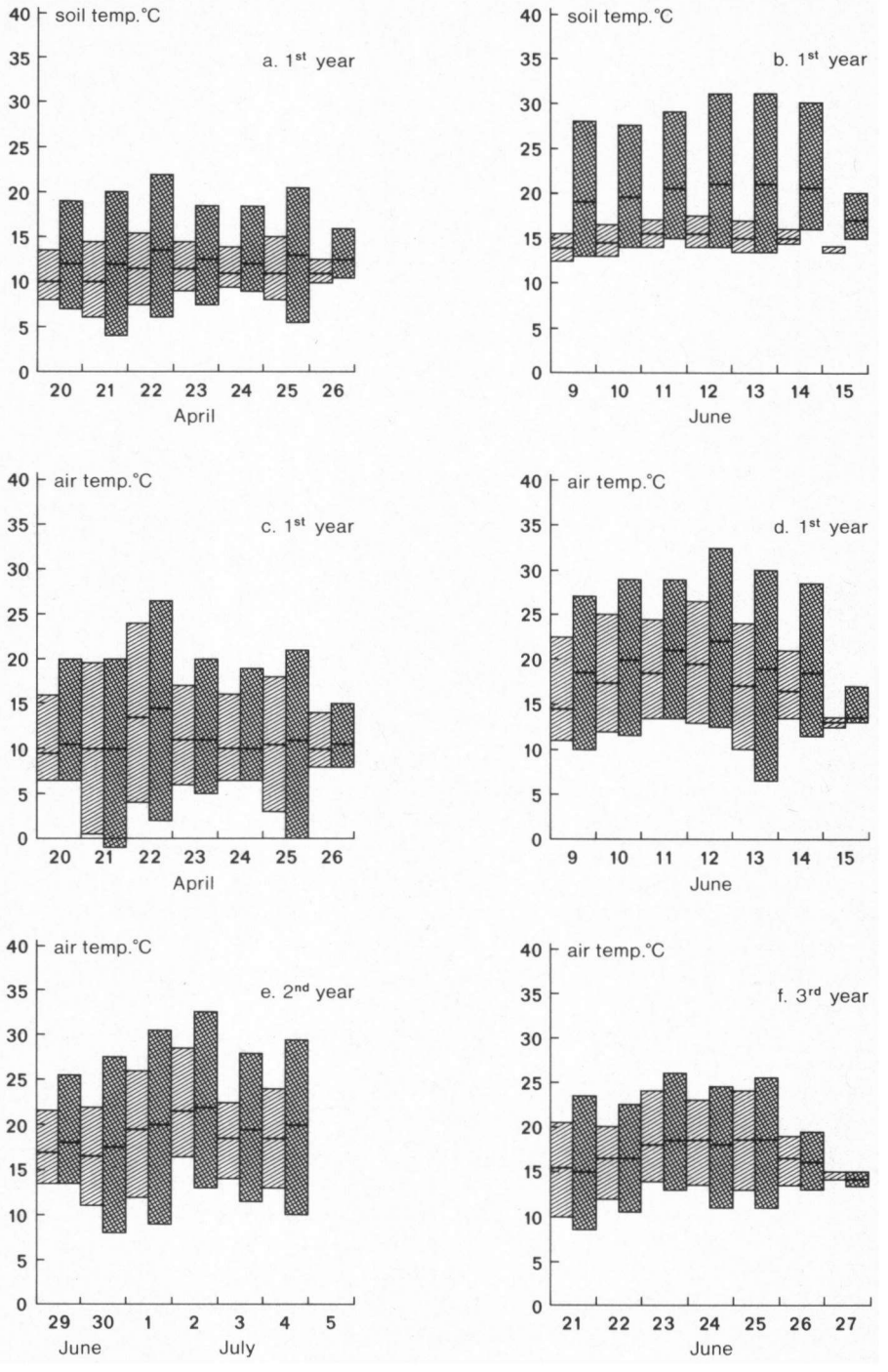

soil temp.°C
a. 1st year
April
soil temp.°C
b. 1st year
June
air temp.°C
c. 1st year
April
air temp.°C
d. 1st year
June
air temp.°C
e. 2nd year
June
July
air temp.°C
f. 3rd year
June

Fig. 3. Maximum, average and minimum temperatures of the air (height 50 cm) and the surface layer of the soil (depth 0.5 cm) in different stages of the coppice cycle compared with the neglected part. ▧ The neglected part of the coppice; ▩ The part of the coppice felled at regular intervals.
a) Soil temperatures the first year after coppicing, April 20–26, 1975
b) Soil temperatures the first year after coppicing, June 9–15, 1975
c) Air temperatures the first year after coppicing, April 20–26, 1975
d) Air temperatures the first year after coppicing, June 9–15, 1975
e) Air temperatures the second year after coppicing, June 29, July 4, 1975
f) Air temperatures the third year after coppicing, June 21–27, 1974

Temperature regime

The differences in average air temperature between the neglected part and the felled area are small *(fig. 3)*. The greatest differences were measured in the summer of the first year after coppicing. In the second year, at about the same time of the year, the differences were less and in the third year they completely disappeared. However, there were still some differences in maximum and minimum temperatures. The maxima are somewhat higher and the minima somewhat lower than in the neglected part.

The main differences in temperature regime were found in the top layer of the soil. In spring the average temperature at a depth of 0.5 cm in the felled area was several degrees higher than in the neglected part. When the differences in radiation strongly increased, combined with a lower water content of the topsoil and a still underdeveloped vegetation, as was the case in June, the result was a distinctly higher average temperature and during daytime a high maximum temperature in periods of sunshine. The temperature in the neglected part showed relatively little fluctuation in 24 hours.

3.2 Growth of Geum urbanum under a closed tree canopy

When the ashtree canopy has closed, the appearing and disappearing foliage is the dominating factor for the field layer. Physiological processes in *Geum urbanum (fig. 4)* were measured in the neglected part of the coppice throughout the seasons.

Geum has a leaf rosette throughout the year from which in late March or early April a number of stems start to sprout in the leaf axils as soon as growth conditions become favourable. During summer the plant goes through blooming and seed formation, while the leaf rosette continues to grow. In late summer or autumn the stems die. The leaf rosette is left intact and persists throughout winter *(fig. 5)*. In the course of the winter the plant looses many of its old rosette leaves, mainly because of grazing, whereas new small leaves are formed rather slowly. The underground part consists of a short rhizome and roots. The rhizome grows a little each year where the leaf rosette is attached, but gradually dies off at the other end.

Throughout the season of 1974 the growth and development of six plants was measured. All of them appeared to react in the same way qualitatively, but their weight varied considerably: from 2.5 to 9 g dry weight in the above-

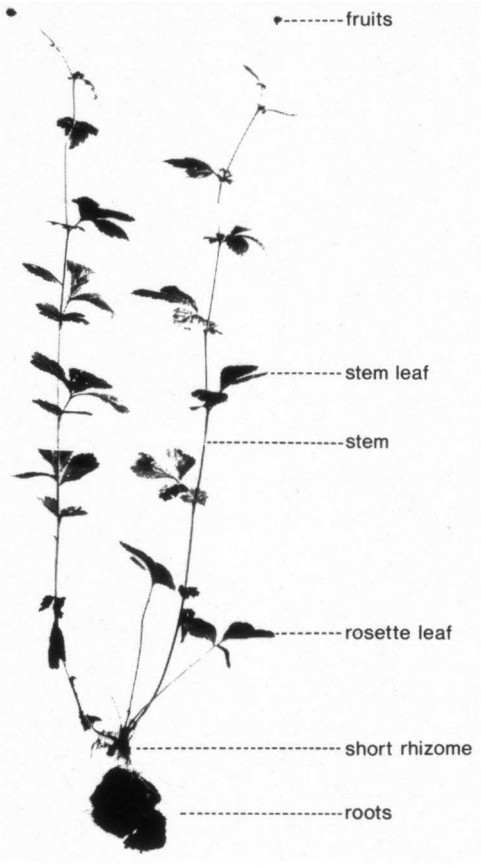


Fig. 4. *Geum urbanum* in summer (July) in the neglected part of the coppice.

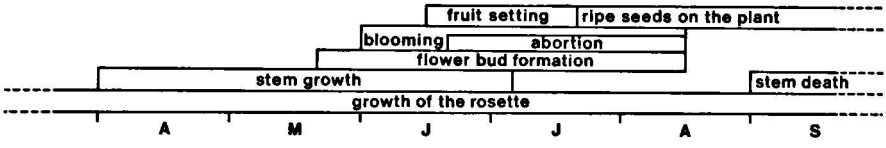
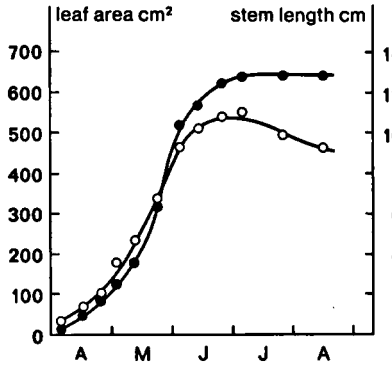


Fig. 5. Phenological stages of *Geum urbanum* in the neglected part of the coppice.

ground parts. *Figs. 6* and *7* show the results of one representative individual. The increase in dry weight of the aboveground part, starting in April, was more or less exponential; in May this phase terminated with the expansion of the tree foliage and the consequent decrease in light intensity. Stem growth, however, accelerated in late May until the blooming in early June. The underground part increased in weight much less which accounts for an ever decreasing part of the total weight. In June there was still some increase in weight and leaf area; the light intensity continued to decline until late June. During summer the leaf



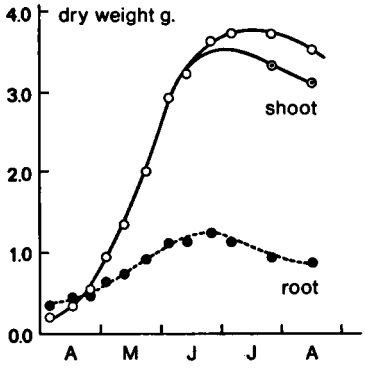


Fig. 6. Stemgrowth and leaf area increase of *Geum urbanum* in the neglected part of the coppice; one plant throughout the season.
●——● added stem length of the two stems;
○——○ total leaf area of the plant.

Fig. 7. The course of the dry weights of *Geum urbanum* in the neglected part of the coppice; One plant throughout the season, living biomass only. ○——○ aboveground part; ⊙——⊙ aboveground part without seed; ●- - -● Underground part.

rosette remained of about the same size, old leaves died as new leaves were formed. In July the number of rosette and stem leaves began to decrease because more leaves died than were formed. Every leaf formed in April had died in July (a number of rosette leaves and the first two stem leaves). This was accompanied by a decline in plant weight of the underground part as well as the aboveground part. During the period of deep shade in summer the plant was able to preserve a more or less constant weight, while the generative development was completed. Most of the seed formation took place in the fruits formed after the first blooming in early June. After that the plant bloomed regularly throughout the summer but with lessening success. Many flower buds and young fruits aborted. The ripe seeds of these plants were smaller than those of the plants in the garden, which were grown in full daylight.

After the beginning of shading, lighter leaves appeared to be formed and the already existing leaves turned somewhat lighter at the same time. The average specific leaf weight (SLW) declined *(fig. 8)*. It is possible that in this case there was some distribution of dry matter from old leaves to young growing parts. After September when the stems had died, the SLW of the remaining rosette increased in the course of the autumn, possibly in connection with the decreasing temperature and the ageing of the leaves. In January and February no measurements of SLW were carried out; but it can be assumed that the results are similar to those of December. In April the SLW is lower, so a rapid decline must have occurred in March because of lighter spring leaves being formed.

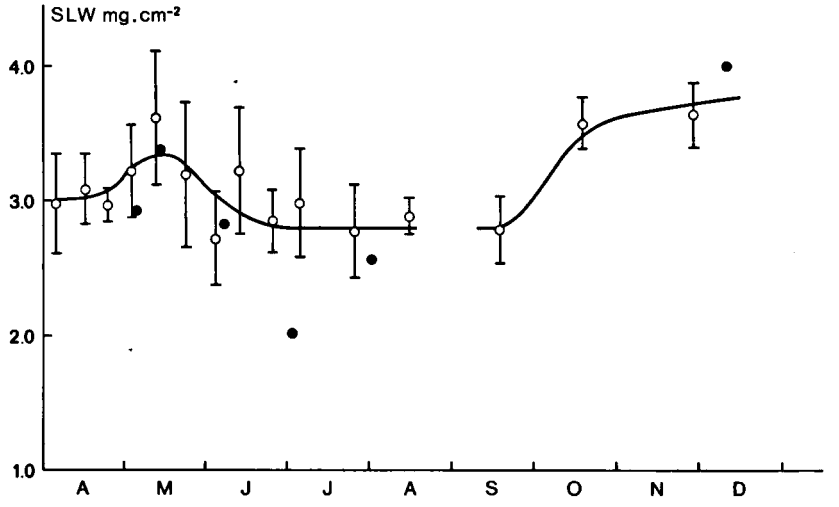


Fig. 8. The specific leaf weight (SLW) of *Geum urbanum* in the neglected part of the coppice. In spring and summer rosette and stem leaves, in autumn after stem death rosette leaves only. ○ All living leaves 1974; ● the average of some representative leaves, 1975; 95% confidence intervals indicated.

3.3 CO_2-exchange characteristics

In *fig. 9* the changing photosynthetic capacity throughout the year of *Geum urbanum* in the neglected part of the coppic is shown. In winter a low level was maintained, but in March new spring leaves had appeared with a much higher photosynthetic capacity, which was maintained till May. The high light intensity penetrating to the field layer in March, April and early May could be used efficiently for assimilation. However, as soon as the light intensity started to decline with the expansion of the tree foliage in early May, the photosynthetic capacity of the *Geum* leaves declined too, until June when a level was reached which was about 1/3 of the former. In this case it made no difference whether a leaf was measured that was formed in the spring light phase and had experienced a strong decline in light intensity afterwards (2nd stem leaf) or a leaf formed in a relatively low light intensity and which had consequently experienced a much smaller decline (5th stem leaf). It was remarkable that in winter the leaves had a photosynthesis-light curve, measured at 12 °C, similar to that of shade leaves in summer, measured at 20 °C, although the winter leaves were much thicker.

The light compensation point showed a comparable decline in May, correlated with the decreasing light intensity and the photosynthetic capacity. But from measurements in 1974 it appeared that in early April the compensation point at 20 °C was even higher than in early May. However, temperature is lower in early April and it is possible that the light compensation point remained about the same under conditions prevailing in the field. The value of the compensation point is temperature dependent, since it depends not only on the

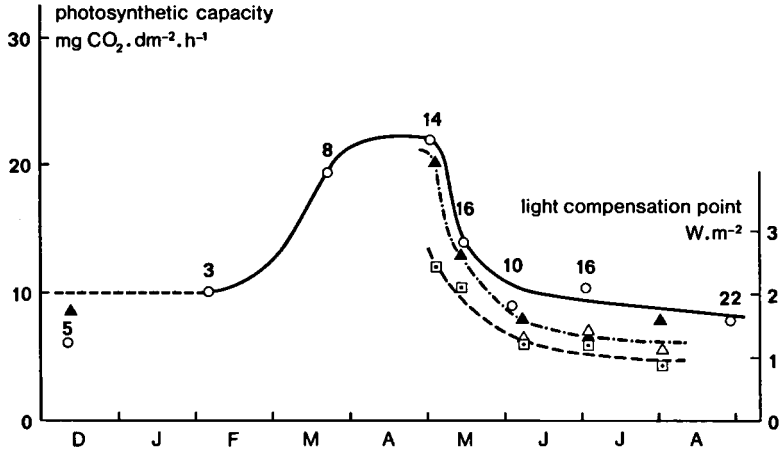


Fig. 9. Photosynthetic characteristics of the leaves of *Geum urbanum* in the neglected part of the coppice; 1974–1975.
- - - - O———O– Photosynthetic capacity; $^{14}CO_2$-method; field conditions, temperatures indicated.
Photosynthetic capacity; URAS-method; 20°C:
upper leaves – ▲– – – – –▲ –; lower leaves △–·–·–△–
– ⊡ – – – –⊡– Light compensation point 20°C.
The maximum photosynthesis could not be measured in december in the field with available light. The maximum measured value is indicated but the photosynthetic capacity is higher. The value of the photosynthetic capacity, obtained with the URAS-method, was determined at 12°C.

slope of the photosynthesis-light curve at limiting light intensities, but also on the level of dark respiration.

The results of the two independent methods of photosynthesis measurements appeared to agree rather well. The results of the $^{14}CO_2$-method are generally somewhat higher than those of the URAS-method. On June 3rd this was slightly different: the field temperatures were extremely low for this time of the year (10°C) with temperatures about freezing point at night. Photosynthesis might have been suboptimal, although this is not the case in spring at such temperatures. Shifts throughout the season in optimum temperature for photosynthesis and sensitivity to cold nights might have been of importance (LARCHER 1969).

The kind of photosynthesis-light curve obtained by means of the $^{14}CO_2$-method is shown in *fig. 10*. In spring the indicated maximum photosynthesis appeared to be reached on a clear day, which means that the rate of assimilation is high compared with a summer day. The assimilation on a clear summer day was much less. In diffuse light about (3 W/m^2) the rate of photosynthesis remained far below the capacity. In sunflecks, illuminating the woodland floor, the photosynthetic capacity could sometimes be reached. The leaves of *Geum* were in direct sunlight for periods of less than a second to about 15 minu-

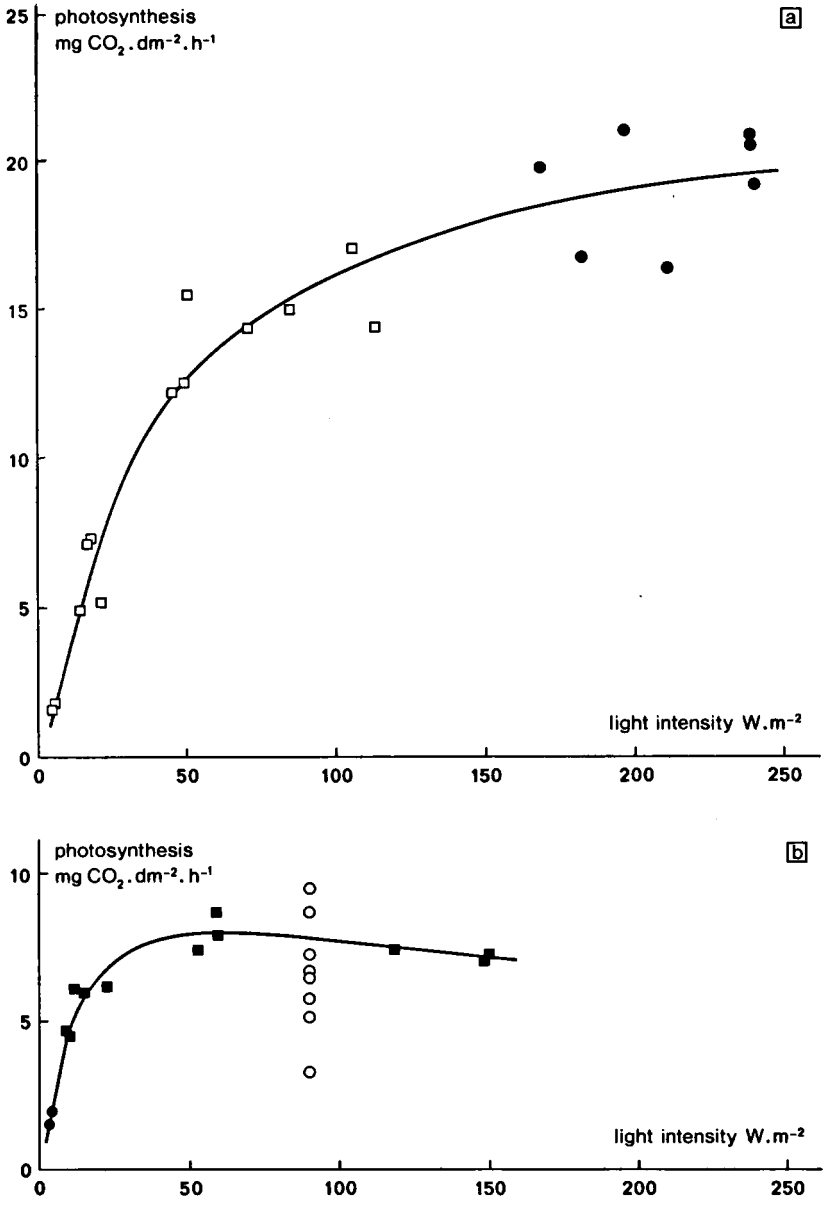


Fig. 10. The photosynthesis-light curves of the leaves of *Geum urbanum* exposed to the prevailing light conditions under the tree canopy in the neglected part of the coppice.
a) March 21, 1975, rosette leaves in spring.
● sunlight; □ artificially shaded.
b) August 28, the 5th and 6th stem leaves in summer.
● diffuse daylight under the tree canopy;
○ direct sunlight in moving sunflecks of different duration and intensity, see text; ■ additional lighting with an incandescent lamp.

Table 1. The average rate of photosynthesis in mg $CO^2/dm^2.h$ ($^{14}CO_2$-method) the first year after coppicing, in full sunlight ($\pm$ 300 W/m^2).

	1–7–1975	28–8–1975
Geum urbanum	8,8	–
Cirsium palustre	24,9	20,1
Carduus crispus	28,3	36,6
Valeriana officinalis	–	23,0

tes; the light intensity varied very much too, ranging from 10 to 250 W/m^2. The measurements were carried out on leaves in sunflecks of reasonable duration and intensity: a few minutes at least and a light intensity of at least 50 W/m^2 with an average of 90 to 100 W/m^2. The photosynthetic capacity was not always reached in sunflecks. A leaf having been exposed to light of a low intensity needs some time to reach its maximum photosynthesis after the intensity has increased to above the saturation level. The rates of photosynthesis below the capacity measured in the sunflecks will have been before the moment of reaching the capacity. In overcast weather the light intensity remains very low and so does the assimilation.

The first year after coppicing only occasional measurements were carried out with the $^{14}CO_2$-method in full sunlight. Full sunlight of about 300 W/m^2 is assumed to be enough to give light saturated photosynthesis. It is clear from *table 1* that *Geum urbanum* had a very low rate of photosynthesis in the felled area, compared with the woodland. On August 28 the species had virtually disappeared. The two thistle species had a much higher rate under the same conditions and *Valeriana*, a perennial of the felled area, only a slightly lower one. So the insufficient adaptation of *Geum* to the prevailing conditions after coppicing compared with the species of the felled area, appeared also in the photosynthetic behaviour of the species.

4. DISCUSSION

Changes in light intensity in the course of the year in deciduous woodlands in Western Europe have been described among others by ANDERSON (1964), PIERIK (1965), and EBER (1971a). Especially Andersons' observations show a peak in absolute light intensity penetrating to the forest floor in April. In woods of the association Alno-Padion to which the woodland under investigation belongs, the field layer turns green before the shrub and tree canopy does. So the field layer benefits from the relatively short period of high light intensity by building up an assimilation apparatus earlier than the tree canopy does. Hence adaptations of the woodland plants to low temperatures are important (GORYSHINA 1972). It was found that in winter at temperatures close to freezing point the assimilation of *Geum* did not cease to continue and there was also some leaf growth.

The photosynthetic capacity was high in March and April and when the tree foliage expanded it decreased. This has been described for other species too. GORYSHINA (1972) mentions it for *Aegopodium podagraria* and KOYAMA & KAWANO (1973) for *Maianthemum dilatatum*. SPARLING (1967) and TAYLOR & PEARCY (1976) have described this phenomenon for a great number of species; however, it is difficult to compare the data of Sparling, because he expressed photosynthesis on a leaf weight basis and does not mention leaf area data.

The concept "shade plant" should be used carefully and by no means can be applied to all woodland plants. It can in any case not be applied to the spring geophytes (BLACKMAN & RUTTER 1947, LÖHR 1952), but in general not to all other woodland plants either. Many of them will show sun plant characteristics in spring, then they will change physiologically and in summer they will show shade plant characteristics. *Geum urbanum* is an example of a woodland plant which seems to need the spring light phase to produce enough biomass to be able to survive. It would be interesting to study how other woodland plants deal with the changing light factor in a deciduous woodland (COOMBE 1966).

In general the maximum photosynthesis of woodland plants measured in summer is reported to be lower than those found for *Geum* (6–7 mg $CO_2/dm^2.h$. LUNDEGÅRDH (1921) found 4.8 for *Oxalis acetosella* and SCHULTZE (1972) 1.7 for *O. acetosella* and *Athyrium filix-femina*, HOLMGREN et al. (1965) for *Circea lutetiana* 4–5 and KOYAMA & KAWANO (1973) for *Maianthemum dilatatum* 4 mg $CO^2/dm^2.h$.

The fact that many plants in the field layer of temperate deciduous woodlands benefit from the spring light phase, explains the phenomenon that the main biomass production in the herb layer takes place in that period. This has been shown in studies of KUBIČEK & BRECHTL (1970), HUGHES (1975) and EBER (1971b). In most cases the highest biomass is found in June after a rapid increase in April and May. In the course of the summer there is sometimes a gradual decrease.

When we compare the results obtained with the two independent photosynthesis neasurement methods, they appear to be slightly different. As it is supposed that the $^{14}CO_2$-method approaches the gross photosynthesis and the URAS-method measures the net photosynthesis, it can be assumed that the results of the former method are higher. Dark respiration mostly amounts to some 10% of the maximum photosynthesis, whereas photorespiration is supposed to be 20–30% of it in C_3-plants (LAWLOR & FOCK 1975).
The $^{14}CO_2$-method should therefore give results which are some 30–40% higher, but it is in fact only 10–25%. Factors that could have caused this discrepancy are:
1) In the $^{14}CO_2$-method a lower CO_2-concentration (265 ppm) was used than in the URAS-method.
2) Photosynthesis in the field could have been farther from the optimum than in the measurements carried out under controlled conditions.
3) In the period of 45 sec between first contact with $^{14}CO_2$ and death of the

tissue there could have been some $^{14}CO_2$-efflux, which affects the results in a negative way.

The fact that *Geum urbanum* can not realize a high assimilation and growth after coppicing and *Cirsium palustre* is hardly able to grow in the woodland, indicates that shade tolerance and tolerance of high light intensities might be of importance in the observed succession (BLACKMAN & WILSON 1951). However, *Geum* is able to grow in a high light intensity in the spring light phase of the woodland and subsequently adapts itself to a lower intensity. The ability for this adaptation might be of importance as well. Besides, *Cirsium* is a biennial and must establish itself by means of seed every two years. So factors affecting seed germination might be important too. There are *Cirsium* seeds in the woodland soil but they do not germinate until after coppicing. Future experiments will deal with the importance of the light factor in the succession in the field layer during the coppice cycle.

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