ACTA UNIVERSITATIS AGRICULTURAE ET SILVICULTURAE MENDELIANAE BRUNENSIS

Volume LX 31 Number 5, 2012

PLANT PHYSIOLOGY AT THE INSTITUTE FOR PHILOSOPHY IN BRNO IN MENDEL'S TEACHER F. DIEBL TEXTBOOK FROM 1835

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Received: February 17, 2012

Abstract

ŠEBÁNEK, J.: *Plant physiology at the institute for philosophy in Brno in Mendel's teacher F. Diebl textbook from 1835*. Acta univ. agric. et silvic. Mendel. Brun., 2012, LX, No. 5, pp. 277–282

Gregor Mendel attended lectures of F. Diebl, professor of natural history and agricultural science at the Institute of Philosophy in Brno. Diebl published his lectures in a textbook "Abhandlungen über die allgemeine und besondere Naturgeschichte, Brünn 1835." From the textbook the level of scientific knowledge in plant biology is obvious, with which the later founder of a new field of biology – genetics got acquainted. Diebl considered germination to be a specific method of fermentation transforming seed starch into a sugary matter which nourishes the germinating plant. In the physiology of nutrition he distinguished nutrition from the soil via roots from nutrition from the air via leaves. The former is based primarily on the humus theory of A. Thaer (1809) because not until 5 years after the publication of Diebl's textbook J. Liebig initiated the mineral theory. Diebl's presentation of photosynthesis was based on information available at that time about the release of oxygen by green plants under conditions of light and the uptake of CO_2, but he had no knowledge about the passage of CO_2 into the leaves through stomata. Remarkable is Diebl's discovery that respiration increases during flowering. Electricity is considered to be a force significantly supporting the life processes of plants. Diebl also noticed the difference between diurnal and night evaporation of water from the leaves. In his textbook growth is connected with nutrition only, as it was the entire 19th century. Stem thickening from the cambium is described very simply. Bud and root regeneration is given the term reproduction which today is commonly used in relation to sexual reproduction. Diebl considered nyctinastic movements (bending or unbending of the leaves) and closing of the flowers at night to be "sleep". He described fertilisation in a primitive way, because it was not until 1848 that the first exact description came out.

plant physiology in textbook from 1835, germination, nutrition, growth and reproduction, period of rest, plant propagation

INTRODUCTION

Plant Physiology as an independent discipline of natural sciences emerged as late as 1848 at Vienna University after the habilitation of Franz Unger (1800–1870) and 9 years later at Prague University after the habilitation of Julius Sachs (1834–1897). It is however remarkable that the first textbook on plant physiology appeared in Brno in what is now the Czech Republic as early as 1850. It was written in German but the author was Czech, Eugen Netolička (Krekule, 1998). Formerly plant physiology was only a part of natural history and that is how it was conceived by František Diebl (1770–1859), Professor of General Natural History and Agricultural Science at the Institute for Philosophy in Brno, in his book "Abhandlungen über die allgemeine und besondere Naturgeschichte, Brünn 1835 (gedruckt bei R. Rohrer)". Diebl was the teacher of G. J. Mendel who during his studies of theology attended Diebl's lectures on natural history and agricultural science at the Institute for Philosophy in Brno and in 1846 passed his exam there (Orel, 2003).

To realise the extent, depth and character of knowledge about plant physiology as it was presented in 1835 is not only interesting but it is also instructive. It was 176 years ago, before the

principal discoveries about mineral plant nutrition, photosynthesis and about growth, development, morphogenesis, reproduction and heredity emerged.

Diebl defined plant physiology as a science about the life activities and performance of plants aiming on the one hand to preserve its own life (germination, nutrition, growth, regeneration, dormancy) and on the other hand to preserve the progeny (breeding, seed formation, other methods of propagation, duration of life, age and death).

Germination

The germination of seeds with a live embryo is dependent on external factors, such as humidity, temperature and the presence of air as active factors, and on the period of rest (dormancy) as a passive factor. By the period of rest however Diebl obviously did not mean dormancy as the inability of seeds to germinate when all external conditions for germination are met and what stratification or post-harvest maturation may help overcome. Most probably he had in mind only the latent condition of live seeds in the period of their drying. Air has a vitalising effect on germination because of oxygen. Diebl explained the release of CO_2 by the breathing germinating plant in a peculiar formulation saying that "air dissolves plant carbon by means of oxygen" ("Die Lebensluft auflöset den Kohlenstoff durch ihren Sauerstoff").

Diebl indicated germination as "live seed fermentation (belebte Keimungsgärung)". When the seed swells after taking up water it begins to transform starch into a sugary matter, as can be seen when malting cereals. This sugary solution nourishes the germinating seed at the time when the seedling is not yet able to uptake nutrition from the soil and air.

Diebl then went on to describe the morphological aspects of germination. The embryo contains "archetypes" of the future plant, i.e. the rootlet going downwards and the plumule going upwards. Inserted to the "cervix" are cotyledons which later on dry up on the seedling. From this it is evident that Diebl had in mind only epigeous cotyledons. For that matter even Mendel did not see a component of the embryo in the substantial part of the pea seed content, i.e. hypogeic cotyledons.

Nutrition

Plants absorb nutrient substances (nutrients) from the soil and the atmosphere. Diebl therefore divided nutrients into atmospheric and "telluric", i.e. related to the ground. The most important atmospheric and telluric nutrient is water in which solids are dissolved. Light is necessary for plant nutrition from the air because through light the water dissolves, carbonic acid disintegrates and carbon fixation occurs. In this way the plants acquire "firmness, maturity and sweetness". A number of findings about CO_2 photosynthesis preceded Diebl's publication of the textbook because as early as 1775 Joseph Priestley discovered that a mouse shut in a container survived only if the container contained a green plant. Four years later Jan Ignenhousz found out that a plant must be lighted and that all the carbon in the plant body comes from atmospheric CO_2 which the plant decomposes, the carbon is utilised in the plant body and the oxygen returned into the air. In 1804 T. de Saussure discovered that water is indispensable in photosynthesis and that the proportion of released oxygen to the taken in CO_2 is equal to one. C. Daubeny did not discover the dependence of the intensity of photosynthesis on the intensity of light until one year after the publication of Diebl's textbook. Many other discoveries important in terms of photosynthesis (e.g. chloroplasts, chlorophyll and the penetration of CO_2 into the leaf through stomata) appeared even later (Nátr, 1998a). Nonetheless Diebl's interpretation of photosynthesis is surprisingly brief.

Diebl further stated that apart from light temperature is very important for plant nutrition because heat supports evaporation and the flow of fluids. However he was not familiar with the term transpiration. He pointed out that plant respiration and growth releases heat and that the temperature of plants is always a little higher than the temperature of the surrounding atmosphere, particularly during flowering. That respiration is higher at the time of flowering is indeed a remarkable observation. For respiration he uses the same term as for germination, i.e. "Gärung", hence "fermentation". However the German word "Gärung" may have a wider meaning, such as agitation, disturbance.

Interesting is Diebl's statement about the positive effect of electricity on plants; he claims that vegetation is more luxuriant after a storm and that germination of seeds is quicker under the effect of electricity.

The soil supplies the plant ducts with nutrients in the roots and partakes in the dissolution of nutrients under adequate humidity, temperature and access of air; it therefore represents the stomach and intestines of the plant. Indeed precious little was known about the uptake of nutrients by the roots. Yet still 60 years ago the opinion was accepted of the simple intake of salts dissolved in water. Science became familiar with passive and active intake of ions, ion exchange and ion transmitters as late as the third quarter of the 20th century (Dykyjová, 1962; Nátr, 1998b).

In terms of soil science Diebl briefly pointed out that soil (clay, sandy, gravel, siliceous etc.) is composed of mineral substances (incl. potash and common salt). Apart from that soil also contains decomposed plant and animal remains in the form of humus in which "the majority of the best nutrient substances for plant nutrition" are contained; it is a dark brown or black fungous matter. A dark coloured extract from substances soluble due to the putrefactive process pass from it into hot water giving rise to humus acid together with

potassium components producing water-soluble salts of humus acids. Humus originates naturally by decomposition of the remains of plant and animal bodies and their excrements. It consists of hydrogen, carbon, oxygen, nitrogen, phosphorus and small amount of iron. Nitrogen and phosphorus come particularly from decomposition of animal bodies and their excrements.

It is obvious that Diebl indeed knew (as Woodward remarked as early as 1699) that plants do not feed on water only, but also on mineral nutrients from the soil. Yet he was still fully under the influence of Albrecht Thaer's (1752–1828) humus theory of plant nutrition which held out the whole first half of the 19th century. The theory of mineral nutrition did not begin until 5 years after the publication of Diebl's textbook, in the book of J. von Liebig (1803–1872) "Die organische Chemie und ihre Anwendung in der Agrikultur und Physiologie" (1840). The experimental basis to the mineral theory of plant nutrition was given by J. J. Boussingault's pot experiments in which he applied mineral fertilisers and which were conducted at the very time of the publication of Diebl's textbook. As late as 1858 J. Sachs made up the first nutrient solution of mineral salts for cultivating plants in hydroponics (Nátr, 1998b). Diebl interpreted plant nutrition by describing the "flow of fluids" in the plant body. Nutrients taken in by roots go up via the wood to the apex of the stem and then via the phloem downwards. As early as 1727 Stephan Hales found out that the branch above the ring removing the phloem did not wilt and that the water containing the nutrients passed through the wood (Strassburger, 1908). On the other hand the flow of fluids through the phloem downwards is retained by the ring, above the ring swelling occurs and a callus is formed whose task is to bridge the wound caused by the ring. Diebl described the positive effect of this ringing on fertility and development and quality of fruit of fruit trees. He also mentioned the upward pressure of the root, even though he did not use this term. But he described how in early spring the upward flow of fluids is aroused e.g. in vine, maple and birch. However he pointed out that the flow of fluids in the plant body cannot be regarded as circulation but that it is merely a certain relationship between the "force of the roots" (i.e. upward flow of fluids) and the "force of the leaves" (i.e. downward flow of fluids).

When he described the leaves in relation to their function Diebl observed that the underside had more "stomata" than the top side, but that both served to take up components of the atmosphere and "to exhale useless substances". Not until 1868 J. B. Boussingault discovered that CO_2 entered the leaves through the stomata (Peklo, 1923; Nátr, 1998a).

Diebl described that evaporation from the leaves is higher during the day than at night without knowing the conception of transpiration and the role of stomata in it. When he described how "evaporation altogether ceases with drops of dew" Diebl most probably had in mind guttation which occurs when the air is saturated with water vapours.

Growth and Reproduction

Here the term reproduction does not mean propagation but regeneration. According to Diebl growth means every enlargement of the plant body in length, width and height and also thickening of body parts which become firmer and harder. Growth is influenced by nutrition and its effect. In this way Diebl naturally emphasised the trophic nature of growth because that is how growth had been perceived during the entire 19th century. It is true that the impulse to the discovery of regulation (hormonal) effects on growth came from Darwin as early as 1880, but not until the early 20th century R. Dostál (1908) expressed the hypothesis of the existence of substances of a regulating nature.

Diebl's explanation of the thickening of dicotyledonous plants is that the growth of wood and phloem is connected with a flow of fluids between the phloem and wood and as a consequence annual rings appear visible in the wood and that the older inner parts of the wood are harder than the younger external part. Diebl's description of cambium is very original. It is supposed to be a nutritive mucous fluid with a slight flavour of gum which performs the role of blood. On the outside it forms the phloem and inwards wood. If we separate part of the phloem with bark from the wood in early spring droplets of cambial solution will appear on the uncovered wood from which very thin fibres will begin to form. Allegedly in this way it is possible to observe how tissue substituting the removed phloem is formed.

The term reproduction means regeneration but Diebl did not use this term. It is a process during which the plant restores its integrity if it had lost one of its parts. On stem cuttings roots and buds arise. This is for instance how vine is propagated from cuttings. When he mentioned the rooting of stem cuttings Diebl had in mind "de novo" regeneration of buds, but he also described regeneration from buds existing on the plant before wounding. He mentioned the "shooting" of cut clover. In the terminology of the types of regeneration B. Němec (1905) maintained the term "reproduction" for this type of regeneration as was generally used by Diebl. Later Němec distinguished "de novo" regeneration, reproduction and restitution, where in the case of the root apex the lost part regenerates in the original form. Therefore the term "reproduction" used to the present day for one type of regeneration has its roots in history. The term is not suitable today because it is commonly used for sexual propagation only.

Period of rest ("sleeping")

If the fruit tree produces many fruits in one year, in the following year growth and the "circulation of fluids" are usually weaker and the tree bears fewer fruit or none at all. In Diebl's opinion this is the

summer period of rest; but most important in woody species is winter rest which always brings "recovery and strengthening". This simple anthropomorphic interpretation of dormancy is understandable for the time of publication of Diebl's textbook; not until W. J. Johannsen (1857–1927) in his research divided dormancy (period of rest) into internal (voluntary) of hormonal nature and external (forced by cold) but particularly research carried out from the 1930s.

In connection with the period of rest Diebl also mentioned "plant sleep". He meant movements which in fact have nothing to do with dormancy, such as the unbending of leaf petioles of kidney bean during the day and bending during the night; wood-sorrel folding its leaves at night; or on the contrary the unfolding of crown-vetch leaves at night, all of which are nyctinastic movements. Needless to say Diebl was not familiar with nasty or tropism but he observed the movement of stems tracking the sun, the movement of stamen in flowers of some plant species as a result of mechanical stimuli and climbing stems clinging to a support. Diebl noticed that flowers of some plant species close at night resembling sleep; flowers of some species however open at night. The opening and closing of these flowers is most likely a response to light or temperature (photonastic or thermonastic movements) (Kavina, 1942). Diebl specifically mentioned Linné's well-known "flower clocks". The table I. below gives a few examples:

I: *Examples of Linné's "flower clocks*

Type of plant	Opening of blossoms (h)	Closing of blossoms (h)
Leontodon tuberosum	4–5	15
Dianthus prolifer	8	13
Hieracium auricola	8	14
Mesembryanthemum crystallinum	9–10	15–16
Nymphaea alba	7	17
Cactus grandiflorus	9–10	24

When describing these movements Diebl pointed out that it was not a demonstration of the plant's will but that it was a mere "game" connected with the ability to respond to stimuli. It is interesting that here he did not mention the purposefulness of these movements in the life of the plant. The interpretation of tropism by Cholodny and Went came a full 90 years after the publication of Diebl's textbook (Went and Thimann, 1937).

Plant propagation (sexual and asexual)

"Procreation is the most important process in nature without which our beautiful Earth would have long been a desolate wilderness. The wise Creator equipped His creatures appropriately to fulfil this task ….. ". This is Diebl's introduction to this chapter. Although already Theofrastos (372–287 B.C.) knew that the date palm had to be pollinated to bring fruit, for a long time it was believed that plants are asexual organisms. It was not until 1694 that Rudolph Jacob Kamerarius proved the sexuality of plants in his experiments.

Pollen is transferred to the stigma by insects or by the wind and it is most easily performed in plants which have flowers of different sex. Pollen grains on the stigma are stimulated by the fluid released by the stigma. They begin to "open" and exude an "ethereal fertilisation matter". In this primitive way Diebl explained pollen germination and fertilisation. Diebl's textbook was actually published 13 years before the first description of fertilisation of fern by the Polish botanist Count M. Leszczyc – Suminski in 1848. Seven years later the German botanist N. Pringspheim described fertilisation of the Vaucheria alga and as late as 1898 the Russian botanist Sergěj Davrilovič Navašin used lily and fritillary to describe fertilisation of flowers of seed plants (Kavina, 1942).

After fertilisation the first to wilt are the anthers, then the petals and calyx fall off (sometimes they hold on to the fruit), the ovary and/or the receptacle swell, the seed cores develop into seeds. The fruit becomes larger; its colour and taste change and the fruit are dry or soft, pulpy or juicy. The seed-ovary (placenta) joint loosens and the fruit falls off. In some plant species seed production is extremely abundant. As an example Diebl gives tobacco; one seed can produce 360,000 new seeds.

Interesting is Diebl's opinion that the period between fertilisation and fruit maturity can be compared with the period of gravidity of animals and fruit falling with egg-laying. The duration of "gravidity" of plants perceived in this way varies, from several days to 2 years.

The shape of seeds or fruit may sometimes be unusual; for instance double fruit or fruit abnormally grown together. Various "freaks of nature", varieties, shape deviations and changes in the colour of flowers may appear, "sometimes these properties may be transferred to the progeny". Not until 30 years after the publication of Diebl's textbook, in 1865, Diebl's pupil G. J. Mendel discovered the first laws of heredity when crossing pea. At the end of the chapter Diebl briefly mentioned vegetative propagation of plants with shoots, runners, bulbs, tubers etc. He again mentioned propagation with cuttings, by regeneration of roots and buds and in woody species he emphasised grafting and inoculation which had

been known in antiquity by Greeks and Romans; as early as 1684 the Czech exile Jiří Holík invented one of the most successful methods of grafting (Geißfußpropfen) (Kavina, 1942).

Diebl also commented on propagation with daughter bulbs and tubers, with runner e.g. in strawberry and he pointed out how some plant species may become troublesome weeds by way of division of the rhizomes (e.g. the quackgrass). The length of life, ageing and death in plants can be divided into three stages:

- juvenility, when parts of the plant body are juicy, fine, their growth is strong, but they are not very prolific;
- maturity, when the fluids solidify, parts of the body are more consistent, growth intensity is lower and the plant is highly prolific;
- old age, when the ducts contract, harden and clog, the fluids thicken, their flow slows down and eventually the plants dry up. Death follows.

Interesting is Diebl's finding that the plant begins to age and die virtually from the beginning of its life; for instance leaves, sexual organs, bark, the tops of shoots of some woody species die off, the duramen dies off completely. Today these phenomena which Diebl presented are called apoptosis (process of programmed cell death).

Many plants end their life prematurely in response to the effect of internal or external factors. Diebl did not specify the internal factors (because of their hormonal nature he could not know them), but it is amazing that he mentioned them at all. External factors include heat, drought, frost, high humidity, hailstorm, insects, fungous diseases, herbivores, weeds inhibiting cultural plants etc.

SUMMARY

Prof. František Diebl (1770–1859) lectured general natural history and agricultural science at the Institute for Philosophy in Brno. During his studies of theology in Brno Gregor Mendel attended his lectures and in 1846 he passed his prescribed exams there. In 1835 Diebl published a textbook on his lectures called "Abhandlungen über die allgemeine und besondere Neturgeschichte". The focus of the present study is on that part of the textbook which deals with plant physiology which was not an independent university discipline before 1848. In his textbook Diebl described the process of seed germination, plant nutrition, growth, reproduction, dormancy, sexual and asexual propagation, ageing and death. He considered germination to be a specific method of fermentation transforming seed starch into a sugary matter which nourishes the germinating plant. Apart from the external conditions of germination (water, temperature, air) he also mentioned the period of rest of the seeds as an internal factor. In the physiology of nutrition he distinguished nutrition from the soil via roots from nutrition from the air via leaves. The former is based primarily on the humus theory of A. Thaer (1809) because not until 5 years after the publication of Diebl's textbook J. Liebig initiated the mineral theory. Diebl's presentation of photosynthesis was based on information available at that time about the release of oxygen by green plants under conditions of light and the uptake of CO_2, but he had no knowledge about the passage of CO_2 into the leaves through stomata. Remarkable is Diebl's discovery that respiration increases during flowering. Electricity is considered to be a force significantly supporting the life processes of plants. Diebl also noticed the difference between diurnal and night evaporation of water from the leaves.

In his textbook growth is connected with nutrition only, as it was the entire 19th century. Stem thickening from the cambium is described very simply. Bud and root regeneration is given the term reproduction which today is commonly used in relation to sexual reproduction.

By the period of rest in woody species Diebl understood winter "recovery" after summer activities of growth and propagation. When a year of high yields is followed by low or zero yields he talks of a summer period of rest. The substance of voluntary summer and autumn period of rest in contrast to winter rest forced by cold had not been known at the time of Diebl's publication. Diebl considered nyctinastic movements (bending or unbending of the leaves) and closing of the flowers at night to be "sleep". He described fertilisation in a primitive way, because it was not until 1848 that the first exact description came out. At the end of his article on plant physiology Diebl described ageing and the causes of death. He also mentioned dying off of parts of the plant body during life which is today indicated as apoptosis.

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