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Growth analysis of Scots pine (*Pinus sylvestris* L.) seedlings cultivated in a wide range of experimental conditions

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Abstract

The work of this laboratory for many years with Scots pine seedlings has allowed to collect quite unique information as to the accumulation and distribution of dry matter and the reaction of plants to various environmental influences. It seems worthwhile to publish the main experimental data almost *in extenso* because they may be used in future work for building mathematical models of plant growth. The presented experimental data enabled to discuss controversial points of quantitative analysis of plant growth such as: the time instant and the initial value of growth to be taken as the starting points (t_o, W_o); exponential approximation of the growth curve; inadequacy of allometric approach in modelling vegetative growth of plants, etc. The discussion aims at defining more closely the essential notions of growth analysis.

Key words: growth analysis, Pinus sylvestris, adaptive growth

INTRODUCTION

Accumulation of dry matter in permanent structures of a plant, which takes place during vegetative growth, is often considered to be exponential at early stages and allometric during the whole process of growth. Both assumptions, however, are only rough approximation to reality since phenotypical deviations from the "idealized" growth curve are usually large. A growing plant changes its proportions not only because of its natural ontogenetic trend, as is the case in many animals, but also in response to environmental influences what makes the allometric approach inadequate.

The environmental effects on dry matter accumulation and distribution in plants are, however, not sufficiently recognized because usually large agricultural crops are the objects of research, the measuring and weighing of which is extremely difficult and laborious. Thus, sampling can seldom be sufficiently abundant to give representative means; besides, the root system is often neglected making some growth analytical characteristics meaningless or confusing.

Tree sedlings, especially of conifers in the first growing season, appeared to be convenient objects for studying vegetative growth. They are small enough to be harvested in appropriate numbers of replicates, they do not lose needles at the end of the first growing season, and their assimilatory and nonassimilatory parts are well distinguishable (what is not always the case with crop plants). Scots pine seedlings have, moreover, another advantage as experimental plants, namely, an extremely high phenotype adaptability to a wide range of environmental situations (rather exceptional with narrow crop genotypes).

By analysing a certain number of our own experimental results and by comparing them with available literature data one should be able to discuss important problems related to modelling of plant growth: limited occurrence of the exponential growth stage, maximum values and seasonal changes of growth characteristics, inadequacy of allometric approach in describing vegetative growth of plants, response of plant organs to a change in environmental conditions, and consequences of this for the interpretation of the discrepancy between plant and animal growth.

The applied methods may seem quite primitive as compared with the technical means of modern research. But there exists no way of revising ambiguous views on accumulation and distrtibution of dry matter other than tedious cultivation, watering, harvesting, partitioning, drying and weighing the particular parts of the investigated plant; this explains the number of coauthors of this laborious study.

MATERIAL AND METHODS

Seedlings of Scots pine, always of the same provenience from Central Poland, were cultivated under various, laboratory or out-of-doors, semi-controlled conditions, specified in detail for the particular experiments described below. In laboratory experiments artificial light sources were applied: fluorescent mercury vapour lamps LRFR — 400 W (in one case 250 W) or fluorescent tubes 40 W, giving, at the level of plant tops, about 70, 50, or 30 Wm^{-2} of PAR, respectively. In greenhouse experiments plants were exposed to natural fluctuations of daylength and light intensity (latitude 51° 40'); pots standing out-of-doors on trolleys were shifted under glass for rainy periods and nights.

A mixture of sand, poor forest soil, and peat (1:2:1), watered every day to constant weight, was used as medium in the majority of pot experiments. Numerous experiments were also carried out in water culture where either Ingestad (1962/63) solution (called in this paper "standard") or our own, modified, solution (called "luxurious") were used. The modification consisted in: 1) an increased concentration of nitrogen salts (according to suggestions of Ingestad (1970)), 2) higher proportion of nitrate to ammonium salts (what was empirically proved as suggested by Ingestad (1970)), 3) application of calcium nitrate as an additional source of nitrogen (according to the experience of van den Driesche (1971)), and 4) adjustment of other elements towards a more suitable composition of the solution (N:K:P=100:40:6 against 100:100:40 in the standard solution, whereas 100:65:13 is assumed by Ingestad (1979) as the optimum for pine). Then, the modified (luxurious) solution consisted of ($g \cdot dm^{-3}$): NH_4NO_3 — 1.280, $Ca(NO_3)_2 \cdot 4H_2O$ — 0.441, KH_2PO_4 — 0.053, K_2HPO_4 — 0.101, K_2SO_4 — 0.311, $CaCl_2 \cdot 6H_2O$ — 0.429, $MgSO_4 \cdot 7H_2O$ — 0.247, and microelements according to Ingestad (1962/63). Only root-tips were immersed in the solution so aeration was accomplished by means of the major part of the root-system continuously maintained above the water level. The solution was changed every two weeks in laboratory experiments and every four weeks in greenhouse experiments.

Classical, growth analytical characteristics, i.e. leaf weight ratio, relative growth rate, and unit leaf rate (for review see: Květ et al. 1971, Evans 1972) were calculated from the mean values of dry weight of particular organs. Weight of primary needles and cotyledons was used instead of the surface area as measure of the size of assimilatory organs for two reasons: because the shape of pine needles is difficult to measure planimetrically and because the interpretation of growth characteristics is easier (leaf weight ratio is then simply a fraction of leaf weight in the total dry weight of a plant).

The mean values and their standard deviations were calculated on the basis of a different, rather large, number of replicates (specified at particular experiments); the data refer to average (idealized) individuals, representing the whole investigated populations. Dry weight data are given in mgs, RGR and ULR in mgs $g^{-1} \cdot d^{-1}$.

RESULTS

The first (preliminary) experiment was carried out with germinating embryos (seedlings) grown in sand, under continuous illumination. It was carried out in order to characterize the earliest developmental stages and the reaction of plants to transient inhibition of growth. It appeared (Fig. 1) that under most suitable germination conditions the heterotrophic phase of growth lasted only one week. The maximum value of the relative growth rate was attained between the 3rd and 4th day and amounted to 0.600 d^{-1} (what meant almost doubling of the embryo weight in one day). When cotyledons began to photosynthesize the value of RGR stabilized at the mean level 0.102 d^{-1} for the period between the 8th and 14th day from imbibition. While weight gain was inhibited by transient shading after new exposure to light the plants resumed vigorous growth with mean RGR equal to 0.125 d^{-1}.

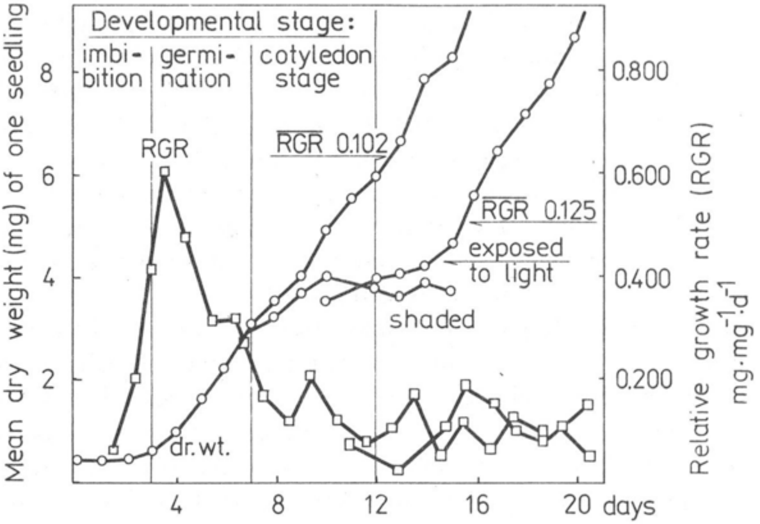

Fig. 1. Dry matter accumulation (—o—o—) and relative growth rates (—□—□—) of embryos (or seedlings) grown in sand culture under continuous light (12 fluorescent tubes, 40 W each); means of 4 × 50 = 200 embryos (or seedlings) prepared each day; between 7th and 15th day one part of seedlings was transiently shaded. Doubled or even tripled points, on certain days, mean the number of samples augmented, respectively. (Experiment 1)

The experimental data of seedling growth can easily be approximated by an exponential curve with even highly significant coefficients of correlation (Fig 2 — data from experiment 2). With the logarithmically transformed data, however, a curvilinear trend is noticeable quite early. This slight departure from linearity often is disregarded if variance of the subsequent harvests is high, as it was artificially achieved in Fig. 2 (and is typical when only few plants represent the mean). For the experimental data from Fig. 2 the calculation of the mean value of RGR as the rate of exponential growth seemed to be justified for only five initial harvests (between the 1st and 5th week).

Table 1

Experiments in water culture, plants grown under artificial light

Exp. No.	Day	7th	14th	21st	28th	35th	49th	70th	91st	112th
Exp. 2	dr. wt., mg	5.8 (±1.5)	10.2 (±2.6)	17.8 (±4.7)	29.2 (±7.2)	55.0 (±11.8)	160 (±45)	509 (±175)	1122 (±228)	1954 (±350)
	LWR	0.48	0.62	0.71	0.76	0.77	0.74	0.68	0.66	0.66
Exp. 3	day	21st	49th	77th	106th					
	dr. wt., mg	44.2 (±10.6)	249 (±13.2)	539 (±52.7)	831 (±38.5)					
	LWR	0.74	0.78	0.78	0.77					
Exp. 4	day	14th	21st	28th	35th	42nd	56th			
	dr. wt. (S), mg	11.1 (±1.9)	23.5 (±5.0)	51.2 (±7.7)	101 (±17.8)	165 (±28.8)	428 (±80)			
	dr. wt. (L), mg	11.9 (±2.2)	23.7 (±3.2)	50.4 (±7.7)	92 (±14.6)	176 (±20.8)	447 (±82)			
	LWR (S)	0.59	0.68	0.72	0.73	0.71	0.69			
	LWR (L)	0.57	0.70	0.72	0.74	0.73	0.67			

Exp. 2 — mercury vapour flurescent lamps, 4×400 W, 16h day, luxurious solution, means of 15 plants.
Exp. 3 — mercury vapour flurescent lamps. 4×250 W. 16h day. standard solution. means of 2 samples (72 plants in each sample).
Exp. 4 — flurescent tubes 12×40 W. 24 h day. standard solution (S). or laxurious solution (L), means of 20 samples (5 plants in each sample).

Table 2

Experiments in water culture, plants grown out-of-doors

Exp. No.	Day	21st	51st	81st	126th	156th	176th
Exp. 5	dr. wt., mg	20.4 (±2.0)	102.5 (±17)	410 (±101)	1449 (±370)	2005 (±403)	2128 (±398)
	LWR	0.57	0.67	0.66	0.61	0.51	0.48
Exp. 6	day	14th	42nd	70th	98th	126th	154th
	dr. wt. (S), mg	10.8 (±0.67)	54.7 (±6.2)	271 (±40.4)	667 (±151)	1211 (±146)	1576 (±273)
	dr. wt. (L), mg	11.1 (±0.85)	57.5 (±4.9)	236 (±26.9)	689 (±68)	1287 (±83)	2131 (±466)
	LWR (S)	0.57	0.68	0.68	0.68	0.56	0.50
	LWR (L)	0.58	0.72	0.68	0.66	0.60	0.57

Exp. 5 — standard solution, means of 90 plants; first harvest 1980.05.26.

Exp. 6 — standard solution (S), or luxurious solution (L), means of 5 samples, (5 plants in each sample); first harvest 1981.05.05.

Table 3

Experiments in pots (soil culture), plants grown out-of-doors, watered daily to constant weight 60% of capillary capacity

Exp. No.	Day	21st	35th	50th	64th	78th	92nd	106th	120th	134th	148th
Exp. 7	dr. wt., mg	22.9 (±1.6)	36.1 (±5.4)	73.2 (±5.6)	132 (±7)	230 (±25)	372 (±24)	493 (±50)	629 (±61)	748 (±10)	828 (±60)
	LWR	0.66	0.62	0.65	0.69	0.67	0.63	0.56	0.54	0.49	0.47
Exp. 8	day	14th	28th	42nd	56th	77th	98th	119th	140th	161st	182nd
	dr. wt., mg	6.5 (±0.42)	12.3 (±1.3)	38.9 (±3.0)	76.8 (±9.0)	156 (±2.9)	174 (±33)	218 (±16)	292 (±14)	305 (±47)	320 (±21)
	LWR	0.50	0.59	0.66	0.63	0.60	0.55	0.50	0.43	0.43	0.44

Exp. 7 — moderate watering, 60% of c.c., means of 5 samples (30 plants in each sample); first harvest 1975.06.11.
Exp. 8 — moderate watering, 60% of c.c., means of 3 samples (about 15 plants in each sample); first harvest 1981.05.14.

Table 4

Experiments in pots (soil culture), plants grown out-of-doors, watered daily to constant weight 60% or 20% capillary capacity

Exp. No.	Day	21st	35th	49th	64th	77th	105th	133rd	174th				
Exp. 9	dr. wt. (M)	6.15	22.8	40.4	62.9	80.5	121	153	197				
	dr. wt. (D)	2.9	11.8	25.0	36.2	31.9	52	50	64				
	LWR (M)	0.46	0.67	0.67	0.64	0.56	0.63	0.55	0.51				
	LWR (D)	0.46	0.64	0.65	0.62	0.52	0.58	0.52	0.50				
Exp. 10	day	21st	41st	57th	70th	97th	111th	125th	139th	153rd			
	dr. wt. (M), mg	11.7 (±1.4)	33.7 (±1.9)	52.1 (±2.3)	78.0 (±6.0)	127 (±8.1)	147 (±16)	156 (±13)	162 (±19)	163 (±7)			
	dr. wt. (D), mg	11.7 (±1.4)	25.7 (±2.8)	44.5 (±4.8)	74.4 (±14.6)	92.0 (±8.9)	96.9 (±7.6)	105 (±5.1)	122 (±13)	145 (±14)			
	LWR (M)	0.65	0.64	0.63	0.57	0.51	0.48	0.46	0.44	0.44			
	LWR (D)	0.65	0.63	0.61	0.56	0.45	0.43	0.41	0.41	0.37			
Exp. 11	day	11th	25th	40th	54th	68th	82nd	96th	110th	124th	138th	152nd	166th
	dr. wt. (M), mg	5.6 (±0.7)	18.2 (±2.2)	32.8 (±2.4)	39.7 (±1.5)	61.3 (±8.3)	111 (±9.5)	172 (±5.6)	260 (±12)	416 (±63)	440 (±88)	593 (±70)	521 (±52)
	dr. wt. (D) mg	5.6 (±0.7)	18.3 (±2.2)	34.2 (±3.6)	47.1 (±2.8)	52.7 (±5.3)	65.8 (±10)	83.5 (±12)	116 (±15)	127 (±11)	170 (±20)	175 (±33)	187 (±32)
	LWR (M)	0.55	0.63	0.64	0.65	0.58	0.63	0.63	0.63	0.57	0.49	0.46	0.45
	LWR (D)	0.55	0.63	0.64	0.65	0.52	0.50	0.52	0.53	0.51	0.44	0.43	0.40

Exp. 9 — moderate watering, 60% of c.c. (M) or dryness, 20% of c.c. (D); means of 40—80 plants, weighed as one sample; first harvest 1980.06.10.

Exp. 10 — moderate watering, 60% of c.c. (M) or dryness, 20% of c.c. (D); means of 5 samples, 20—25 plants in each sample; first harvest 1982.06.09.

Exp. 11 — moderate watering, 60% of c.c. (M) or dryness, 20% of c.c. (D); means of 4 samples, 12—15 plants in each sample; first harvest 1983.05.11.

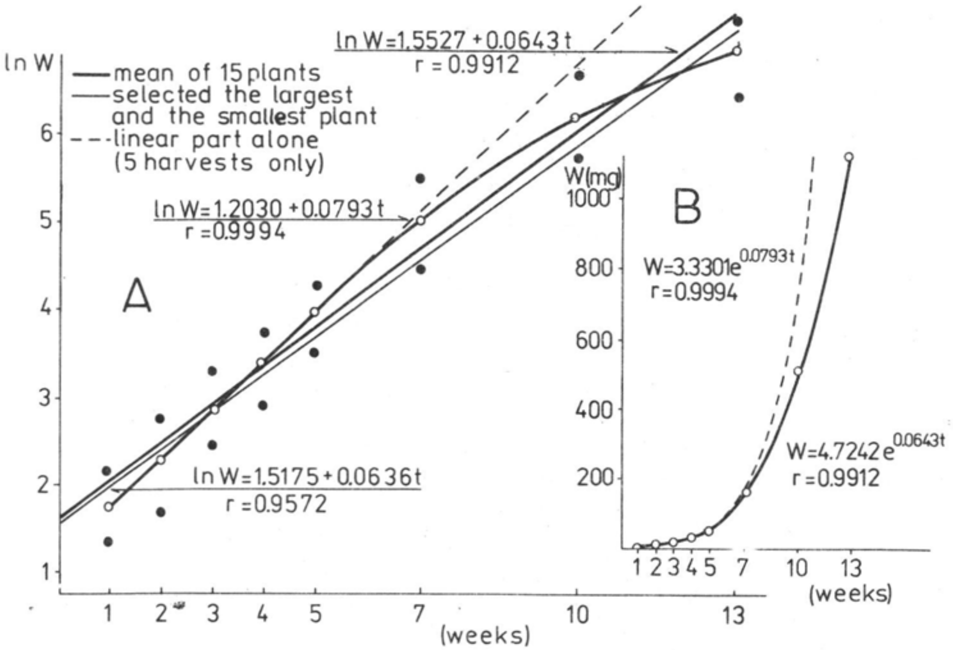

Fig. 2. Exponential function fitted to the data from experiment 2 (Table 1), A — logarithmically transformed means (—o—o—), or the largest and the smallest plants selected in each sample (● ●). B — original mean data of dry matter accumulation (—○—○—) as the deviation from exponential curve (- - -) determined from the initial five points

Experiments with seedlings grown over the whole growing season under different growth conditions indicated that, not only the course of dry matter accumulation, but also the leaf weight ratio (i.e. the fraction of dry matter accumulated in assimilatory organs) were highly variable (Tables 1-4, experiments 1-11). This caused an altered pattern in seasonal changes of relative growth rate and of unit leaf rate (Figs. 3 and 4). The fraction of dry matter accumulated in needles depended very much upon illumination, watering, and nutrient supply (Figs. 5 and 6). Leaf weight ratio, relative growth rate, and unit leaf rate were highly affected by sudden changes in growing conditions, e.g. in the nutrient status or photoperiodic treatment (Fig. 6, Tables 5 and 6, experiments 12-15).

DISCUSSION

The initial weight and the time of the beginning of growth are usually assumed, rather arbitrarily, as the moment of the first sampling. Since many growth models base upon these values, and appeared to be very sensitive to an even slight inaccuracy in this respect, a more precise

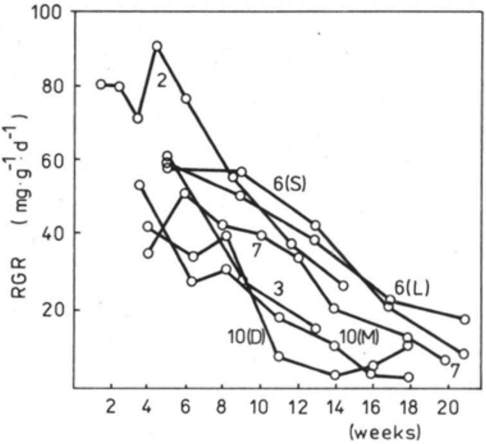

Fig. 3. Seasonal drift in value of the relative growth rate; as example data from selected experiments (numbers and letters indicate particular experiments described in Tables 1-4)

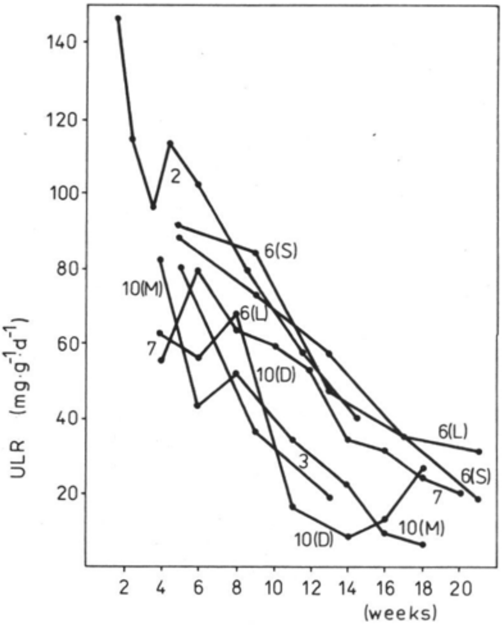

Fig. 4. Seasonal drift in value of the unit leaf rate; as example data from selected experiments (number and letters indicate particular experiments described in Tables 1-4)

definition and an adequate biological interpretation of the starting point would be desirable. Blackman (1919), the first author who investigated exponential growth of plants, assumed seed weight as the initial value of growth. This, however, means a rough simplification since at early stages of growth the embryo lives at the cost of storage materials from the

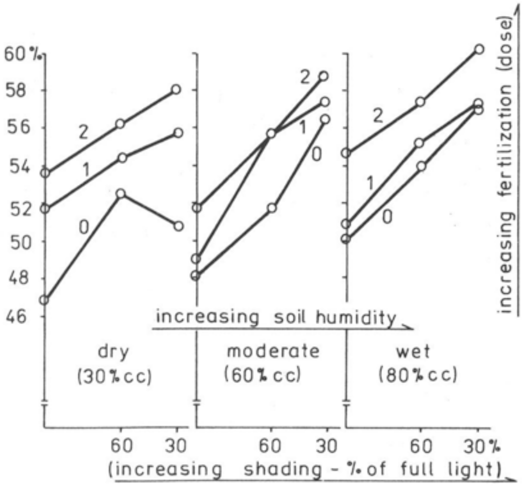

Fig. 5. Leaf weight ratio (or fraction of needle dry weight) in seedlings cultivated out-of-doors, in pots, under differentiated soil humidity, shading, and nutrient supply; (0, 1, 2 — relative measure of applied fertilization). (Experiment 14)

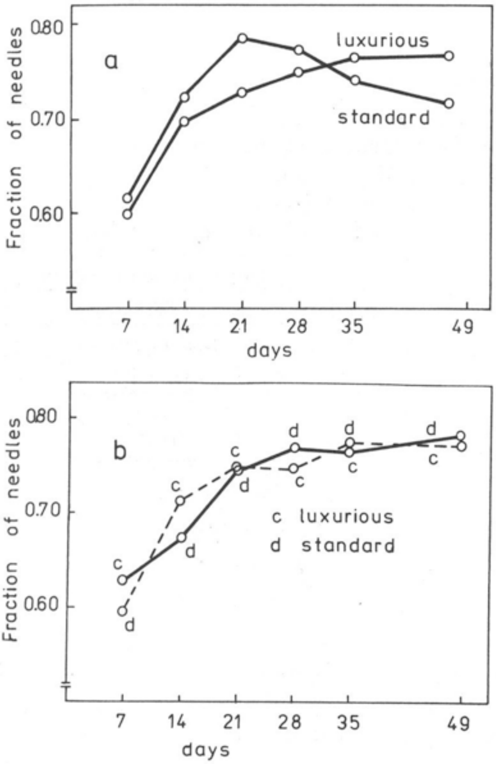

Fig. 6. Leaf weight ratio (or fraction of needle dry weight) of seedlings cultivated in water culture, under continuous fluorescent light, at constant (a) or alternated (b) nutrition regimes. (Experiment 15)

Table 5

Exp. 12. Sand culture at illumination from fluorescent tubes (12 × 40 W), 24 h, 16 h and 8 h day length; on 24th day of growth plants were transferred into continuous light; means of 50 seedlings weighed as one sample

Characteristic	Day from germination					
	day length	7th	day length	23rd	day length	38th
Dr. wt., mg	24 h	3.11	24 h	11.15	24 h	27.65
	16 h	2.61	16 h	8.00	24 h	24.72
	8 h	2.42	8 h	4.89	24 h	15.17
LWR	24 h	0.49	24 h	0.67	24 h	0.70
	16 h	0.48	16 h	0.65	24 h	0.71
	8 h	0.49	8 h	0.57	24 h	0.66
RGR mg·g^{-1}·d^{-1}	24 h		80	24 h		61
	16 h		70	24 h		75
	8 h		44	24 h		76
ULR, mg·g^{-1}·d^{-1}	24 h		135	24 h		88
	16 h		121	24 h		110
	8 h		82	24 h		121

Table 6

Exp. 13. Water culture at mercury vapour fluorescent lamps (4 × 400 W), 16 h day, means of 16–21 plants; seedlings grown in standard (Ingestad) solution (S) and transferred to luxurious solution (L) at the age of 10 weeks

Characteristic		Day from germination		
		70th	88th	116th
Dr. wt.	S	188 (±46)	449 (±89)	910 (±204)
	L	188 (±46)	460 (±103)	1065 (±298)
LWR	S	0.69	0.62	0.53
	L	0.69	0.62	0.58
RGR	S	32		25
	L	33		30
ULR	S	50		44
	L	51		50

megagametophyte only, this causing a transient decrease of the total dry weight of the germinating seed. As a result the heterotrophic stage of growth and its high RGR value are not interpretable in terms of the classical concept of growth analysis (Żelawski and Sztencel 1981). It appears that constant values of RGR, and, consequently, the exponential phase of growth, are limited to an only very short period when assimilatory organs are fully developed and active, i.e. when the natural trend of decreasing unit leaf ratio is still compensated by the increasing leaf fraction (since RGR = ULR × LWR, see, for review, Żelawski and Sztencel 1981). In seedlings of Scots pine it may fall to the time of emergence and fast development of primary needles, but under less favourable environmental conditions, particularly in the field (low temperature, short days, etc.), it may also be delayed up to several weeks (see e.g. exp. 7 and 8). In the case of a delay of formation of leaves the exponential phase of growth is hardly discernible: the rate of decrease in ULR may then exceed the rate of increase in LWR; (later all three growth characteristics decrease with a rate predominantly controlled by the environmental conditions).

Taking all this into account, and assuming that in the germinating embryo the accumulation of dry matter highly depends on the transfer of substance from the maternal megagametophyte, one should assign the starting point of growth to the time of autotrophic development, when the exponential phase occurs; such a phase is presumed to occur when the assimilatory organs (LWR) and their activity (ULR) reach maximum values.

Consequently, the initial value of RGR should be maximum since further growth is simply a departure from exponentiality (Figs. 2 and 3). In fact, under conditions favouring growth, the maximum RGR occurred early: under continuous light, following transient shading it took place in the third week after germination and amounted to 0.125 d^{-1} — a value which seems to be the highest ever reported for Scots pine (Fig. 1). For comparison the mean maximum values, reported by other authors, were as follows: Rutter (1957) — 0.033 d^{-1}, Ingestad (1962/63) — 0.080 d^{-1}, Jarvis and Jarvis (1964) — 0.071 d^{-1}, Grime and Hunt (1975) — 0.051 d^{-1}; one should expect, however, that the quoted data concern somewhat later stages of growth and perhaps less favourable growing conditions.

Field conditions, and particularly natural daylength (under this latitude varying between about 13 and 17 hours in the growing season), impose certain disturbances upon the growth characteristics and their spontaneous drift appearing under fixed photoperiods. Usually the increasing daylength shifts the maximum values of RGR and ULR towards the summer solstice. Yet, the field conditions mean, as a rule, certain stress effects by which the formation of assimilatory organs is restrained.

Under favourable conditions the most intensive formation of needles takes place in Scots pine seedlings during the early stages of growth, before the plant reaches about 100 mg of dry weight. An increasing "investment" of photosynthetic products into the roots and stem occurs during the remaining part of the growing season. Partitioning of matter is then phenotypically variable and reflects the plant response to environmental factors. As a result the proportion of assimilatory tissue in the total dry weight of a plant could differ highly towards the end of the growing season: from nearly 80% (abundant fertilization and watering, and moderate shading) to almost 35% (in soil culture, with low watering and fertilization) — exp. 3 and 10, Tables 1 and 4.

Such a phenotype differentiation, though often less pronounced than in pine, is known for various plants, but quantitative data, concerning the response of dry matter distribution to changes in environmental conditions, are rather scanty. In experiments with *Impatiens parviflora* (Evans and Hughes 1961, 1962, Hughes and Evans 1962) adapted to shade 4.5-week-old plants, when transferred from low to high light intensity, increased their relative growth rate and decreased the leaf area ratio, as compared with the control plants.

In our experiments with seedlings of Scots pine, transiently shaded and then exposed to light, the relative growth rates also increased (Fig. 1) and the leaf weight ratio decreased (Tarasiuk 1985). On the other hand, shortening of photoperiods, due to a diminution of daily photosynthesis, reduced the relative growth rate almost proportionally to the daylength and lessened the leaf weight ratio (Table 5); new exposure to continuous light caused a resumption of growth and augmented both the RGR and the LWR. Changes in the nutrient status, most easily attainable in water culture (Table 6), inhibited the natural decrease of RGR and LWR, when seedlings were transfered from the standard to "luxurious" solution. If the solutions were alternated week by week the course of formation of needles was irregular but the trends, remained specific for the solution applied: formation of needles was accelerated in the standard, as compared with the "luxurious", solution (Fig. 6).

The presented experimental data indicate the difficulties of constructing a quantitative theory of plant growth. Ontogenesis, and the related weight gain, are often presumed to be a consequent realization of the genetic program which is only accelerated or inhibited by favourable or stress conditions, respectively. Although, many heterotrophic organisms grow in such a way, revealing an *a priori* imposed (allometric) pattern of proportions between organs (see for review: Walter and Lamprecht 1976, Żelawski and Lech 1980), plants grow according to the activity of their photosynthesizing portions; this makes the partitioning of photosynthetic products crucial, and the allometry rules invalid in the analysis of plant growth. Physiologists are not always aware of this principal difference between plant and animal growth and they often apply rigid mathematical models formulated for describing the weight gain of heterotrophic organisms. Richards' equation (1959, 1969), quite commonly applied in plant research, derived from the von Bertalanffy (1957) theory of animal growth by purely formalistic transformation of parameters, is a good example of such a model; it does not fit the objects showing adaptive growth because it also contains an allometric background.

Unfortunately, the allometric point of view is deeply inverterated because the logarithmic transformation of data facilitates disregard of actually existing trends. Even those who generally accept the adaptive character of photosynthetic products distribution are sometimes inclined to assume deviations from linearity in the logarithmic relationship between organs as an only insignificant departure from allometry. For instance, Ledig et al. (1970) and Drew and Ledig (1980), who investigated seedlings of loblolly pine, though less responsive than Scots pine, took for granted the allometry rules as a typical mode of growth during the first two years, at least.

Yet, the construction of a theory of plant growth encounters another difficulty related to the unrealistic, and usually nonrealized, task of maintaining constant conditions during the process of growth. Even under "controlled" conditions in growth chambers illumination, at least, is a very heterogenous factor because of self-shading effects (Kramer and Clark 1947, Żelawski et al. 1973) and owing to the square dependence of light intensity from the distance of the light source. Since the growing plant changes its photosynthetic conditions, as well as its water and nutrient status, by the growth process itself, there is very little chance to experimentally disclose a "pure" dependence of dry matter accumulation of external factors and to recognize a "natural" growth pattern that would appear if the conditions were absolutely constant. One can only guess that a photosynthesizing plant should exhibit a natural inclination primarily to "invest" as much organic matter as possible (i.e. as genetically permissible) in the leaves. Formation of other than assimilatory organs is partly postponed until an environmental stress begins to enforce a transfer of photosynthetic products into the meristematic tissues of these organs. The adaptive changes in the allocation pattern proceed within the genetically determined "life strategy" of the species, while phenotypes are a "tactical solution" of this strategy (Jones and Wilkins (1971), Evans (1972), Harper (1977)). The more flexible the genotype the larger its phenotype variability, ecological niche, and natural range of distribution.

Any change in external factors that exceeds the range of the genotype adaptability, may cause decay of the relevant object. As an example a rather poor survival of tree seedlings, transplanted from too rich nursery conditions into a less favourable forest rejuvenation area, could be quoted.

Long-lived organisms, like forest trees, must exhibit higher phenotypical variability than herbaceous plants. This is especialy clearly seen when individuals in an open space and in the stand are compared. Since tree growth has a cumulative character the changes in allocation pattern, caused by environmental effects, become less and less effective with increasing size and age; this explains the diminishing adaptability of older tress.

The results of the presented experiments have been used as the basis for a dynamic model of vegetative plant growth in which the partitioning of photosynthetic products has been taken into account (Żelawski and Szlenk 1984, Szlenk and Żelawski 1984).

In conclusion one can say that:

1. The exponential phase of growth, in seedlings of Scots pine, is limited to a very short period when the assimilatory organs are fully developed, relative growth rate is maximum and presumably constant, and the natural decline in the unit leaf rate is compensated by an equivalent increase in the leaf weight ratio.
2. The strating point of growth, important in building mathematical models in which the initial weight is involved, should be assigned to the time instant when the maximum values of leaf weight ratio and relative growth rate are reached.
3. The phenotypical response of dry matter allocation, bringing about adaptive changes in the proportion of assimilatory to nonassimilatory organs, excludes the allometric approach in quantitative analysis of dry matter accumulation in plants.

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REFERENCES

Bertalanffy L. von, 1957. Quantitative laws for metabolism and growth. Quart. Rev. Biol. 32: 217-231.

Blackman V. H., 1919. The compound interest law and plant growth. Ann. Bot. 33: 353-360.

Drew A. P., Ledig T. F., 1980. Episodic growth and relative shoot/root balance in Loblolly pine seedlings. Ann. Bot. 45: 143-148.

Driesche R. van den, 1971. Response of conifers to NO_3 and NH_4-N sources. Plant and Soil 34: 421-439.

Evans G. C., 1972. The Quantitative Analysis of Plant Growth. Blackwell Scientific Publications, Oxford-London-Edinburgh-Melbourne.

Evans G. C., Hughes A. P., 1961. Plant growth and the aerial environment. I. Effect of artificial shading on *Impatiens parviflora*. New Phytol. 60: 150-180.

Evans G. C., Hughes A. P., 1962. Plant growth and the aerial environment. III. On the computation of unit leaf rate. New Phytol. 61: 322-327.

Grime I. P., Hunt R., 1975. Relative growth rate: its range and adaptive significance in a local flora. J. Ecol. 63: 393-422.

Harper J. L., 1977. Population biology of plants. Academic Press, London-New York-San Francisco.

Hughes A. P., Evans G. C., 1962. Plant growth and the aerial environment. II. Effect of light intensity on *Impatiens parviflora*. New Phytol. 62: 154-174.

Ingestad T., 1962/63. Macroelement nutrition of pine, spruce and birch seedlings in nutrient solutions. Medd. St. Skogsf. Inst. 7: 1-131.

Ingestad T., 1970. A Definition of Optimum Nutrient Requirements in Birch Seedlings. I. Physiol. Plant. 23: 1127-1138.

Ingestad T., 1979. Mineral Nutrient Requirements of *Pinus silvestris* and *Picea abies* seedlings. Physiol. Plant. 45: 373-380.

Jarvis P. G., Jarvis M. S., 1964. Growth rates of woody plants. Physiol. Plant. 17: 654-666.

Jones D. A., Wilkins D. A., 1971. Variation and adaptation in plant species. Heinemann Educational Books Ltd., Polish edition 1977, PWN, Warszawa.

Kramer P. J., Clark W. S., 1947. A comparison of photosynthesis in individual pine needles and entire seedlings at various light intensities. Plant Physiol. 22: 51-57.

Kvˇet J., Ondok P. J., Neˇcas J., Jarvis P. G., 1971. Methods of growth analysis. In: Plant Photosynthetic Production. Šestak Z., Čatsky J., Jarvis P. G. (eds.), Dr W. Junk N. V. Publishers, The Hague. pp. 343-384.

Ledig F. T., Bormann F. H., Wenger K. F., 1970. The distribution of dry matter growth between shoot and roots in Loblolly pine. Bot. Gaz. 131: 349-359.

Richards F. J., 1959. A flexible growth function for empirical use. J. Exp. Bot. 10: 290-300.

Richards F. J., 1969. The quantitative analysis of growth. In: Plant Physiol. F.C. Steward (ed.), Vol. VA, Academic Press, New York-London. pp. 3-79.

Rutter A. J., 1957. Studies in the growth of young plants of *Pinus sylvestris* L. I. The annual cycle of assimilation and growth. Ann. Bot. N.S. 21: 399-426.

Szlenk W., Żelawski W., 1984. A dynamic model of plant growth. Preprint 7, Matematisk Institut, Aarhus University.

Tarasiuk S., 1985. The reaction of growth of Scots pine (*Pinus silvestris* L.) seedlings to change of light intensity. Ann. Warsaw Agric. Univ. 35, Ser. Forestry and Wood Techn. (in press).

Walter R., Lamprecht J., 1976. Sovremennye teorii i uravnenija rosta. In: Termodinamika biologicheskikh procesov. A. Zotin (ed.), Izd. Nauka, Moskva. pp. 98-112.

Żelawski W., Lech A., 1980. Logistic growth functions and their applicability for characterizing dry matter accumulation in plants. Acta Physiol. Plant. 2: 87-94.

Żelawski W., Szaniawski R., Dybczyński W., Piechurowski A., 1973. Photosynthetic capacity of conifers in diffuse light of high illuminance. Photosynthetica 7: 351-357.

Żelawski W., Szlenk W., 1984. Vegetative growth in plants: A dynamic model. Physiol. Plant. 62: 253-259.

Żelawski W., Sztencel I., 1981. Relative growth rate and its ontogenetic drift in growth analysis of plants. Acta Physiol. Plant. 3: 85-94.

Analiza wzrostu siewek sosny zwyczajnej (Pinus sylvestris L.) rosnących w różnych warunkach doświadczalnych

Streszczenie

Badania siewek sosny, prowadzone od lat w naszym zespole, umożliwiły zebranie dość unikalnego materiału, dotyczącego akumulacji i rozmieszczenia suchej masy w roślinach

i reakcji tych roślin na rozmaite wpływy czynników zewnętrznych. Wydaje się pożyteczne opublikowanie tych danych prawie *in extenso* bowiem mogą być one w przyszłości wykorzystane do budowy modeli matematycznych opisujących i wyjaśniających przebieg wzrostu rośliny. Przedstawiony materiał eksperymentalny umożliwił przedyskutowanie niektórych kontrowersyjnych zagadnień ilościowej analizy wzrostu: jaki moment czasowy i jaka masa rośliny (t_o, W_o) winny być przyjmowane jako początkowe wartości procesu wzrostu?; czy i ewentualnie kiedy przybliżenie krzywej wzrostu za pomocą równania wykładniczego jest dopuszczalne?; dlaczego opis allometryczny nie jest odpowiednim sposobem modelowania wzrostu wegetatywnego roślin? itd. Przeprowadzono dyskusję, która powinna ułatwić dokładniejsze zdefiniowanie podstawowych pojęć ilościowej analizy wzrostu.