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SPECTRAL TRANSMISSION CURVES OF SOME TYPES OF LEAF CANOPIES WITH A NOTE ON SEED GERMINATION

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SUMMARY

Measurements show that dense leaf canopies transmit very little radiation in the wavelengths 400–700 nm and many times as much radiation in the longer wavelengths.

It is shown that germination of seeds requiring either light or darkness can be inhibited under a dense canopy but the ecological importance of this phenomenon is not proved.

1. INTRODUCTION

As early as 1936 MEISCHKE drew attention to the fact that germination of many seeds is inhibited by far red light, a wavelength band which is very strongly transmitted by green leaves. He concluded that under natural conditions this inhibition might occur under dense vegetation and showed in an experiment that light filtered through a leaf could inhibit seed germination.

In 1962 the present author made measurements of the spectral transmission of several types of woodland canopies and its effect on seed germination. The results which were hidden in a brief report (STOUTJESDIJK 1964) and are published here more extensively.

In the meantime some papers pertinent to the subject have appeared which were cited by VAN DER VEEN (1970) who, not knowing the work of Meischke, repeated his experiment, showing that seeds of several species failed to germinate under an *Alocasia* leaf or under dense vegetation in a greenhouse. Both Meischke and van der Veen showed that not only photoblastic seeds but also seeds requiring darkness can be inhibited by the light under vegetation.

While from the data in the literature there was no doubt that the light in a forest is relatively rich in far red and near infrared, there was a lack of accurate data as suitable instruments were not available.

The first to make accurate measurements of the radiation spectrum on a forest floor was KNUCHEL (1914) who used a spectrophotometer. Unfortunately his measurements cut off at 650 nm.

SEYBOLD (1936) and EGLE (1937) made measurements with glass filters which already extend to ca 720 nm, but of necessity the wave bands were not sharphly defined. These measurements clearly show that the light in a forest is relatively rich in far red and near infrared.

Only recently suitable interference filters have become available, which make satisfactory field measurements possible.

DIRMHIRN (1964) made measurements (between 400 and 1100 nm) under a group of walnut trees by means of a monochromator with interference filters. FEDERER & TANNER (1966) made measurements with a similar instrument under different stands in a wavelength range of 400–740 nm.

In the present paper measurements of the transmission spectrum of several leaf canopies are presented as well as some experiments on the influence of light conditions under a canopy on seed germination.

2. METHODS

Comparative measurements of the radiation intensity in a range of wavelength bands were made inside and outside several forest stands. The wavelength bands were isolated by means of interference filters. The instrument used (*fig. 1*) is virtually the same as that deviced by Sauberer (SAUBERER & DIRMHIRN 1958). A 'wedge' interference filter was used as monochromator.

The filter is 6 × 25 × 200 mm and the wavelength transmitted changes continuously from one end of the filter to the other. The filter can move in a flat tube, the light is admitted by a row of cylindrical holes which define the angle of indicence of the light (*fig. 1*).

Two Schott filters were used, covering the ranges 400–740 nm and 870–2000 nm, respectively. The gap between the two was partially covered by an interference filter with maximum transmission at 769 nm.

Up to 700 nm a selenium cell was used as a detector, over 700 nm a silicium cell was used. A silicium cell would be sensitive enough to cover the whole range but in the region 400–500 nm the filter transmits an appreciable amount of radiation of double that wavelength. Especially under a canopy where there is very little radiation in the former wavelength range and much in the latter this can give rise to grave errors. Therefore it is advisable to use in the short wavelengths a selenium cell which is not sensitive to radiation in this secondary transmission maximum.

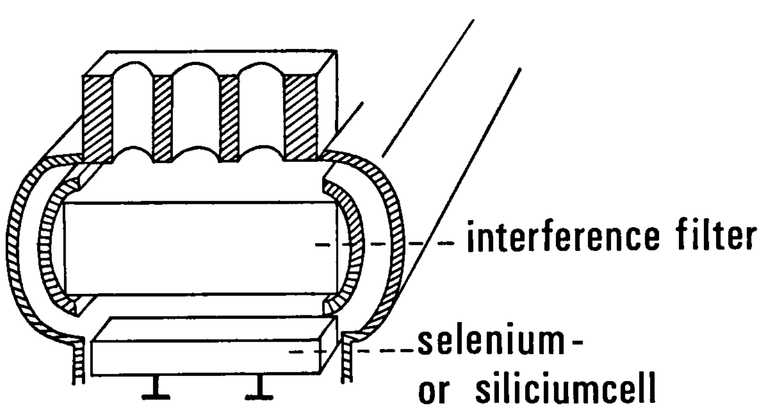

Fig. 1. Cross-section of interference filter in tubular mount.

To take measurements the instrument was pointed downward at a flat white surface and measurements of the diffusely reflected radiation were taken at intervals of 20 nm (50 nm in the infrared). The measurements were made both in the open and under a canopy and then the relative amount of radiation transmitted was calculated for every wavelength step. All measurements were made with a clear sky. Relative intensities below ca 0.1 % could not be measured.

3. RESULTS

3.1. The transmission spectrum of some leaf canopies

Results are pictured in *figs. 2* and *3*. A brief characteristic of the stands follows.

1. Hawthorn shrub. Dunes Oostvoorne. Dense canopy of *Crataegus monogyna*, undergrowth a few scattered individuals of *Melandrium rubrum*.
2. Beech wood. Mildenburg, Oostvoorne. Dense canopy of *Fagus sylvatica*. Forest floor practically bare.
3. Mixed wood. Overbos, Oostvoorne. Some tall trees of *Quercus robur*.

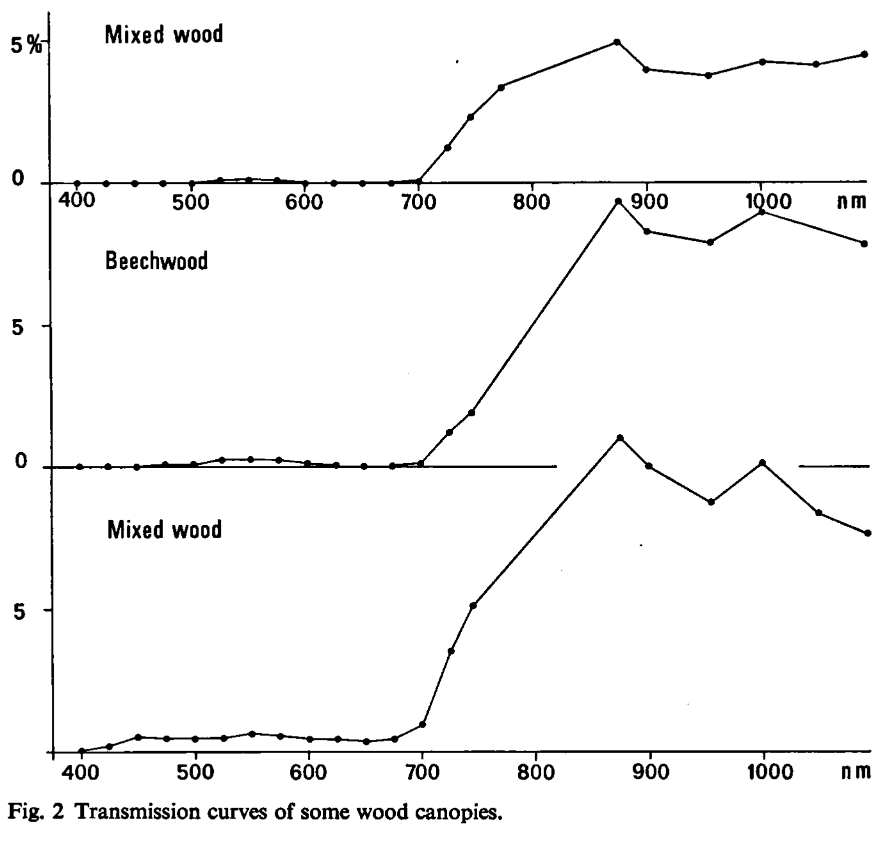

Fig. 2 Transmission curves of some wood canopies.

Lower tree and high shrub layer of *Betula verrucosa*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *Alnus glutinosa*, *Sorbus aucuparia*, *Lonicera periclymenum*. Shrub layer up to 3 m high. *Crataegus monogyna*, *Sorbus aucuparia*, *Lonicera periclymenum*, *Acer pseudoplatanus*, *Humulus lupulus*. Herb layer with scattered individuals of *Polygonatum odoratum*, *Viola* spec., *Equisetum arvense*, *Geranium robertianum*, *Melandrium rubrum*, *Geum urbanum*, *Rubus* spec., *Lapsana communis*.

4. Mixed wood. Mildenburg, Oostvoorne. Canopy of *Quercus robur*, *Betula verrucosa*, *Fagus sylvatica*, *Ulmus* spec., *Acer pseudoplatanus*, *Crataegus monogyna*. Herb layer 15% with *Urtica dioica*, *Stachys silvatica*, *Melandrium rubrum*, *Rubus* spec.
5. High alder shrub. *Alnus glutinosa* dominant with *Quercus robur*, *Fraxinus excelsior*, *Acer pseudoplatanus*, *Humulus lupulus*. Herb layer 20% with *Eupatorium cannabinum*, *Urtica dioica*, *Scutellaria galericulata*, *Glechoma hederacea*.

The data pictured in the graphs clearly show the high amount of radiation over 700 nm transmitted as compared with the very small transmission in the shorter wavelengths. As could be expected, a minor peak is also found at 550 nm in the green part of the spectrum.

In the darkest woods the discrepancy visible/far red is strongest. This could be expected: if a canopy of a certain density transmits e.g. 5% in the visible range and 20% in the infrared, then a canopy of double that density will transmit 0.25% in the visible and 4% in the infrared. Jordan (1969) used the ratio of near red (675 nm) and far red (800 nm) transmission as a measure for canopy density.

To find from the transmission curves the actual energy distribution under the canopy, the composition of the daylight outside the forest is to be known. This was not measured directly, but from a typical energy distribution curve for cloudless weather (DIRMHIRN 1964), the energy distribution inside the forest was calculated for one case (*fig. 3*).

The general shape of the energy distribution curve is not greatly different from the transmission curve and the statement that radiation in the shorter wavelengths is weak as compared with far red and infrared remains true.

3.2. Germination experiments

The results justified the assumption that under natural conditions inhibition of seed germination by far red and infrared radiation might occur. Therefore seeds of several species of higher plants and fern spores were sown under the canopy of a dense hawthorn shrub and outside of it, but shielded from direct sunlight. This means that the light contains less far red and relatively more blue than the direct sunlight.

To exclude influences of humidity and other properties of the substrate the seeds and spores were sown in petri dishes on wet filterpaper. As direct sunlight was avoided, temperature differences between the dishes inside and outside the shrub did not exceed 1 °C.

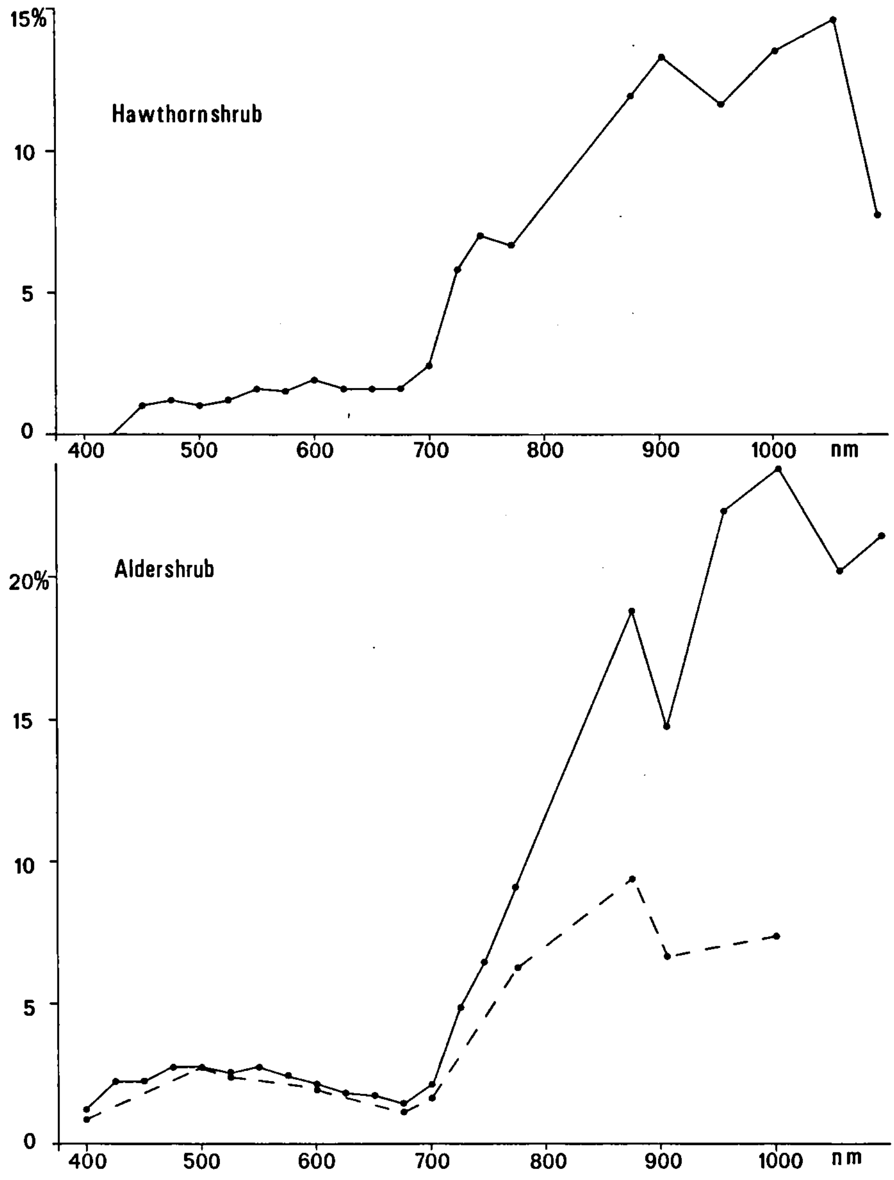

Fig. 3. Transmission curves of two shrub canopies. The dotted line shows the calculated energy distribution under alder shrub.

The results of these experiments are compiled in *table 1.*

Table 1.

	% of seeds germinated			
	in lab.	north of lab.	Hawthorn shrub	dark
Betula pubescens	52	51	0	2
Cirsium palustre	–	75	11	3
Cynosurus cristatus	65	73	3	1
Bromus tectorum	0	0	0	100
Epilobium hirsutum	80	98	0	14
Salix cinerea	100	100	100	100
Salix repens	–	100	100	97
Pinus sylvestris	–	80	73	64
Sagina maritima	–	100	99	96
Sagina procumbens	–	87	12	1
Sagina nodosa	–	23	5	0
Polypodium vulgare	100	100	100	100
Dryopteris filix-mas	100	100	100	0

The data show that both seeds which require light and those which require darkness for gemination can be strongly inhibited under a leaf canopy. Large seeds seem to be insensitive to light (MAYER & POLJAKOFF-MAYBER 1963) but the *Salix* species show that very small seeds can be completely insensitive too. The *Sagina*'s show that closely related species can react completely different.

The spores of *Dryopteris filix-mas* are photoblastic but there is no inhibition under the leaf canopy. In Meischke's opinion some wavelengths always stimulate germination (e.g. red light) while others always inhibit it. In normal daylight both effects exist side by side. In light-requiring seeds the stimulating effect prevails, in darkness-requiring seeds the inhibiting effect prevails. Meischke found that 'Dunkelkeimer' can germinate in monochromatic light of a stimulating wavelength. In this scheme *Dryopteris* spores would have a relatively high sensitivity for stimulating wavelengths and a very low sensitivity for inhibiting ones.

While we may be satisfied that under ecological conditions inhibition of seed germination would be possible, it is by no means proved that far red inhibition actually plays a part in the regulation of seed germination under natural conditions. Other barriers may be more important, like dryness of the substrate or the necessity of a period of frost. It is significant in this respect that in suitable light birch seeds can germinate quite readily in summer in a petri dish but that seedlings are found only as a rarity on the natural substrate at that time of the year, while in spring seedlings are quite numerous.

Van der Veen suggested that far red inhibition may keep seeds dormant in a forest till an opening is formed. For temperate conditions this seems unlikely, as seed germination occurs mainly in spring when the trees are still leafless.

Mayer c.s. speak of "residual genetic properties which no longer have any direct survival value and which are retained as long as they have no harmful effect".

It would also be possible to think of properties which not yet have survival value, i.e., belong to a pool of 'useless' features upon which natural selection can act in the future.

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