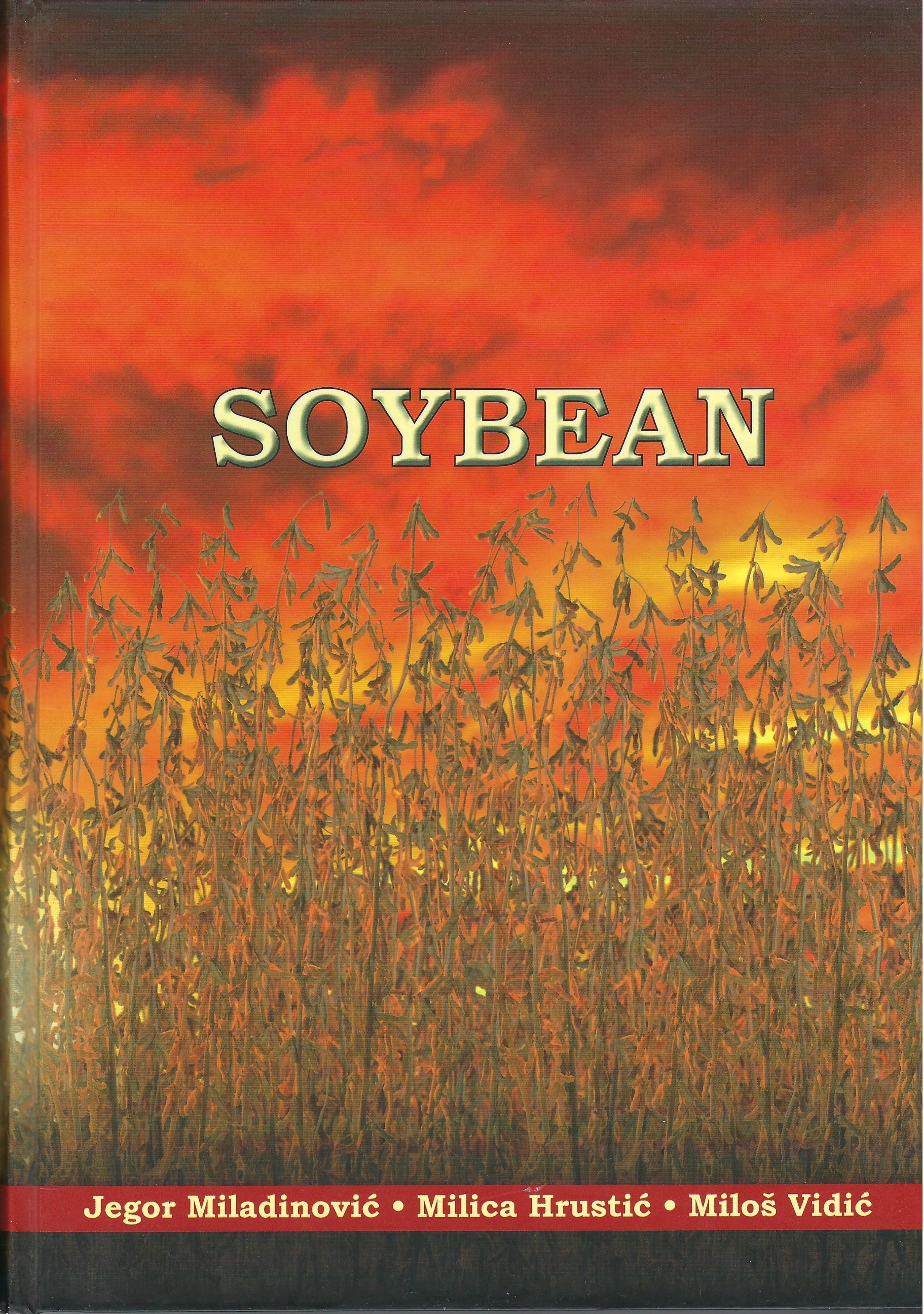
SOYBEAN



Jegor Miladinović • Milica Hrustić • Miloš Vidić

SOYBEAN

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Institute of Field and Vegetable Crops, Novi Sad
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SOYBEAN

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FOREWORD

This is a translated edition of the book titled “Soja” published in Serbian language in 2008, which displayed the accumulated knowledge on fundamental and applied soybean research, as well as soybean breeding efforts at Institute of Field and Vegetable Crops in Novi Sad, Serbia.

Global importance of soybean is continually growing, with soybean planted areas reaching almost 99 million ha in 2009 and production of soybean grain exceeding 222 million tons. According to these indicators, soybean is the most important industrial plant worldwide, both as a basic source of protein nutrients for cattle, poultry and fish and as the most important source of plant oil.

Simultaneously with increased interest in growing this plant species, scientific research on soybean has also been enhanced, especially regarding fundamental research. For the most part, this book deals with achievements of Serbian researchers. Chapters dealing with soybean morphology and its requirements during growth and development have been updated and revised. Content of chapters dealing with production technology, seed production and importance, as well as chapters giving an overview of diseases and pests affecting soybean is somewhat characteristic for Serbian climate and soil. Therefore, the authors would particularly recommend to foreign readership the chapters dealing with quantitative and qualitative genetics of soybean prepared for this edition by leading experts and professors from University of North Carolina and University of Iowa. Outline of the most recent achievements in the field of soybean breeding has also been prepared by scientists from the USA, where such research is most developed.

Chapter dealing with soybean importance and origin gives a chronological survey of soybean breeding results at Institute of Field and Vegetable Crops. The previous decade was outstandingly dynamic and successful in this area, witnessed by impressive results. The number of soybean varieties developed at Institute of Field and Vegetable Crops released in Serbia has doubled, while there was a ten-fold increase in the number of varieties released abroad - from four varieties released in 2000 to 49 released so far.

Hence we believe that this edition will be useful to everyone involved in soybean production, especially to students and scientists conducting research on soybean.

Authors would like to thank all who have participated in preparation of this book in any way, and especially to reviewers whose efforts and pieces of advice largely contributed to the form and content of this book.

Special gratitude is extended to the Ministry of Science and Technological Development of the Republic of Serbia for financially aiding the printing of this book.

In Novi Sad, in February 2011.

Authors.

SOYBEAN MORPHOLOGY AND STAGES OF DEVELOPMENT

Jegor Miladinović, Vuk Đorđević

MORPHOLOGY

Root system

Soybean is characterized by a taproot system, typical for the class *Dicotyledonae*. However, when lateral roots emerge during later stages of development, most often the taproot cannot be distinguished from them, which is why soybean root system would best be described as diffuse (Lersten and Carlson, 1987). Soybean root system consists of a taproot, lateral roots, and adventitious roots. According to the time of occurence, root system could be distributed as primary, secondary, tertiary and higher order roots.

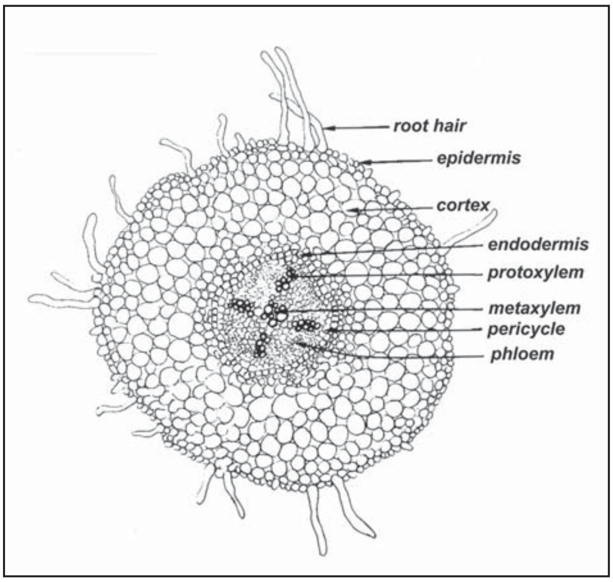
Formation of root nodules is influenced by the activity of nitrogen-fixing bacteria *Bradyrhizobium japonicum*. Root system growth and development are conditioned both by variety and external factors (climate and soil). Number of authors obtained significant differences in growth rate, diameter and number of roots and root dry matter accumulation among genotypes grown in the same environmental conditions (Mitchell and Russell, 1971; Kaspar et al., 1978; Zobel, 1980). On the other hand, Stone and Taylor (1983) and Kaspar et al. (1981) found that growth and development of soybean root system are significantly affected by environmental conditions, especially soil temperature.

Root anatomy

Transverse section of the primary root shows three different parts – the epidermis (rhyzodermis), the primary cortex and the stele (Figure 2.1).

Figure 2.1

Transection of primary root in root hair zone (from Lersten and Carlson, 1987)



The rhyzodermis consists of tabular cells radially elongated along the root axis. These cells are of simple structure, with thin walls that allow easy adoption of water and nutrients. In search of the nutrients, individual cells of rhyzodermis elongate and form root hairs, thus significantly increasing the overall root absorbing surface. The precise increase cannot be determined with certainty, but it is considered that root hairs comprise about 85% of the total area of the entire root system absorbing surface (Carlson, 1969). According to the study by Dittmer (1940, as cited in Lersten and Carlson, 1987) root hairs can be found on all roots, except the taproot where secondary growth removes the epidermis (Table 2.1).

Table 2.1

Data on roots and root hairs of mature, field grown Ilini soybean (from Dittmer, 1940)

Root type	Average root diameter	Average root hair length x diameter	Number of root hairs
	mm	µm	mm-1 root length
Primary root*	2.50	-	-
Secondary roots	0.65	110 x 17	606
Tertiary roots	0.31	90 x 14	210
Quaternary roots	0.23	90 x 14	170

** – Secondary growth caused loss of most epidermis and root hairs*

Cortex is a fundamental tissue that consists of parenchyma cells, located between the rhyzodermis and the stele. In the primary root it consists of 8 to 11 layers of slightly elongated cells with much intercellular space, while in branch roots the narrower cortex has 4 to 9 layers (Lersten and Carlson, 1987). Cortical cells close to the rhyzodermis are considerably smaller than intervening cortical cells and form the exodermis. The innermost cortical cell layer forms endodermis with a continuous suberized casparian strip encircling its radial walls.

The stele consists of radially structured vascular bundle and pericycle. The pericycle is a cylinder of parenchyma that has the capacity to produce new cells and plays a key role in formation of the lateral roots and secondary dermal tissue during secondary thickening. Lateral roots arise in the pericycle at loci directly opposite the ridges of the tetrarch xylem and develop acropetally at approximately 90-degree intervals in four longitudinal rows on the taproot (Mitchell and Russell, 1971). This symmetry is, however, hardly noticable due to the twisting of the main root during growth in soil. Lateral roots are tetrarch or triarch in structure, while tertiary, quarternary, and successive orders of smaller branch roots may be triarch or diarch, and depending on the structure they grow in two, three or four rows around the axis of the primary root (Carlson, 1973).

The most part of soybean root system consists of four to seven heavily branched major lateral roots that emerge from the base of the taproot. Those roots, called basal, are larger in diameter than those growing from the lower parts of the taproot (Zobel, 1980). According to Mitchel and Russell (1971), after lateral growth of 20 cm to 36 cm, major lateral roots abruptly turn downwards and rapidly grow to a depth of almost 2 m under favorable conditions.

Higher order roots are formed whenever conditions are favorable, but the active life span of feeder rootlets is between 10 to 20 days. Afterwards, roots continually dry and die off as they exhaust the resources available in their immediate vicinity, while parental root remains and initiates growth of new rootlets (Huck and Davis, 1976).

Not much is known about adventitious roots. According to Tanaka (1977), they develop from the underground part of the hypocotyl, with growth and function similar to the major lateral roots whose length and diameter they are able to reach. As with other parts of the root system, their growth and development are significantly affected by soil conditions, especially temperature (Stone and Taylor, 1983).

Growth and Development of the Root System

Since growth and development of soybean root system during vegetation period is rather uneven, number of authors tried to trace the precise outlines of root development (Mitchell and Russell, 1971; Sanders and Brown, 1979; Mason et al., 1980). The most accurate determination was suggested by Mason et al. (1980), for they connected the growth and development of soybean root system with the stages of development of above ground plant parts proposed by Fehr and Caviness (1977).

According to this determination, there are five stages of soybean root system development: early vegetative growth (VE - V6), pre-flowering period (V6 - R1), flowering (R1 - R3), pod formation and growth (R3 - R4) and seed growth and maturity (to R6).

Early vegetative growth

Development of root system onsets with seed germination and radicle emergence out of which the taproot forms. During this period the root grows much faster than above ground plant parts reaching daily growth of 2.5 cm to 5 cm given the favorable soil moisture (Mitchell and Russell, 1971), only to reach depths of 0.8 m to 1 m at the end of this stage (Sivakumar et al., 1977). Lateral roots start growing horizontally three to seven days after germination, often reaching length of 25 cm to 30 cm at the end of the phase, and can be found at 3 cm from surface at the most, depending on temperature and soil moisture (Mitchell and Russell, 1971). Secondary and tertiary roots also start growing in the layer of 0 cm to 15 cm, where major mass of soybean root is often found. The percentage of root size found in this layer primarily depends on soil moisture. At the end of vegetation period in dry cultivation, Mayaki et al. (1976) measured 51% total plant root mass in this layer, while this percentage was 67% in irrigated plants. At the end of this phase, when the plant reaches stage V6, ratio of above ground plant dry weight to root dry weight is approximately 3.8 (Sivakumar et al., 1977).

Pre-flowering period

In this stage the growth of the main root slows down, while the lateral roots reach maximum horizontal length. Higher order roots start growing along the whole length of the root while total root dry weight increases. Ratio of above ground plant weight to root reaches the value of 6.8 until stage R1 and inreases during vegetation period due to rapid growth during the reproductive phase (Kaspar, 1985).

Flowering

In the flowering stage, above surface plant parts grow rapidly again, as well as the root. In this period, Mason et al. (1980) determined the increase of total root dry weight in comparison to the previous growth stage by 84% and increase in length by 165%, being the highest increase of all the stages in vegetation period, which is in accordance to the results of Kaspar et al. (1978). Nonetheless, the root growth is slower than the growth of above surface plant parts and ratio between them during R2 stage reaches the value of 9 (Sivakumar et al., 1977). Further increase in length is mostly into deeper soil layers, while the most part of dry weight is still in the layer up to 30 cm. Lateral roots had by this time stopped growing horizontally and started growing rapidly downwards, which can be explained by higher temperature and lower soil moisture closer to the surface (Mitchell and Russell, 1971).

Pod formation and growth

Root is still growing, but slowlier than in the flowering stage. If the soil is well provided with moisture, new root growth is visible in the layer up to 30 cm. Since this occurs rarely in this stage, most often there is only the downward elongation.

Seed growth and maturity

In this stage root growth is significantly slowed as compared to the previous stage, since the plant uses almost all organic matter created in the process of photosynthesis for seed formation and filling. Dry matter increase in soil layer up to 15 cm is mostly connected to the secondary thickening of the taproot and lateral roots (Kaspar, 1985), while growth into depth is mostly finished before seeds start filling. Total root dry weight reduces due to older parts of the root system dying off, while the ratio of above ground plant dry weight to root dry weight reaches the value of 10 (Sanders and Brown, 1976).

Root nodules

Root nodules are an important part of the soybean root system. Similarly to other legumes, soybean plant enters into a symbiotic relationship with nitrogen-fixing *Bradyrhizobium* bacteria living in root nodules, whence their name nodule bacteria. These bacteria take carbo-hydrates from the plant providing it with nitrogen by converting inorganic nitrogen (N2) from the atmosphere into ammonia (NH3) which is readily usable by plants. Typical for soybean is the species *Bradyrhizobium japonicum*, gram-negative, rod shaped bacteria, capable of penetrating thin rhyzodermis cell walls or root hairs, progressing to the primary cortex. Visible 7 to 9 days after infection, nodules are formed by intensive division of bacterial cells and desintegration of host cells. During the third week from infection, the infected root tissue produces leghemoglobin intensivelly coloring the nodules pink, which remain thus colored while active. When leghemoglobin forms, bacteria cease division and nitrogen-fixation commences (Bergersen, 1963).

During the fourth week from the infection, nodules reach their full size (3 to 6 mm) most often being oval shaped, although they could be of irregular shape. A subtle increase of nodule number and size is observed during vegetation period (Zobel, 1980). Nodules actively fix nitrogen for 50 to 60 days, when they dry off and die. One plant can host as many as few hundreds of nodules, mostly concentrated in the shallow soil layer of up to 20 cm, but these could also be found at depths over 1 m (Grubinger et al., 1982). Nodule number is conditioned both by internal factors (genetic and physiological) and external factors (soil nitrogen level) (Gibson and Harper, 1985; Harper, 1987). At least 40 genes are directly involved in the process of nodulation and nitrogen-fixation, from regulation of a certain soybean variety`s compatibility towards a certain *B. japonicum* strain, via infection intensity, to nodule development (Rolfe and Gresshoff, 1988).

Stem

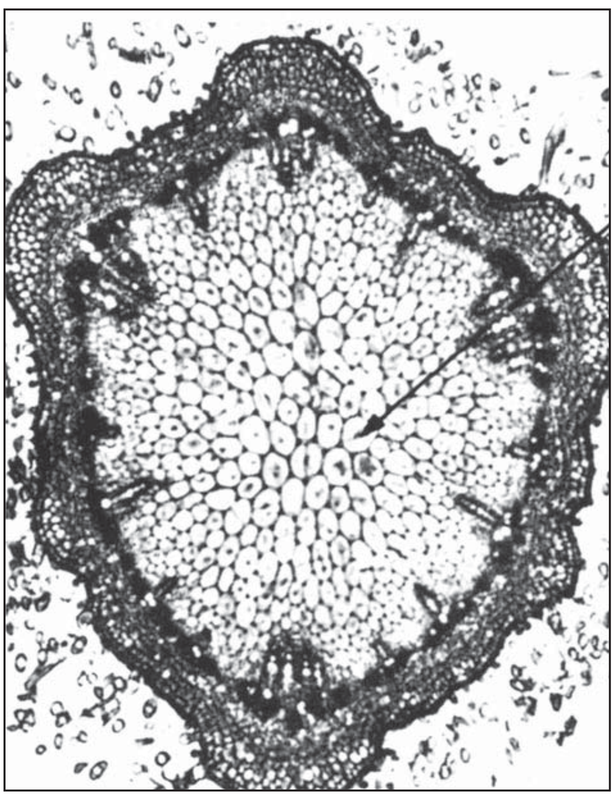
There are two basic types of the soybean stem – the prostratum, with vining growth habit, and the erect type. The first is typical for wild soybean species and can reach heights of 2 to 3 m. Commercial varieties, however, have an erect stem, the height of which, affected by variety and environmental conditions may be 30 to 130 cm. Soybean stem is green, due to the presence of chlorophyll in the parenchyma cells, covered in hairs and mostly branched. On stem there are joints or nodes, clearly visible thickenings which carry leaves; a portion of the stem between two nodes is called an internode. The first node carries the cotyledons, the second node carries the first pair of leaves (prophylli), while other nodes carry alternated trifoliolate leaves.

Stem anatomy

Soybean stem transection clearly shows layers of the stele, primary cortex and epidermis (Figure 2.2).

Figure 2.2

Stem transection (according to Curry, 1982; as cited in Lersten and Carlson, 1987)



The middle of the stem is occupied by a voluminous parenchyma pith tissue made up of large cells without chlorophyll. During the first part of the vegetation period, this tissue serves as storage, while later, due to secondary thickening, the cells move away from each other leaving the stem hollow. Pith is surrounded by a zone of vascular bundles intersected by parenchyma tissue cells, which connects the pith to the primary cortex, thus comprising the network of individual veins, or eustele.

The zone of vascular bundles consists of xylem, positioned towards the pith, and phloem that transports the assimilates, positioned towards the exterior. Xylem and phloem are separated by the rest of undifferentiated cambium. Primary xylem comprises protoxylem and metaxylem. Owing to their non-thickened wall parts, first set protoxylem elements are capable of following the elongation process during stem growth. As elongation growth finishes, protoxylem loses its function, which is taken over by a later differentiated metaxylem whose coiled structure enables an additional slight elongation. Similarly, the phloem is also divided into protophloem and metaphloem, which in addition to sieve-tube cells also has companion cells. During secondary stem growth, the secondary xylem and phloem are created to form a complete cylinder at lower plant parts (where the secondary thickening lasts longest) (Cumbie, 1960).

In the internodal stem parts there are vascular bundles (veins) thicker than usual, from which collateral veins extend and are traceable towards the base as traces of leaf vascular bundles. At each node, three such traces part from the stele and merge into a leaf vascular vein.

The primary cortex is separated from the stele by a layer of endodermis cells, made up of a green assimilation storage parenchyma tissue, externally enveloped by collenchyma. In some soybean varieties, this layer stores the pigment anthocyanin whose presence affects flower color. Varieties that have anthocyanin display purple flower color, while varieties lacking anthocyanin have white flowers.

On the surface, stem ends in epidermal cell layer lacking chlorophyll with a cutinized external wall. Typical for soybean is that epidermal cells elongate into hairs, whose color, density and position are a significant feature in commercial varieties. Varieties with a dominant *Pd1* gene have a larger number of hairs per unit of epidermal area (Bernard and Singh, 1969; Bernard and Weiss, 1973). Hairs are white to dark brown, positioned most often erect to the stem, although they can be appressed. There are even varieties lacking hairs.

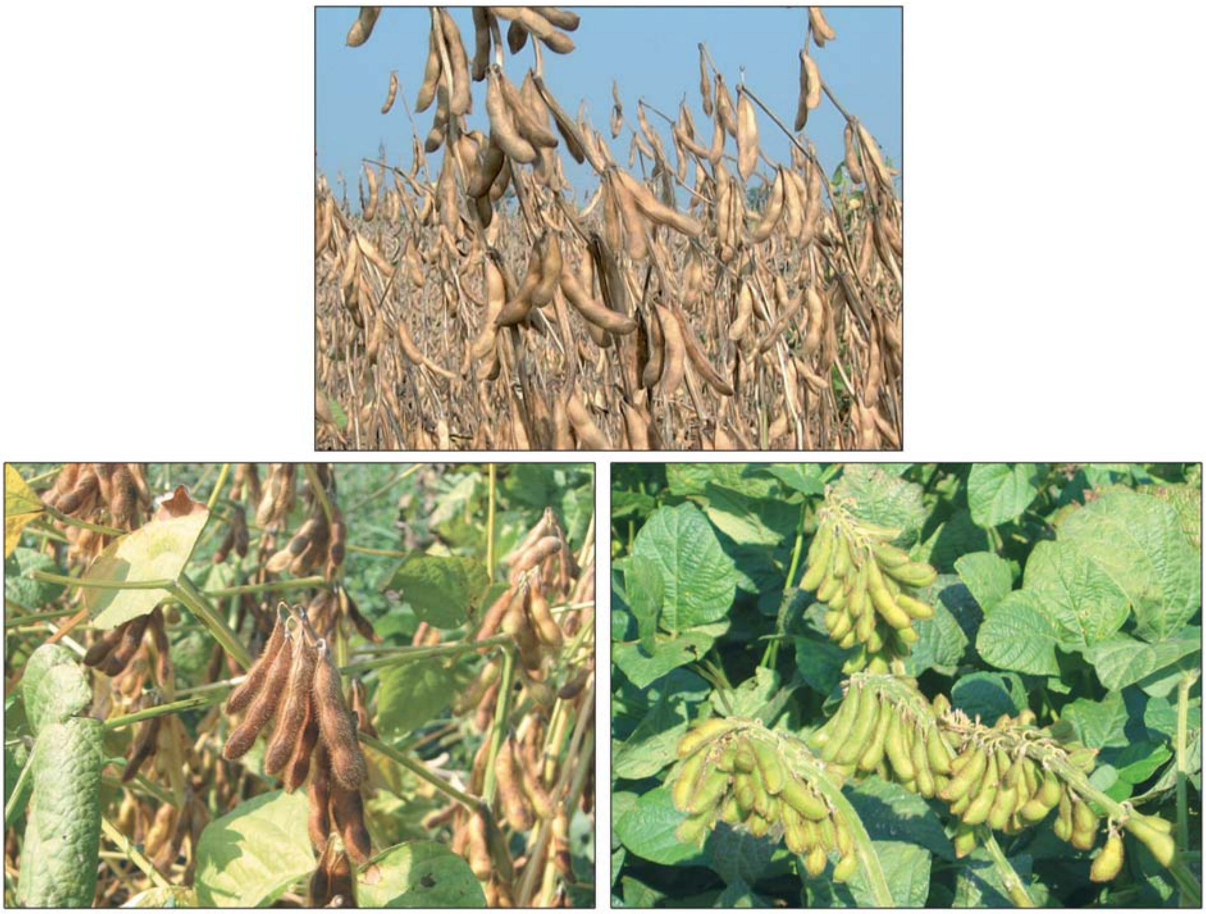
Stem growth and development

Stem development begins with shoot (hypocotyl) emerging above the soil surface. Two cotyledons and a plumule (shoot bud) are observable on the shoot, which grows straight upwards in the erect habit plant. The first stem node carries the cotyledons. Above cotyledons, at the second node, there is a pair of the opposite first unifoliolate leaves.

The third and all other nodes carry typical trifoliolate leaves. In each leaf axil there is a bud which may develop into a branch, a flower or remain as an undeveloped, i.e. dormant bud (Vratarić, 1986). Depending on variety and environmental factors, soybean plant is more or less brached, with common primary branches, while the secondary branching is rare in soybean plants (Dzikowski, 1936). Further stem development is affected by growth type. There are three growth types of soybean plants: indeterminate, determinate and fasciated (Figure 2.3).

Figure. 2.3

Stem growth types (original) *(photo: V. Đorđević)*



Description: indeterminate (top), determinate (left) and fasciated (right)

Varieties of indeterminate (unlimited) growth type have a vegetative cone at stem top. Terminal leaf is often smaller than lower leaves. Until beginning bloom stage they form around 67% of total dry matter. Stem growth and vegetative weight formation prolongs even after beginning bloom stage. Indeterminate varieties are more susceptible to lodging than determinate ones.

Varieties of determinate (limited) growth type finish stem with an inflorescence. After beginning bloom plants cease growing, adversely affecting yield in drought conditions. These varieties form around 80% of vegetative mass until beginning bloom (Lin and Nelson, 1988). Terminal leaf is of the same size as lower leaves. Determinate varieties branch more and are more resistant to lodging than indeterminate ones. Varieties grown here are indeterminate. After formation of the first few leaves, vegetative cone of plants with a fasciated stem divides and forms several merged stems, resulting in two to three leaves at one node. Such plants form a long inflorescence at stem top resulting in a dense pod cluster. As of yet, there are no such commercial varieties developed to display such a stem type.

Leaf

There are three different types of soybean leaves: the first pair of cotyledon (seed) leaves, the second pair of primary (unifoliolate) leaves and true (triofoliate) leaves. The cotyledons are parts of the embryo, attached to the embryonic stem, and they emerge to the soil surface by germination. Round in shape and enveloped in epidermis with stomata, they can be yellow or green in color. Their function is of a food and photosynthesis storage until the plant fully acquires autothrophic nutrition, following which they dry off and drop.

In each cotyledon axis there is a bud from which one unifoliolate (primary) leaf shoots, meaning that each unifoliolate leaf has its node, but these two are for practical reasons regarded as one (Figure 2.4). These leaves are positioned opposite each other at petioles measuring 1 to 2 cm in length, while the leaflet is oval shaped and 2 to 5 cm long.

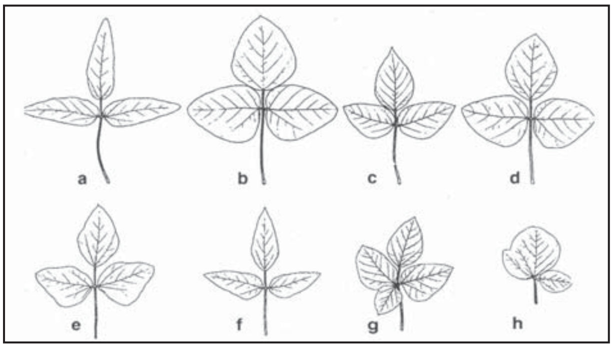
Figure 2.4

The first pair of leaves - prophylli *(photo: G. Mulić)*

All other nodes carry trifoliolate leaves, which are typical for soybean, and alternate up the main stem. Trifoliolate leaves are composed of three leaflets and a petiole. Leaflets may be oval or spear shaped (Figure 2.5). Sometimes it might happen that the true leaf is composed of four, or even seven leaflets (Figure 2.5g), or that lateral leaflets merge with the terminal one (Figure 2.5h). A leaflet is 4 to 20 cm long and 3 to 10 cm wide, light to dark green in color. Leaflet color and size are varietal properties, the same as degree of attachment between petiole and stem. During vegetation period leaves turn yellow and are shed, although there are varieties that do not shed leaves even in maturity.

Figure 2.5

Different leaflet shapes (Dzikowski, 1936, as cited in Lersten and Carlson, 1987)



At the point of petiole attachment to the stem, a pair of opposite lateral bracts or stipules are visible. On these leaf-like outgrowths seven main nerves accompanied with several smaller ones can be observed.

At the petiole base, apart from stipules, a certain thickening might also be observed (*pulvinus*, Dzikowski, 1937, as cited in Lersten and Carlson, 1987). The second smaller thickening is found where leaflets are attached to the petiole. These thickenings, also known as stipels, function as joints since they enable a change of leaflet orientation during day and night due to changes in osmotic pressure.

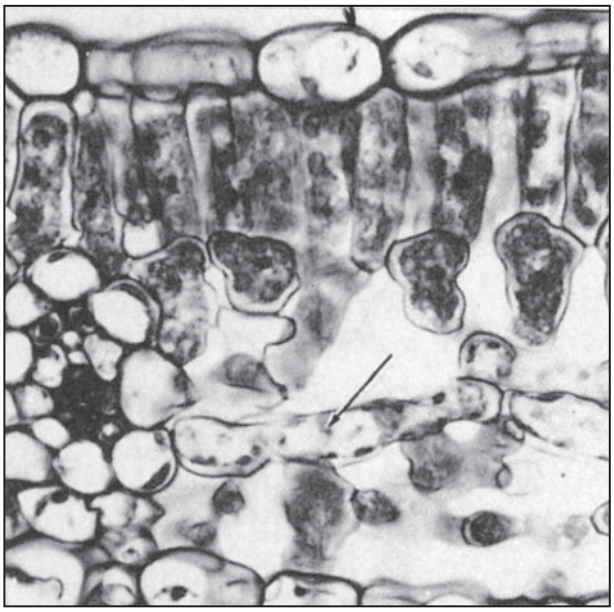
Leaf anatomy

As stated in the stem anatomy paragraph, leaf vascular tissue is made from three separate vascular bundles which are already merged into a larger bundle at basal petiole thickening. As soon as the stem vascular bundles merge, vascular tissue is differentiated into the eustele. Vascular tissues of all leaf parts are created by branching of petiole eustele.

The most important part of the leaf is a leaflet. True soybean leaf is made of three leaflets of identical composition – there are two lateral leaflets and one terminal (Figure 2.6). Leaflet composition is dorsoventral and adapted to its basic functions – photosynthesis and transpiration.

Figure 2.6

Transection of a leaflet (from Lersten and Carlson, 1987)

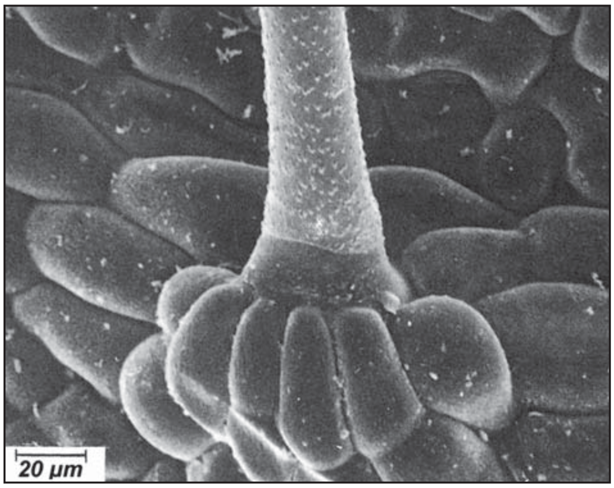


On both leaflet surfaces, epidermal cells are covered with a thin cuticle from which epicuticular wax forms protecting the leaf from heat and excessive water vapor. Continual string of these cells is interrupted by the stomata. Stoma complex comprises a pair of kidney-shaped cells (guard cells) which enclose a pore, the neighbouring epidermis cells (subsidiary cells) and one layer of mesophyll cells. Gas exchange is regulated between the plant and environment through the pore of the stoma complex. Stomata number is affected by light, heat, and moisture, as well as variety. Based on their research on 43 soybean varieties, Ciha and Brun (1975) reached a conclusion on significant differences in stomata number among varieties, as well as the connection between stomata number and drought resistance. The authors found that there is an important difference in stomata number on upper and lower leaf surfaces. Upper side has 81 to 174 stomata per mm^2, and lower 242 to 345 stomata per mm^2.

Typical for soybean leaf are hairs (trichomes), comprising two cells – a short basal one, surrounded by epidermis cells, and a terminal one 0.5 to 1.5 mm long (Figure 2.7).

Figure 2.7

Lower part of a leaf hair (Flores and Espinoza, 1977, as cited in Lersten and Carlson, 1987)



According to the research of Woolley (1964), leaf hair length in the variety Hawkeye is around 1 mm, distanced from each other also 1 mm, and they comprise around 10% of the total leaf area. The same author established that leaf hairs reduce wind blow on the leaf area up to 40%. Plants with denser hairs have physiological and agronomical advantages, since they are less exposed to the pest attacks (Johnson and Hollowell, 1935; Singh et al., 1971; Levin, 1973), water loss through transpiration under high temperatures and drought conditions is reduced (Weigand, 1910; Ghorashy et al., 1971; Ehleringer et al., 1976; Ehleringer and Mooney, 1978) and they have a higher capability of sun radiation reflection as compared to the plants with fewer hairs (Gausman and Cardenas, 1973; Nielsen et al., 1984).

Between upper and lower parts of the epidermis there is the mesophyll, made up of two layers of vertically distributed elongated cells towards the upper leaf surface. It is called the palisade parenchyma because of its characteristical cross section appearance. Palisade parenchyma is also called the assimilation tissue, since these cells are rich in chloroplasts. Lugg and Sinclair (1980) determined that upper, more sun-lit leaves can even form the third layer of assimilation parenchyma cells. Towards the lower leaf surface there are two to three layers of spongy parenchyma cells containing fewer chloroplasts. This mesophyll part contains cells of irregular shape with distinctly wide intercellular spaces, related to a higher stomata number at the lower leaf surface. Such composition of the spongy parenchyma enables uninterrupted gas exchange between the plant and environment.

Leaf blade vascular tissue is situated between the palisade and the spongy parenchyma, while its internal structure is identical to the structure of the stem vascular tissue.

Flower

Soybean flower (Figure 2.8) forms successively at leaf axil on stems and branches from the base upwards.

Figure 2.8

Soybean flower *(photo: G. Mulić)*

The first flowers are often initiated on the fifth, sixth or higher nodes, rarely or never being initiated on lower nodes (Carlson and Lersten, 1987). Flower ranges from 3 to 8 mm in size and white or various shades of purple in color, depending on the presence or absence of anthocyanin, purple being dominant over white. Flowers are borne in the axillary raceme cluster, which mostly comprise 3 to 5 flowers.

Stem in determinate varieties ends in the terminal inflorescence in which up to 35 flowers may be initiated. For varieties of this growth type it is characteristic that growth ceases with beginning of flowering. In indeterminate varieties, however, growth and development are simultaneous – plants keep growing even after flower initiation. These varieties also have the terminal inflorescence, with two to three axillary inflorescences tightly initiated due to short internodes at stem top.

As previously mentioned, soybean plant initiates flowers successively, thus on one plant there could simultaneously be found flower buds, open flowers and pods in seed-filling stage. Affected by variety, planting date and environmental conditions, soybean flowering period in this area lasts from end of May through mid August.

Typical for soybean is a high rate of flower abortion, i.e. more flowers are initiated than pods. This phenomenon is yet to be satisfactorily explained. According to Van Shaik and Probst (1958), the long inflorescence, higher number of flowers and high rate of flower abortion are features inherited quantitatively, with dominant and complementary gene effect, while heritability for flower abortion percentage ranges from 29 to 93%. The same authors concluded that it is difficult to develop a variety with a high flower initiation capacity and a low flower abortion rate, for they found a positive correlation between flower abortion and flower number per node. Pod number per node is an important yield component that affects yield more than seed weight (Heindl and Brun, 1984), which is in agreement with conclusions of Wiebold et al. (1981) who stated that soybean yield can be increased by reducing flower abortion, i.e. by increasing pod number. Probability for flower abortion for flowers found lower on the inflorescence is often less than 10%, while it is over 50% for higher positioned flowers (Wiebold and Panciera, 1990). For this reason it is recommended to breed for lower flower abortion rate, especially of those on inflorescence top, according to Sharma et al. (1990).

Flower anatomy

Soybean has a bisexual, typically papilionaceous flower characteristical for *Papilionoidae*, consisting of tube-like corolla, composed of five uneven separate petals covered in hairs, and a five-pieced calyx. The largest most outward petal more or less envelops the flower and is called vexillum. Two lateral much smaller petals enclosing the pistil from the sides are called alae, while two front petals are merged comprising a naviculum. Flower is zygomorphic, i.e. it can be divided by only a single plane of symmetry.

Inside the calyx there are ten stamina, nine of which are positioned on filaments comprising a whorl around the pistil, while the remaining one is free and positioned below the stigma.

The pistil is monocarpic, with one to four seed embryos. Development of the seed embryo is of *Polygonum* type. The style leans backwards towards the free stamen. Similarly to the corolla, the pistil is covered in hairs, which are lacking from sepals and stamina. At the base, between pistil and stamen there are nectaries.

Stamina compose a whorl around the pistil and consist of a supporting stalk (filament) and an anther which opens and releases the pollen onto the stigma, most often a day before the flower opens, thus greatly reducing the percentage of cross-pollination (< 0.5%). A large number of pollen grains are dropped on the stigma, whence they germinate into a pollen tube and progress through the style finally reaching the ovary. More than 90% of pollen tubes atrophy even before reaching the ovary, leaving only a small number apt for fertilization (Carlson and Lersten, 1987).

Protruding into the embryonic sac, the tip of the pollen tube bursts and releases its content of two sperm cells. One sperm cell unites with the ovule forming a diploid zygot, the first cell of the future embryo, while the second sperm cell unites with the secondary nucleus of the embryonic sac, forming a triploid nucleus of the endosperm, which in soybean does not develop further. The proembryo is formed as a result of zygote division, from whose cells positioned towards the interior of the embryonic sac embryo is later created. Other proembryonic cells become basal cells (suspensors), which push the embryo into the secondary endosperm, the nutritious tissue formed out of endosperm nucleus and the rest of embryonic sac plasm. With embryo division, the radicle emerges from the end facing the micropyle, while cotyledons emerge from the end facing chalaze, with an apical shoot meristem between them.

Pod

Soybean fruit is the pod, whose number ranges from two to more than twenty in one inflorescence, and up to 400 on a mature soybean plant (Carlson and Lersten, 1987). Owing to a high percentage of soybean flower abortion, this number is ofter much lower.

Pod shape and size vary significantly among varieties, and even among pods on one plant under the influence of environmental factors. Soybean pods can be straight, slightly bended or sickle shaped, ranging 2 cm in length in wild soybean to 7 cm in some cultivated soybean varieties (Figure 2.9). Depending on the seed number, pod length is most often between 4 and 6 cm (Frank and Fehr, 1981).

Figure 2.9

Pod *(photo: G. Mulić)*

Pod color can be light yellow, brown or black, including all shades and transitions among these three colors, which depends on the presence of carotene and xanthophyll, color of hairs, and presence of anthocyanin (Dzikowski, 1936). Darker pod color is dominant over lighter pod color.

There could be one to five seeds in a pod, which depends on varieties and environmental conditions. Varieties grown here there are most often 2 to 3 seeds in a pod (Hrustić, 1984) (Figure 2.10).

Figure 2.10

Pod with mature seeds *(photo: G. Kuzmanović)*

Mature wild soybean pods split and shatter seeds, which is very disadvantageous in commercial varieties from an agronomic standpoint. Modern commercial varieties, developed by soybean breeding, have firm pods that split only under stress (Miladinović et al., 1996).

Pod internal structure

The first pods on the soybean plant are visible around two weeks after initiation of the first flowers. Owing to the successive soybean flowering, on the same plant there could simultaneously be just initiated pods and pods bearing green seed. Pod develops from the ovary, directly following fertilization as the stigma and the style dry and fall off. Pod development is slow at first, becoming faster after flowering is over. Flower corolla is visible at the base of the pod and remains until end of maturity.

As in other plants from this family, pod is made of one carpel which involutes and merges its margins by a ventral seam. The main nerve of the former leaflet resembles dorsal seam. The main part of both seams consists of vascular bundles, created from the former leaf, one being on the dorsal seam, and two on the ventral seam.

The epidermis above the vascular bundles of both seams involutes, forming clearly observable ducts which extend into the layer of parenchyma cells.

In the earlier developmental stages, the pod is covered with a layer of epidermal cells which sporadically form hairs. Below this layer, there is a wide zone of parenchyma tissue embossed with the vascular system and a thin layer of inner parenchyma from which membranous endocarp develops (Carlson and Lersten, 1987). With maturity, the walls of epidermis cells thicken and are externally covered with cuticle. A layer of short fibers forms below the epidermis cells, while vascular tissue connecting main seam bundles is placed inside the following parenchyma layer. Below parenchyma, there is a thin layer of sclerenchyma fibers, responsible for pod shattering (Carlson and Lersten, 1987). The cited authors state that inner sclerenchyma cells, whose fibers are parallel to the vertical cell axis, shorten while drying more than cells of the external sclerenchyma layer, which displays cross orientation of the fibers, causing the pod to twist around the vertical axis and split at seams.

The last layer of flat parenchyma cells is called the endocarp. According to Krul (1978, as cited in Yaklich and Cregan, 1981) this layer regulates seed moisture in mature pods.

Seed

Seed of most commercial soybean varieties is oval shaped, but can include all shapes between round and elongated, almost linear shape. Thousand seed weight ranges from 20 g in wild soybean to over 500 g in some cultivated soybean varieties. Commercial varieties most often have middle-sized seeds of 150 to 190 g thousand seed weight (Hrustić, 1984: Relić, 1996: Miladinović, 1997).

As with most legumes, soybean seed does not include endosperm but is comprised of an embryo enclosed by the seed coat. Mature embryo comprises two large cotyledons, plumules, with two primary leaves enclosing leaf primordia, epicotyl, hypocotyl and radicle.

The part of the seed where it was attached to the pod is called the hilum. Hilum shape, color and size are varietal features. Hilum shape varies from linear to oval, and color may be black, brown, yellow or green, including all shades of these colors, and may or may not differ from the color of seed coat. At one hilum end there is a little channel, chalaza, and at the other end there is micropyle, a small opening between the tips of integuments, through which the radicle emerges. Gas exchange between the embryo and environment occurs mostly through micropyle, due to cutinized walls of outer cell layers in seed coat epidermis. In some varieties, when seed separates from pod, hilum epidermal cell layer lingers on funiculus, causing a white scar along the middle of hilum (Dzikowski, 1936).

Seed coat comprises three parts: epidermis, hipodermis and internal parenchyma. It can be smooth or wrinkled, glossy or matte as affected by variety.

Epidermis is made of a layer of cells shaped like palisade, with walls externally cutinized. In colored seeds, this layer harbors pigments such as anthocyanin in vacuoles, chlorophyll in plastids and different pigment decomposition products (Carlson and Lersten, 1987). Soybean seed can be yellow, green, brown or black, including all shades and transitions among these colors, but it may also be bicolored (Figure 2.11).

Figure 2.11

Soybean seed *(photo: J. Miladinović)*

Tully et al. (1981) established that black seeds are more resistant to low temperatures, which can be explained through reduced water permeability of the pigmented seed. This is in accordance with the results of Dickson (1971) who analysed another legume – common bean (*Phaseolus vulgaris* L.).

Below the epidermis there is the hypodermis, a layer of pillar cells with large intercellular spaces due to uneven thickness of the cell walls.

The tissue of inner parenchyma is composed of 6 to 8 layers of flat thin-walled cells. This tissue is uniform through the whole seed coat, except on hilum which distinguishes three layers - outer, which leans on hypodermis and may contain pigments giving hilum a more intensive color; middle layer composed of thin flat cells and bundles of spiral vessels branching around hilum, and inner layer, mostly typical parenchymal one (Dzikowski, 1936).

Cotyledons make up the largest portion of total soybean seed weight and volume. Each cotyledon is more or less crescent and covered by epidermis. Stomata are present on both sides of the cotyledons.

On the inner, flat side of cotyledon, mesophyll cells are more tightly linked and arranged in two or three palisade layers, whereas on the other side these layers are not visible. Interior of cotyledon consists of spongy parenchyma cells filled with aleurone granules and oil droplets. Calcium oxalate crystals are dispersed through the whole cotyledon inside.

Most soybean genotypes have yellow cotyledons (Williams, 1950), while some can also be green. Together with the different combinations of seed coat pigments, they provide soybean seed with a wide color spectrum.

Plumule is about 2 mm long with two opposite primary leaves, each with a pair of basal stipules. Embryonic stem comprises epicotyl and hypocotyl, made up of epidermis, cortex and pith. It is often around 5 mm long, depending on seed size, and ends in a radicle

Seed chemical composition

Based on dry weight, mature soybean seed regularly contains around 40% proteins, 20% oil, 17% cellulose and hemicellulose, 7% sugar, 5% fiber and around 6% ash (Rubel et al., 1972). The importance of soybean in food and feed production primarily comes from the high contents of seed protein and oil.

Depending on varieties and environmental conditions, seed protein content varies from 30% to 53%, while commercial varieties most often contain 39 % to 42%. Based on the sedimentation constant, reserve proteins of soybean seed are divided into three large groups: 2S (α-conglycinin) comprising mostly protease inhibitors, 7S (β-conglycinin) and 11S (glycinin) (Clarke and Wiseman, 2000).

Soybean proteins contain almost all essential amino acids and are most similar to proteins from animal sources. Amino acids present in soybean seed are lysine (6% to 7%), histidine (3%), arginine (12% to 13%), threonine (4% to 5%), phenylalanine (5%), tryptophan (2%), serine (5% to 6%), glutamine (20%), proline (4% to 5%), glycine (4%), leucine (8%), tyrosine (4%), alanine (5%), valine (4% to 5%), methionine (1%), cysteine (1%), isoleucine (5%), and some 400 free amino acids aside (Leáenko et al., 1987)

Depending on variety and environmental conditions, seed oil content varies from 12% to 24%, and in commercial varieties from 19% to 22%. Soybean oil contains around 10% palmitine (16:0), 3% stearine (18:0), 20% oleine (18:1), 55% linoleic (18:2) and 7% to 8% linolenic (18:3) acid (Swern, 1972). Owing to especially high content of linolenic acid, soybean oil lacks favorable technological features for human consumption as compared to sunflower oil.

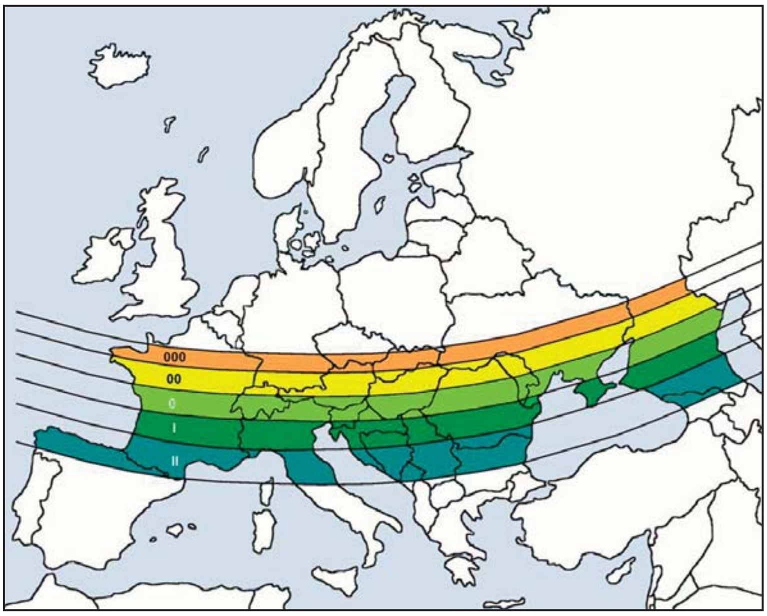
MATURITY GROUPS

Soybean plant is sensitive to photoperiods, meaning that the point when plants enter vegetative and reproductive stages depends directly on the day length. This dependence has caused the division of soybean varieties into 13 maturity groups (Hartwig, 1973). Marks for maturity groups are 000, 00, 0 and Roman numerals from I to X. Soybean varieties designated with 000 are adapted to the conditions of longer days and have a long critical photoperiod, i.e. they are photoperiodically insensitive and are successfully grown at higher latitudes, while varieties marked with X are adapted to the conditions of shorter days and are successfully grown at lower latitudes (Criswell and Hume, 1972). Differences among maturity groups are conditioned by photoperiodical demands of the varieties and if grown at the same latitude, differences in maturity are on average 10 to 18 days. Critical photoperiod progressively decreases from higher to lower latitudes. Requests for photoperiod thus limit the distribution of varieties to a narrow latitudinal belt to which a certain variety is adapted (approximately 200 km, Scott and Aldrich, 1983; Zhang et al., 2007). If a variety is grown at latitude higher than the one it is adapted to, it will flower and mature later or it might not even reach full maturity until the first frost appears. A variety grown at lower latitude in relation to the area it is adapted to will flower earlier, have decreased vegetative weight and mature earlier, consequently causing decreased yield.

For each soybean growing area there is an “optimal” maturity group, meaning that varieties belonging to a previous group are early for that area, and those belonging to a following group are late for that area. In our conditions varieties belonging to maturity group I are the basic varieties, those belonging to maturity group 0 are early, and those belonging to maturity group II are late (Figure 2.12). Under agro-ecological conditions common for our area and optimal planting date in mid April (Rajičić, 1987), vegetation period (from emergence through maturity) for varieties belonging to maturity group I is 120 to 135 days. Varieties belonging to maturity group 0 end their vegetation period in 110 to 120, while varieties belonging to maturity group II take 135 to 145 days for full vegetation period. Due to stress conditions, such as unusually high or low temperatures, pertaining drought, etc., and interaction between variety and environment (Jocković et al., 1994; Miladinović, 1997) vegetation period can be shorter or longer than the stated one.

Figure 2.12

Maturity groups of soybean varieties grown in Europe *(J. Miladinović)*



Phases of growth and development

Soybean development is a continual process which begins with seed emergence, and ends with mature seed and harvest-ripe soybean. Plant development during vegetation period could be divided in two phases – vegetative and reproductive, which could also be subdivided into several stages, or phenophases. Even though few such determinations have been proposed in both Soviet and US research communities, nowadays the determination and alpha-numeral marks proposed by Fehr and Caviness (1977) are widely accepted.

Aim of describing developmental phases

Depending on variety, maturity group, planting date, environmental factors, and applied agronomy, plant development can be decreased or increased. If there were no unique terminology, this would hinder the communication among experts, representatives of agro-industry and a wide range of producers. For example, if a herbicide producer recommends a its application when plants reach developmental stage of 6 leaves, and during application it is not known which leaves should be included into the identification of that particular stage, the herbicide would probably be applied inadequately (Fehr and Caviness, 1977). Stages of soybean development described by Fehr and Caviness can be used for any soybean variety grown at any location, and the descriptions can be used to identify the stage of a single plant or a whole field of soybeans.

Objectiveness and preciseness of the descriptions reduce the risk of different evaluation by persons identifying the stage of a plant to the minimum, which is the main reason why these descriptions are widely accepted in our country.

Separate descriptions have been used for identification of vegetative (V) and reproductive (R) phases of development, so that differences in relations between these two phases with different growth types do not influence the procedure of stage identification.

Vegetative growth

Vegetative development of soybean plants begins when cotyledons appear (i.e. emerge) above soil surface and this stage is designated with a VE, where V stands for vegetative phase, and E for emergence. Soybean development depends on temperature, day length, variety and other factors, meaning that there could be significant differences in days needed for the plant to reach next phase. The main factor influencing vegetative development is temperature. Low temperatures decrease seed germination and leaf development, while high temperatures increase them. Thus, depending on the temeprature, days from planting through emergence (VE) could vary from 5 to 15.

Soon after emergence (3 to 10 days), the first pair of unifoliolate leaves appear above cotyledons. When unifoliolate leaves unroll (two edges of each leaflet are not touching), the plant is in VC (cotyledons) stage.

For further determination of vegetative stages, nodes with fully-developed leaves are taken into account. A leaf is considered fully developed (nodes are counted) when leaf at the first upper node is unrolled sufficiently such that the two edges of each leaflet are no longer touching. The first node counted is the one of the unifoliolate leaves. When first trifoliolate leaves unroll, formed at the node above unifoliolate leaves, the plant enters stage V1. It may be 3 to 10 days between stages VC and V1 depending on the environmental conditions. Further vegetative stages are designated with a combination of the letter V and a number (1, 2, 3, to n) denoting number of nodes with fully developed leaves. It usually takes 3 to 8 days for the plant to reach the next stage, from V2 onwards.

Varieties grown here have an indeterminate stem growth type, which means that vegetative stage of development lasts until the end of vegetation period. When the first flower appears, vegetative and reproductive developments of the plant overlap. Depending on maturity groups and environmental conditions, the first flower appears at stages V4 to V6.

It should be pointed out that only nodes on the stem are counted, disregarding those on the branches

Reproductive development

Reproductive stages, designated with the letter R (reproductive) and a numeral, encompass flowering, pod and seed development, and plant maturation.

As with vegetative stages, determination of reproductive stages considers only the stem, for if it is broken or otherwise damaged, reproductive development on the newly-formed branches will be late, which is why branches are not taken into account. The same factors as with vegetative stages influence number of days needed for the plant to reach the next reproductive stage. High temperatures and short days enhance reproductive development, while low temperatures and long days reduce it.

One open flower at any stem node marks the beginning bloom stage, which is designated with R1. As a rule of thumb, R1 and R2 appear simultaneously in determinate types, while period between R1 and R2 in indeterminate types takes 3 days. Full bloom stage (R2) means one open flower at one of upper two nodes on the main stem with fully developed leaves. Full bloom may last from 5 to 15 days.

Plant reaches stage R3 (beginning pod) when the pod is 5 mm long at one of four uppermost nodes on the main stem with fully developed leaves. As the previous stage, this stage can also last from 5 to 15 days.

Pod 2 cm long at one of four nodes with fully developed leaves marks the full pod stage R4. Depending on weather conditions and maturity group, this stage may last for 4 to 16 days.

Beginning seed stage R5 means that 3 mm long seed forms inside pod at one of uppermost nodes with fully developed leaves. When pod at one of these nodes contains green seed which fully fills pod cavity, the plant enters the stage R6. The period of these two developmental stages is mostly affected by moisture available to the plant. Plant remains in stage R5 for 7 to 21 days, and in stage R6 from 9 to 30 days.

When one normal pod reaches mature color, the plant enters beginning maturity stage R7 lasting often 7 to 18 days.

When 95% of pods are mature color, the plant has reached full maturity stage R8. Seeds contain 15% moisture and it takes few more days of dry weather before harvest-ripe fit for combining.

Descriptions of vegetative and reproductive stages represent development of the individual plants. Average stage of the crop is the one in which are 50% of the plants in a field.

SUMMARY

Soybean is an erect annual plant with a hairy stem reaching 30 cm to 130 cm in height depending on environmental factors. Soybean root system is diffuse, with a taproot usually indistinguishable from the lateral roots. Root system is characterised by root nodules whose creation results from a symbiotic relationship between the soybean plant and nitrogen–fixing Bradyrhizobium bacteria. Trifoliolate leaves are typical for soybean, while the flower is bisexual and typically papilionaceus, purple or white in color. Pod contains one to five seeds as affected by the environmental factors. The most important components of soybean seed, proteins (about 40%) and oil (about 20%) are the main reason for soybean cultivation. Due to photoperiod sensitivity, soybean varieties are divided into 13 maturity groups, from 000 for varieties grown at higher latitudes, to X for varieties grown at lower latitudes. Plant development could be divided into two phases – vegetative (V) and reproductive (R), which are in turn further subdivided into more phenophases, designated with numbers.

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