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depending upon the species. All species, except the unleached seeds of *Plantago insularis*, when stored at 50°C, reached their maximum germination within the first 5 weeks of storage. Continued storage at 50°C resulted in a progressive loss in viability. After storage at 75°C, the seeds of all species failed to germinate. Throughout the 10-week period, the refrigerated (4°C) seeds germinated only as well as the initial planting of fresh seeds.

Since seeds of most of the species studied show vastly improved germination when given a 50°C treatment for 1-4 weeks, this technique has been employed in subsequent studies as a convenient method for growing plants from fresh seeds soon after collection. To achieve comparable germination with seeds stored at room temperature, a maturation period of up to 5 months is needed. Several generations of plants may be grown within a single year if seeds from each generation are given heat treatment.

In several replicated trials of the 50°C treatment, the percentage germination varied somewhat from that shown in Table 1, but nevertheless, germination was improved in each case over that of untreated seeds. One source of variability may have been the difference in degree of maturation of the seeds at the time of collection. In

addition, these native populations are probably characterized by a range of genetically conditioned variations in the physiology of germination. Large numbers of seeds were collected and thoroughly mixed to increase the probability that these sources of variability were randomly distributed among the plantings.

The results were essentially the same from seeds planted in sand and from seeds planted on moist filter paper. This would indicate that leaching is not a necessary factor in most instances. Germination of *Plantago insularis*, however, was unaffected by heat treatment yet attained 100% when seeds were kept in a stream of flowing water for about 24 hours prior to planting.

The results of heat pre-treatment suggest that in the field the prevalent high temperatures following seed dispersal may help promote seed maturation among many species of desert plants.

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## PLANT PIGMENTS IN WOODLAND SOILS<sup>1</sup>

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*Abstract.* Low concentrations of carotenoids and chlorophyll derivatives are present in the organic matter of surface horizons of woodland soils. Before leaf fall chlorophyll breaks down more rapidly than carotenoids, while the reverse is true in soils. Pigment concentrations in the organic matter of sediments from productive lakes are usually much higher than concentrations in the litter and humus layers of woodland soils. This suggests that the contribution of woodland litter and humus to the organic matter in such sediments is outweighed by contributions from aquatic macrophytes and phytoplankton.

The degree of preservation of plant pigments in organic lake sediments is now recognized as a helpful guide to present and past productivity (Gorham 1960, 1961, Fogg and Belcher 1961, Belcher and Fogg 1964). Although much of the organic matter in these sediments may come from the drainage basins of the lakes, little attention has been paid to plant pigments in terrestrial soils, probably on the assumption of low levels in aerobic situations. Chlorophyll derivatives (mainly pheophytins or pheophorbides) are in fact low in woodland soils (Gorham 1959, Gorham and Sanger 1964).

This paper examines the abundance of carotenoids as well as chlorophyll derivatives in organic soils under oak (*Quercus ellipsoidalis* and *Q. borealis*) and pine (*Pinus strobus*) at Cedar Creek in central Minnesota. The two pine stands are quite homogeneous, while the two oak stands are more mixed, with considerable proportions of other trees (*Acer rubrum*, *Pinus strobus*,

*Ostrya virginiana*, *Betula papyrifera*) and an abundance of shrubs (*Corylus* spp.).

#### METHODS

Samples of organic horizons 5-6 cm thick were taken within 30- by 30-cm quadrats at four sites between June 17 and 30, 1964, and separated into upper ( $L_1$ ) and lower ( $L_2$ ) litter layers and moderately decomposed (F) and well-decomposed (H) humus layers. Tree leaves and litter were also collected at various times (see Table 2).

Pigments were extracted in the dark with acetone, usually from representative samples of about 2 g fresh weight. Chlorophyll derivatives were measured with a Beckman DU spectrophotometer at the red peak between 660 and 670 m $\mu$  (Gorham and Sanger 1964). Aliquots of acetone were saponified with methanolic potassium hydroxide in the dark and carotenoids were extracted into light petroleum ether. Hypophasic carotenoids (with two or more hydroxyl groups) were further partitioned into 90% methanol, the epiphasic pigments (without hydroxyl groups) remaining in the petroleum ether. Monohydroxy compounds may be found in both phases. Both epi- and hypophasic carotenoids were measured spectro-

<sup>1</sup> We are indebted to Dr. W. H. Marshall, Director, Cedar Creek Natural History Area, for permission to collect samples. The senior author gratefully acknowledges support from the National Science Foundation (Grants G23309 and GB2448) and the Graduate School, University of Minnesota.

TABLE 1. Pigments in four soil horizons—expressed in units per gram organic matter

Soil horizon and stand	Water (% fresh wt)	Organic matter		Chlorophyll derivatives (CD)	Epiphasic carotenoids (EC)	Hypophasic carotenoids (HC)	CD		EC/HC
		(% dry wt)	(g dry wt per m <sup>2</sup> )				EC + HC	HC	
White pine stand #1									
L <sub>1</sub> .....	66	92	320	0.65	0.065	0.19	2.5	0.34	
L <sub>2</sub> .....	67	82	590	1.50	0.077	0.26	4.5	0.30	
F.....	54	61	470	1.66	0.059	0.18	6.9	0.33	
H.....	37	21	300	0.62	0.046	0.14	3.3	0.33	
Total <sup>a</sup> .....	54	51	1680	1.22	0.064	0.20	4.6	0.32	
White pine stand #2									
L <sub>1</sub> .....	31	95	480	0.32	0.11	0.41	0.6	0.27	
L <sub>2</sub> .....	64	86	640	1.33	0.096	0.38	2.8	0.25	
F.....	49	61	1340	0.66	0.013	0.045	9.7	0.29	
H.....	41	33	640	0.35	<0.013	<0.03	>8.1	—	
Total <sup>a</sup> .....	48	57	3100	0.64	0.044 <sup>b</sup>	0.16 <sup>b</sup>	3.1	0.28	
Oak stand #1									
L <sub>1</sub> .....	40	88	440	0.41	0.094	0.22	1.3	0.43	
L <sub>2</sub> .....	55	75	460	1.20	0.11	0.37	2.5	0.30	
F.....	45	63	800	0.58	0.035	0.10	4.3	0.35	
H.....	38	34	750	0.25	nil	0.047	5.3	—	
Total <sup>a</sup> .....	43	53	2450	0.56	0.049	0.16	2.7	0.31	
Oak stand #2									
L <sub>1</sub> .....	14	88	390	0.40	0.17	0.50	0.6	0.34	
L <sub>2</sub> .....	24	77	310	0.89	0.068	0.27	2.6	0.25	
F.....	35	59	900	1.08	0.060	0.22	3.9	0.27	
H.....	43	41	750	0.55	0.039	0.11	3.7	0.35	
Total <sup>a</sup> .....	36	56	2350	0.77	0.072	0.24	2.5	0.30	

<sup>a</sup>Calculated taking different horizon weights into account.

<sup>b</sup>Assuming half the detectable limit for the sample below that limit.

TABLE 2. Pigments in woodland leaves and soils—expressed in units per gram organic matter

Item	Number of samples	Organic matter (% dry wt)	Chlorophyll derivatives (CD)	Epiphasic carotenoids (EC)	Hypophasic carotenoids (HC)	CD		EC/HC
						EC+HC	HC	
Leaves (mixed except for April 13 and 21)								
Midsummer 1964.....	6 <sup>a</sup>	94	26 <sup>b</sup>	9.9	16.7	1.0	0.59	
Freshly fallen, Oct. 15, 1964.....	1	93	0.30	0.49	1.60	0.14	0.31	
On trees, Nov. 20, 1964.....	1	95	0.04	0.17	0.48	0.06	0.35	
On oak tree, Apr. 13 and 21, 1965.....	2	96	<0.01	0.08	0.41	<0.02	0.20	
On soil surface, Apr. 20, 1965.....	1	93	0.23	0.22	0.56	0.29	0.39	
Soil horizons (average values)								
L <sub>1</sub> .....	4	91	0.45	0.110	0.33	1.0	0.33	
L <sub>2</sub> .....	4	80	1.23	0.088	0.32	3.0	0.28	
F.....	4	46	0.97	0.042	0.14	5.4	0.31	
H.....	4	32	0.44	<0.025	<0.08	>4.2	—	

<sup>a</sup>Two samples each of *Quercus ellipsoidalis* and *Pinus strobus*, and one sample each of *Corylus* sp. and mixed ground flora.

<sup>b</sup>As pheophytin, = chlorophyll × 0.63.

photometrically at 445 m $\mu$  in their respective solvents. Complete spectra revealed considerable distortion in some F and H samples with low carotenoid concentrations. These can therefore be regarded as only approximate values. The analytical results for individual soil profiles are presented in Table 1. Pigment concentrations are expressed as units per gram of organic matter, one unit being equivalent to an optical density of 1.0 in a 10-cm cell when dissolved in 100 ml of solvent (Gorham 1959). Average pigment concentrations in soils, as well

as data for leaves and litter, are given in Table 2. Total organic matter in these non-calcareous soils was measured by loss on ignition.

#### RESULTS

The data indicate that pigment concentrations in the organic matter of the upper litter layer average between 1% and 2% of those in green leaves. Concentrations of carotenoids decline in the deeper layers, especially between the L<sub>2</sub> and F layers. These pigments are therefore

decomposed at a rate greater than that for soil organic matter as a whole. Chlorophyll derivatives, however, are highest in the L<sub>2</sub> and F layers, so that they are decomposed at less than the overall rate between the L<sub>1</sub> and L<sub>2</sub> litter layers. This may be so from the time the leaves fall, since freshly fallen leaves show a lower concentration of chlorophyll derivatives per unit organic matter than any of the soil layers.

Data for green and brown leaves indicate that concentrations of all three types of pigment decline very sharply before leaf fall. Leaves overwintering on oak trees exhibit a striking decline in chlorophyll derivatives, with much lower concentrations than those of the L<sub>1</sub> soil layers.

The relative rates of pigment decomposition are shown by ratio changes. While leaves are turning brown on the trees, chlorophylls are degraded much faster than carotenoids, as shown by a decline in CD/EC + HC ratio from 1.0 in green leaves to < 0.02 in overwintered brown oak leaves (Table 2). In the soil the situation is reversed, with chlorophyll derivatives decomposed less rapidly than carotenoids, as shown by a rise in CD/EC + HC ratio from 0.14 in freshly fallen leaves to 5.4 in the F layer of the soil. The ratio EC/HC exhibits little change, except for a drop from about 0.6 to 0.3 as leaves turn brown.

There do not appear to be any marked differences between profiles under oak and those under pine, although the ratio of chlorophyll derivatives to carotenoids is apparently somewhat higher under pine (4.6, 3.1) than under oak (2.7, 2.5). The same is true of living leaves to a lesser degree, two samples of fresh pine needles showing higher ratios (1.1, 1.1) than two samples of oak leaves (0.90, 0.89).

Pigment concentrations in the organic matter of the total woodland humus layers are compared with those of aquatic soils in Table 3. Lake muds are very much richer than the woodland soils in all three pigments, chiefly because of the anaerobic situation provided in all but the surface skin of the aquatic sediments. In the absence of oxygen, pigment degradation may be greatly inhibited in lake muds.

The high maximum pigment levels in the aquatic sediments come from very productive lakes. In these lakes a large proportion of sedimentary organic matter must

TABLE 3. Pigment concentrations in 4 woodland soils and 31 profundal lake muds from Minnesota—expressed in units per gram organic matter

Pigment	Source	Maximum	Minimum
Chlorophyll derivatives	Terrestrial	1.2	0.6
	Aquatic	14.2	1.1
Epiphasic carotenoids	Terrestrial	0.07	0.04
	Aquatic	26.6	0.4
Hypophasic carotenoids	Terrestrial	0.24	0.16
	Aquatic	31.4	0.8

come from aquatic production, since upland litter washed in from the drainage basin is bound to be very low in pigments (see Table 2).

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## GROUND WATER AND VEGETATION IN TWO PEAT BOGS IN NORTHERN MINNESOTA

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*Abstract.* Plant cover and water quality of bog waters are related to the surrounding ground-water flow systems in two bogs—one perched above and isolated from the regional ground-water system, the other nonperched and continuous with the regional system. The nonperched bog has higher pH, higher specific conductivity, and greater variety in plant cover than the perched bog.

Several studies have discussed the relationships between mineral-influenced bog waters and vegetation patterns in peatlands (Gorham 1956, Graham and Satterlund 1959,

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and Heinselman 1963). Others have also related pH and ionic composition directly to bog floristics (Sjörs 1950, Pierce 1953). But few have had the opportunity to relate bog-water conditions to the surrounding ground-water flow system. This has been investigated in recent