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ON THE PHOTOREACTIVITY OF SOME HARDWOOD SPECIES STUDIED BY THEIR LEAF CHARACTERISTICS

by

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In studying the reaction of tree species to light radiation, it is essential to find out whether the morphological and physiological modifications, caused by changes in light environment, are specific. As sylvicultural practice has repeatedly tried to classify tree species, starting from their empirically observed light demand or tolerance, the unequivocal determination of specific photoreactivity could be put to practical use, even if it would only allow a critical appreciation of the existing classifications.

A far better knowledge is needed about the light absorption to arrive at a more accurate interpretation of tree growth. This applies to all fundamental questions concerning the exchange and transformation of enegry, but also to the more practical problems of individual tree care and appropriate treatment of the forest stand.

The present paper is a summarizing synthesis of the research work on the reaction of tree species to light radiation, done at our « Research Centre of Sylviculture » during the last years. It deals with an indirect approach to the problem, as it only gives information about some morphological and physiological differences between the leaves of a restricted number of tree species, grown under different conditions of light radiation.

1. The morphology of tree leaves

To measure length, thickness and weight of leaves of common oak (*Quercus robur* L.), collected in a mixed oak forest of the atlantic type (*Quercetum atlanticum*) at Landskouter — Gontrode near Ghent, different tree positions and three crown layers in each tree, were taken into consideration :

Social positions of tree	Crown layers
I Completely isolated	U Upper crown layer $(> \frac{2}{3})$
II Surrounded on all sides	M Middle crown layer $(\frac{2}{3} / \frac{1}{3})$
III Completely overshaded	L Lower crown layer $(< \frac{1}{3})$

As expected and entirely normal, the leaves get thinner and progressively develop into a tolerant type as the quantity of available light radiation diminishes along the lines I → II → III and U → M → L. (Tab. 1) However, differences between leaves taken from

TABLE 1

Variation of some morphological characteristics of leaves of common oak (Q. robur L.)

Position of tree	Crown layer	Thickness in mm	Length in mm	Thickness principal nerve in mm	Dry weight/g
I	U	0.205	103	0.816	0.0102
	M	0.192	102	0.777	0.0091
	L	0.174	110	0.731	0.0070
Mean value I		0.190	105	0.783	0.0086
II	U	0.171	107	0.734	0.0088
	M	0.133	102	0.659	0.0054
	L	0.119	100	0.570	0.0040
Mean value II		0.141	103	0.654	0.0061
III	U	0.124	83	0.493	0.0046
	M	0.123	83	0.492	0.0043
	L	0.122	80	0.490	0.0041
Mean value III		0.123	82	0.492	0.0043
Mean value	U	0.167	97	0.680	0.0079
	M	0.149	96	0.644	0.0063
	L	0.138	96	0.597	0.0051

different crown layers only exist as far as dominant (I) and codominant (II) trees are concerned and no such differences are observed between leaves collected from suppressed or completely overshaded trees.

This fact eventually leads to the assumption, that the oak-leaf reacts by morphological modifications to a decrease in intensity of light radiation, but only down to a certain minimal level of light intensity. Below that point the leaves do not react any more : they have developed into a marginal tolerant type with a low potential for activity. In the light environment, corresponding with this marginal leaf type, assimilation is slowed down so as only to permit survival of the leaves and a very reduced growth activity of the trees.

Similar conclusions result from the study of some morphological leaf characteristics of 5 hardwood species, the sampling being made separately in the upper half (1) and the lower half (2) of the crown and the measurements being regularly spaced over the vegetation period.

The data reproduced in tab. 2 thus represent mean values for a group of 180 individual measurements pro object (tree species/ crown layer). These groups are made up of 9 series of 20 individual measurements each; the series were evenly spaced over a 4-months period (June-September) by regular intervals of 2 weeks.

From the determination of thickness and weight only, the following provisional conclusions can be drawn :

TABLE 2

Variation of morphological leaf characteristics of some hardwood species

Species	Crown layer	Thickness leaf/ 0.001 mm	Fresh weight leaf/cm^2	Factor $Q = dm^2/g$
Beech	1	178	17,0	0,5904
	2	91	7,7	1,3126
Common oak	1	236	23,0	0,4380
	2	146	11,5	0,8728
Hornbeam	1	142	13,6	0,7424
	2	98	7,6	1,3327
Field maple	1	161	15,6	0,6457
	2	133	11,4	0,8808
Ash	1	143	12,6	0,8041
	2	120	9,0	1,1151

1° Considering leaves from the upper crown layer only, ash and hornbeam rather represent a tolerant type, oak shows the general characteristics of the light type or intolerant type, whereas beech and maple more or less seem to be of a transitional type between ash and oak.

2° Comparing within each species leaves from the two crown layers, lower values are always found for the leaves collected in the lower stratum.

The most important differences between leaves from different crown layers are found for oak, hornbeam and beech. This gives at least an indication about the degree of response of these species to changes in light environment; it is simultaneously demonstrated that ash and maple have a higher degree of stability in this respect.

It may be worth mentioning that for all species variations in weight of leaves are more important than the variations of their tickness.

3° The factor of GRULOIS ($Q = \frac{dm^2}{g}$) varies in the opposite sense of the values for weight and thickness of the leaves. The analysis of its variation however leads to exactly the same conclusions as reached by considering weight and thickness.

All measurements indicate, that an important degree of variation of the leaftype exists within each species and that for each single tree these variations are no less important. It thus occurs, that the differences between mean values for samples taken in the two crown layers are more important for each of the species hornbeam, beech and oak than they are between the species themselves if the comparison is based on leaves collected in the upper crown layer. These facts illustrate the very curious character of the relationship existing between species that are found growing together. (There exists e.g. no significant difference in weight, thickness and Q - value between oak-leaves from the lower crown layer and hornbeam - leaves from the upper crown layer, although very important differences between the two species can be shown if the comparison is limited to leaves from the upper crown layer).

Maple-leaves show little and ash-leaves practically no difference between crown layers.

If it can be proved, that these morphological particularities are acceptable for the characterisation of the energetic type of leaves and tree species, the present observations lead to the deduction, that the different reaction of tree species to changing light conditions, also changes their relative position to each other continually and even considerably, which is of importance for the practice of sylvicultural treatment and stand manipulation.

And, in fact, if leaves of the upper crown layers are chosen as material for comparison, ash must be characterized as a species with relatively high light demands.

It is also not unimportant to conclude that, judging from the same basis, ash and maple seem to belong to the same energetic type.

2. The transgression of light radiation

In the transgresso-reflector (2,5) leaves were exposed to a constant beam of artificial light with a total intensity of 3.200 Lux and the following characteristics, obtained by interposing suitable monochromatic interference filters between light source and photoelectrical measuring cell :

Component	λ-max filter	Light intensity in Lux
White	No filter	3.200
Yellow	580 nm	340
Green	545 nm	140
Red	705 nm	12
Blue	440 nm	10

The light radiation, generated by the source, gets divided into three parts :

Part 1 :	Reflected by leaf surface
Part 2 :	Absorbed by leaf
Part 3 :	Going through the leaf

Part 3, the light radiation going through the leaf, is also called transgression light. As the quantity of reflected light is nearly constant, the intensity of transgression light, can be used to characterize the leaf.

2.1. *Light transgression through leaves grown in a natural light environment.*

Transgression of light through the leaves of 9 tree species was measured at four points, evenly spaced over the vegetation period.

Each basic series (measurements at one point and for each species) was made up of 50 individual measurements (50 leaves).

Leaves were collected at the top of 6-year old trees growing in the nursery under normal light conditions.

A first analysis permits to conclude, in a general way and for each species separately, that the outgoing light radiation diminishes as the vegetation period progresses (Tab. 3). As the intensity of light

TABLE 3

Light intensity in Lux of the white transgression light.
(Artificial light source = 3.200 Lux)

Species	June	July	August	September	Mean value period
	n = 50				$N_p = 200$
Beech	670	432	250	314	417
Red oak	647	392	322	254	404
Hornbeam	522	408	251	191	343
Sessile oak	621	301	202	200	331
Chestnut	505	338	174	138	289
Ash	425	326	200	182	283
Field maple	434	309	160	143	261
Birch	341	278	170	151	235
Black alder	388	260	149	133	232
Total	506	338	209	190	311
	$N_s = 450$				

reflection shows no significant variation, it thus becomes evident that the quantity of light absorbed by the leaves of all species continually increases from the beginning till the end of the growing season. For all practical purposes this phenomen means, that all tree species towards the end of the vegetation period react as relative light demanding species as compared to their photocharacteristics in early spring.

However, although this general line of conduct applies to all species, measurable differences between the species persist, essentially concerning the level of intensity of the transgression light, but also regarding the quantitative aspects of the modification of light absorption in the course of the growing season.

Using the intensity of transgression light as a measure, tree species can be classified in the following way (decreasing values for lightression;transg increasing values for light absorption), considering however thatsuch a classification hasonly a limited signification :

Increase of absorption
Decrease of transgression
More light demanding

Start vegetation period	*End vegetation period*
Beech	Beech
Red oak	Red oak
Sessile oak	Sessile oak
Hornbeam	Hornbeam
Chestnut	Ash
Field maple	Birch
Ash	Field maple
Black alder	Chestnut
Birch	Black alder

An additional analysis (t - test) allows to conclude that no significant differences exist between the following pairs or groups of species :

Beech = Red oak	Hornbeam = Sessile oak
Birch = Black alder	Chestnut = Ash = Field Maple

If such a similarity of species can also be proved by studying other aspects of their behaviour and reactions, better founded rules for stand treatment could be formulated.

Regarding the changes in intensity of transgression light occurring in the course of the growing season, three groups can be made (Tab. 4) :

1st. group : Decrease with 50-60 % between June-September Relatively photostable species : Beech, birch, ash.

This is a rather unexpected grouping, not entirely covering the classification made by sylvicultural practice, that usually considers beech as a tolerant species and ash/birch as typical species with high light demands.

2nd. group : Decrease with 60-70 % between June-September Relatively photolabile species : Red oak, hornbeam, black alder, field maple and sessile oak.

3rd. group : Decrease with more than 70 % between June-September. Extreme photolabile species : chestnut.

These changes are taking place rather slowly in leaves of ash, birch and hornbeam (Light intensity in July still 75 % and more of value for June), but quick changes are typical for sessile oak (Light intensity in July only 48 % of value for June).

As to the reaction of the leaves to light radiations with a different wave length (Tab. 5), a confirmation of former observations (5) is to be found in the fact, that the leaves of the 8 species under observation react in the same way to light radiation with λ-max = 580 nm (yellow) as they do toward the unaltered light radiation with a complete spectrum (white).

The reaction to light radiation with λ-max = 705 nm (Red light), however, is slightly different :

a) Judging from mean values for the intensity of transgression light representative for the whole growing season, the absorption of red light is for all species slightly less important than for the total white light.

b) The intensity of red light radiation after passing through the leaves of beech, birch and ash attains in September still 50 % of the values observed in June, whereas for the other species it reaches no more than 30 — 40 % of the June — value.

TABLE 4

Relative values for the intensity of white transgression light

	Beech	Red oak	Sessile oak	Hornbeam	Chestnut	Field maple	Ash	Black alder	Birch
June	100	100	100	100	100	100	100	100	100
July	64	60	48	75	66	71	76	67	81
August	37	49	32	46	34	36	47	38	49
September	46	39	32	35	27	32	42	34	44
June	100	96	92	80	75	64	63	57	50
July	100	100	69	94	78	71	75	60	64
August	100	128	80	100	69	63	80	59	68
September	100	80	63	60	43	45	57	42	47

These facts suggest an unsuspected degree of similarity between beech, birch and ash; they also allow differentiation between otherwise highly similar species as beech / red oak and ash/ maple.

Quite different is the transgression through the leaves of light with shorter wave length, i.e. with λ-max = 440 nm (blue) as compared to white light, but it is most puzzling to observe that the absorption of the light with shorter wave length goes in quite the opposite direction for green and for blue.

Table 5

The intensity of transgression light originatlng in differend regions of light spectrum (mean values in Lux for total vegetation period).

Intensity of transgression light in % of intensity going out from artificial light source. (below)

Tree species	White	Red	Yellow	Green	Blue
Beech	417	1,833	42,76	24,64	0,391
Red oak	404	1,813	41,43	23,83	0,326
Hornbeam	343	1,543	35,47	20,53	0,337
Sessile oak	331	1,562	33,60	18,97	0,352
Chestnut	289	1,347	29,40	17,53	0,188
Ash	283	1,295	27,44	17,09	0,279
Maple	261	1,240	25,41	15,49	0,183
Birche	235	1,197	22,69	14,54	0,187
Black alder	232	1,187	22,86	14,17	0,125
Beech	13	15	13	18	4
Red oak	13	15	12	17	3
Hornbeam	11	13	10	15	3
Sessile oak	10	13	10	14	4
Chestnut	9	11	9	13	2
Ash	9	11	8	12	3
Maple	8	10	7	11	2
Birche	7	10	7	10	2
Black alder	7	10	7	10	1

Green light is relatively less absorbed (relatively high portion of initial light radiation going through the leaves) than all other light types, including wihte light; blue light radiation (λ-max = 440 nm) on the contrary is absorbed to a very high degree and there is a maximum light transgression of only 4 % of the initial light radiation of the artificial light source going through the leaves of beech and sessile oak against a minimum of 1 % for black alder (Tab. 5).

TABLE 6

Procentual values of the transgression light radiation at end of vegetation period (Sept.) as compared to corresponding light radiation in June

Tree species	Radiation type				
	White	Red	Yellow	Green	Blue
Beech	47	51	43	43	37
Red oak	39	38	33	41	37
Hornbeam	37	41	31	36	30
Sessile oak	32	33	27	34	29
Chestnut	27	35	24	28	7
Ash	43	51	38	40	47
Maple	33	40	29	32	33
Birch	44	50	40	44	40
Black alder	34	38	30	33	23
Total	38	41	33	37	32

The reaction to the blue light radiation is also very different, permitting a clear differentiation between species and proving the energetic importance of the light radiations with shorter wave length.

Present observations lead to the following conclusions (Tab. 6) :

1⁰ Ash is clearly different from the other species in letting through a relative higher amount of blue light at the end of the vegetation period than is the case for the total white light radiation (September - value in % of June - value).

2⁰ The changes in blue light absorption in the course of the vegetation period are also less important for ash. At the end of the observation period the blue transgression light still arrives at 47 % of the value for june, whereas it only reaches between 7 and 40 % for the other species.
This shows once more the photostability of ash.

3⁰ Significant is also the high degree of blue light absorption (and reflection) by chestnut at the end of the vegetation period as the intensity of light transgression falls back to 7 % of the value measured in June.

The unequal absorption by leaves from different species or at different moments of light radiations with a different wave length, shows that light absorption is specific and selective to a certain degree. It also indicates, that significant, but unequal changes are taking place in the course of the vegetation period, so that the relative position of the species, eventually based on light absorption, continually changes.

In a general way, a classification of the species based on increasinh light absorption ro decreasing light transgression, gives the same results when made for the red, green and yellow comqanents or for the total white light radiation.

Beech and oak react as relative tolerant species all over the growing season; ash acts as a light demanding species in June, but as a transitional species in September; maple, birch and alder act as relative light demanding species 'all over the season; the position of sessile oak, hornbeam and chestnut is fairly variable.

The reaction to blue light radiation gives a modified picture of the situation. Beech, red oak, sessile oak and hornbeam react as relative tolerant species all over the year as blue light absorption is fairly low.

Ash reacts as a relative light absorbing species in spring, but as a species with low absorption in september. This phenomen is mostly due to its high degree of photostability.

Maple, birch and black alder show at all times a relatively high absorption of blue light.

As to certain particularities of the species, the following constatations could be of practical importance :

1⁰ Ash shows a very low absorption of blue light as compared to its absorption of light radiations with another wave length.

2⁰ A real difference between ash and maple exists regarding the significant difference of blue light absorption.

3⁰ Beech really differs from red oak by its significantly lower absorption of yellow and red light radiation, especially at the end of the growing season.

4⁰ Chestnut absorbs an extremely high quantity of blue light, especially at the end of the vegetation period.

2.2. *The influence of light quality*

Seedlings of ash, hornbeam, beech and oak were cultivated in phytotron units under different light conditions (white, blue, green and red light), but using a standard illumination period of 12 hrs a day over a growing period of one year (second year).

In each unit 9 ACEC TL-Lamps were used, with a potential of 300 W/qm floor surface and creating the following light intensities :

White light	4.860 Lx	Blue light	4.750 Lx
Green light	6.800 Lx	Red light	3.450 Lx

Transgression of white light through the leaves was measured during the second growing season in series of 20 individual measurements for each object, repeated four times (middle of May, June, August and September). Very little variation in light reflection was observed and as a constant light source was used to measure the degree of light transgression, the collected data could, under the given circumstances, also serve as a measure for the degree of light absorption.

By grouping all the collected data (4 species, 4 light environments, 4 measuring points) in an adequate way, it is possible to test consecutively the fundamental differences between species, between light environments and between measuring points, without trying to determine the interaction between the factors under consideration (Tab. 7).

TABLE 7

Mean values for the intensity (in Lux) of the total light transgression (white light) ($N = 320$)

Tree species	Lx	Light environment	Lx	Time of measurement	Lx
Ash	428	White	398	May	487
Hornbeam	418	Blue	352	June	422
Beech	383	Green	405	August	380
Oak	369	Red	444	September	310

Oak/hornbeam	5,363°°°	Beech/Ash	5,038°°°
Oak/Ash	7,602°°°	Beech/Hornbeam	3,453°°°
Oak/Beech	1,520	Ash/Hornbeam	1,114
Red/Green	4,195°°°	Green/White	0,927
Red/White	5,113°°°	Green/Blue	6,125°°°
Red/Blue	9,761°°°	White/Blue	5,334°°°

It thus appears, that, in a general way, ash and hornbeam react as relative tolerant species, with no significant difference between the two; oak and beech react as species with relatively higher light demands, but also with no significant differences between the two.

In a similar way, the general inpact and typical influence of the qualitative light environment on all species and for the whole growing season, can be proved.

As compared to leaves grown under white artificial light, leaves that developed under a light radiation of about the same intensity but with λ max = 440 nm (blue) take on an outspoken intolerant type. Leaves grown under light with λ max = 705 nm (red) are more of the tolerant type, whereas no significant modifications are caused by green light (λ max = 545 nm) in comparison to white light.

These observations indicate that the increase of red light radiation increases the tolerance of tree species and that increase of blue light radiation is accompanied by increasing light absorption.

Whether these phenomena are revelant as far as some physiological functions or the whole of energy absorption and transformation are concerned, must be made out by specialized research.

Quite in line with former conclusions is the fact, that the intensity of transgression light diminishes in the course of the growing season, meaning that the leaves gradually change into a relative intolerant type and that all species are more light demanding and less tolerant at the end of the vegetation period.

A second grouping of measurements, neglecting only the eventual importance of the time at which they were taken (Tab. 8), confirms the signification of blue and red light radiation, but only as far as hornbeam and ash are concerned. In fact, both species show the lowest values for light transgression for leaves grown under blue light, the highest values for leaves grown under red light.

Beech only reacts to red light (increase of transgression = increase of tolerance) and oak seems to be indifferent to the variations of light quality as provoked in these experiments.

The interpretation of the present observations for practical purposes of stand regeneration or sylvicultural treatment, must be considered as rather premature at the moment.

It nevertheless becomes evident that, due to a different reaction of tree species to changing light conditions, the relative position of the species to each other changes continually, so as to arise serious doubts about the value of the classical division into tolerant and intolerant species or into species with high and with low light demands. These characteristics are variable and are to be inter- preted in function of growing conditions.

And, in fact, no real differences in the degree of transgression

TABLE 8

Mean values (Lux) for the intensity of white transgression light, calculated for the whole growing period separately for species and chosen light environments

Light environment	Tree species	Mean values (Lx)
White	Ash	420
	Hornbeam	438
	Beech	341
	Oak	386
Blue	Ash	361
	Hornbeam	349
	Beech	331
	Oak	368
Green	Ash	430
	Hornbeam	441
	Beech	395
	Oak	356
Red	Ash	496
	Hornbeam	446
	Beech	467
	Oak	368

(absorption) of standard white light through the leaves exist between ash, hornbeam, beech and oak grown under blue ($\lambda_{max} = 440$ nm) artificial light : they all react as in tolerant species.

Grown under white or green ($\lambda_{max} = 580$ nm) light, ash and hornbeam react as tolerant species compared to beech and oak, reacting as species with higher demands.

Under red light ash, hornbeam and beech constitute the group of tolerant species and the unchanged intensity of transgression makes oak a relative light species.

Noteworthy also that ash and hornbeam are only different from each other when grown under red light, ash reacting as the most tolerant.

The same can be said of beech in its relative position to oak.

This continual shifting of relative positions is confirmed in studying the changes in light transgression taking place in the course of the vegetation period. (Tab. 9).

As already observed before, the intensity of light transgression decreases in the course of the growing period, but the changes are less important for plants grown under artificial light (Max. 7.000 Lx — Constant photoperiod 12 hrs) than for those growing

TABLE 9

Mean values in Lux for the intensity of total light transgression (white light) at four different measuring points

Relative values a) Reference : May - values
b) Reference : Ash

Tree species	May	June	August	September
Ash	445	461	450	353
Hornbeam	550	430	381	313
Beech	523	368	347	296
Oak	430	427	341	280
Ash	100	104	101	79
Hornbeam	100	78	69	57
Beech	100	70	66	57
Oak	100	99	79	65
Ash	100	100	100	100
Hornbeam	124	93	85	89
Beech	118	80	77	84
Oak	97	92	76	79

in the nursery under natural conditions (September - values 57 to 79 % of May - values against 32 to 46 %) (Cfr. Tab. 3).

Using as a reference a species with a high degree of photostability such as ash, the following conclusions can be drawn :

a) Between June and September no essential difference between ash and hornbeam occurs, but in May hornbeam behaves as a relatively more tolerant species.

b) No difference oak-ash for the period May-June, but afterwards oak behaves as a relative light or intolerant species.

c) At the beginning of the vegetation period beech behaves as a relative tolerant species in comparison to ash, but very soon and already in June the situation is reversed.

d) All observations give proof of the high degree of photostability of ash as well as of the great variability in light temperament of beech.

The silvicultural interpretation of the described phenomena still needs a lot of experimenting with regeneration and treatment techniques. System analysis and study of theoretical models should be used if possible to replace the classical semi-empirical experimentation methods.

2.3. *Influence of photoperiod*

Exposing 1-year old seedlings of hornbeam, oak, ash and maple during the second year of growth to a radiation of white artificial light with a constant intensity of 4.860 Lx, but using four units with a different photoperiod (2 - 4 - 8 - 16 hrs a day) morphological (Tab. 10) and physiological (Tab. 11) differences between species manifested themselves.

TABLE 10

Variation of length (mm) and thickness (0,001 mm) of leaves developing under different photoperiodic conditions (time of measurements = End of May)

Tree species	Photo-period	Thickness of leaf/0.001 mm		Length of leaf/mm	
		Mean value	t-value	Mean value	t-value
Oak	2	94	1,0128	56,5	2,1550°
	4	97	4,1015°°°	63,6	4,3815°°°
	8	112	2,1538°	76,7	2,4345°
	16	100		90,4	
Hornbeam	2	76	2,2528°	43,8	0,9404
	4	83	3,1627°°	45,5	4,5443°°°
	8	93	4,4935°°°	54,6	1,1498
	16	108		58,7	
Ash	2	100	1,7622	31,4	6,4204°°°
	4	106	3,8545°°°	43,2	4,3329°°°
	8	126	0,1831	61,2	1,9064
	16	125		51,6	
Field maple	2	95	2,0261	39,5	2,5189
	4	106	5,5786°°°	48,7	0,1120
	8	152	6,9084°°°	48,3	1,2283
	16	117		51,9	

The thickness of the leaves of all four species increases as the photoperiod gets longer (Tab. 10). Differences between the 4 hrs and 8 hrs-period seem to be most important for all species and maximum thickness is mostly attained with a 8 hrs-period.

The lenght of the leaves varies in the same general sense (max. difference between 4 hrs and 8 hrs. period) for ash, oak and hornbeam, but no significant variation is observed for maple.

The variation in the intensity of light transgression through leaves brings confirmation of the morphological variation due to changes in photoperiod : Light transgression diminishes and light absorption increases as the photoperiod gets longer. (Tab. 11). All four species under observation react more as tolerant species

TABLE 11

Intensity in Lux of white transgression light for four different photoperiods

Tree species	Photoperiod	May	
		Mean value	t-value
Oak	2	593	9,6938°°°
	4	336	8,6407°°°
	8	156	3,0310°°
	16	303	
Hornbeam	2	632	2,6056°
	4	543	8,9860°°°
	8	259	—
	16	259	
Ash	2	450	7,5678°°°
	4	327	0,3585
	8	335	0,8074
	16	366	
Field maple	2	428	1,3797
	4	478	7,0869°°°
	8	197	1,9226
	16	276	

(decrease of light demands? More efficient transformation of light radiation energy?) as light conditions get worse and a lower total amount of light energy is available over a given period of time. The efficiency of light transformation, on the other hand, seems to diminish and all species react more as typical intolerant demanding species as light conditions get better, meaning by this the lengthening of the photoperiod or an important increase of the total amount of available light energy over a given period of time.

There is also some indication that, for a given light intensity and tree species, a threshold value for the duration of the photoperiod exists, beyond which no further reaction of the leaves is to be expected.

In the present experimentation this threshold point must be situated for oak, hornbeam and maple between 4 hrs and 8 hrs, but for ash it lays between 2 hrs and 4 hrs. This means in fact that the photoreaction of ash is stabilized after a shorter illumination period or at a lower daily amount of light radiation energy.

The higher degree of photostability of ash can also be illustrated by the far less important variation of the intensity of transgression light (values for May) :

	Max.	Min.	Quotient
Ash	450	327	1.38
Oak	593	156	3.80
Hornbeam	632	259	2.44
Maple	478	197	2.43

This phenomen explains the continual change of position of ash towards the other species. For the short photoperiod (2hrs) ash reacts on an equal level with maple (450 Lx/428 Lx = intensity of light transgression) as a relative light species in comparison to oak (593 Lx) and to hornbeam (632 Lux). For the longer photoperiods (8 hrs/16 hrs) ash is no longer on the same level with maple. He reacts as a relative tolerant species in comparison to oak and hornbeam and to maple as well.

3. Respiration and photosynthesis

Morphological variation of the leaves and differences in light absorption must necessarily correspond with a modification of certain physiological processes, at least as far as their quantitative aspects are concerned.

To prove this point, respiration and photosynthesis in the leaves of american red oak (*Quercus borealis L.*) and sessile oak (*Quercus petraea* L.) were measured.

To this effect leaves were taken from two-year old plants, grown during the second year under white artificial light (light intensity: 4.860 Lx; Photoperiod 8 hrs = 8 W) and under red artificial light (light intensity: 3.450 Lx; Photoperiod 4, 8 and 16 hrs = 4 R, 8 R, 16 R).

As a control (C) plants belonging to the same sample but grown under natural light conditions in the nursery were used.

Referring to former observations (Tab. 3/5) from which was drawn the conclusion that red oak reacts as a relative tolerant species in comparison to sessile oak, it immediately appears that the two species are also dissimilar in regard to respiration and photosynthesis (Tab. 12).

For plants, grown in the nursery under natural light conditions (C), leaves of sessile oak show the highest values for respiration and real photosynthesis, but the balance-value (apparent photosynthesis) is sensibly higher for red oak. This is a rather puzzling constatation, illustrating the character of differences in physiological activity between species. The values for apparent photosynthesis

TABLE 12

a. Mean values for gas exchange pro hr in μlO_2 pro qcm leaf surface and determined for leaves grown under different conditions of light environment. b. Relative values

Tree species	Photoperiod	Respiration	Real photosynthesis	Apparent photosynthesis	Respiration	Real photosynthesis	Apparent photosynthesis
Sessile oak	8 W	3,243 ± 0,050	4,408 ± 0,084	1,165 ± 0,042	31	36	71
	4 R	3,897 ± 0,168	4,828 ± 0,050	0,930 ± 0,184	37	40	56
	8 R	2,757 ± 0,159	3,729 ± 0,109	0,972 ± 0,117	26	31	59
	16 R	2,162 ± 0,075	3,067 ± 0,117	0,905 ± 0,075	21	25	55
	C	10,466 ± 0,578	12,117 ± 0,209	1,651 ± 0,201	100	100	100
Red oak	8 W	3,553 ± 0,117	5,246 ± 0,084	1,693 ± 0,075	36	44	85
	4 R	2,120 ± 0,235	3,209 ± 0,369	1,089 ± 0,117	22	27	55
	8 R	2,899 ± 0,075	4,031 ± 0,101	1,132 ± 0,075	30	34	57
	16 R	3,268 ± 0,201	4,383 ± 0,176	1,115 ± 0,142	33	37	56
	C	9,821 ± 0,193	11,816 ± 0,034	1,995 ± 0,134	100	100	100

on the other hand bring a confirmation of the higher growth intensity of red oak, already observed by forest practice.

It seems also quite normal, that respiration and real photosynthesis reach the highest values for plants grown under natural light, as, in fact, the amount of available light energy is much higher than in the phytotron units with artificial light. At the same time however, the differences for apparent photosynthesis or the values for the gas exchange balance are less important : Leaves of red oak grown under white artificial light with a daily period of 8 hrs (8 W) show an intensity of apparent photosynthesis (1,693 μlO_2), that is only slightly inferior to the value for the leaves of the control plants (1,995 μlO_2).

This is to be explained by the fact that a decrease in light intensity or in the amount of available light energy slackens down the processes of both respiration and real photosynthesis. Its impact on respiration however is more important and this inequality is responsible not only for the stabilisation of the balance-values, but also for the fact, that apparent photosynthesis seems less influenced by changing light conditions, although its impact on the underlying and very real phonemena is considerable.

Hereby it is illustrated how inefficient the indirect approach to biophysiological phenomena can be and how dangerous the interpretation of the action of environmental factors on plant growth by only assessing the final or periodical results of growth.

The eventual influence of the light quality can be assessed in this experiment by making a comparison between 8 W and 8 R for respiration and photosynthesis.

It is possible to calculate the factor $Q = 100 \frac{8\ W}{8\ R}$, which gives the following results :

	Sessile oak	Red oak
Respiration	118	123
Real photosynthesis	118	130
Apparent pnotosynthesis	120	150

These relative values indicate that, under comparable conditions of light intensity and photoperiod, white artificial light stimulates respiration and photosynthesis more than red artificial light.

The differences are more important for leaves of red oak than for those of sessile oak.

As to the unequal reaction of different tree species to variations in light environment, the present experiment shows that the values for apparent photosynthesis for red oak are under all circumstances a little higher than the corresponding values for sessile oak.

The same applies to respiration and real photosynthesis for plants grown under white artificial light (8 W), although the control plants (C-natural light) give quite an opposite picture and here the values for sessile oak are higher as those for red oak.

Still quite another pattern appears for the plants grown under red artificial light (R), where at the same time the influence of the illumination period was studied. (Tab. 12/13).

From this series of experiments the following conclusions can be drawn :

1° The lengthening of the photoperiod causes an increase of the intensity of respiration and real photosynthesis for red oak (4 R > 8 R > 16 R), but quite as important a decrease for sessile oak (4 R > 8 R > 16 R).

2° However, no significant differences are observed between plants developing under different photoperiods as far as the assimilation balance (apparent photosynthesis) is concerned and this for red oak as well as for sessile oak (4 R = 8 R = 16 R). However in all circumstances the values for red oak are a little higher than the corresponding values for sessile oak.

3° Photoperiodic variations influence respiration more strongly than real photosynthesis and sessile oak also more strongly than red oak. (Tab. 13).

TABLE 13

Index values for respiration and photosynthesis for different photoperiods

	Sessile oak			Red oak		
	4 R	8 R	16 R	4 R	8 R	16 R
Respiration	100	71	55	65	89	100
Real photosynthesis	100	77	64	73	92	100
Apparent photosynthesis	100	105	97	98	102	100

This phenomena must really be considered as photoreactions and the determination of assimilation going on in leaves of common oak (Qercus robus L.), collected at the top of trees growing in different social positions (Tab. 1, Tab. 14), confirms it.

It can even be demonstrated that common oak reacts in quite the same sense as red oak : Analogous to the reaction of red oak

TABLE 14

Respiration and photosynthesis (µl O_2 pro hr. and qcm.) for common oak in different social positions

Social position tree	Respiration		Real photosynthesis		Apparent photo-synthesis
	Measure-ment	t-Value	Measure-ment	t-Value	
Dominant	47,88	25,722°°°	53,40	53,342°°°	5,52
Dominated	37,38	47,250°°°	44,88	109,640°°°	7,50
	24,06		32,62		8,56

to the lengthening of the photoperiod, respiration and real photosynthesis are intensified with improvement of the social position of the tree.

In both cases the increase of physiological activity corresponds with an increase of the amount of available light energy; in both cases also respiration is more affected than real photosynthesis.

Apparent photosynthesis on the other hand develops in quite an opposite direction as maximal values are found for trees in the lower stratum and a minimum for dominant trees.

This phenomen can not be explained on first view, but the chlorophyl content of the leaves could presumably be of some importance.

4. The chlorophyl content of leaves

A correct analysis of photoreactivity inevitably leads to the study of the active pigments in leaves and their importance.

The interpretation of the chlorophyl content of leaves must however be done with great care and circumspection as demonstrated by the results for common oak (Quercus robur L.) (Tab. 15).

In fact, if total chlorophyl content is expressed in relation to a fresh weight unit, no difference can be observed between the leaves collected from trees with highly varying social positions; if total chlorophyl content is expressed pro surface unit, a significant difference between the leaves can be demonstrated and a maximum is measured for trees in a dominant position.

In order to avoid exageration, the first method was adopted in further investigations.

TABLE 15

Chlorophyl content of leaves of common oak collected on trees in different social position

Position tree	mg chlorophyl/g Freshweight of leaves		mg Chlorophyl/Surface Unit (1,1 cm^2)	
	Mean value	t-Wert	Mean value	t-value
Dominant Dominated Overshaded	2,4553 2,4960 2,6588	0,337 1,562	0,0502 0,0398 0,0333	2,797°° 4,257°°°

A clearer insight results from the determination, separately, of chlorophyl a, chlorophyl b and total chlorophyl (7) in the leaves of five tree species, the morphological characteristics of which were already studies in the same context (Tab. 2). Care was taken to analyse leaves from the upper crown layer (1) and from the lower crown layer (2) separately (Tab. 16).

TABLE 16

Chlorophyl content (mg/g freshweight leaf) in leaves of different tree species

Tree species	Social position	Chlor. a	Chlor. b	Chlor. tot.	a/b
Field maple	1	1,6647	0,9131	2,6761	2,00
	2	1,8299	0,8942	2,8597	2,06
Ash	1	1,5698	0,7417	2,5257	2,14
	2	1,6098	0,8337	2,4529	2,10
Hornbeam	1	1,11682	0,7092	1,8364	1,65
	2	1,6763	0,9032	2,5894	1,86
Beech	1	1,1083	0,6312	1,7644	1,77
	2	2,2253	1,2363	3,4471	1,82
Oak	1	0,9007	0,5143	1,4561	1,90
	2	1,6851	0,8691	2,7129	1,97

It first of all appears, that the index

$$Q = \frac{\text{chlorophyl a} - \text{content}}{\text{chlorophyl b} - \text{content}}$$

is nearly constant with values between 1,6 and 2,2 and there seems to be no significant difference between the leaves from different crown layers. The highest values are found for ash and maple, the lowest for beech and hornbeam, oak being more or less transitional, but the differences between the species are not very important.

However, about the same relations between the species are found if starting from the chlorophyl – content (a, b and total) with only a slight change of position for oak : Maple and ash have the highest chlorophyl content, followed by hornbeam and beech, but the lowest values are found for oak.

Maple and ash are very close to each other for c.a. and c.t. but ash shows a considerable lower c.b. content.

In a similar way hornbeam and beech are comparable to each other, except for c.b., the content of which is considerable higher for hornbeam. This even leads to the constatation that, although ash and hornbeam are really different from each other as for as c.a., c.t. and a/b are concerned, their leaves have about the same content of chlorophyl b.

Relative values (Upper crown layer)

	Chlorophyl a	Chlorophyl b	Chlorophyl total
Maple	100	100	100
Ash	94	81	94
Hornbeam	70	78	69
Beech	67	69	66
Oak	54	56	54

The differences in chlorophyl content of the leaves of different species give already a certain clue to their potential differences in physiological reaction. The picture of the relationship between species gets more complete but more intricate at the same time, if the differences between leaves from different crown layers are also taken into consideration.

TABLE 17

Value of index 1/2 (cfr. tab. 16) = relation chlorophyl content of leaves belonging to different crown layers

Tree species	Chlorophyl a	Chlorophyl b	Chlorophyl tot.
Field maple	110	98	107
Ash	103	112	97
Hornbeam	143	127	141
Beech	201	196	195
Oak	187	169	186

Three facts seem to be importance :

1° In a general way, the chlorophyl content (a, b and t) of the leaves collected in the lower crown layer is higher than the chlorophyl content of leaves from the upper crown layer. In reverse this means, that higher chlorophyl content stands for a more outspoken tolerant leaf type. This applies as well to leaves as to species.

2° For the same species, unimportant differences in chlorophyl content between leaves from different crown layers lead to the characterisation of this species as « photostable », whereas big differences are corresponding with the predicate « photolabile » (Tab. 17.)
In this respect, ash and maple must be considered as photostabile species (relation 1/2 varies between 97 and 112); beech and oak react as photolabile species (relation 1/2 varies from 169 to 201) and hornbeam is to be placed in between (relation 1/2 varies between 127 and 143).

3° The relationship between species is greatly dependant on the light environment conditions under which they are growing together.

In fact, if the chlorophyl content of leaves is judged an acceptable parameter to assess the photoreactive character or the « light temperament » of tree species and if it is taken for granted that the clorcphyl content varies with macro- and microclimatic light conditions so as to cause great variation between trees from the same species and even between leaves collected on the same tree, it is amply proved that a great deal of precaution must be taken in qualifying a tree species. Emperical observation can only lead to conclusions with restricted signification; a schematic classification of tree species based upon their relative position to each other as a consequence of similarities or differences regarding light absorption, is not to be attempted as the reaction of species to changing light conditions is quite different from the quantitative and qualitative point of view.

These facts also prove how much wisdom is contained in the opinions of leading sylviculturists as Schaedelin and Leibundgut, where both stress the importance of continual observation, warn against generalisations and oversimplications in the concepts of stand treatment and give so much importance to the care for the individual tree and to the uniqueness of the forest stand.

5. Final conclusions and general summary

A certain number of measurable characteristics of tree leaves (morphological characteristics, absorption of light radiation, intensity of respiration and photosynthesis) are clearly linked with the presence of physiologically active pigments in the leaves.

Leaf characteristics are highly and inequally influenced by changing conditions of light environment, especially those related to light intensity, light quality and duration of the daily illumination period. These modifications do not only apply to light radiation as created under laboratory conditions, but also to light conditions ensuing from the place in the crown of a single tree, the social position of the tree in a forest stand and the site factors in general.

There are also changes taking place due to the progression of the vegetation period, at the end of which all species are less tolerant or more light demanding. The reaction of the leaves towards light radiation out of different regions of the spectrum is also different. The so-called blue light radiation ($\lambda_{max} = 440$ nm) seems to be of the greatest importance in this relation, as species react quite different to its action.

The biggest variation in leaf characteristics due to changing light environment was measured for oak and beech, which both react quickly and are qualified as « photolabile species ». No important variations occur in leaves of ash and maple, which therefore are qualified as « photostable species ».

As a consequence of variable reactions to changing light conditions, the relationships between the species are continually modified, even in such a way that their potential for dominance is not constant.

The classical division into tolerant and intolerant species or classification of the species based upon the degree of light demand, is highly inaccurate and it seems preferable to speak of relative light demands and relative tolerance. All these observations and conclusions bring about a clear confirmation of the necessity to recognize the individuality of the single tree, the special character of each growth condition, the own structure of each forest stand, the specific reaction to one sided modifications of environmental factors. This is especially important for an intensive sylvicultural practice.

They also prove the necessity for more physiological and biochemical research to arrive at a better understanding of growth and its mechanism.

Sylviculture in fact must try to regulate, on an expanded scale, the phenomens of growth, which is the exchange, absorption and transformation of energy.

A practical interpretation and regulation of fundamental laws of physiology and growth will be possible as soon as a clinical form of sylviculture is created and the adequate instrumentarium developed.

ZUSAMMENFASSUNG

Es besteht ein deutlicher Zusammenhang zwischen morphologischen Blattmerkmalen, der Durchlässigkeit des Baumblattes für die Lichtstrahlung, bestimmten physiologischen Prozessen wie Atmung und Photosynthese und dem Vorkommen von Blattpigmenten.

Sehr unterschiedliche Aenderungen an diesen Faktoren werden hervorgerufen durch Variation von Beleuchtungsstärke, Beleuchtungsdauer und Lichtqualität. Diese stimmen ihrerseits überein mit Unterschiede nach sozialer Position des Baumes und nach Position des Blattes in der Baumkrone.

Auch im Laufe der Vegetationszeit treten kontinuierlich Aenderungen auf (Zunahme des Charakters von Lichtart), wobei die Reaktion des Blattes gegenüber Strahlung herkünftig aus verschiedenen Sprektrumteilgebieten sehr ungleich sein kann. Die Strahlung aus dem blauen Gebiet (λ max = 440 nm) scheint in dieser Hinsicht eine besondere Rolle zu spielen.

Die feststellbaren Variationen sind bei einigen Baumarten wie Buche und Eiche sehr gross : sie werden deswegen als « photolabile Baumarten » bezeichnet. Geringe Variationen treten dagegen auf bei den « photostabilen Baumarten » wie Esche und Ahorn. Zwischen den beiden Gruppen bestehen Uebergange, wie z.B. durch Hagebuche gebildet. Infolge der ungleichen Variation und Reaktion von verschiedenen Baumarten auf veränderliche Lichtstrahlungsbedingungen, ändern sich die gegenseitigen Positionen der Baumarten ständig. Deswegen ist es angewiesen nur von « relativen Lichtbaumarten » und von « relativen Schattenbaumarten » zu reden.

Die obigen Feststellungen und Beobachtungen weisen deutlich hin auf die Eigenart jedes Wuchszustandes, sowie auf die spezifischen Variationen die aus wechselnden ökologischen Bedingungen entstehen.

Sie beweisen auch die Notwendigkeit der intensivierten physiologischen und biochemischen Foschung zur Erklärung der Wuchserscheinungen und Energieverarbeitung.

Diese Grundlagenforschung wird eine direkte praktische Bedeutung erhalten, sobald akurate klinische Methoden ausgearbeitet worden sind, die eine schnelle, komplete und genaue Ansprache jedes Wuchszustandes erlauben.

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