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A STUDY OF THE EARLY DEVELOPMENT OF

THE ROOT SYSTEMS OF VARIOUS

GRASS SPECIES;

AND

A STUDY OF THE IMPORTANCE OF VARIOUS

ROOTS, PARTICULARLY THE SEMINAL

ROOTS, TO LOLIUM PERENNE.

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Thesis submitted in part fulfillment for the Degree of M. Agr. Sc.
in Plant Husbandry, University of New Zealand, by M. E. Yates.

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SECTION I.INTRODUCTION.

New Zealand is essentially a land of pastures. Greater reliance is placed on pastures for the sustenance of stock by the farmer in New Zealand than probably anywhere else in the World. The study of pastures is therefore of paramount importance to the national welfare of New Zealand and their improvement will be reflected in raised living standards and at the same time will provide more food for the hungry world of today.

There is no doubt that New Zealand is favoured by an equable climate and well distributed rainfall which enables her to derive a considerable portion of her wealth from grasslands. Nevertheless we have had to adopt farming methods to suit the environment so that the greatest benefits may be derived from the natural advantages with which New Zealand is endowed.

New Zealand has proceeded a long way since the early days of her farming when little was known of the environmental requirements of individual pasture species in order that they may produce to their maximum. It is unquestionable that much of the progress already made in grassland husbandry in this country is due to the wide range of trials conducted by the Department of Agriculture and Grasslands Division, D.S. and I.R., particularly over the last quarter of a century. Much has been learnt in the past and investigations being pursued at the present time will no doubt be reflected by improved methods of grassland husbandry with consequent increased pasture production in the future.

The original technique of pasture establishment was to sow a wide range of species in the hope that at least one specie would persist and form a sward. This idea changed as the farming community came to know the environmental conditions

necessary for the persistence and production of the individual species. In this way seeds mixtures became simpler containing those species suited to the particular environment of the land being laid down to pasture. However, despite the sowing of the correct species there are numerous other factors warranting consideration before high pasture production can be obtained. Thus methods of pasture establishment and pasture management have been investigated and improvements have been effected through the application of the results obtained. Breeding work on the more important pasture species has been performed and resultant improved strains have been made available to the farmer per medium of the Seed Certification Scheme. Applications of artificial fertilizers have also played a major part in the improvement of New Zealand's pastures.

It is evident from the above that most research in New Zealand, directed towards maximum yields of high quality herbage, has considered only the aboveground parts of the pasture plants. However, it must be remembered that the aboveground parts of plants are dependent on the underground organs for the supplying of water, nutrients and the storage of reserves as well as acting as a mechanical support for the plant. Moreover, it has been demonstrated that there exists significant interrelationships between leaf production and underground development. When one considers that the main aim of grassland husbandry is to produce and maintain maximum production of high quality herbage this interrelationship thus indicates the great importance of the underground parts. Therefore an understanding of the functions of roots, their relationship to the aboveground organs and the response of plants to the various environmental factors affecting the roots is practically indispensable.

We all realize that a child has to be nursed if it is to survive and fit into place in this world. The same is true also of pastures. In the establishment period of a pasture it has to be nursed so that it will ultimately

produce to a high level and in the case of permanent pastures, be persistent. In the past, and the same even applies today, poor pasture establishment has limited the production obtainable from pastures in a great number of instances. No matter how good the seed, a pasture will not be very successful if environmental conditions are not conducive to rapid and successful establishment.

It is known that, with members of the Gramineae family, the seminal roots are the first roots to develop and support the developing plant until such time as the nodal root system becomes functional. In view of this it is surprising that little work has been performed on the relationship between this seminal root system and pasture establishment. Further investigations on their importance in the early life of a pasture, their response to environmental conditions and the relative value of the various seminal roots and the nodal roots to the plant are thus worthy of pursuance.

In this experiment, by means of root amputations, an effort was made to evaluate the importance of the various seminal roots and the nodal roots to perennial ryegrass (Lolium perenne) in the presence and absence of superphosphate. The degree of tillering, herbage yields and the survival of plants were used as standards of judgment of the plants' response to the varying treatments.

SECTION II.

REVIEW OF LITERATURE.

When one reviews the literature it is soon seen that most attention has been focused on the aboveground parts. A lesser amount deals with the underground organs and there is a scarcity of material regarding the seminal roots of plants. Further, there is very little on the interrelationships between the above- and belowground organs even though they have been shown to be closely interrelated.

This state of affairs is no doubt due, to a large degree, to the great difficulties which one has to overcome when adequate observations are to be made on root development in order that reliable results can be obtained and correct interpretations of these results arrived at. Some of the more important difficulties that one is liable to come up against are:-

- (1) Variation in plant material.
- (2) Soil variations under natural environmental conditions.
- (3) As a result of (1) and (2) large numbers of plants have to be observed.
- (4) Tedious work involved in observations on root development.
- (5) Lack of efficient yet speedy techniques.

Notwithstanding these difficulties, many workers have made observations on root development but there is still a large field available for detailed and pertinent research on underground development and importance of roots.

A. TERMINOLOGY.

It is at once obvious when the literature is perused that many synonyms are used to denote the different types of roots. To prevent any misunderstanding I shall enumerate these synonyms and also the terms that will be used throughout

the remainder of this paper.

Jacques (1) discusses the types of roots of the nodal root system of perennial ryegrass. He lists them as follows:-

- (1) Purely absorptive roots.
- (2) Storage as well as absorptive roots.
- (3) A type intermediate between the above.

He states, however, that the functioning and significance of these types is still a matter of conjecture and requires to be fully investigated.

However, members of the Gramineae family possess two distinct root systems and within these two there are distinct types of roots. When the seed germinates the seminal or primary root system develops and consists of one to several main roots and their branches. The primary seminal root develops first and in some cases is the only seminal root to develop. It is also known as temporary and primary root. In the majority of cases, however, more seminal roots develop after the appearance of the primary seminal root. These are known as lateral roots. Unfortunately the use of this term may lead to confusion in that branches of the nodal roots are referred to as lateral roots. Thus for the purposes of clarity the lateral roots of the seminal root system will be referred to as the lateral seminal roots. Figure 1 illustrates these various types of roots.

Later on in development, more especially when the plants begin to tiller, a root system begins to develop from the nodes at or near the soil surface. This root system is known as the secondary root system. Other terms given to these roots are crown roots, adventitious roots and nodal roots. Through the remainder of this paper I shall refer to them as nodal roots.

To summarise then a list is given below of the terms used and the synonyms met with in the literature on root systems.

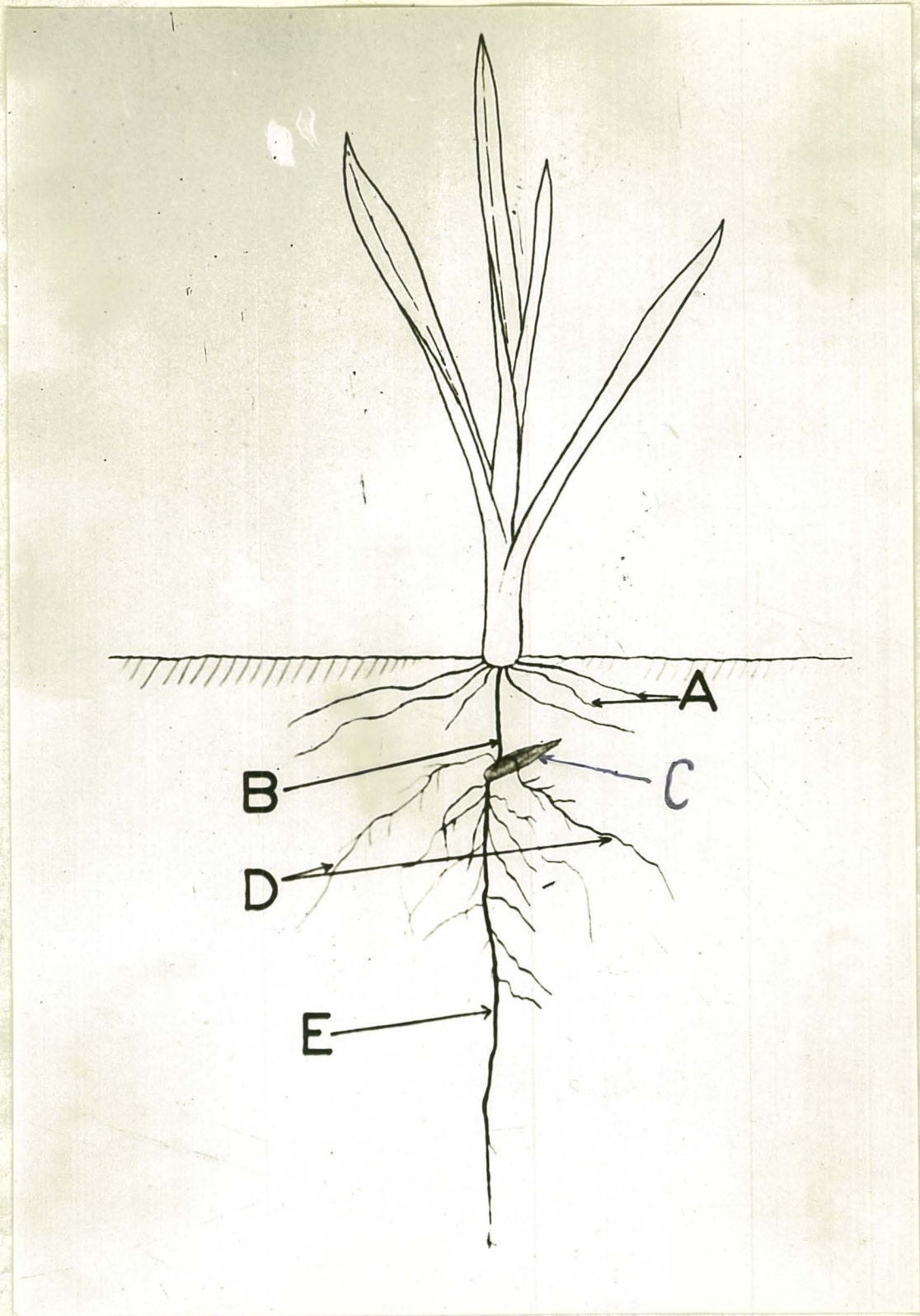


FIGURE I.

Diagrammatic representation of the various roots of the gramineae family.

A. Nodal roots.

B. Internode.

C. Seed.

D. Lateral seminal roots.

E. Primary seminal root.

Term Used	Synonyms
Nodal Roots	Crown, adventitious, secondary roots.
Primary Seminal Roots	Temporary, Primary Root
Lateral Seminal Roots	Lateral, Temporary and Primary Roots
	} Make up the Seminal or Primary Root System.

B. GENERAL DEVELOPMENT OF THE SEMINAL ROOTS.

Upon germination the embryonic plant previously dormant in the seed is released. Plants of the grass family possess two distinct root systems which develop at different periods. The seminal root system develops immediately upon germination and usually consists of several roots, the number of which depends on the species of plant.

According to Pavlychenko (2) the number of seminal roots varies within narrow limits and is apparently governed by a definite genetic factor. The following, extracted from results obtained by him, support his statement:-

Annual Grain Crops.

Crop	Number
<i>Avena fatua</i> (Wild oats)	3.0
<i>Avena sativa</i> (Cultivated oats)	3.1 - 3.5
<i>Triticum aestivum</i> (Wheat)	3.6 - 5.0
<i>Secale cereale</i> (Rye)	4.5 - 5.3
<i>Hordeum distichon</i> (Barley)	6.5 - 8.5

Perennial Grasses.

Specie	Agropyron cristatum			Agropyron pauciflorum			Bromus inermis		
	5	15	30	5	15	30	5	15	30
Days after emergence									
Av. No. of Seminal Roots per plant.	1.6	2.6	2.4	1.5	1.2	1.1	2.3	2.0	2.0

Further, it will be observed that the number of seminal roots was smaller in the perennial grasses studied than in the annual grain crops. However, it must be realised that the above figures apply only to the conditions under which the experiments were conducted. Environmental factors such as climate and soil conditions modify the average numbers of seminal roots but the variation within species is limited under the same conditions.

McCall (3) with respect to wheat states that "When the seed is exposed to moisture water is absorbed and the seed swells. At appropriate temperatures the embryo begins to push out both the coleorhiza and the coleoptile, the former somewhat more rapidly than the latter. The seed coat is ruptured, the coleoptile turns upward and the primary (seminal) root pierces the coleorhiza and turns downward. Shortly after the primary (seminal) root has pierced the coleorhiza the lower pair of lateral (seminal) roots emerge through the axis cortex, followed soon after by the second pair of lateral (seminal) roots just above the first pair."

The young seedling is entirely dependent on this seminal root system until later, during the period of tillering, the second root system, the nodal root system, develops from the lower nodes of the main stem and of the tillers. Once the nodal root system is established the seminal root system is no longer an absolute necessity, it finally dies and its place is taken over by the nodal root system.

To appreciate fully the significance of seminal roots for the survival of a plant one must recognise that during development prior to emergence the size of the plant increases about four times. This is supported by results obtained in a study by Pavlychenko (4). The seminal roots of various crop plants at emergence were of the following length:-

Specie	In Greenhouse	In Field
Marquis wheat	12.62 ins.	24 ins. approx.
Hannchen barley	14.75 "	27 " "
Banner oats	6.6 "	14 " "
Wild oats	6.95 "	13 " "

With respect to later development, Weaver and Zink (5) obtained the following figures working with various grasses. At 21 days after planting when the plants were $1\frac{1}{2}$ to 5 inches high the seminal roots were 6 to 10 inches deep. Nodal roots and tillers were only just beginning to develop. At 41 days the grasses were about 8 to 10 inches tall and well tillered. At this stage the seminal roots reached a depth of $7\frac{1}{2}$ to 27 inches and the nodal roots were often equally deep. At 90 to 123 days when the grasses were 9 to 19 inches tall, the seminal roots, despite a large number of nodal roots, extended deeply and frequently to 24 inches in depth. Microscopic examination showed about half to two-thirds of the seminal root system to be intact. (Based on the condition of the cortex).

These figures then serve to indicate the tremendous development of the seminal roots and how important they are to developing plants even until they reach an age of three months at which time the nodal root system is extensive and fully functional. It will also be realised that any serious damage to the seminal root system prior to the development of the nodal roots will cause the death of the plant. Further, damage caused to the seminal root system once the nodal roots have begun to develop may have serious effects on the development of the plant depending, however, on the stage to which the nodal roots have developed.

C. LENGTH OF LIFE OF SEMINAL ROOTS.

Since root study necessitates much more difficult technique due to their inaccessability, the length of life of the seminal roots, and also the nodal roots, remains a disputed question.

The seminal roots are often designated as temporary in general text books and even in special books on grasses of

recent publication notwithstanding that experimental evidence has proved this conclusion to be incorrect. For example Robbins (6) states: "The primary roots, those that arise directly from the seed, are temporary, dying after the permanent roots are able to support the plants." More recently Nelson (7) states: "The function of the seminal root system is temporary and is to provide for the supply of the seedling stage only. Later on it dies." Hitchcock (8) states: "The primary root persists only a short time after germination, its place being taken by secondary roots (nodal roots) produced from the nodes of the young culm."

However, observations and experimental trials have shown that the seminal root system is by no means temporary in all cases. Members of the Gramineae family have been observed as reaching maturity while existing on only the seminal root system.

Locke and Clarke (9) observed that in two different instances where extremely dry surface soil, packing or crusting of the soil prevented normal development of the nodal roots, the seminal roots furnished sufficient moisture to maintain growth of wheat plants to maturity or until rain occurred and the permanent roots developed normally. Simmonds and Sallans (10) found through amputation studies that the wheat plant may produce seed when dependent almost entirely upon the seminal roots. Simmonds (11) at a later date stated that the seminal roots remain functional throughout the life of the plant. Krassovsky (12) working on the physiological activity of seminal roots demonstrated that the seminal roots of wheat, barley and rye were active up to the time of harvest. Results obtained by Pavlychenko (4) in studies over a period of nine years gives conclusive evidence that, in annual grasses in arid climates, seminal roots function throughout the entire growing season, and what is more important, they are frequently the only roots supporting the plant from emergence to maturity.

The above deal with annual species. Studies on the seminal roots of perennial grasses are very meagre.

Stoddart (13) in 1935 found that the seminal roots of Andropogon furcatus all lived to an age of 18 months and some were still functioning at the end of two years. This indicates then that the seminal roots may live in excess of two years. Rapport (14) reports that the tap root (primary seminal root) of Lolium perenne was discernable after three months and growth was still proceeding. Weaver and Zink (5) observed that the seminal roots of fourteen perennial grasses were usually deep and spread widely whilst they remained alive and active as absorbing organs for $3\frac{1}{2}$ to 4 months.

From the above evidence then, one can conclude that where the climate and soil conditions are favourable for nodal root development the seminal roots die, once the former are capable of supporting the plant. This has apparently led to the conclusion that the seminal roots are temporary. However, where climate and soil conditions are unfavourable, or where artificially induced conditions have retarded nodal root development then the length of life of the seminal roots is increased.

To sum up then one may say that the seminal root system is normally short-lived but under adverse conditions it may persist for longer periods and may even allow the plant to reach maturity.

D. TILLERING AND ROOT DEVELOPMENT.

The interrelationships between the two root systems and tillering have not been thoroughly investigated. Results obtained on this aspect by various workers are usually mentioned more or less incidentally to the main theme of the various papers.

Olmsted (15) observed that plants with no nodal roots were retarded in growth as compared with plants bearing functional nodal roots. Glendinning (16) found that tillering was closely associated with the establishment of the nodal root system in Heteropogon. McCall (3) mentions that where the nodal roots fail to develop the wheat plant does not tiller to any extent even though the seminal root system is capable of

carrying the plant to maturity. According to Weaver (17) the production of tillers is successful only when the nodal root system penetrates into the moist soil and meets the increased demand for water.

Krassovsky (12) determined that the seminal roots supply principally the main stem and the nodal roots the tillers. The removal of the seminal roots during the period of stalking depressed the development of the main stem and lengthened the period of vegetation whereas the removal of the nodal roots checked tillering and hastened maturity. One can, on the basis of Krassovsky's results, draw the conclusion that the seminal roots serve the main stem whilst the nodal roots supply the tillers.

It is evident then from the above that the removal of nodal roots or the failure of nodal roots to develop, has a definite effect on tillering, in that tiller production is suppressed.

E. THE IMPORTANCE OF THE VARIOUS ROOTS.

It is of importance here to consider the developmental anatomy of the Gramineae family in relation to the importance of the various roots. It has been already stated that the primary seminal root is the first root to appear followed by the first and second pair of lateral seminal roots. At a later date the nodal roots make an appearance and finally tend to take over the functions of the seminal roots.

McCall (3) states: "As the food supply from the endosperm is conveyed along the scutellum trace, its most direct route leads to the first node and into the coleoptile. The portion of the scutellum trace passing on the first node is much larger than the branches leading to the coleoptile. Thus it appears that the connection of this large trace to the node insures that the primary seminal root is well supplied with materials for growth." This is supported by the fact that most workers have observed the growth of the primary seminal root to be most rapid. McCall (3) showed this to be due to a most efficient conducting system which connects the first node to all the

bundles of the root axis. The coleoptile, in wheat, is somewhat slower in growth even though it is connected directly to the food supply and is probably due to the fact that the coleoptile has only two bundles supplying it and depends on diffusion to a large extent.

The first pair of lateral seminal roots are also directly connected to the first nodal plate and as a result they are in a position to draw directly on the labile food supply. Consequently they emerge almost immediately after the primary seminal root and the growth of them is almost as rapid as that of the primary seminal root.

The second pair of lateral seminal roots frequently do not develop or if they do so they are much slower in growth and do not become as extensive as the primary and first pair of lateral seminal roots. In the case of wheat McCall (3) says that this is the result of the less favourable placement of them in relation to the food stored in the endosperm. To reach them the food must pass either from the first node or through the relatively smaller connections from the coleoptile bundles. In the former case they have to compete with the primary and first pair of lateral seminal roots and in the latter case with such structures as the coleoptile and the plumule. That the amount of food material available through these channels is not always adequate is shown by the fact that in a large number of cases this pair does not develop or if it does develop their slower growth shows the result of their less favourable position.

From the above, some basis is thus given for the relative development and extent of the various seminal roots. As a result, the value of the various seminal roots to the plant varies according to their ability to develop quickly and extensively.

Sallans (18) found that the various roots of the wheat plant contribute independently of each other to the water and mineral supply of the plant as was indicated by the final yield of grain. His data given below illustrates that, of the

seminal roots, the primary seminal root contributes most to the final yield. The first pair of lateral seminal roots are of approximately equal importance whilst the second pair of lateral seminal roots are of much less importance.

Amputation Treatments	Dry top weights 1938	Yield of grain 1939
None	4.135	2.075
Primary seminal root	3.555	1.605
1st pair lateral seminal roots	3.602	1.855
2nd pair lateral seminal roots	3.792	1.860
All seminal roots	1.535	1.220

Thus we see that the value of the seminal roots is closely linked with their development.

The contribution of the nodal roots to the wheat plants' yield of grain is much more variable than is the case with the individual seminal roots. Sallans (18) states: "At Saskatoon in 1939 the nodal roots individually were less valuable than the other classes taken singly. In the aggregate, however, they contributed 61% of the total yield. At Indian Head in 1938 they contributed 63.6% of the total yield." With respect to variability in 1929 at Indian Head the nodal roots produced 65.5% of the check yield whilst in 1930 they produced only 36% as much grain.

The importance of the seminal roots in the early stages of development was supported by further data of Simmonds and Sallans(10). In their work, amputations of seminal roots on 21st July resulted in no reduction of yield whereas amputations on June 9th caused a loss of 64% in yield as shown in the controls. At the latter date the nodal roots were just developing and were not in a position to take over the supplying of water and minerals to the plant. Hence the earlier in the developmental stage of the nodal roots that the seminal roots are amputated the more marked is the loss of these roots.

Krassovsky (12) found that in wheat, barley and rye that the seminal roots were more effective in water absorption,

absorbing almost double the amount of water per unit of dry weight in comparison to the nodal roots. This further emphasises the importance of the seminal root system in annual grain crops.

With respect to perennial grasses very little is known about the importance of the various roots. Much contradictory evidence has been put forward concerning the persistency of the seminal roots and this has no doubt led to the belief that they are of no great importance to a plant once it has established. Work employing amputation studies would no doubt help to clarify the position.

F. CONCLUSIONS.

We have seen that the seminal roots are of great importance to annual grain crops often enabling them to reach maturity in the absence of nodal roots due to unfavourable conditions. However, reduction in yield and tillering results with the non-development of the nodal roots. Work by Simmonds and Sallans has illustrated the relative importance of the various roots to the wheat plant.

Work on perennial grasses is somewhat scarce but it has been shown that they are important at least until the nodal roots have developed.