herbicides used. Dicryl was used exclusively in the growth chamber studies. Since it is active as an inhibitor of the Hill reaction (*5*) one would expect a greater inhibition of growth during the daylight hours than at night, and this does occur. The occurrence of this phenomenon does not explain, however, why a compound administered at night is less inhibitory the following day than it is when administered during the light period, unless degradation or dilution by translocation occurs during the night. Of the chemicals tested dicryl, C-2059, and DCMU are considered to be inhibitors of the Hill reaction, but, in contrast to the first two, DCMU (the most active of the three) showed no evidence of diurnal activity. The mode of action of the fourth chemical, EPTC, is uncertain, but it is thought to act as a mitotic poison (*6*). The basis of its diurnal selectivity is problematic.

Despite the inconclusive nature of the tests performed in the growth chamber, there is a strong diurnal rhythm of sensitivity to herbicides in the field. The differences are large enough to warrant consideration of the practical importance of the time of day at which chemicals are applied. Preliminary tests fail to show the same diurnal response by soybean seedlings, and this suggests that rhythmic sensitivity might be used as a selective factor in herbicide action. The rhythmic nature of the response to the herbicides tested seems to be caused primarily by one or more rhythmic environmental factors, since under constant temperature and light the rhythm is not clearly defined.

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References and Notes

1. A. Sollberger, *Biological Rhythm Research* (Elsevier, New York, 1965).
2. A. Carlson and F. Serin, *Acta Pharmacol. Toxicol.* **6**, 181, 187 (1950); W. M. Davis, *Experientia* **18**, 235 (1962); S. T. Emlen and W. Kem, *Science* **142**, 1682 (1963); R. J. Ertel, F. Halberg, F. Ungar, *J. Pharmacol. Exp. Therap.* **146**, 395 (1964); E. F. Lutsch and R. W. Morris, *Science* **156**, 100 (1967); P. R. Wiepkema, *Nature* **209**, 937 (1966).
3. C. L. Cole and P. L. Adkisson, *Science* **144**, 1148 (1964).
4. B. Polcik, J. W. Nowosielski, J. A. Naegele, *ibid.* **145**, 405 (1964).
5. N. E. Good, *Plant Physiol.* **36**, 788 (1961).
6. L. J. Audus, *The Physiology and Biochemistry of Herbicides* (Academic Press, New York, 1964).
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Photosynthetic Utilization of Internal Carbon Dioxide by Hollow-Stemmed Plants

Abstract. *The hollow stems of wet-meadow and bog plants often contain relatively large amounts of carbon dioxide. The internal carbon dioxide apparently originates from respiration of root and stem cells. Some of this carbon dioxide is fixed photosynthetically by stem tissues and is thus recycled within the plant. Such internal stem photosynthesis would be advantageous, particularly in the early stages of growth in cold, wet, high-altitude environments.*

Many herbaceous plants characteristic of moist mountain meadows and bogs have hollow stems. Such a hollow stem is part of a system of lacunar air passages which connects the leaves with the roots. Thus, air and individual gases can move internally from one part of the plant to another by diffusion and mass movement through such a porous aerenchyma (*1*). We found that these stems often contain much higher concentrations of carbon dioxide than is present in the external air and that the concentration varies with light and temperature. There is usually a carbon dioxide flux upward inside the stem which originates from respiration in the roots, rhizomes, and in the rapidly growing stems themselves. Our experiments show that much of this carbon dioxide is apparently utilized in photosynthesis by green-stem tissue and is thus recycled within the plant.

We first became aware of the carbon dioxide flux within the stem while measuring photosynthesis and respiration of plants in wet subalpine meadows at 3100-m elevation in the Medicine Bow Mountains, Wyoming. These wet meadows are characterized by many species of grasses, sedges, and dicotyledonous plants. Typical dicots are *Delphinium barbeyi* Huth, *Mertensia ciliata* (James) G. Don., and *Senecio triangularis* Hook. Plants of all of these species grow very rapidly after snowmelt in June, and all have hollow stems with many chloroplasts in the cortical tissue. There are also some chloroplasts in the outer pith cells.

We extracted gas samples, with a hypodermic syringe, from the stems of these plants in the field and injected the samples into a closed, infrared gas-analyzer system. The concentration of carbon dioxide in the stems ranged from two to over fifty times the carbon dioxide content in the ambient air. Shading the plants increased the carbon dioxide concentration in the stem.

Both carbon dioxide and oxygen fluxes and gradients have been previously described in plants growing in wet habitats (*1*); the downward flux of oxygen which is derived both from photosynthesis and from ambient air through the stomates has been emphasized. The oxygen is utilized in root and rhizome respiration; the aerenchyma serves not only as a diffusion pathway during the day, but as a reservior of oxygen at night.

No evidence for the utilization of the internal stem carbon dioxide in photosynthesis has been presented, although such utilization seems likely. For example, Hartman and Brown (*2*) found that the aerenchyma in *Elodea canadensis*, a submersed vascular plant in lakes, acts as a reservoir for carbon dioxide which is utilized in photosynthesis to such an extent that the internal supply is depleted by midafternoon.

To investigate possible relations between internal carbon dioxide and photosynthesis of subalpine meadow plants, we measured carbon dioxide exchange within the stems of plants of *Mertensia ciliata* (grown in the greenhouse) by connecting the internal atmosphere of the plant with an open infrared gas-analysis system (*3*) (Fig. 1). Ambient air, drawn by polyethylene tubing from above our laboratory building, could

Table 1. Photosynthesis within the stem of *Mertensia ciliata*, as indicated by the decrease in detectable carbon dioxide flux with increase in light.

Light intensity on vertical surface (10^3 lu/m^2)	Temperature (°C)			Stem CO_2 flux (μg/min)	Gross photosynthesis (μg cm^{-2} min^{-1})
	Soil	Stem air	Chamber		
Dark	22	18	20	9.7	
33	22	20	20	7.3	0.11
36	22	21	22	6.8	.13
44	22	22	22	6.3	.15

be passed in individual streams through both the stem of the plant and the Plexiglas chamber surrounding the plant shoot. By means of stopcock switches, "chamber" air or "stem" air could be alternately sent through the infrared analyzer.

At temperatures of 20°C (both air and soil) and a steady flow rate through the *Mertensia* stems of 0.2 liter per minute, it was possible to measure upward fluxes of CO_2 in stems. These fluxes ranged from 5.3 to 9.7 μg per minute in the dark. When vertical stems (with leaves) were illuminated from above and from the sides with about 44×10^3 lu/m^2 (as measured on vertical surface at stem position), the fluxes decreased to a range of 2.4 to 6.3 μg per minute. Differences in flux between full light and dark ranged from 2.9 to as much as 5.6 μg per minute. The decreases in upward flux came within less than a minute after the lights were turned on. Such rapid decreases could be due only to photosynthesis. The data from one of these experiments and the decrease in the internal carbon dioxide flux with increasing light are shown in Table 1. Internal stem photosynthesis was not saturated with our laboratory maximum of 44×10^3 lu/m^2; in the field, light values on vertical surfaces can be much higher.

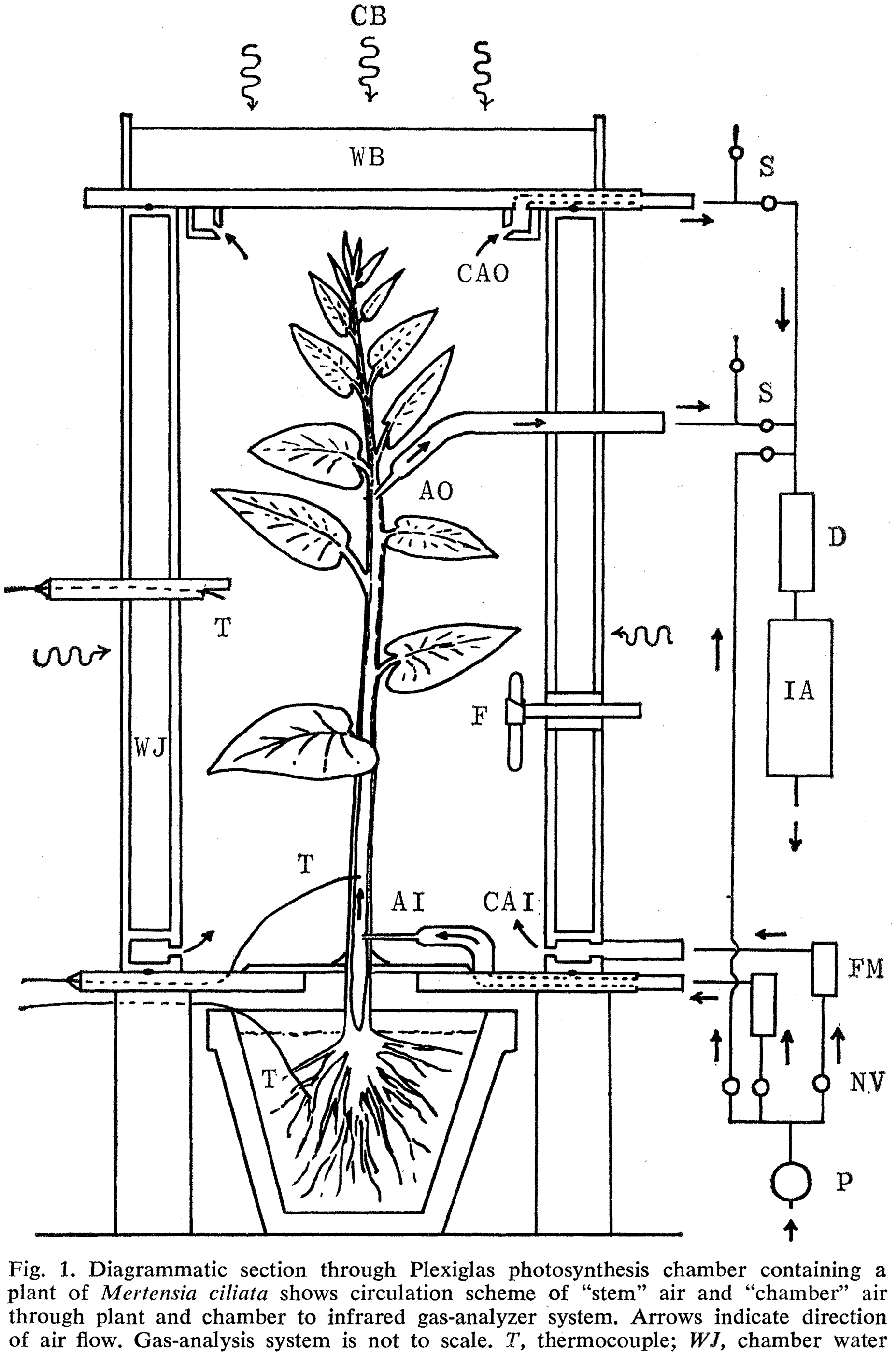

Fig. 1. Diagrammatic section through Plexiglas photosynthesis chamber containing a plant of *Mertensia ciliata* shows circulation scheme of "stem" air and "chamber" air through plant and chamber to infrared gas-analyzer system. Arrows indicate direction of air flow. Gas-analysis system is not to scale. *T*, thermocouple; *WJ*, chamber water jacket; *WB*, water barrier; *CB*, "Cool Beam" lights; *AI*, hypodermic needle stem air input; *AO*, glass capillary stem air output; *FM*, flow meter; *NV*, needle valve; *P*, pump; *IA*, infrared gas analyzer; *D*, "Drierite" columns and filter; *S*, stopcock; *F*, fan; *CAI*, chamber air input; *CAO*, chamber air output.

To approximate natural conditions of CO_2 flux in the stem, air flow was stopped for various periods of time up to 15 minutes in the light or dark. This allowed us to measure the relative accumulation of carbon dioxide in the stem up to the time of resumption of flow. The results (Fig. 2) indicate the effect of light and photosynthesis in reducing the concentration of carbon dioxide in the stem.

Gross photosynthesis resulting from uptake of internal carbon dioxide was calculated from the uptake rate on the basis of internal surface areas of the hollow stems. At temperatures of 20°C and light intensities of about 44×10^3 lu/m^2, gross internal stem photosynthesis ranged mostly between 0.13 and 0.15 μg of CO_2 cm^{-2} min^{-1}. Some measurements, however, were as high as 0.35 μg cm^{-2} min^{-1}. Because a whole plant was enclosed in the photosynthetic chamber, it was possible to compare internal gross photosynthesis rate with that (*4*) of the whole external plant, including leaves. At ambient carbon dioxide concentrations of about 0.58 mg per liter, internal stem gross photosynthesis on a unit area basis ranged from 19 to 36 percent of the rate occurring in leaf tissue. In one set of measurements at an ambient level of 0.57 mg of CO_2 per liter, gross internal stem photosynthesis was 0.13 μg of CO_2 cm^{-2} min^{-1}. The concentration of carbon dioxide in the chamber outside the plant was then dropped to 0.39 mg per liter, thus approximating the CO_2 concentration at an altitude of 3100 m. Gross internal stem photosynthesis was then 0.02 μg of CO_2 cm^{-2} min^{-1}, whereas the rate for the rest of the plant dropped from 0.70 to 0.56 μg cm^{-2} min^{-1}. Apparently, the gross internal stem photosynthesis rate is relatively independent of low, ambient concentrations of carbon dioxide whereas photosynthesis in the leaves, of course, is not (5).

The upward carbon dioxide flux was increased both in the light and in the

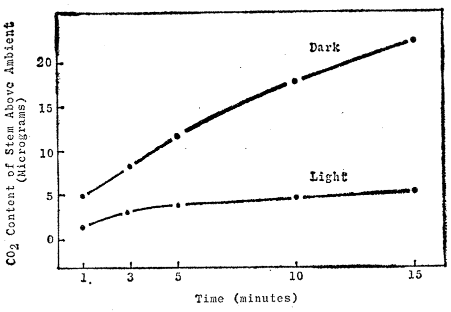

Fig. 2. Relative accumulation of carbon dioxide in the stem of *Mertensia ciliata* in the dark and light, as measured for 15 minutes. Zero, ambient carbon dioxide concentration (0.585 mg per liter).

dark by increasing the temperature of the root environment while holding stem temperature constant at 20°C. In the dark, the flux showed a straight-line relation with root temperature from 3.8 μg per minute at 19°C to 10.6 μg per minute at 38°C. Lowering the root temperature decreased the flux. These data indicate that a fair proportion of the carbon dioxide flux in a mature plant is coming from the roots or rhizomes, or both. To determine this proportion in a mature plant of *Mertensia*, the plant was sealed in the chamber (Fig. 1), and the flux through the intact stem was measured in the dark at 18°C as 6.2 μg per minute at a flow-rate of 0.2 liter per minute. The stem was then cut near the base and connected directly to the input air line, and the joint was sealed with silicone rubber. The flux originating in the stem proper was measured as 2.8 μg per minute. Input and output air lines were then connected to the stump and sealed, and flux measurements were made under the same conditions. The flux from the stump (therefore from the roots) was 3.4 μg per minute. These two figures add up to 6.2 μg per minute, the flux through the intact plant at the start. In this experiment, the root system contributed 55 percent of the flux, whereas the shoot contributed 45 percent. The proportions of the internal carbon dioxide flux undoubtedly vary with age of plant, temperatures, partial pressure of ambient carbon dioxide, and soil aeration.

During early growth conditions after snowmelt at high altitudes, stems of wet-meadow plants may be 1 or 2 dm high before leaf expansion. At this time, respiration rates are very high, and external photosynthesis is very low (*6*). Under these circumstances, most of the plant's photosynthesis is probably within the stem where the partial pressure of CO_2 is considerably above ambient and where temperatures are more favorable for photosynthesis. To measure internal stem temperatures under field conditions, a hypodermic-needle thermistor probe was inserted in the hollow stem of a young plant of *Delphinium barbeyi* emerging from a snowbank at 3100 m. For several days and nights, these internal temperatures were compared with those of the external air as measured by a shielded thermistor. In full sunlight, internal stem temperatures between 10 a.m. and 3 p.m. ranged from 30° to 37°C, while ambient air temperatures ranged from 13° to 16°C. When the shadow of a tree crossed the plant, the internal temperature dropped to that of the ambient air; at night, both temperatures dropped to freezing. In the laboratory, uptake of carbon dioxide within the stem decreased when the temperature of the air passing either through the stem or through the chamber was lowered. Since our field results indicate relatively high internal temperatures and an internal atmosphere rich in carbon dioxide, hollow stems apparently provide a favorable environment, similar to that of a greenhouse, for photosynthesis under low ambient temperatures and the low partial pressures of carbon dioxide at high altitudes.

The hollow stem has a structural advantage in rapidly growing plants of cold, high-altitude, wet meadows where the growing season is short. Apparently, it also has a physiological advantage in that some of the respiratory carbon dioxide may be used in photosynthesis within the stem, thus making more efficient use of carbon dioxide at high altitudes where the partial pressure of ambient carbon dioxide is relatively low (*5*). During early stages of growth after release from snow cover, root and stem respiration rates are relatively high even at low ambient temperatures. Under these conditions, internal stem photosynthesis may be the major photosynthetic system of the plant until the leaves are fully expanded and the weather becomes warm.

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References and Notes

1. A. Barthelemy, *Ann. Sci. Natur. Bot.* [5] **19**, 131 (1874); V. M. Conway, *New Phytol.* **36**, 64 (1937); M. H. van Raalte, *Ann Jard. Bot. Buitenzorg* **50**, 99 (1940); H. E. Laing, *Amer. J. Bot.* **27**, 861 (1940); D. A. Barber, M. Ebert, N. T. S. Evans, *J. Exp. Bot.* **13**, 397 (1962); J. M. Teal and J. W. Kanwisher, *ibid.* **17**, 355 (1966); W. T. Williams and D. A. Barber, *Symp. Soc. Exp. Biol.* **15**, 132 (1961); D. A. Barber, *J. Exp. Bot.* **12**, 243 (1961); K. B. Vallance and D. A. Coult, *ibid.* **2**, 212 (1951); D. A. Coult and K. B. Vallance, *ibid.* **9**, 384 (1958); H. van der Heide, B. M. de Boer-Bolt, M. H. van Raalte, *Acta Bot. Neerl.* **12**, 231 (1963); W. Armstrong, *Nature* **204**, 801 (1964); J. M. Teal and J. W. Kanwisher, *Limnol. Oceanogr.* **6**, 388 (1961); ———, *J. Exp. Bot.* **17**, 355 (1966).
2. R. T. Hartman and D. L. Brown, *Ecology* **48**, 252 (1967).
3. The infrared analyzer used for both laboratory and field measurements was a Beckman Instruments model 15, calibrated for 0 to 600 ppm of carbon dioxide. We thank J. J. Godfrey for assistance in the construction of the assimilation chamber.
4. Gross photosynthesis of whole plant represents net photosynthesis and dark respiration.
5. W. D. Billings, E. E. C. Clebsch, H. A. Mooney, *Science* **133**, 1834 (1961).
6. E. B. Hadley and L. C. Bliss, *Ecol. Monogr.* **34**, 331 (1964).
7. Supported by NSF grants GB-1219 and G-5501.

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Autosomal Linkage between the Albumin and Gc Loci in Humans

Abstract. *Naskapi and Montagnais families segregating for albumin Naskapi give evidence for close linkage of the* Gc *and albumin loci with a high probability. One possible case of crossover is included in the data.*

We have recently reported a "new" variant of serum albumin that occurs in North American Indians (*1*). This protein, which has been called albumin Naskapi, is inherited as a simple autosomal trait, and its presence is determined by the gene Al^{Na} that appears to be allelic with the gene Al^{A} that determines the presence of the common albumin (albumin A). The group specific substance system (Gc) was discovered by Hirschfeld (*2*); Gc is a protein that migrates in the alpha-globulin region on agar-gel and paper electrophoresis and in the post-albumin region on starch-gel electrophoresis. There are three common phenotypes (Gc 1-1, Gc 2-2, and Gc 1-2) that are controlled by two genes, Gc^1 and Gc^2, segregating at an autosomal locus. Other rare phenotypes are also known.

In this report, we present evidence for close linkage between the loci that determine these two inherited traits, using family material from the Naskapi and Montagnais Indians of the Labrador peninsula. A brief preliminary report has been published (*3*).

Naskapi and Montagnais Indians belong to the Algonquin language group.