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Liisa Kaarina Simola: Effect of different sucrose concentrations and gibberellic acid on anatomy of *Bidens radiata* Thuill. and *B. pilosa* L.

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EFFECT OF DIFFERENT SUCROSE CONCENTRATIONS AND GIBBERELLIC ACID ON ANATOMY OF BIDENS RADIATA THUILL. AND B. PILOSA L.

BY

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Abstract

The anatomy, especially of roots and stems, has been studied in several parts of *B. radiata* and *B. pilosa* grown in pots in greenhouses. The structure of these plants was compared with that of plants cultivated in sterile cultures with sucrose as carbohydrate source. The effect of gibberellic acid (10 ppm) with different sucrose concentrations was also tested. *B. radiata* was more tolerant of high sucrose concentrations (7 and 10 %) and of the presence of gibberellic acid than *B. pilosa* and it even flowered under these conditions. A characteristic feature of *B. radiata* is the occurrence of aerenchyma in stem and root cortex. No real interfascicular rays are formed during secondary growth. Some older parts of *B. pilosa* roots have a pith and they are polyarch. The younger parts as well as all roots growing in sterile cultures do not have any pith and their steles are mostly tetrarch. Gibberellic acid stimulates secondary thickening and lignification of xylem in roots and stems. The anatomical structure usually becomes simpler in sterile moist conditions but some new features also emerge. Chlorenchyma occurs in the root cortex and in cultures it is also formed by the cambium in some roots.

I. Introduction

Up to now there have been relatively few comprehensive experimental studies on the effect of environmental factors on the morphogenesis and anatomy of higher plants. Conclusions have been drawn from plants grown in their natural environments and many clear correlations have been detected between some climatic factors and certain morphological and anatomical features of plants. The difficulty of regulating environmental factors has been one of the main difficulties in studies of this kind. Methodical advances in sterile culture, by which the effects of the growth medium can be studied,

and new technically well equipped growing cabinets, known as phytotrons, have created quite new possibilities for experimental anatomy.

In sterile culture, most plants and tissues will not grow without any organic carbon source. Sucrose has proved to be the best carbohydrate source for most plants and its optimum concentration usually varies from 2 to 5 per cent (GAUTHERET 1941, 1959 and BALL 1959). Many embryo cultures need very high sugar concentrations for their growth (*Capsella* up to 18 %, *Lathyrus* 8 %) (RAGHAVAN & TORREY 1963, PECKET & SELIM 1965 and RAGHAVAN 1966). The concentration of sucrose needed for root differentiation of young embryos is higher than that for shoots (YATES & CURTIS 1949 and HONMA 1955). A high sucrose concentration also promotes the secondary growth of some root cultures (TORREY & LOOMIS 1967).

Gibberellic acid is known to stimulate the flowering of plants and elongation of the internodes. It also promotes extension growth of lateral roots of excised tomato roots (BUTCHER & STREET 1960) but at a higher concentration (5 ppm) it has a slight inhibitory effect. At a concentration of 10 ppm gibberellic acid depresses the growth of most callus tissues (NICKELL & TULECKE 1959). On the other hand, there is some evidence that gibberellic acid stimulates the action of cambium and the formation of secondary xylem in some woody stems (BRADLEY & CRANE 1957 and WAREING 1958).

The anatomical structure of the genus *Bidens* is very poorly known and reports on the secondary growth of the stem of *B. tripartita* are contradictory (KOSTYTSCHEW 1924 and GRÁF 1938). A heterophyllous leaf sequence can be seen in *B. pilosa* (NEUBAUER 1959). In the present work the main anatomical features of different plant organs of two morphologically relatively dissimilar species *B.*(*Platycarpaea* DC.) *radiata* Thuill. and *B.*(*Psilocarpaea* DC.) *pilosa* L. have been studied. *B. radiata* is a hygrophilous Eurasian species but *B. pilosa* has a much wider distribution (South and North America, Asia, Africa, Australia, and recently spreading in Europe), with a concentration in America (SHERFF 1937, HEJNÝ 1960 and WAGENITZ 1966).

The aim of this study was

1) To grow these two species in greenhouses under unregulated and relatively natural conditions in order to compare their anatomical structure

2) To study the effect of very moist conditions on the anatomy of these plants under sterile conditions.

3) To study the effect of different sucrose concentrations on the anatomy with and without gibberellic acid.

The present comprehensive anatomical study is part of a larger project concerning the effect of gibberellic acid and various sucrose concentrations on the morphogenesis of several angiosperms under sterile conditions (WARIS, GRANÖ & SIMOLA in preparation).

II. Material and methods

Achenes of *Bidens radiata* Thuill.[1] and *B. pilosa* L.[2] were sterilized with H_2O_2 (10 per cent) for one hour, after which they were left in sterile distilled water for one or two days. After this the achenes were husked in a sterile cabinet in 1 per cent calcium hypochlorite solution.

One embryo was put in each culture flask (750 ml) via the S-shaped side tube. These culture vessels were filled with 250 ml of nutrient solution A, as described by WARIS (1967), containing sucrose (Merck p.a.) 1, 7, 10 and 15 per cent). In some experiments gibberellic acid (10 ppm) was added to this medium before autoclaving. The pH was determined with a Beckman pH-meter (Expandomatic). The initial pH varied from 5.8 to 6.1. The cultures were illuminated for 16 hours with sets of six 80 w Airam Flora-lux fluorescent tubes placed at a height of about 50 cm above the shelves with the flasks. Under these conditions the temperature reached extremes of 19° (night) and 25°C (day) but it mostly varied between 21° and 23°C. The growing time varied from 7 to 18 weeks, depending on the rate of development of the culture.

In order to compare the effect of these very moist conditions with more natural ones, some plants were grown in greenhouses in pots containing a mixture of peat moss and garden humus soil. The plants were illuminated with Philips HPLR lamps 400 w and the temperature varied from 15° to 35°C, depending on the amount of sunshine. Some cultures of *Bidens pilosa* were grown in pots but in the same conditions of temperature and illumination as the sterile cultures.

Growth under sterile conditions in a medium containing 1 per cent sucrose with or without gibberellic acid was studied in *B. pilosa*. This plant did not grow in the high sugar concentrations tested (10 and 15 per cent). Samples of *B. radiata* were studied from plants grown in 7 per cent sucrose with and without gibberellic acid and in 1 and 10 per cent sucrose without gibberellic acid because the growth of this species in the two latter sugar concentrations was very slight in the presence of gibberellic acid. The cultures studied were thus:

B. pilosa	*B. radiata*
1 % sucrose	1 % sucrose
1 % sucrose + gibberellic acid	7 % sucrose
	7 % sucrose + gibberellic acid
	10 % sucrose

Several sections (transverse and longitudinal) of fresh material were cut by hand with a razor blade in order to see the chloroplasts, which are usually destroyed during fixation and embedding. Some sections were stained with phloroglucinol-HCl (JENSEN 1962) or aniline sulphate in order to determine the degree of lignification. The phloem was easier to delimit when acid phosphatase activity was localized (cf. FREY 1954, and BRAUN & SAUTER 1964 a, b). Peroxidase activity was also tested in some root transections (cf. JENSEN 1962).

Acetocarmine-glycerol was used for epidermis preparations, and ruthenium red, Sudan Black and Sudan III for detection of some special structures and in order to give more contrasts for photographing. The preparations were usually mounted first in water, then in glycerol or glycerin jelly.

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[1] Achenes of *B. radiata* were collected in Hollola, Finland.

[2] Achenes of *B. pilosa* were obtained from Abidjan, the Ivory Coast.

III. Results

1. *Bidens pilosa* L.

Shoots

A non-flowering plant *B. pilosa* (length about 75 cm) had 13 internodes when grown under natural conditions under the same temperature and light conditions as the sterile cultures (cf. Fig. 3). Its structure is described here as that of the normal plant. Most internodes have a narrow cortex and a large pith (the parenchyma containing chloroplasts). Angular collenchyma is present, especially at the edges and outside the vascular bundles in the cortex. Chlorenchyma cell groups are also present in the cortex. The vascular bundles (about 23) form a cylinder. The large vessels of the metaxylem are usually in rows. The amount of phloem is very small; sclerenchyma fibre groups are associated with it. Interfascicular cambium (cf. Fig. 9) develops as early as the tenth internode[1] and some secondary xylem differentiates at the 6th internode. The middle internodes have a very similar structure to the upper ones, although the pith is larger and contains dead cells filled with air in the middle. They have a somewhat smaller quantity of vascular bundles.

Secondary growth is prominent in the two lowest short internodes. The pith is smaller but consists of bigger chloroplast-containing cells than in the upper internodes. The cambium effectively forms secondary xylem elements (about 35—40 cell layers) which all lignify and die. No real secondary interfascicular rays can be seen and no acid phosphatase activity could be established. Xylem elements with a large cell lumen differentiate radially between the metaxylem and -phloem (cf. Fig. 10). No real secondary phloem is formed but parenchyma. In transection the stem is nearly round.

The epidermis of the lower internodes contains anthocyanin. Small groups of anthocyanin-containing parenchyma cells are also seen in younger internodes in the middle of the collenchyma-containing edges. The epidermal cells are long and narrow. They contain chloroplasts. Stomata are arranged in vertical rows. Multicellular trichomes occur especially in the youngest internodes.

In transection, the petioles are half-moon-shaped. The edges, however, are prolonged and orientated upwards and contain chlorenchyma, collenchyma and one small vascular bundle (cf. Fig. 11). About 14 vascular bundles are arranged in a half circle. Three of them have a large xylem and are much bigger than the other eleven. Most of the tissue is chlorenchyma and chloroplasts are more abundant in the outer parts.

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[1] The internodes are counted upward from the transition region of the root and stem, as always in this paper.

The epidermal cells of the lower surface of the leaves have undulant cell walls but the walls are straight near the veins. The stomata are anomocytic and very frequent. The cells of the upper epidermis have somewhat less undulant lateral cell walls. Stomata are rare but trichomes consisting of 3—4 cells in a row are found.

The seedlings of *B. pilosa* grown in sterile cultures with 1 % sucrose and gibberellic acid had several long thin aerial branches and effective formation of thin adventitious roots (Fig. 2). The plants grown without gibberellic acid had only some rather short aerial shoots (Fig. 1) and these had fewer and shorter internodes than in the seedlings cultivated with gibberellic acid. In both experiments the leaves were thin and rather simple, but they had a long petiole.

The fifth internode of a plant grown with gibberellic acid had a cylinder of 12 small collateral vascular bundles, and a sclerenchyma fibre bundle was associated with each of them. The transection was roughly tetrangular. The pith was rather large and the cortex narrow. Cambium formed some secondary xylem. The activity of the cambium and the formation of secondary xylem was more prominent in the lower internodes (cf. Figs. 13—15). The differentiation of the xylem elements with big diameter of the cell lumen in transection was common between the metaxylem and phloem. No real secondary phloem or interfascicular rays were formed. Collenchyma was found as small groups under the epidermis. The bulk of the cortex consisted of chlorenchyma.

The stem of a plant cultivated without gibberellic acid did not have secondary xylem formation, but the cambium formed external and internal chlorenchyma. The cells of the primary cortex and pith also contained abundant chloroplasts (cf. Fig. 16). Some giant cells were found in the epidermis and these cells had high peroxidase activity. The cortex was rather large and sometimes clear aerenchyma was seen. The upper internodes had a cylinder of 12 small collateral vascular bundles and small groups of sclerenchyma fibres were associated with them.

Roots

The roots of *Bidens pilosa* grown in humus soil in greenhouses (cf. Figs. 17—20) or under artificial light only had a structure which is very rare in dicotyledons. The main root near the transition region as well as its thicker lateral roots and adventitious roots growing out from the cut stems had a large pith and a polyarch stele (up to about 24 protoxylem bundles, usually octarch) (cf. Figs. 18—19). These two features are typical of several monocotyledons (Esau 1965). The youngest parts of the long lateral or main roots of *B. pilosa* were usually hexarch or tetrarch and did not have any pith (cf. Fig. 20). This must have been due to some changes in the differentiation region during the development of the plant.

The cortex and pith of *B. pilosa* roots consisted of ground parenchyma, and the secondary phloem had developed well. The secondary xylem of the main root contained elements having a large cell lumen. The elements of secondary xylem in a root with a pith usually have relatively thick cell walls and only a small cell lumen (cf. Fig. 18).

Effective branching of roots and their brownish red colour are characteristic features seen by eye in *Bidens pilosa* grown in 1 per cent sucrose with or without gibberellic acid (cf. Figs. 1 and 2). The epidermal cells and some parenchyma cells of the cortex have enlarged abnormally and root hairs are not very frequent. These epidermal cells have a relatively high peroxidase activity and a lignified cell wall could also be demonstrated with phloroglucinol and aniline sulphate reagent. The root cortex was large and the relatively large roundish parenchyma cells contained some chloroplasts.

Intercellular spaces were frequent but not very wide. The vascular cylinder was small in most roots grown under sterile conditions and only weak secondary thickening could be detected if the roots developed without gibberellic acid. The young stele was diarch or only monarch but the cortex was wide and consisted of tumorous cells. If the roots had developed in a medium containing gibberellic acid the secondary growth was very prominent in most roots even in the young parts (1 cm from the tip). The secondary phloem contained chloroplasts as well as a root cortex.

2. *B. radiata* Thuill.

Shoots

The shoot of *B. radiata* grew about 35 cm long in the greenhouses. It had several flowering branches and 7 internodes. The anatomy of the stem depended on the internode studied and also, naturally, on the age of the plant. In a fullgrown plant the lower internodes were almost cylindrical but the upper ones were somewhat furrowed. The stem cortex mainly consisted of aerenchyma containing chloroplasts. The cell rows anastomosed in the upper internodes and formed a thin network around the vascular cylinder. In a thicker stem the cells and intercellular spaces expanded tangentially. Under the epidermis a homogeneous layer of chlorenchyma one cell deep was always found. Angular collenchyma was found only as discontinuous patterns (one cell layer usually) in very young thin internodes without any functional interfascicular cambium.

The number of vascular bundles increased in the stem from the base to the top. The four upper internodes of the seven in the plant studied had from 20 to 22 collateral vascular bundles. The oldest internodes had from 12 to 13

triangular vascular bundles, and in a younger plant one could see that 4 or 5 of them were clearly larger than the others. Each vascular bundle had a relatively large sclerenchyma fibre bundle outside the phloem. Chloroplasts occurred in both phloem and xylem parenchyma as well as in the pith of young internodes (Fig. 23).

Intervascicular cambium was formed in the 6th internode counted from the top. No real phloem was formed to the outside and all cells cut off towards the inside lignified and died (Fig. 21). The two lowest internodes mostly consisted of secondary xylem (Fig. 22). The pith was rather small in them and in the middle contained numerous dead cells filled with air. The diameter of the third internode was clearly greater than that of the lower ones, due to the expansion of the pith. The intercellular spaces in the pith are very small schizogenous ones. The cells have pectin substances in their walls like the cells of the proto- and metaphloem and the chlorenchyma of the cortex.

The epidermal cells contained chloroplasts. The cell walls were straight and the whole structure of the epidermis very much resembles that of *B. pilosa*. Only the epidermal cells of the lowest internodes contained anthocyanin. The inner cell wall of the epidermis had collenchymatous thickenings. Trichomes were present especially on the epidermis of young parts of the stem. They had four paired cells at the base and usually terminated in a row of 10 cells.

The petiole was half-moon-shaped in transection, with prolonged edges which contain homogeneous mesophyll. The ground tissue of the petiole also contained abundant chloroplasts. Aerenchyma with short vertical cell rows were found always on the upper side and sometimes even on the lower side of the petiole. Five collateral vascular bundles were detected and the three in the middle were larger than the two other. Trichomes formed of 5—9 cells in a row occurred on the upper epidermis.

Stomata were moderately frequent on the upper surface of the leaves. The epidermal cells had normally undulant cell walls but near the veins these were straight. On the lower surface the cells had even more undulant walls and stomata were very abundant. The epidermis of the stem had long narrow cells with straight cell walls. Stomata were found in some vertical cell rows consisting of shorter cells. The epidermal cells contained chloroplasts.

The plant grown in 10 % sucrose without gibberellic acid had a branched flowering shoot and strongly developed roots (cf. Fig. 7). The two distalmost internodes had a cylinder of 28 relatively small collateral vascular bundles. Rather large groups of sclerenchyma fibres were associated with most of them (cf. Fig. 27). The pith was relatively large and mostly consisted of rather big roundish parenchyma cells. Cambium had already developed in the middle internodes of the stem but some secondary xylem and phloem were

found in the second internode (cf. Fig. 28) and several transectioned adventitious roots could be seen in the large intercellular spaces of the cortex. They were from hexarch to octarch and their pith also lignified and well developed root hairs could be seen. The aerenchyma of the stem cortex contained numerours chloroplasts. The cells were relatively small and arranged in rows. Some homogeneous layers of chlorenchyma were seen under the epidermis.

The *Bidens radiata* seedlings grown in 7 % sucrose without gibberellic acid had only one short (4—5 cm) shoot, which did not form branches (Fig. 6). The leaves were small and simple. The upper part of the stem was deeply furrowed, the lower one being cylindrical. The whole stem had a clear pith with roundish parenchyma cells containing some chloroplasts. The intercellular spaces were schizogenous and small. The vascular bundles were very small (15) and no sclerenchyma fibre bundles were connected with them. The cambium had already developed in the upper part but its action was only slight even in the lower part of the stem and the cells (4—5 layers) formed did not lignify. The cortex was the main part of the stem. It consisted of slightly radial aerenchyma with chloroplasts. In the older stem this tissue was more compact around the vascular cylinder. In the young stem the epidermis contained chloroplasts but in the older ones it was brown and the cambium formed under it gave rise to new brownish cells.

In *Bidens radiata* grown in 7 % sucrose with gibberellic acid most of the shoots were short (about from 5 to 7 cm long) and they had several very short branches bearing small simple leaves without petioles. (Fig. 5) Some of the growing points formed aerial long shoots which had an anatomical structure different from that of the shorter shoots. In the short stems prominent secondary xylem formation could be seen. The pith was relatively small and in the lower part of the stem it was lignified (Fig. 26). No interfascicular areas could be found. The cortex consisted of very loose aerenchyma and the stem was deeply furrowed. In the upper part of the stem as well as in the short branches a cylinder of 7—8 small collateral vascular bundles could be seen. They also had small sclerenchyma groups outside the phloem.

The long flowering aerial shoot had a very large pith. The 11 triangular vascular bundles were connected by secondary xylem (about 3—10 layers). The cortex contained aerenchyma. Clear small sclerenchyma bundles could be seen outside the protophloem (Fig. 25).

B. radiata cultivated in 1 % sucrose without gibberellic acid (Fig. 4) had several long shoots with long internodes. The plant did not flower but the stem had a rather similar structure to the long flowering aerial shoots grown in 7 % sucrose with gibberellic acid. Slight secondary xylem formation was seen in the lower part of the stem.

Roots

Roots of *Bidens radiata* grown in humus soil in the greenhouse also had a clear aerenchymatic cortex with rather large intercellular spaces. The cortex was, however, narrow and the vascular cylinder relatively large (Fig. 24). Secondary thickening could be seen even in relatively thin young roots, which were usually hexarch. In older roots the amount of secondary xylem with large vessels was considerable. A narrow phloem cylinder was formed. Only some vestiges of cortex could be seen.

The root anatomy of *B. radiata* was not very much affected by the sugar content in the nutrient medium. In thin young roots the root hairs were relatively long. The epidermis was red, even over the mitotic part of the root tip (10 % sucrose without gibberellic acid). The cortex had a radial structure and the parenchyma cells did not contain chloroplasts in the youngest parts. Between about 18 radial cell rows relatively large intercellular spaces could be seen (Figs. 31 and 32).

The vascular cylinder is tetrarch. Metaxylem began to form at a distance of about 12 cm from the transition region of root and stem in roots (about 20 cm long) grown in 10 % sucrose without gibberellic acid. In somewhat older parts of the same root the xylem plate was clear and the parenchyma cells of the cortex had lengthened (Figs. 31—32) and contained chloroplasts (8 cm from the transition region). The epidermal cells were abnormally large. In an older part of the root (6 and 4 cm from the transition region) these cells were also prominent and in transverse section the outline of the root was wavy. The parenchyma cells of the cortex had divided and lengthened. Each ray usually had two cells at the outer end of the row. The greater part of the cortex consisted of intercellular spaces (cf. Fig. 29). Around the vascular cylinder the aerenchyma formed a rather compact network containing considerable numbers of chloroplasts (cf. Fig. 30). Owing to the very meagre secondary thickening the vascular cylinder was relatively small. Under the epidermis two layers of chlorenchyma cells could be seen. It was apparent that the pericycle formed chlorenchyma around the vascular cylinder both in the transition region of root and stem and in the older part of the root (cf. Fig. 30). In transverse section made at a distance of 1.5 cm from the transition region lateral roots could be seen sectioned in the root cortex. These were either tri- or tetrarch even within the same section. The adventitious roots growing out from the lower part of the stem were usually tetrarch, but tri- and pentarch roots could also be seen. Roots 4 cm long had already begun secondary thickening at a distance of about 2 cm from the tips.

Roots grown in 7 % sucrose with or without gibberellic acid did not form secondary xylem. The stele was mostly tetrarch, sometimes tri- or hexarch. In roots cultured without gibberellic acid some tumorous formations were

detected, especially in the older parts of the root. These consisted of large brownish parenchymatous cells of the root cortex. They did not have any special organization or structure, but had a lignified cell wall. Otherwise the anatomical structure was fairly normal and strongly resembled that of the young roots grown in 10 % sucrose (Fig. 31). In both experiments the main part of the root cortex consisted of chloroplast-containing aerenchyma, but the cortex was much larger in roots grown without gibberellic acid. The radial cell rows contained about 15 cells instead of 1—3 and the intercellular spaces were very large.

In *B. radiata* grown in 1 % sucrose without gibberellic acid fewer lateral roots were formed than in 10 % sucrose (cf. Figs. 4 and 7). The roots were greenish white in color except for the red root tips. The root was tetrarch and had a very similar structure to that grown without gibberellic acid in 10 % sucrose but the cortex was thinner and not so many tumorous cells could be seen in the epidermis.

IV. Discussion

It proved possible to cultivate *B. pilosa* and *B. radiata* seedlings in sterile conditions, although not all experiments were successful. Therefore it is only in a few sucrose concentrations (*B. pilosa* 1 %, *B. radiata* 7 %) that it has been possible to compare the effect with and without gibberellic acid (10 ppm). It is apparent that *Bidens* species are more tolerant of the inhibitory effect of relatively high concentrations of gibberellic acid than most other plants. Even at a concentration of 5 ppm gibberellic acid has a slight inhibitory effect on the growth of excised tomato roots, and at a concentration of 10 ppm it inhibits the growth of most tissue cultures (NICKELL & TULECKE 1959, BUTCHER & STREET 1960). Root development was very good in *B. pilosa* grown in 1% sucrose with gibberellic acid (cf. Fig. 2). *B. radiata* was more tolerant of high sugar concentrations and it even flowered in these conditions.

The different sugar concentrations did not have clear effects on the development of roots, which may be due to the fact that the sugar concentration slowly decreased in the medium. In *B. radiata* the high sugar concentration (without gibberellic acid) stimulated root growth and branching (cf. Figs. 6 and 7).

The leaves of the cultures in sterile conditions were thin and the petiole of *B. pilosa* was long (cf. Figs. 1 and 2). In *B. radiata* small leaves without any petiole were seen in some experiments. Branching of the shoot was stimulated by gibberellic acid (cf. Figs. 2 and 5) in both species.

The following features are common to *B. radiata* and *B. pilosa* cultivated in natural conditions. The stem has a large parenchymatous pith usually contain-

ing chloroplasts and a rather narrow cortex and one cylinder of collateral vascular bundles. The number of vascular bundles is highest in the middle of the stem. No interfascicular rays develop in the secondary xylem and no real secondary phloem, but parenchyma is formed outside the cambium in the stem. Vessels differentiate in the fascicular area more rapidly than in the interfascicular area. KOSTYTSCHEW (1924) contended that in the stem the vascular cambium does not form conducting xylem elements in *B. tripartita* and in most other vascular plants, but only parenchyma. GRÁF (1938), however, established the formation of interfascicular cambium and differentiation of vessels in the secondary xylem in this plant. My results bear out the latter's results.

There are several differences between the two species. *B. radiata* has aerenchyma in the cortex of the stem and only some small groups of collenchyma. The stem of *B. pilosa* contains collenchyma especially in the edges and outside the small sclerenchyma bundles associated with the vascular bundles. The sclerenchyma groups associated with the vascular bundles are bigger in *B. radiata* than in *B. pilosa*.

The roots have a rather dissimilar structure. The root of *B. radiata* is usually tetrarch or hexarch. Its cortex, like the stem, contains aerenchyma. This is in good correlation with its habitats in nature, which are frequently moist (HEJNÝ 1960). The short roots of *B. pilosa* usually have octarch steles, but the young parts of the long roots have triarch, tetrarch or hexarch steles and no pith. Near the transition region of root and stem the number of protoxylem bundles is difficult to count (cf. Fig. 18). These dissimilarities within a plant may be due to some changes in the differentiation region during development. It has been proved that the concentration of IAA influences the number of xylem bundles formed in the *Pisum* root (TORREY 1957). Both pith and a polyarch stele are very rarely found in roots of dicotyledons, but they are common in several monocotyledons. A pith has also been found in some succulent *Senecio* species (HARE 1941—1942). Two different anatomical types of roots have also been found in *Hordeum* (JACKSON 1922). It has been established that in several plants the number of xylem bundles in the root varies and is usually dependent on the size of the root (WARDLAW 1928, and TORREY 1955). So a thin root has fewer xylem bundles than a thick one. This fact must be taken into consideration when the anatomical characteristics of roots are used in systematics.

The epidermises of stem and leaves were very similar in the two species studied, but the trichomes of the upper epidermis of *B. pilosa* were shorter. Several vascular bundles were present in the petiole in both species.

The formation of aerenchyma is very prominent in *B. radiata* in moist conditions. High sugar concentrations, especially, tended to increase the growth of the cortex. In the stem of *B. pilosa* well developed aerenchyma was found only

in plants which had been cultivated with 1 % sucrose without gibberellic acid.

The secondary growth of both roots and stems, as well as the lignification of the secondary xylem, were stimulated by gibberellic acid in all experiments. These processes were very weak in plants growing without extra gibberellic acid. In the flowering shoots, however, some secondary xylem formation was seen, which may have been due to gibberellic acid formation in the flowering plant. Sometimes in experiments with gibberellic acid on *B. radiata* the secondary xylem was formed of relatively thin-walled, lignified, dead parenchyma (cf. Fig. 26). Usually vessels developed more rapidly in the fascicular cambium than in the interfascicular cambium (cf. Figs. 14 and 25). It has been demonstrated that gibberellic acid stimulates the formation of secondary xylem in several woody plants (BRADLEY & CRANE 1957 and WAREING 1958). The cambium derivatives so formed are small and unlignified but a mixture of β-indolylacetic acid and gibberellic acid causes a wide zone of new wood consisting of fully lignified vessels (WAREING 1958). It is known that the differentiation of xylem elements requires a balance not only between the plant hormones concerned but also between these and sucrose (JEFFS & NORTHCOTE 1966). It is apparent, however, that the type of reaction is highly dependent on the species.

In roots of *B. pilosa* grown with gibberellic acid and in the stem of *B. radiata* grown without gibberellic acid (7 % sucrose) chlorenchyma was formed instead of secondary phloem. The vascular cylinder of the root was usually rather small and xylem elements with wide cell lumina did not differentiate. No pith was formed in the roots of *B. pilosa* and the roots were mono-, di-, tri- or mostly tetrarch. Gibberellic acid stimulated adventitious root formation in *B. pilosa*.

The roots of *B. pilosa* (1 %) and *B. radiata* (7 % sucrose) cultivated in sterile conditions contained tumorous cell groups formed from the cortex (cf. TRYON 1955). These cells are very large and brownish and have a lignified cell wall. They also exhibit a high peroxidase activity. This result is consistent with the histochemical observations of the lignification and peroxidase activity of the xylem in *Allium* but that was stimulated with IAA (DE JONG 1967).

Secondary growth was found only in roots cultured in the presence of gibberellic acid or in a very high sucrose concentration (*B. radiata* 10 %) but the latter plant even flowered and was possibly able to synthesize adequate amounts of the growth substances needed for the secondary growth of roots and stems. It seems obvious that the formation or transport of some growth substances is not effective enough in the shoots. It is known that secondary thickening is not normally found in excised roots but the formation and function of cambium can be stimulated by β-indolylacetic acid, cytokinetin and certain other substances (DORMER & SREET 1948, TORREY 1951, 1957, 1963, FRIES 1954, LOOMIS & TORREY 1964 and TORREY & LOOMIS 1967).

The flowering shoot of *B. radiata* grown with 7 % sucrose with gibberellic acid had an anatomical structure quite different from the nonflowering branches. The cortex was narrower, the pith was larger and did not lignify, and secondary xylem was formed but not so effectively as in the shoots which did not flower.

The present studies show that several parts of a plant organ must be investigated in order to obtain a true picture of the anatomical structure of a plant and to make comparisons between different species. Sterile cultures give valuable evidence of the plasticity of the plant's anatomy and of the factors that influence this. Both *B. radiata* and *B. pilosa* preserve several characteristic features under these moist conditions but on the average their structure was simpler in sterile cultures than under natural conditions. Such a tendency is found in several amphibious species.

Summary

The anatomy, especially of roots and stems, has been studied in *Bidens radiata* and *B. pilosa* grown in sterile cultures with sucrose as carbohydrate source and in plants grown in pots containing humus soil in the greenhouse. The effect of gibberellic acid (10 ppm) was also tested. *B. radiata* was more tolerant of high sucrose concentrations (7 and 10 %) and of the presence of gibberellic acid than *B. pilosa* and it even flowered under these conditions.

The cortex in both stem and root of *B. radiata* contains aerenchyma and the amount of this tissue is greatly increased in the moist conditions of sterile cultures, especially in the presence of high sugar concentrations. The pith of the stem is large and the cortex narrow in *B. radiata* and *B. pilosa* grown in normal conditions. One circle of collateral vascular bundles occurs in the stem and their amount is highest in the middle of the shoot. In *B. radiata* chloroplasts are found in the parenchyma of the primary phloem and xylem of the stem. No real interfascicular rays or xylem parenchyma could be seen in the secondary xylem of older stems in the two species studied. The cells in the interfascicular area, however, have different structure from other parts of the secondary xylem.

Gibberellic acid stimulated the secondary growth of the stems in both *B. pilosa* and *B. radiata* in sterile cultures. The pith remained small and sometimes even lignified in the lower part of the *B. radiata* stem grown in 7 % sucrose. Its long aerial flowering shoot had a dissimilar anatomical structure (large pith, slight secondary growth). Large amounts of collenchyma were not formed in the stem cortex in moist conditions, as they are, in natural conditions in the stem of *B. pilosa*.

The number of xylem bundles in the roots varies within a species. Tetrarch roots are most common under sterile conditions. The oldest part of the main root as well as of the lateral and adventitious roots of *B. pilosa* have a clear pith and the root seems to be polyarch. The younger parts, however, do not have any pith and it is never found in sterile cultures. Large tumorous cells sometimes grow out from the root cortex and have a lignified cell wall and a high peroxidase activity.

Several vascular bundles occur in the petioles. The leaves are amphistomatic and the stomata anomocytic. The epidermal cells of the leaves have undulant cell walls but those of the stems are straight under normal conditions.

These experiments demonstrate that the anatomy of a plant can be modified by the growing conditions but the reaction type is dependent on the natural structure of the plant and in moist experimental conditions the structures formed are somewhat simpler than in nature.

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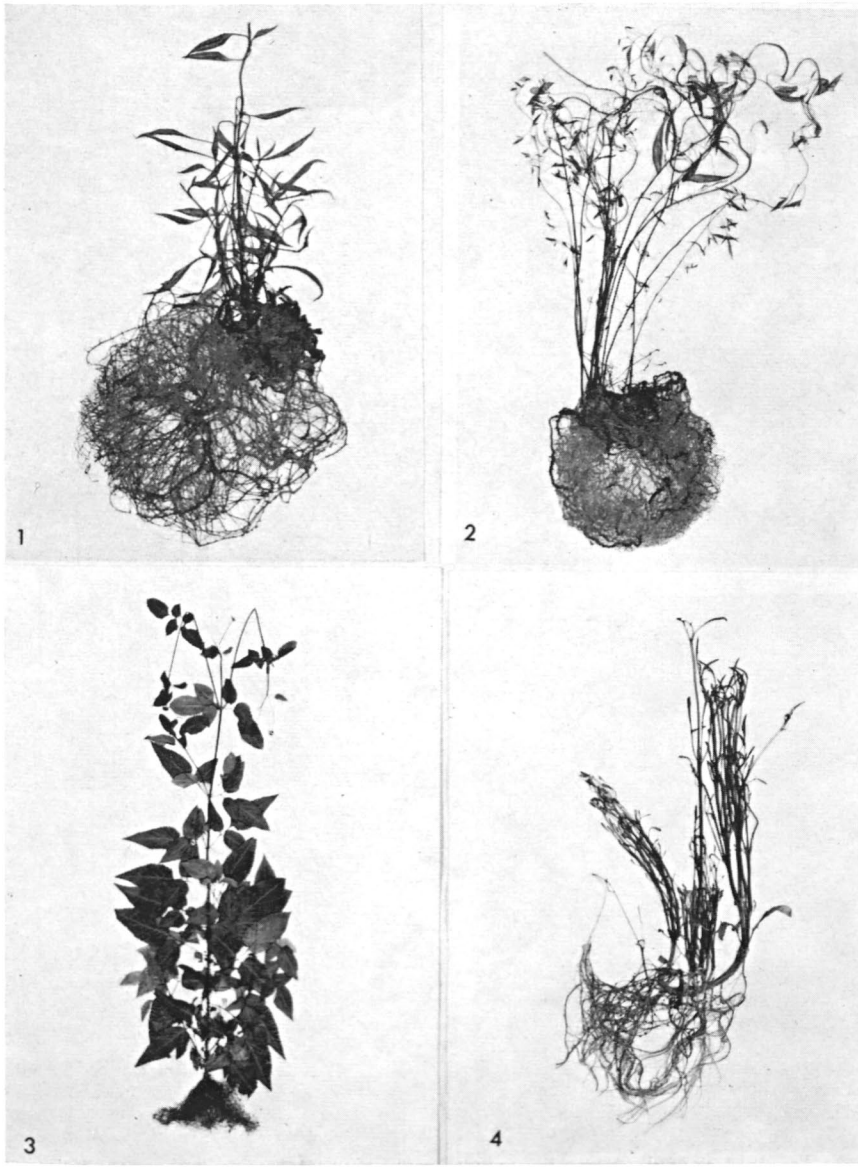


FIG. 1. *B. pilosa* grown under sterile conditions for 16 weeks with 1 % sucrose as carbohydrate source. 1:3.

FIG. 2. *B. pilosa* grown under sterile conditions for 18 weeks with 1 % sucrose and 10 ppm of gibberellic acid. 1:4.

FIG. 3. *B. pilosa* grown in the soil under artificial light at the same temperature as the sterile cultures. 6:100.

FIG. 4. *B. radiata* grown under sterile conditions for 9 weeks with 1 % sucrose. 2:9.

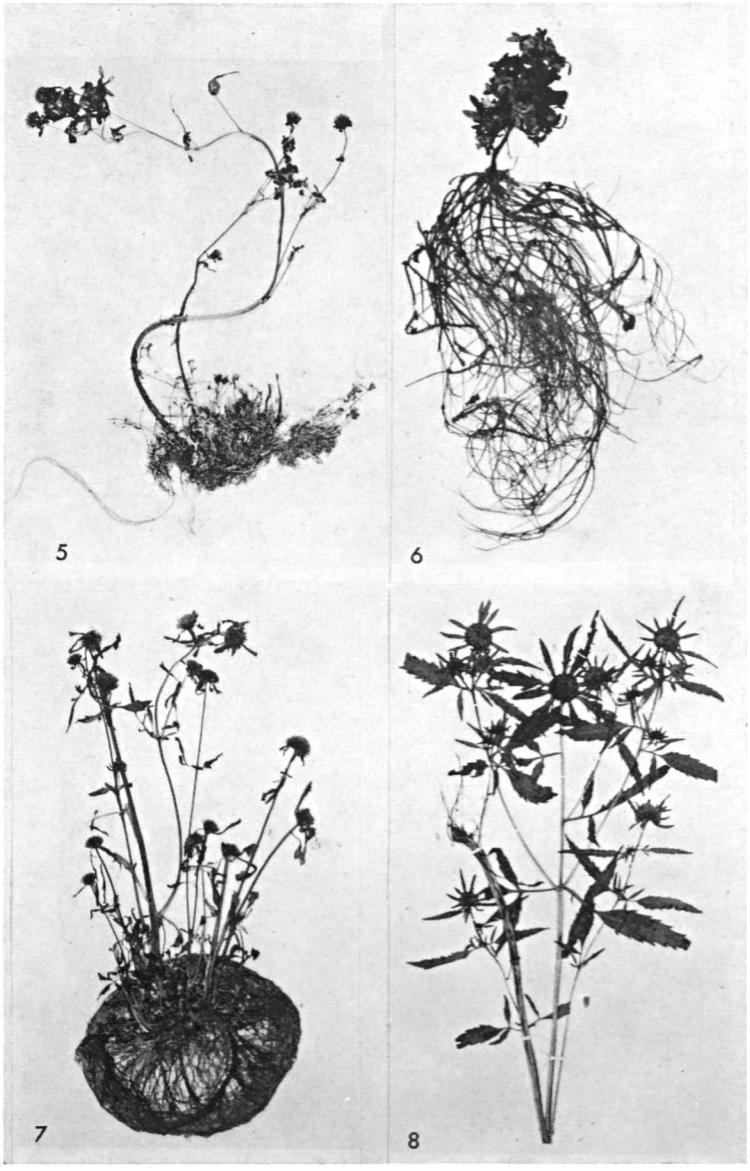


FIG. 5. *B. radiata* grown with 7 % sucrose with gibberellic acid 10 ppm for 16 weeks. Two long and several short flowering shoots. 1:4.

FIG. 6. *B. radiata* grown for 15 weeks with 7 % sucrose. One short shoot. Tumorous formationsts. on roo 2:3.

FIG. 7. *B. radiata* grown for 7 weeks with 10 % sucrose. Several aerial flowering shoots. 1:4.

FIG. 8. A herbarium specimen of *B. radiata* grown in nature, Hämeenlinna, Finland. 1:6.

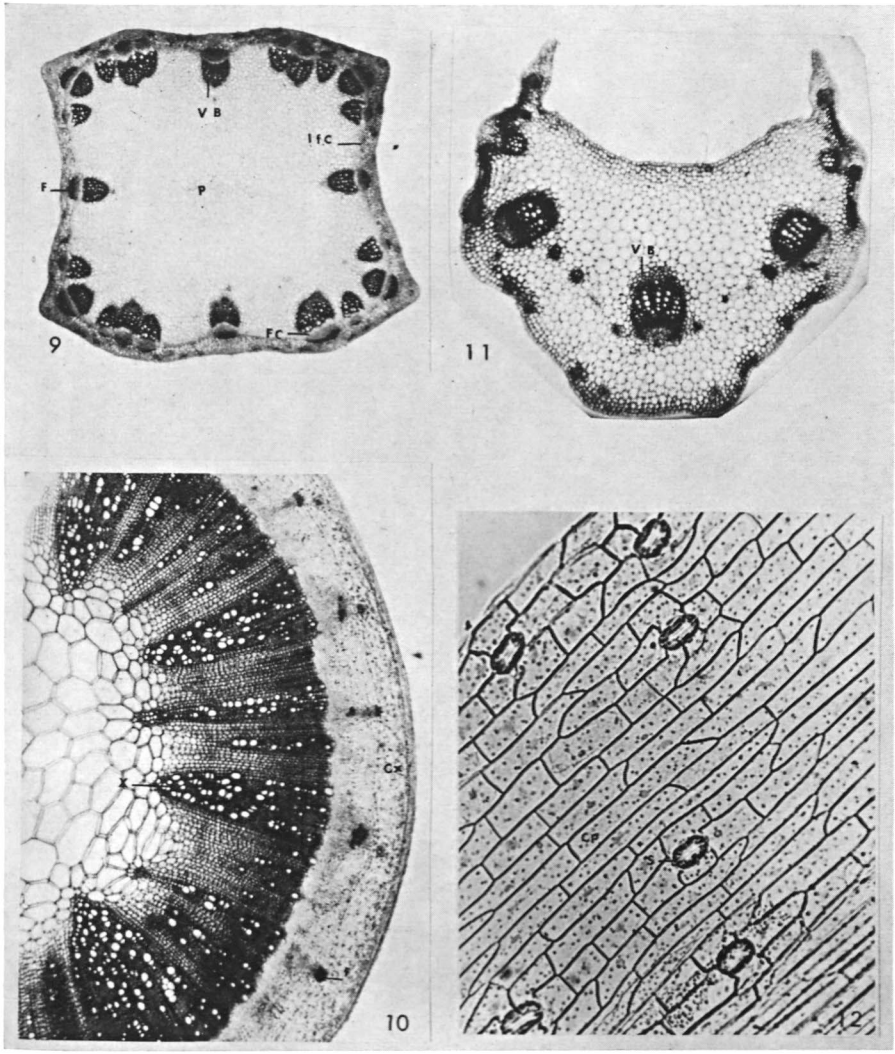
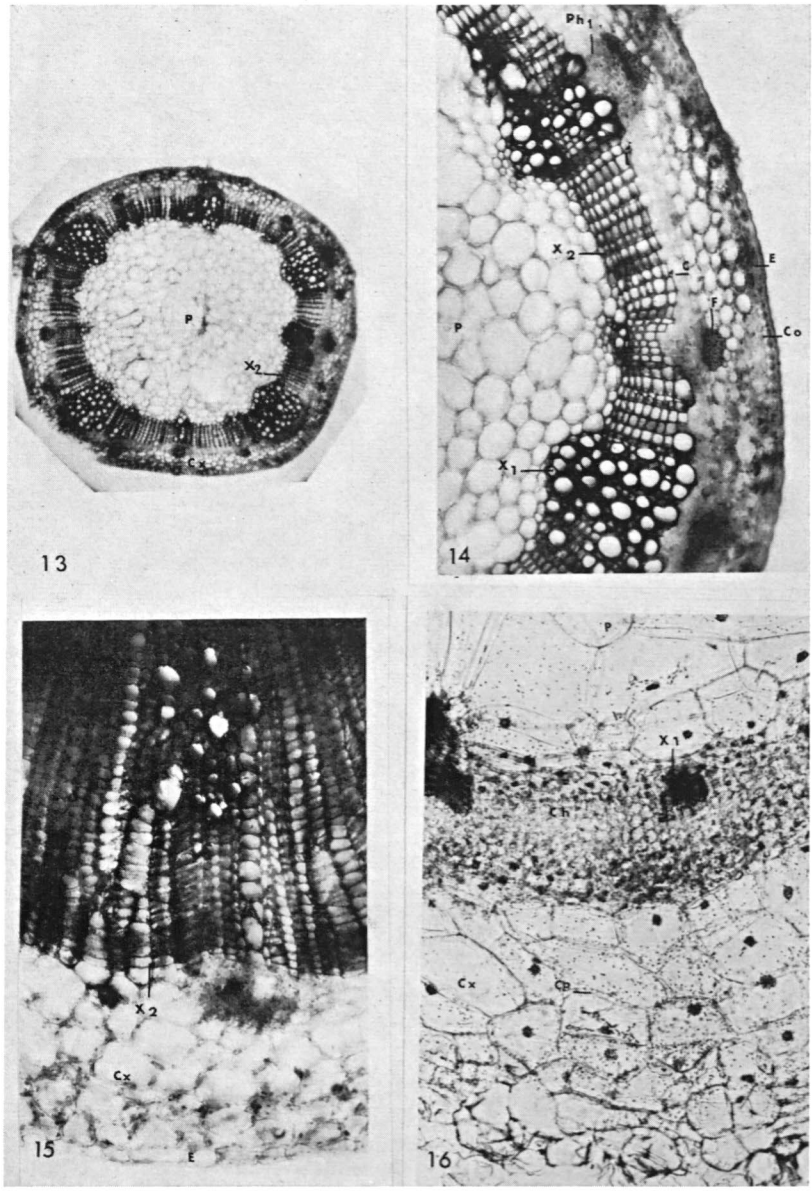


FIG. 9. Transection of the 10th internode (counted upwards from the transition region) of flowering *B. pilosa* grown under natural conditions. Large pith (P), circle of collateral vascular bundles (VB), interfascicular cambium (IfC), collenchyma in edges and outside the vascular bundles in the cortex, sclerenchyma fibre bundles associated with vascular bundles (F), fascicular cambium (FC). Stained with phloroglucinol-HCl. 13x.

FIG. 10. Transection of the first internode of the stem of flowering *B. pilosa*. The cells of the pith have enlarged. Secondary xylem formation strong. Differentiation of large conducting cells in xylem (X) is more prominent in the regions outside the protoxylems bundles. No interfascicular regions. The cortex (Cx) contains chlorenchyma and fibre bundles (F). 23x.

FIG. 11. Transection of *B. pilosa* petiole under natural conditions. Large and small vascular bundles (VB). 20x

FIG. 12. Epidermal cells of the stem of *B. pilosa* under natural conditions. Stomata (S) and chloroplasts (Cp). 120x.



FIGS. 13—15. Transections of the stem of *B. pilosa* (plant in Fig. 2) grown under sterile conditions.

FIG. 13. 3th internode; large pith (P), secondary xylem (X_2), narrow cortex (Cx). 20x.

FIG. 14. The same section at greater magnification. Proto- and metaxylem (X_1), secondary xylem (X_2), cambium (C), protophloem (Ph_1) and fibre bundles (F), no clear secondary phloem cylinder, chlorenchyma, collenchyma (Co), epidermis (E, inner cell wall sometimes has collenchymatous thickenings). 80x.

FIG. 15. First internode numerous layers of secondary xylem (X_2), no interfascicular rays and secondary phloem, cortex (Cx, chlorenchyma), epidermis (E). 120x.

FIG. 16. Transection of the stem of *B. pilosa* grown with 1 % sucrose without gibberellic acid. Pith (P) and cortex (Cx), parenchyma containing chloroplasts (Cp) especially around the nucleus. Proto- and metaxylem (X_1), chlorenchyma (Ch, small cells) formed by the cambium. 67x.

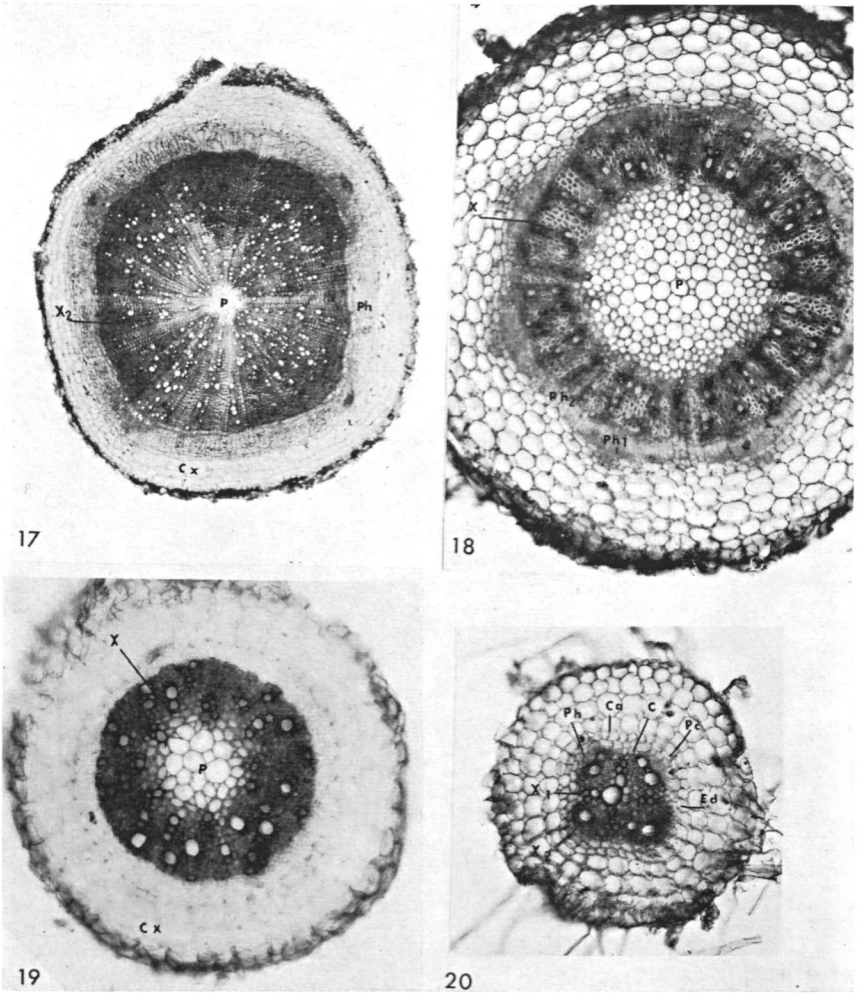


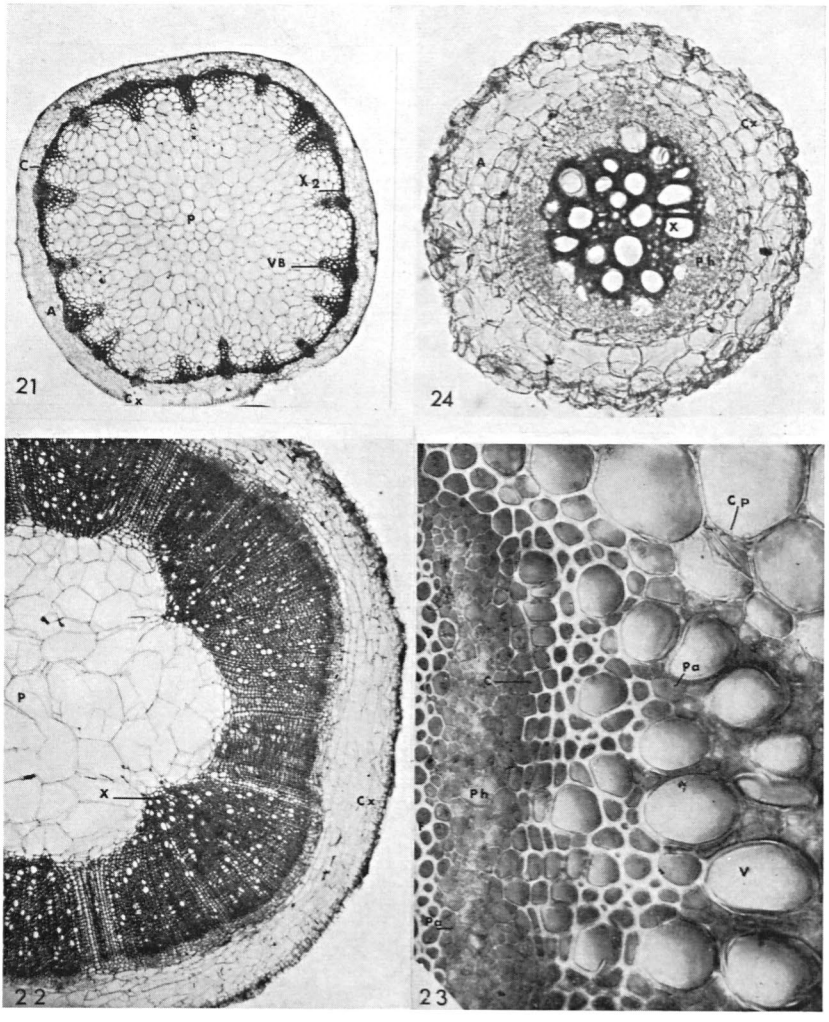
FIG. 17. Transection of the main root (0.5 cm from the transition region) of *B. pilosa* grown under natural conditions. Pith (P), secondary xylem (X_2) elements with wide cell lumen), phloem (Ph), cortex (Cx). 17x.

FIG. 18—20. Lateral root (25 cm long) of *B. pilosa* grown out from the part of the main root which has no pith.

FIG. 18. The basal part of the lateral root, clear large pith (P), xylem (X) with numerous rays of strongly lignified cells, the xylem elements usually with a relatively narrow cell lumen, secondary phloem (Ph_2) primary phloem (Ph_1) in eight bundles. 67x.

FIG. 19. About 15 cm from the tip. Pith (P), xylem (elements with large cell lumen), cortex (Cx). Stained with phloroglucinol-HCl and ruthenium red. Pectic substances in the epidermal cell walls. 67x.

FIG. 20. 10 cm from the tip of a tetrarch root with secondary growth. Phloem scanty (Ph), cambium (C), pericycle (Pc), endoderm (Ed), Casparian spot (Ca), parenchyma cells of the cortex, small schizogenous intercellular spaces, primary (X_1) and secondary xylem (X_2). 67x.



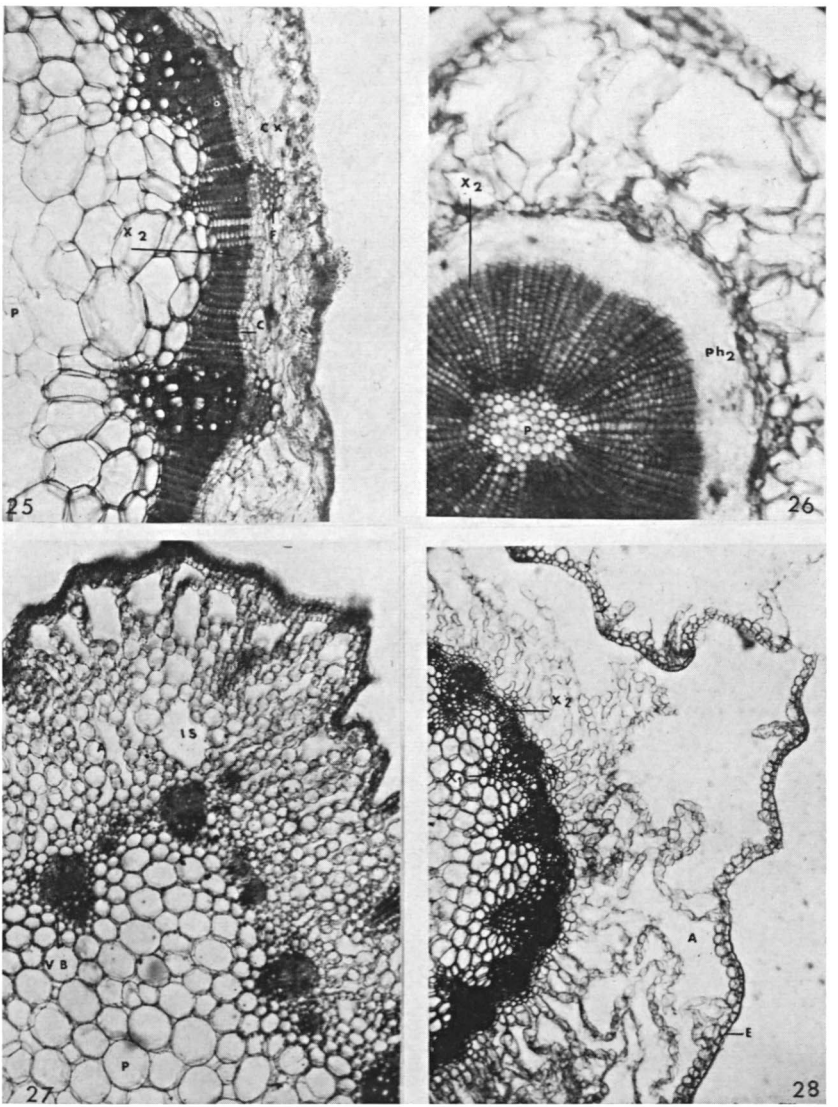
FIGS. 21—23. Transections of stems of *B. radiata* grown under natural conditions.

FIG. 21. Fourth internode. Large pith (P), circle of collateral vascular bundles (VB), cambium (C) forming secondary xylem (X_2) but not phloem. Cortex (Cx) consisting of aerenchymatic (A) chlorenchyma. 10x.

FIG. 22. First internode. Pith with large cells (P), xylem (X), no real interfascicular rays, cortex (Cx). 23x.

FIG. 23. Part of a vascular bundle of the fourth internode. Large vessels (V) of the metaxylem, xylem parenchyma and phloem parenchyma (Pa) with chloroplasts (Cp), cambium (C), phloem (Ph), fibres (F). 270x.

FIG. 24. Transection of the root of *B. radiata* grown under natural conditions. Xylem (X) with elements having a large cell lumen, phloem (Ph), cortex (Cx), aerenchyma (A) with relatively large intercellular spaces. 60x.



FIGS. 25—26. Transections of stems of *B. radiata* grown under sterile conditions with 7 % sucrose and gibberellic acid.

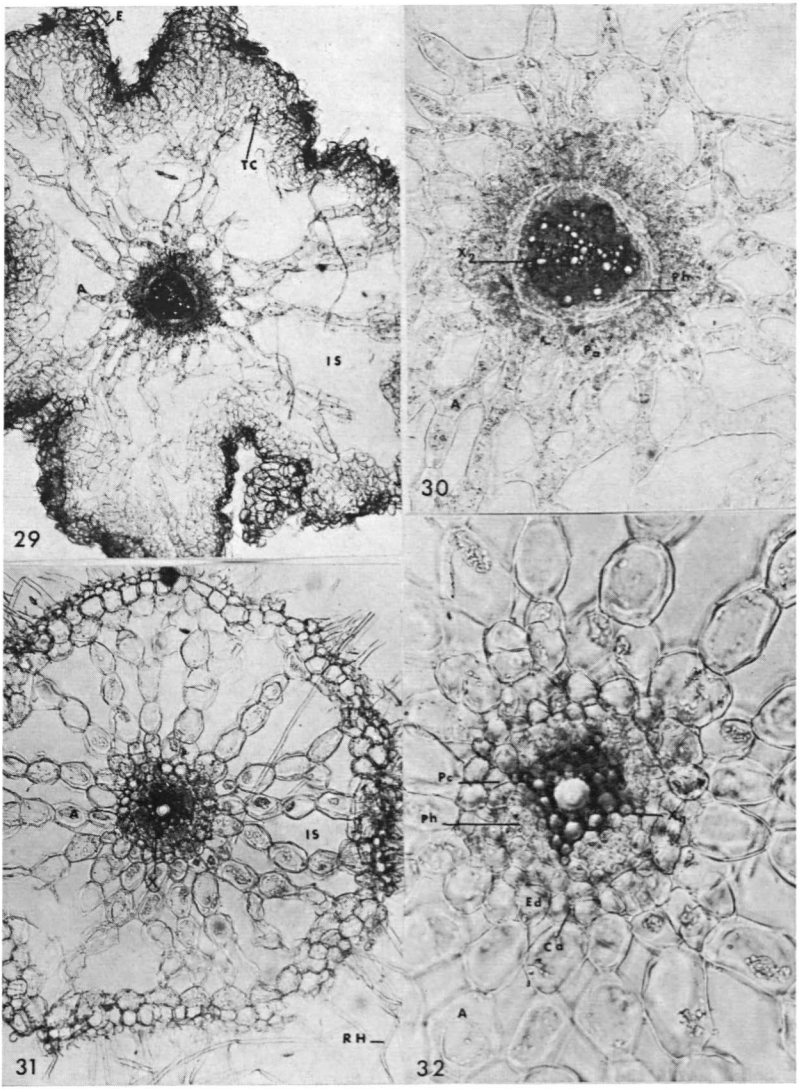
FIG. 25. The lower part of the long aerial stem in Fig. 5. Large pith (P), narrow cortex (Cx), cambium (C), secondary xylem (X_2) containing cells with large lumina only in the region of the vascular bundles, fibre bundles (F). 60x.

FIG. 26. Anatomical structure of the lower part of the stem of the plant in Fig. 5. Secondary growth prominent, also the pith has lignified. No xylem (X_2) elements with a large cell lumen. Secondary phloem (Ph_2), relatively much loose aerenchyma with large intercellular spaces, no interfascicular rays. 60x.

FIGS. 27—28. Transection of stem of *B. radiata* grown with 10 % sucrose without gibberellic acid.

FIG. 27. Fourth internode (cf. Fig. 7). Pith (P) with small schizogenous intercellular spaces vascular bundles (VB) of different sizes, aerenchyma containing chloroplasts, intercellular spaces (IS), epidermis. 13x.

FIG. 28. Second internode. Proto- and metaxylem (X_1), secondary xylem (X_2), aerenchyma (A), epidermis (E). 13x.



FIGS. 29—31. Transection of *B. radiata* roots grown under sterile conditions (plant in Fig. 7) with 10 % sucrose.

FIG. 29. 4 cm from the transition region of root and stem. Epidermal (E) cells large, brownish and lignified, under them big unorganized tumorous cells (TC), root hairs rare, cortex wide, aerenchyma (A), intercellular spaces (IS) large, vascular cylinder relatively small. 23x.

FIG. 30. The same section as in Fig. 29. Aerenchyma (A) and ground parenchyma (Pa) containing chloroplasts around the vascular cylinder, secondary xylem (X_2), phloem (Ph). 60x.

FIG. 31. About 8 cm from the transition region, root hairs (RH), aerenchyma (A) with radial cell rows (chloroplasts), intercellular spaces (IS) and xylem (X). 60x.

FIG. 32. The same root at greater magnification, proto- and metaxylem (X), phloem (Ph), pericycle (Pc), endoderm (Ed), Casparian spot (Ca), aerenchyma (A). 120 x.

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