REVIEW

Dedicated to the anniversary of Prof. Ing. Jiří Petr, DrSc., Dr.h.c.

CROP PHYSIOLOGY OF OILSEEDS: A COMPARATIVE ANALYSIS BETWEEN RAPESEED (BRASSICA NAPUS L.), SUNFLOWER (HELIANTHUS ANNUUS L.), AND LINSEED LINUM USITATISSIMUM L.)

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This review deals with a comparative description of the yield development for different oil-bearing species, i.e. rapeseed, sunflower, and linseed. Yield performance of each species is conditioned by their special morphology and physiology. Although all three oil crops are specifically adapted to climate and soil conditions, the life cycle of these species can be divided into four principal stages: germination and seedling emergence, juvenile growth, flowering and post-anthesis growth. During the early stages of germination and seedling emergence, controlling the distribution of plants per unit area is especially important for yield stability. In this paper juvenile growth describes the period from emergence (E) to flowering (FI). During this phase flower initiation takes place. For all three species flowering is the most sensitive stage to environmental stress when vegetative and reproductive development occur concomitantly. Finally, the post-anthesis growth is governed by the source/sink relationship between the vegetative and reproductive parts of the plants.

rapeseed; sunflower; linseed; crop physiology; development.

Introduction

in plant breeding and production techniques, have helped oil crops to increase

worldwide. In line with their growing importance, there are now numerous publications concerning their cultivation, breeding and utilization (for review see Diepenbrock, Becker, 1995). However, a comparative description of the yield development for different oil-bearing species is still lacking. Therefore, the present review deals with a physiological analysis of the yield development of three major oilseed crops grown in Europe, i.e., rapeseed (Brassica napus L.), sunflower (Helianthus annuus L.), and linseed (Linum usitatissimum L.).

These species have the common ability to produce storage oil (triacylglycerols) in the developing cotyledons during ripening. Triacylglycerols are well-suited storage substances because of their extremely low oxygene contents and their hydrophobic characteristics. They give a maximum of energy reserves within the accumulating organs for the lowest possible weight and the quantitative storage is the main determinant of the kernel weight.

As to fatty acid composition, different long-chain fatty acids are dominant in the storage oil: erucic acid (rapeseed – old varieties), linolenic acid (linseed), linoleic acid (sunflower), and oleic acid (rapeseed – new varieties; sunflower – high-oleic /HO/ varieties).

It is also obvious that these oilcrops differ greatly in their physiology and breeding history. Moreover, environmental effects such as variation in weather, have a strong impact on yield-determining processes (Petr, 1991). The responses of different oilcrops to environmental conditions vary specifically.

Rapeseed is mostly grown in cool wet climates as a winter annual plant with a growing period of about 320 days. Within this time about 15 t above-ground biomass is accumulated per hectare. Sunflower as summer annual crop with a vegetation period of about 150 days also produces 13–15 t ha⁻¹ biomass. Linseed grows to maturity in about 130 to 150 days producing a biomass of about 7 t ha⁻¹. On the assumption that all three oilcrops develop an average harvest index (HI) of 30%, rapeseed, sunflower and linseed produce kernel yields of 4.5, 3.9–4.5, and 2.1 t ha⁻¹, respectively. Nevertheless, yield performance of each species is conditioned by their special morphology and physiology.

Yield potential

Yield potential of a crop is a theoretical assessment of the maximum yield that can be generated when high yielding biological material is grown in an optimum physico-chemical environment. Yield will include the terms 'biological yield' and 'economic yield'. Total dry matter (root dry matter ex-

cluded) refers to 'biological yield' while the economically useful part of 'biological yield' is classified as economic yield. For oil crops the oil-bearing kernels, which also have high percentages of protein, are the economic parts of the plants. In case of linseed the short fibre of the stalk may also have an added value.

Usually, the seed yield of oil crops is considerably lower by weight than that of cereals, although there is no appreciable difference in canopy photosynthesis. Since substances such as fats and proteins use more energy for their biosynthesis than carbohydrates such as starch, sucrose, hemicelluloses and fructosans, it is possible to explain differences in growth rate of storage organs in terms of their different chemical composition (Penning De Vries et al., 1974; Greef et al., 1993).

A simple estimation of the potential seed yield of oil crops accounts for differences in the harvest index between these crops and, e.g. winter wheat. The harvest index of modern cultivars of winter wheat has shown an increase during recent decades up to 45–50% (Austin et al., 1980; Feil, 1992), while that of oilseed rape increased up to 25–30% (Habekotté, 1997). This comparison, however, might be misleading because the energy content in seeds of oil crops is greater than that of wheat. Thus, a comparison between oil crops and cereals should be done on an energetic basis.

On the example of oilseed rape and wheat, above-ground dry matter, kernel yield, concentration of energy in kernels and straw and harvest index are compared (Table I). For the sake of simplicity, this model assumes that both species produce 20 t ha⁻¹ of above-ground biomass. The harvest index of wheat remains greater than that of the oil crop, even when the energy content is taken into account. Thus, harvest index of oil crops is a major parameter that limits yield. For oilseed rape it is concluded that further increases in the yield are closely linked to an increase in the harvest index (H a b e k o t t é, 1997).

I. Yield and harvest index of winter oilseed rape compared with winter wheat (Diepenbrock, 2000)

	Biomass (t ha ⁻¹)	Kernel yield (t ha ⁻¹)	Harvest index $\frac{DM\ kernels\ x\ 100}{DM\ biomass}$	Energy content* (MJ kg ⁻¹ DM)		Energy harvest index
The state of the s				kernels	straw	$\frac{DM\ kernels\ x\ 100}{DM\ biomass}$
Winter wheat Winter	20	10	50	18.4	18.1	50.4
oilseed rape	20	5 – (6)	25 - (30)	27.6	18.3	33.5 - (39.3)

According to Greef et al. (1993)

Growth and development

Although oilseed rape, sunflower and linseed are specifically adapted to climate and soil conditions, the life cycle of these species can be divided into four principal stages: germination and seedling emergence, juvenile growth, flowering and post-anthesis growth. For all three oilcrops the fitted curve representing dry matter accumulation is sigmoid in shape (Larsen, 1963: Hocking, Steer, 1983; Grosse et al., 1992a). It changes according to genotype and environment and does not represent special events that might occur during development as will be discussed later. Dry matter and yield production are closely related to utilization and interception of photosynthetic active radiation (PAR) during crop growth. For linseed the utilization of absorbed PAR (g dry matter MJ⁻¹ absorbed PAR) is reasonably high, however interception of PAR (GJ PAR ha⁻¹) is lowest by far as compared to winter rapeseed and sunflower (Aufhammer et al., 2000). In consequence, the high utilization of PAR does not compensate for the very short vegetation period as combined with the lowest PAR interception, thus linseed having a much lower yield potential than winter rapeseed or sunflower.

Germination and seedling emergence

The relationships between germination or seedling growth and seed yield are expected to be low (for review see TeKrony and Egli, 1991). However, during the early stages of germination and seedling emergence, controlling the distribution of plants per unit area is especially important for yield stability. Deficiencies in germination and/or emergence result in uneven stands. So seed quality, uniformity of seed placement during sowing, and seedbed conditions have important effects on stand quality. On the other hand, seeds of oil crops can remain viable in the soil for several years. As a consequence, problems from volunteer plants occur quite frequently in the following crops (Sierts et al., 1987; Pekrun et al., 1998).

The phase 'sowing to emergence' includes two distinct subphases, germination (start of imbibition to protrusion of the radicle) and emergence (radicle protrusion to the unfolding of the hypocotyledonary hook above the soil surface) (Bewley, Black, 1985).

For rapid seedling growth it is very important that the storage oil which has a high calorific value is mobilised immediately. Therefore, it might be advantageous for oil crops to have storage substances located almost exclusively in the cotyledons and to have seedlings that grow epigeally. Cotyledons of oilseed rape, sunflower and linseed convert from storage organs into

photosynthetically active leaves. Under the influence of light cotyledons start to green and exhibit considerable assimilation rates.

At higher latitudes successful **rapeseed** production (spring rapeseed) depends on adaption of the crop to the short frost-free period (K o n d r a et al., 1983). Hence, early seeding is desirable but often is limited by low soil temperature. Minimum temperature for rapeseed germination is about 5 °C. With declining temperatures starting from 20 °C the mean germination time increases at progressive rates. However, percent germination does not show any temperature trend (K o n d r a et al., 1983).

For sunflower temperature is the most important factor affecting germination in soils with adequate water and aeration. Minimum temperature for germination ranges between 3 and 6 °C; optimum temperatures are close to 26 °C (Macchia et al., 1985; Gay et al., 1991).

Sunflower shows an irregular shape of the seed and the small size in hybrids compared with open-pollinated cultivars. Seed coating can increase size and make shape more uniform to facilitate sowing (Allen et al., 1983).

During the initial phase of **linseed** germination the seed swells after absorption of soil moisture and mucilage is released from epidermis cells. The mucilage connects the seed with soil particles and thus, pectin substances exuded promote the rhizosphere. Brown-seeded lines possess higher germination percentages than yellow-seeded (Comstock et al., 1963). More recently, Saeidi and Rowland (1999) have reported that yellow seed has lower seed vigour than brown seed in near-isogenic populations, however, at 5 °C there was no difference in germination frequency between brown and yellow seed. Although temperature has no effect on percent germination, the time for 50% of the seeds to germinate at 5 °C was 160 h compared with 30 h at 15 °C (O'Connor, Gusta, 1994).

Juvenile growth

The period of juvenile growth can be drawn from emergence (E) to the stage of flower initiation (FI) at the apex. After an initial phase of leaf development, floral initiation signals the end of production of leaf primordia by the shoot apex and the beginning of generative activity. However, the phenological control before and after FI is rather uncertain. On the other hand, phenological models quite accurately can predict the duration of E to the first anthesis (FA). Temperature, photoperiod and genotype have a clear impact on the control of development to FA. So, in this paper juvenile growth gives a description of the period from emergence to flowering.

The juvenile growth phase of winter oilseed rape lasts from emergence through cessation of growth in winter and stem elongation to the start of

flowering. In autumn, plants should reach the 6–8 true-leaf stage, have a root head diameter of > 5 mm and a shoot length of < 20 mm to withstand subsequent periods of freezing temperatures (Scott et al., 1973a, b; Vullioud, 1974; Schröder, Makowski, 1996). The onset of generative development has already occurred before or during winter. Flower initiation usually takes place from early November (when sown in August) to mid-December (when sown in September) (Geisler, Henning, 1981; Tittonel et al., 1982; Tittonel, 1988). The vegetative apex producing leaves has a flat shape. When the apex swells out, the generative phase hecomes initiated. In basal leaf axils, buds become visible representing the axillary branches which develop quite similarly to the main apex. Next to this, buds without axillary leaves appear around the main apex each giving one flower which then swells out. Thereafter, the flower pedicle lengthens. the four sepals appear and converge. The onset of flower initiation regularly has strong influence on flower, pod and seed number (Tayo, Morgan 1979; Mendham et al., 1981). In general, flower initiation of winter oilseed rape is under control of increasing short-day and vernalizing temperatures. Below 4 °C differentiation of the apex, initiation of axillary buds and flower primordia is still effective (Tittonel et al., 1987; Tittonel. 1988). Thus, under maritime conditions generative development often does not cease during winter. In addition, low temperature and low light intensity during the winter cause a dramatic loss of foliage and, thus, of stored leaf-N as well as a reduced LAI (about 0.5-1.0) (Grosse et al., 1992a, b; Colnenne et al., 1998).

Regrowth of winter oilseed rape starts in early spring when temperature continually exceeds 5 °C. Leaf is a major source of photosynthesis until flowering; thus, it is highly important that the rates of leaf emergence and expansion are high. Dry matter produced during this stage later supports pod growth by mobilising the transiently stored substances (Brar, Thies, 1977; Major et al., 1978). From the start of re-growth until the start of flowering at the beginning of May the leaf area index (LAI) climbs up from 0.5 to 3.5–4.0 m² m⁻². Thereafter the LAI decreases dramatically. A quantitative analysis of pod formation confirmed the linear relationship between the cumulative production of dry matter until flowering and pod density (Habe kotté, 1993). Accordingly, close genotypic correlations were found between the duration of the leaf area index (LAID) until flowering and seed yield (Grosse et al., 1992b).

Once the first pair of true leaves of **sunflower** and **linseed** unfolded the plant begins to shoot at a slow rate without preceding dormancy.

A scale for growth and development of the apex of sunflower has been elaborated by Marc and Palmer (1978, 1981, 1982). Accordingly, the

start of generative development (switch to flower initiation) starts shortly after floral stage 1.3, i.e. 16 to 18 days after sowing. The main generative areas on the apex at floral stage 6 (approximately 36 days after sowing) from outside to inside are i. the 'generative front' with the disposed and differentiating flower primordia, ii. the 'generative ring (or zone)', where initiation of the flower primordia takes place, and iii. the 'generative area' with a high activity of cell division.

The initiation of flowers normally begins at the 8–10 true leaf-stage and probably ends in the 12–15 leaf-stage (Gardner et al., 1986). The duration of E to FI is differentially sensitive to temperature and photoperiod (Rawson, Hindmarsh, 1982; Rawson et al., 1984). Most sunflower cultivars exhibit quantitative long-day or day-neutral responses to photoperiod for the duration of E to FI. However, at least one cultivar has shown a short-day response (Rawson, Hindmarsh, 1982; Goyne, Schneiter, 1988). The minimum and maximum photoperiods that affect developmental rate are estimated as 13 and 15 h (Hammer et al., 1982).

Individual sunflower leaves have a large maximum photosynthesis so that crop photosynthesis regularly increases to relatively high rates at high irradiance despite the generally horizontal display of fully developed leaves in canopies (Connor, Sadras, 1992). The maximum LAI amounts to 7 $\rm m^2~m^{-2}$. The exceptional photosynthetic ability of sunflower leaves compared with other C3 species results from

- numerous and bigger stomata, e.g. in comparison to wheat and soybean (Sutcliffe, 1979)
- lower CO₂-resistance of the stomata than in soybean (Rawson et al., 1977; Potter, Breen, 1980)
- comparable transport capacity of bicarbonate via the chloroplast membrane as for young maize (Poincelot, Day, 1976)
- higher transport rate of electrons and higher rate of carboxylation of the CO₂-fixing enzyme RuBP-carboxylase in comparison to other species (Delaney, Walker, 1978)
- a two-fold higher activity of RuBP-carboxylase in comparison to soybean (Ranty, Cavalie, 1982; Ranty et al., 1982, 1988).

Only within a relatively short period, immediately before reaching the maximum expansion of the leaf area, however, the very high photosynthetic capacity is achieved (Rawson, Constable, 1980; Danuso et al., 1988). Accordingly, Hernandez and Orioli (1982) and Sakac et al. (1988) observed the highest net-assimilation rate (NAR) from 20 to 30 days after sowing. Additionally, the heliotropic movements of the foliage leaves allow the plant to absorb more light and thereby increase photosynthesis (for

review see Long et al., 2001). Shell and Lang (1976) calculated that photosynthesis would be 9.5% greater with heliotropism than with an optimum arrangement of fixed leaves and 23% greater than with spherical distribution.

However, the high photosynthetic potential of sunflower leaves does not necessarily translate into high radiation use efficiency (RUE; g DM MJ⁻¹) of field stands. The values for RUE vary around 2.2 g DM MJ⁻¹ (Kiniry et al., 1992) merely differing from oilseed rape (2.4 g DM MJ⁻¹, Mendham et al., 1981a) and linseed (2.6 g DM MJ⁻¹, Aufhammer et al., 2000).

Floral initiation of **linseed** can be recorded at early stem extension once the plant has reached about 1/6th of its overall height (Larsen, 1961). At this stage the plant is still completely upright; only later when the buds appear does the upper part of the stalk bend slightly. The number of initiated flowers is not complete at a defined instant depending on environmental conditions. The apical buds of the main apex represent the fundamental yield potential. Growth of the main apex largely depends on whether apical dominance is inhibited by the basal branches. The floral initiation starts on the terminal bud with the growth of the pairs of 'bud + leaf', this stage being very important as the transformation to a reproductive stage is fixed now. Although these tissues are not real reproductive organs, they signify the beginning of the floral stage (Douheret et al., 1993). The first pair of 'bud + leaf' appears at 13–15 cm height of the shoot, the ball stamens appear near the 17 cm-height stage, and the staggered gynaeceum is formed at 20 cm height. Up to the start of flowering linseed can reach a maximum LAI of 5 m² m⁻².

Flowering

Flowering is the most sensitive stage to environmental stress when vegetative and reproductive development occur concomitantly. For example, a lack of nutrients or water shortage distinctly affect the yield determining processes. In consequence, the environmental status is decisive for the degree of reduction of generative and reproductive organs initiated during the juvenile development thus, limiting yield performance.

Flower opening over the whole **rapeseed** plant lasts 26 days on average. About 75% of the siliques which provided seeds at maturity are derived from flower buds which appear within the first 14 days of anthesis. The highest potential of flowers and siliques was counted on the main branch and on axillary branches arising from the uppermost three nodes. In total, the final numbers of siliques and seeds of oilseed rape are largely fixed within a 4-week period of flowering. During this phase the source/sink-relationship governs the competition for assimilates which are needed for silique growth

(Keiller, Morgan, 1988; Leterme, 1988). The most limiting process starts shortly after the onset of flowering when the decrease in the total leaf area accelerates due to shading, initially by the flowers and later by the pods (Gabrielle et al., 1998b). The increasing flower cover intensifies photon reflectivity and absorption to 60–65% of incoming radiation (Bilsborrow, Norton, 1984; Yates, Steven, 1987; Leach et al., 1989). At the same time, photosynthesis of the crop decreases by 40% (Robelin, Triboi, 1983). Thus, flowering is the most critical stage influencing the yield of oilseed rape.

In the flowering head of **sunflower** the mostly yellow and sterile ligulate or ray flowers and the fertile disc- or tube flowers are differentiated. The complete process of flowering of a head proceeds from out- to inside, whereby 1–6 garlands begin to bloom each day. The total duration of flowering of a head is 8–12 days; but it can last 14 or more days under unfavourable conditions. In the mature head, the centre is often free from achenes or the achenes do not contain any seeds. The size of this area can vary. Some reasons based on the flowering process have been proposed, i.e. self incompatibility, faulty or lack of fertilization and low attractiviness of the head centre to pollinating insects due to poorly developed nectar glands (Diepenbrock, Pasda, 1995). In consequence, the conditions of fertilization are closely related to the yield component 'achenes per head' which essentially determines the yield per hectare.

The flowering period of **linseed** begins with opening of the terminal flowers of the main apex and continues on the side axes in accordance with the physiological age of the flower buds. Davidson and Yermanos (1965) and Hovland and Dybing (1973) showed that linseed plants produce their blooms in distinct flowering periods alternating with periods of rest. The occurrence of flowering cycles seems to be genetically determined but is influenced by environmental factors as far as frequency and length of individual phases are concerned. Dybing et al. (1988) investigated the relationships among daily flower production, length of flowering, and seed yield. The sum of flowers and the length of the flowering period are closely related. However, no correlations were found with seed yield. Changes in flowering rate with time are much more important for yield than either length of the flowering phase or the total number of flowers produced.

Post-anthesis growth

Post-anthesis growth is governed by the source/sink relationship between the vegetative and reproductive parts of the plant.

After flowering the whole rapeseed canopy is significantly supported by growth of the pods and seed filling. Seed yield is linearly related to PAR that is intercepted during the pod filling phase. In individual pods, developing seeds locally induce growth of pod tissue, representing a major part of the assimilating surface of the crop. Thus, a close relationship between the capacity of sink and source during reproductive growth is maintained. Diepenbrock and Grosse (1995) could show that the maximum surface area of the pods is more or less the same as that of the leaves. From about two weeks after full flowering, the total net CO₂ fixation by pod hulls exceeds that of leaves, because pods are exposed to much higher radiation than leaves (Gammelvind et al., 1996). While the carbon balance changes during this phase, competition for assimilates is responsible for loss. of buds, flowers, pods and seeds (Keiller, Morgan, 1988). During maturation, pod hulls transfer transiently stored carbohydrate to seeds. Exportation starts about two weeks after fertilisation and can account for 60% of the total assimilate for seed filling. In crop stands, however, the overall mobilisation of reserve carbohydrates from roots, stems, leaves and pod hulls contributed at the most 12-17.5% to the final yield (Quillere, Triboi, 1987). At harvest, 10% of the total N in the shoot is located in stems and pod hulls and the remaining N is located in the seed (Schjoerring et al., 1995).

The duration of last anthesis to physiological maturity occupied about 28% of the crop cycle of sunflower (Rawson et al., 1984). The interval between fertilisation and maximum seed weight is referred to as the duration of seed growth. At maturity, the heaviest achenes with the highest oil content can be found in the outer circular positions. Steer et al. (1988) concluded from their results that the outer seeds control the growth of the inner seeds, probably by competition for space on the receptacle and by preferential absorption of assimilates and nutrients. However, there are indications that grain filling is controlled by the source-sink relationship within the whole plant. After anthesis, first head, and then seed, become the dominant sink for photoassimilate. Seed growth is sustained by both current photosynthesis and mobilisation of stored assimilate which results in substantial net loss of biomass from vegetative biomass (Connor, Hall, 1997). Labelled assimilates were found in a sector of the head corresponding to the orthostichy of the leaf exposed to ${}^{13}\mathrm{CO}_2/{}^{14}\mathrm{CO}_2$ (Alkio et al. 2000). Reducing source capacity by cutting off leaves at one side of the stem before anthesis resulted in an increased percentage of unfilled achenes and reduced mass of dry matter per filled achene of the head sector corresponding to the treated half of the plant. These findings suggest that grain filling in sunflower is source-limited.

During the post flowering period of **linseed** the capacity of the sink and distribution of assimilates can limit the yield. An adequate supply of assimilates from leaves during flowering and post flowering are decisive for seed set and also to counteract seed reduction. Major amounts of the assimilates used for seed growth itself are produced by sepals and capsule walls (Deshmukh et al., 1976). Bazzaz and Harper (1977) reported a close correlation between the number of seeds per plant and the number or area of leaves per plant. The developing seed acts as a sink for nutrients and assimilates enhancing their withdrawal from leaves and, thus, accelerating their death. This is further substantiated by the study of Hocking (1995) on the effects of nitrogen supply on the growth, yield components, and distribution of nitrogen in linseed. Remobilisation of N from senescing leaf canopy ranged from 70 to 87%, and was highest for N-stressed plants. About 10% of the N accumulated by seeds was provided by remobilisation from the leaf canopy.

Conclusions and future prospects

On the example of oilseed rape, sunflower and linseed it is demonstrated that crops from different genera reveal specific physiological strategies to produce seed yield. Additionally, these crops differ greatly in their morphology.

To explain crop performance in terms of current knowledge, crop simulation models are under development. Such models are mathematical representations of physiological responses of crop development, growth, and yield to attributes of cultivars and environmental conditions.

In the last two decades modelling methods have developed along two main lines:

- process-oriented modelling based on ecophysiological knowledge while neglecting the architecture of the plant
- architectural modelling which considers the topology and geometry of the plant (Reffye, Houllier, 1997).

Ecophysiological modelling defines plant canopies in terms of functional compartments (e.g. leaves, roots, seeds) and neglects the geometry of the plant. This method encounters difficulties if the modification of the plant architecture itself becomes essential for the functionality of the plant. Therefore, morphogenetic models were created to simulate the architectural development. These models contain formal grammars that describe developmental processes independent on external influences (Lindenmayer, 1968, 1971). More recently, the simulation tool VICA (VIrtual CAnopy) has been developed to combine process- with architectural models (Wernecke et

al., 2000). This approach allows to construct, simulate, and analyse virtual canopies in their spatial three-dimensional dynamic structure, and to calculate photon transfer, especially in heterogeneously structured plant stands.

Hopefully, during the next years the nature and applicability of virtual crop models will significantly make progress to compare crop physiology of different genera to understand the interactions of processes and architecture to provide a functionally and morphologically based explanation of crop performance.

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Fyziologie olejnin: srovnávací analýza tvorby výnosu řepky (*Brassica napus* L.), slunečnice (*Heliantus annuus* L.) a olejného lnu (*Linum usitatissimum* L.). Scientia Agric. Bohem., 32, 2001: 000–000.

Práce přináší srovnání zvláštností tvorby výnosu u tří druhů olejnin – řepky olejky, slunečnice a lnu. Výnosnost každého druhu je podmíněna zvláštnostmi jeho morfologie a fyziologie. Ačkoliv všechny tři druhy jsou rozdílně přizpůsobeny klimatickým a půdním podmínkám, jejich životní cyklus má stejná období růstu a vývoje: klíčení a vzcházení, juvenilní růst, kvetení a postflorální růst. Během počátečních období klíčení a vzcházení je pro stabilitu výnosu důležitá organizace porostu, tj. rozmístění rostlin po ploše půdy. Podrobně je popsán vývin v období juvenilního růstu od vzejití (E) do kvetení (FI). V tomto období se začínají formovat i generativní orgány (květ). Pro všechny tři plodiny je kvetení nejcitlivějším obdobím z hlediska stresu vyvolaného vnějším prostředím, kdy současně probíhá vegetativní i reprodukční (generativní) proces. Růst po kvetení je řízen vztahem zdroj asimilátů – úložná kapacita generativních orgánů a konkurence mezi vegetativní a reprodukční částí rostliny.

řepka; slunečnice; olejný len; tvorba výnosu; vývoj; růst

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