Tropisms and Nastic Movements a Study in Plant Physiology

*Dr.M.Ravikumar, Associate Professor of Botany, Kottureshwara College, Kottur.

Abstract

This paper attempts to study **plant physiology of Tropisms and Nastic Movements Tropisms** are growth **responses** of **plants** with **cell** divisions in meristems leading to elongation of stems and roots. A tropism (from Greek τρόπος, tropos, "a turning") is a biological phenomenon, indicating growth or turning movement of a biological organism, usually a plant, in response to an environmental stimulus. In tropisms, this response is dependent on the direction of the stimulus (as opposed to nastic movements which are non-directional responses). Viruses and other pathogens also affect what is called "host tropism", "tissue tropism", or "cell tropism"; in which case tropism refers to the way in which different viruses/pathogens have evolved to preferentially target specific host species, specific tissue, or specific cell types within those species.

Tropisms are usually named for the stimulus involved (for example, a phototropism is a reaction to sunlight) and may be either positive (towards the stimulus) or negative (away from the stimulus). Tropisms occur in three sequential steps. First, there is a sensation to a stimulus, which is usually beneficial to the plant. Next, signal transduction occurs. And finally, the directional growth response occurs. Tropisms are typically associated with plants (although not necessarily restricted to them). Where an organism is capable of directed physical movement (motility), movement or activity in response to a specific stimulus is more likely to be regarded by behaviorists as a taxis (directional response) or a kinesis (non-directional response). In English, the word tropism is used to indicate an action done without cognitive thought: However, "tropism" in this sense has a proper, although non-scientific, meaning as an innate tendency, natural inclination, or propensity to act in a certain manner towards a certain stimulus. In botany, the Cholodny–Went model, proposed in 1927, is an early model describing tropism in emerging shoots of monocotyledons, including the tendencies for the stalk to grow towards light (phototropism) and the roots to grow downward (gravitropism). In both cases the directional growth is considered to be due to asymmetrical distribution of auxin, a plant growth hormone. Nastic movements are non-directional responses to stimuli (e.g. temperature, humidity, light irradiance), and are usually associated with plants. The movement can be due to changes in turgor or changes in growth. Decrease in turgor pressure causes shrinkage while increase in turgor pressure brings about swelling. Nastic movements differ from tropic movements in that the direction of tropic responses depends on the direction of the stimulus, whereas the direction of nastic movements is independent of the stimulus's position.

Key words: plant physiology , stimulus, Tropisms , Nastic Movements, growth hormone

Introduction

The tropic movement is growth movement but nastic movement may or may not be growth movement. The rate or frequency of these responses increases as intensity of the stimulus increases. An example of such a response is the opening and closing of flowers (photonastic response), movement of euglena, chlamydomonas towards the source of light. They are named with the suffix "-nasty" and have prefixes that depend on the stimuli:

1. Epinasty: downward-bending from growth at the top, for example, the bending down of a heavy flower.
2. Hyponasty
3. Photonasty: response to light
4. Nyctinasty: movements at night or in the dark
5. Chemonasty: response to chemicals or nutrients
6. Hydronasty: response to water
7. Thermonasty: response to temperature
8. Seismonasty: response to shock
9. Geonasty/gravinasty: response to gravity
10. Thigmonasty/seismonasty/haptonasty: response to contact

The suffix may come from Greek νάσσω = "I press", ναστός = "pressed", ἐπιναστια = "the condition of being pressed upon".Although studies that specifically focused on thigmotropism in woody plants do not exist, one study on the effect of wind on the growth of lodgepole pine (*Pinus contorta* Douglas ex Louden) reported that the expanding shoots curved into the wind . Although not acknowledged by the authors as such, this appears to be a positive thigmotropic response to a unidirectional wind flow in the primary growth of a woody plant . Another potential thigmotropic response may have been recorded in secondary tissues, but not reported as such: displaced stems of maritime pine (*Pinus pinaster* Aït.) exposed to wind experienced a greater rate of recovery in the middle and basal stem sections compared to displaced stems not exposed to wind . The increased rate of recovery under windy conditions could not be explained by gravitropism and compression wood formation as both wind and non-wind treatments contained equal amounts of compression wood in their displaced stems, but appears to be complicated by a phototropic response .

Objective:

This paper intends to explore and analyze **tropic and Nastic movements** that are activities of curvature brought about by more growth on one side and less growth on the opposite side of plant organ induced by some external stimuli as part of **Plant physiology**

PARATONIC/ INDUCED MOVEMENTS

Despite the fact that plants are usually seen as stationary organisms, they do, in fact move continuously in different ways, and for different reasons, among others: in search of light, water, nutrients, defense against predators, and reproduction. Several kinds of movements are recognized but the principal ones are nastic, circumnutational, and tropic. **Tropism**, response or orientation of a plant or certain lower animals to a stimulus that acts with greater intensity from one direction than another. It may be achieved by active movement or by structural alteration. Forms of tropism include phototropism (response to light), geotropism (response to gravity), chemotropism (response to particular substances), hydrotropism (response to water), thigmotropism (response to mechanical stimulation), traumatotropism (response to wound lesion), and galvanotropism, or electrotropism (response to electric current). Most tropic movements are orthotropic; *i.e.,* they are directed toward the source of the stimulus. Plagiotropic movements are oblique to the direction of stimulus. Diatropic movements are at right angles to the direction of stimulus. In the latter, the plants move in a direction, under an external stimulus, which induces a different elongation on opposite sides of an organ. The best known, most common, and most easily observable tropisms are gravitropism and phototropism. Plant responses to external stimuli, such as light, gravity, touch, and water, and to endogenous developmental signals set by the biological clock often involve movements. Some are growth movements, others are nongrowth movements, and some have components of both. Movements may also be in response to a directional stimulus (i.e., a tropic movement) or a stimulus that is diffuse (nastic movement).
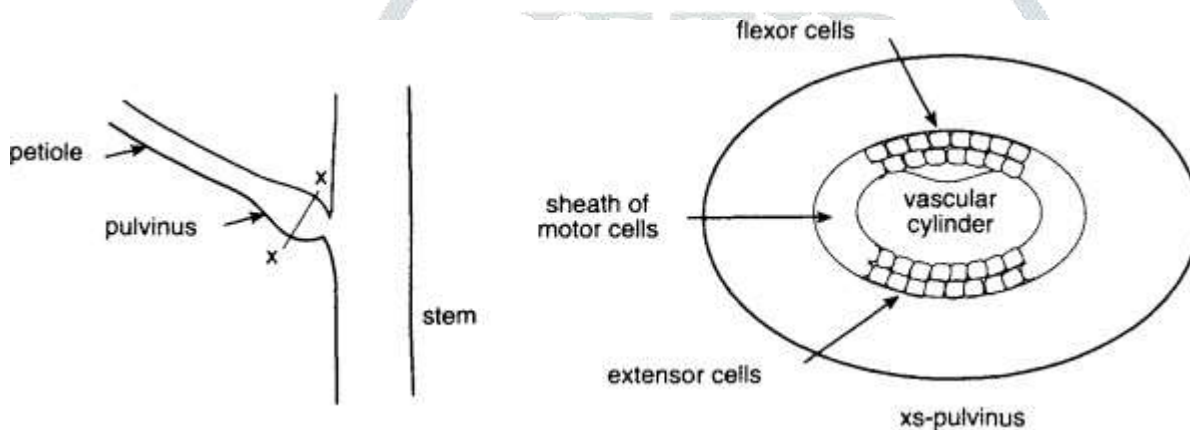
Common examples of growth movements resulting from a directional stimulus are phototropism and gravitropism. Other growth movements may occur in response to mechanical stimuli, such as touch (thigmotropism), or sensing of and growth toward water (hydrotropism) or chemicals (chemitropism), including oxygen (oxytropism). Some growth movements occur in response to a diffuse stimulus and hence are considered nastic movements. For example, shoot tips often describe an oscillatory movement as they grow upward, a movement known as circumnutation. Leaves droop or show an epinastic curvature in their petioles; sometimes they curve upward and show hyponasty.

Nongrowth movements occur in mature parts of the plant. Most of these movements occur in response to directional or diffuse light. Others occur in response to mechanical stimuli, including touch. The best and most common example of nongrowth movement is that provided by stomata. Stomatal pores open and close by reversible turgor changes in guard cells and are regulated by a number of environmental factors, including blue light, as well as by hormones such as ABA. Other examples include movement of chloroplasts in leaf cells of *Funaria* (a moss) and *Lemna* (duckweed), and leaf reorientations (e.g., *Erythrina* spp. and *Phaseolus vulgaris)*, and "rolling" of lamina (e.g., grasses) to avoid excessive solar radiation and transpirational loss. Leaves and flowers of many plants show what are known as "sleep" movements. They open or unfold with sunrise (photonasty) and close or fold with sunset (nyctinasty). These diurnal movements are common in

compound leaves of members of Fabaceae and Oxalidaceae. Flowers of tulip *(Tulipa* spp.) close their petals at night and open them in the morning.

Nastic leaf closure may also result from mechanical stimulation or touch (e.g., the sensitive plant, *Mimosa pudica,* and insectivorous plants, such as Venus fly trap).

A special kind of directional movement, which may involve growth, occurs in solar tracking (heliotropism). The phenomenon is common in many herbaceous plants belonging to diverse families of angiosperms and is shown by mature leaves or flowers. Plant responses to external stimuli, such as light, gravity, touch, and water, and to endogenous developmental signals set by the biological clock often involve movements. Some are growth movements, others are nongrowth movements, and some have components of both. Movements may also be in response to a directional stimulus (i.e., a tropic movement) or a stimulus that is diffuse (nastic movement).

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Heliotropism : herbaceous plants

A special kind of directional movement, which may involve growth, occurs in solar tracking (heliotropism). The phenomenon is common in many herbaceous plants belonging to diverse families of angiosperms and is shown by mature leaves or flowers. As in seed plants, many light-regulated responses in ferns, mosses, and algae are mediated by blue light receptors and phytochromes. These responses are distinguished into two physiological types. One type, a dichroic response, depends on orientation of the electrical vector of light and requires a specific orientation of photoreceptor molecules. It involves perception not only of the quality but also the direction of impinging light. The other type, a nondichroic response, is independent of the electrical vector of light. Among the former are chloroplast movement and phototropic response in algae, mosses, and fern gametophytes. Nondichroic responses include spore germination, tip growth, and cell division in ferns.

Several different blue light receptors and phytochromes occur in these groups of plants, and the existence of two physiologically distinct types of photoreceptors, one mediating dichroic the other nondichroic responses, is predicted. In addition, several responses are regulated by both blue and red/far-red light receptors, thus imparting a great variety and complexity to light-mediated responses in these plants. Until recently, it was difficult to study the light receptors in cryptogams, partly because materials were available only in small amounts and partly because these plants synthesize chlorophyll in darkness, thus making extraction and purification of phytochromes difficult. With the availability of molecular and genetic techniques, however, rapid progress is now being achieved.
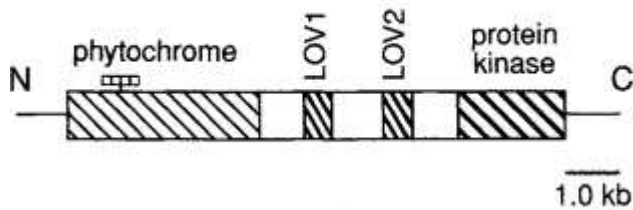
Chloroplast reorientation in response to light in most plants (including angiosperms) is a blue light-mediated response. In several cryptogams, however, including fern protonemata, mosses, and green algae, it is also mediated by red/far-red light. *Mougeotia scalaris* (a filamentous green alga) shows extreme sensitivity to the red light signal and hence has been investigated intensively. In this alga, each cell has a single ribbon-shaped chloroplast, which can be reoriented in response to a single pulse of red light of low fluence. This movement is reversed by a pulse of far-red light given subsequently, which indicates clearly that it is a phytochrome response. In far-red light, the chloroplast is arranged with its thin edge perpendicular to the cell surface. Irradiated with red light it rotates and presents its flat face to the cell surface. Moreover, if a microbeam of plane-polarized light is used to irradiate one-half of the cell while the other half is irradiated with far-red light, the chloroplast twists; the part irradiated with red light presents its flat face, whereas the other half presents its thin edge. Such behavior predicts that the phytochrome molecules are anchored to some intracellular structure, possibly the plasma membrane, which helps rotate the chloroplasts. A gene encoding the apoprotein moiety in the phytochrome of *Mougeotia* has been cloned, but the deduced amino acid sequences show no transmembrane domain. The carboxy terminus, however, contains a motif that is thought to bind to microtubules. Thus, chloroplast movement in *Mougeotia* may be brought about by transduction of the light signal to cytoskeletal elements.

Phototropism chloroplast movement

In contrast to *Mougeotia, Mesotaeniwn caldariorum* (a single-celled green alga), which also shows R7FR-dependent chloroplast movement, is much less sensitive to a light signal. Usually, continuous irradiation with red light or irradiation with several pulses in quick succession is required for chloroplast movement. *Mesolaenium* has been shown to have a cytosolic phytochrome with no transmembrane domain. Thus, the mechanism of phytochrome-regulated chloroplast movement in these algae is still conjectural.

Phototropism by rhizoids of *Bryonia* (a marine coenocytic alga) is reported to be mediated by a blue UV-A receptor. In mosses, *PhyscomitreUa patens* and *Ceratodon purpurem,* however, it is regulated via phytochromes and shows red/far-red reversal. The gravitropic response in mosses appears to be modulated by

blue light. The protonemal filaments of *Ceratodon* grow negatively gravitropicallv (upward) in darkness. This effect is reversed by blue light given simultaneously as the gravitropic stimulus.

In ferns, such as *Acuantian capillas veneris,* blue light receptors and phytochrome act cooperatively to mediate phototropism and chloroplast movement in the gametophyte. The phytochrome involved in both responses is thought to be a dichroic type, probably bound to the plasma membrane, but details are unknown. Some other responses in ferns are also regulated by phytochrome and a blue light receptor. The phytochrome invoked in these responses is the nondichroic type. Moreover, these responses are regulated antagonistically by the blue light receptor and phytochrome. For instance, spore germination in ferns is dependent on exposure to red light. It is a typical phytochrome response in that it shows R/FR reversibility. The red light promotion of spore germination is suppressed by blue light irradiation. Tip growth of the filamentous protonemata is promoted by phytochrome, but is inhibited by B light. Irradiation with B light also promotes apical swelling of protonema (see Fig. 2-44 in Chapter 2) and subsequent cell divisions, leading to two-dimensional growth of the prothallus. Several genes (and many cDNAs) encoding the apoprotein moieties of phytochromes and blue light receptors in these plants have been cloned. Moreover, in some plants, such as **Anaemia** and *Adiantam* among ferns, *Ceratodou* in mosses, and *Mesotaenium* in algae, small families of genes encode phytochromes. For instance, *Adiantinu* has three phytochrome genes, *PHY1, PHY2,* and *PHY3; Ceratodou* has two; and **Mesotaenium** has at least two, possibly many more. In other cryptogams, only one phytochrome gene has been reported (e.g., *Selagimila, Phi/scomitrella, Mougeotia).*

The cryptogamic phytochromes identified to date typically show the structure common to seed plant phytochromes with a chromophore-bearing region, a hinge-like region, a PAS domain, and a histidine kinase-like domain at the C terminus. Cryptogams also show an unusual type of phytochrome, which combines the structural features of phytochrome and a blue light receptor. For example, in *Adiantinu,* two phytochrome genes, *PHY1* and *PHY2,* encode phytochromes with a conventional structure. The third, *PHY3,* encodes an unorthodox protein. The N-terminal of PHY3 is very similar to the N-terminal chromophore-binding domain of PHYA in *Arabidopsis,* but the C-terminal is strikingly similar to NPH1 (the blue light receptor for phototropism at low fluences of light), with both LOV doma ins and all the conserved domains of the catalytic region of a Ser/Thr protein kinase (Fig. 27-11). The moss, *Ceratodou,* has two phytochromes. One has the structure of a conventional phytochrome and the other is an unusual phytochrome. It has a kinase domain but with a different structure than that in PHY3 of *Adiantam.* It also lacks the LOV domain and the blue light

receptor-binding region. Other cryptogams may have still more unusual or novel combinations of photoreceptors.

Blue light receptors in cryptogams are still very much a mystery. Use of molecular techniques, however, has allowed cloning of several *CRY* genes in *Adiantam.* In this fem, five groups of *CRY* genes, members of a small gene family, have been found. The encoded proteins show structural similarities to the protein moieties of cry1 and cry2 in *Arabidopsis.* They probably bind a flavin chromophore, but none of them acts as a photolyase. In summary, many responses in cryptogams are mediated *via* phytochromes and blue light receptors. Some are mediated individually by one type of receptor, others are regulated by both, some synergistically, and others antagonistically. Genes encoding the protein moieties of many of these receptors have been cloned and their structures deduced. In several plants they occur as members of small gene families. The specific roles of these phytochromes and putative blue light receptors are still unknown. They are being elucidated by the use of mutants defective in specific responses. For example, mutants in *Adiantinu* have been isolated that are defective in red light-induced phototropism, but not in red light-induced spore germination or filamentous growth.

Conclusion

When one thinks of fast movement, plants do not usually come to mind. The movements of most plants typically involve a tropism, the growth or turning movement of a biological organism in response to a direction-dependent stimulus, and are normally only notable over the course of hours or days. Classic examples of tropisms include phototropic movements towards light, directional growth or reorientation in response to gravity (gravitropism) and touch-sensitive growth of the roots (an example of thigmotropism) . In addition to tropisms, some carnivorous plants trap prey using nastic movements, or direction-independent, reversible orientational changes in response to direction-independent stimuli. Plants with fast thigmonastic movements have evolved the capability to quickly and dramatically alter their shapes in response to certain external stimuli. Although these mechanically induced active movements may appear to serve different purposes, from a protective mechanism (e.g. the folding of *Mimosa* leaflets) to a hunting function (for example, the rapid closure of the traps of *Dionaea*, *Utricularia* and *Aldrovanda*), some common ground exists. Recent investigations have started to show that most thigmonastic movements result from differential changes of turgor pressure in the tissues, and the opening of certain key ion channels is often involved

References

1. Willis, A.J. (1997). "The Ecosystem: An Evolving Concept Viewed Historically". Functional Ecology. 11 (2): 268–271. doi:10.1111/j.1365-2435.1997.00081.x.

2. Woese, C.R.; Magrum, W.E.; Fox, L.J.; Wolfe, G.E.; Woese, R.S. (August 1977). "An Ancient Divergence Among the Bacteria". Journal of Molecular Evolution. 9 (4): 305–311. Bibcode:1977JMolE...9..305B. doi:10.1007/BF01796092. PMID 408502. S2CID 27788891.

3. Yaniv, Zohara; Bachrach, Uriel (2005). Handbook of Medicinal Plants. Binghamton, NY: Haworth Press. ISBN 978-1-56022-994-0.

4. Yates, F.; Mather, K. (1963). "Ronald Aylmer Fisher 1890–1962". Biographical Memoirs of Fellows of the Royal Society. 9: 91–129. doi:10.1098/rsbm.1963.0006. JSTOR 769423.

5. Zohary, Daniel; Hopf, Maria (2000). Domestication of Plants in the Old World (3rd ed.). Oxford: Oxford University Press. ISBN 978-0-19-850356-9.

6. The Arabidopsis Genome Initiative (2000). "Analysis of the Genome Sequence of the Flowering Plant Arabidopsis thaliana". Nature. 408 (6814): 796–815. Bibcode:2000Natur.408..796T. doi:10.1038/35048692. PMID 11130711.

7. "Auxins". Plant Hormones, Long Ashton Research Station, Biotechnology and Biological Sciences Research Council. Retrieved July 15, 2013.

8. "A Basic Introduction to the Science Underlying NCBI Resources". National Center for Biotechnology Information. March 30, 2004. Retrieved March 5, 2012.

9. "Botany". Online Etymology Dictionary. 2012. Retrieved February 24, 2012.

10. "Early Herbals – The German Fathers of Botany". National Museum of Wales. July 4, 2007. Archived from the original on June 29, 2012. Retrieved February 19, 2012.

11. "Katherine Esau". National Science Foundation. 1989. Retrieved June 26, 2013.

12. "Evolution and Diversity, Botany for the Next Millennium: I. The Intellectual: Evolution, Development, Ecosystems". Botanical Society of America. Retrieved June 25, 2013.

13. "Herbal Medicine". University of Maryland Medical Center. Archived from the original on 2012-03-02. Retrieved March 2, 2012.

14. "Paleobotany". Cleveland Museum of Natural History. Retrieved July 30, 2014.

15. "Physical Map of Brachypodium". University of California-Davis. Archived from the original on August 24, 2011. Retrieved February 26, 2012.

16. "Plants and Life on Earth". Missouri Botanical Garden. 2009. Retrieved March 10, 2012.

17. T. Cavalier Smith 2007, Evolution and relationships of algae major branches of the tree of life. from: Unravelling the algae, by Brodie & Lewis. CRC Press

18. Ševčíková, Tereza; et al. (2015). "Updating algal evolutionary relationships through plastid genome sequencing". Scientific Reports. 5: 10134. Bibcode:2015NatSR...510134S. doi:10.1038/srep10134. PMC 4603697. PMID 26017773.

19. Theodor Cole & Hartmut Hilger 2013 Bryophyte Phylogeny Archived 2015-11-23 at the Wayback Machine

20. Theodor Cole & Hartmut Hilger 2013 Trachaeophyte Phylogeny Archived 2016-03-04 at the Wayback Machine

21. Theodor Cole & Hartmut Hilger 2015 Angiosperm Phylogeny, Flowering Plant Systematics. Freie Universität Berlin

22. Stewart, W.N.; Rothwell, G.W. (1993). Paleobotany and the evolution of plants (2 ed.). Cambridge University Press. ISBN 978-0-521-23315-6.

23. Strother, Paul K.; Battison, Leila; Brasier, Martin D.; Wellman, Charles H. (2011). "Earth's earliest non-marine eukaryotes". Nature. 473 (7348): 505–509. Bibcode:2011Natur.473..505S. doi:10.1038/nature09943. PMID 21490597. S2CID 4418860.

24. Knauth, L. Paul; Kennedy, Martin J. (2009). "The late Precambrian greening of the Earth". Nature. 460 (7256): 728–732. Bibcode:2009Natur.460..728K. doi:10.1038/nature08213. PMID 19587681. S2CID 4398942.

25. Rothwell, G. W.; Scheckler, S. E.; Gillespie, W. H. (1989). "Elkinsia gen. nov., a Late Devonian gymnosperm with cupulate ovules". Botanical Gazette. 150 (2): 170–189. doi:10.1086/337763. S2CID 84303226.

26. P. Kenrick, P.R. Crane (1997) (1997). The origin and early diversification of land plants. A cladistic study. Smithsonian Institution Press, Washington & London. Washington: Smithsonian Inst. Press. ISBN 978-1-56098-729-1.

27. Raven, J.A.; Edwards, D. (2001). "Roots: evolutionary origins and biogeochemical significance". Journal of Experimental Botany. 52 (90001): 381–401. doi:10.1093/jexbot/52.suppl_1.381. PMID 11326045.

28. Del-Bem, L. E. (2018). "Xyloglucan evolution and the terrestrialization of green plants". New Phytologist. 219 (4): 1150–1153. doi:10.1111/nph.15191. PMID 29851097.

29. Heckman, D. S.; Geiser, D. M.; Eidell, B. R.; Stauffer, R. L.; Kardos, N. L.; Hedges, S. B. (Aug 2001). "Molecular evidence for the early colonization of land by fungi and plants". Science. 293 (5532): 1129–1133. doi:10.1126/science.1061457. ISSN 0036-8075. PMID 11498589. S2CID 10127810.

30. Battison, Leila; Brasier, Martin D. (August 2009). "Exceptional Preservation of Early Terrestrial Communities in Lacustrine Phosphate One Billion Years Ago" (PDF). In Smith, Martin R.; O'Brien, Lorna J.; Caron, Jean-Bernard (eds.). Abstract Volume. International Conference on the Cambrian Explosion (Walcott 2009). Toronto, Ontario, Canada: The Burgess Shale Consortium (published 31 July 2009). ISBN 978-0-9812885-1-2.

31. Battistuzzi, F. U.; Feijao, A.; Hedges, S. B. (2004). "A genomic timescale of prokaryote evolution: insights into the origin of methanogenesis, phototrophy, and the colonization of land". BMC Evolutionary Biology. 4: 44. doi:10.1186/1471-2148-4-44. PMC 533871. PMID 15535883.

32. Strother, P.K.; Al-Hajri, S.; Traverse, A. (1996). "New evidence for land plants from the lower Middle Ordovician of Saudi Arabia". Geology. 24 (1): 55–59. Bibcode:1996Geo....24...55S. doi:10.1130/0091-7613(1996)024<0055:NEFLPF>2.3.CO;2.

33. Rubinstein, C. V.; Gerrienne, P.; de la Puente, G. S.; Astini, R. A.; Steemans, P. (2010). "Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana)". New Phytologist. 188 (2): 365–369. doi:10.1111/j.1469-8137.2010.03433.x. PMID 20731783.

34. Wellman, Charles H.; Osterloff, Peter L.; Mohiuddin, Uzma (2003). "Fragments of the earliest land plants" (PDF). Nature. 425 (6955): 282–285. Bibcode:2003Natur.425..282W. doi:10.1038/nature01884. PMID 13679913. S2CID 4383813.

35. Steemans, P.; Lepota K.; Marshallb, C.P.; Le Hérisséc, A.; Javauxa, E.J. (2010). "FTIR characterisation of the chemical composition of Silurian miospores (cryptospores and trilete spores) from Gotland, Sweden". Review of Palaeobotany and Palynology. 162 (4): 577–590. doi:10.1016/j.revpalbo.2010.07.006.

36. Kump, L. R.; Pavlov, A.; Arthur, M. A. (2005). "Massive release of hydrogen sulfide to the surface ocean and atmosphere during intervals of oceanic anoxia". Geology. 33 (5): 397. Bibcode:2005Geo....33..397K. doi:10.1130/G21295.1.

37. Butterfield, N. J. (2009). "Oxygen, animals and oceanic ventilation: An alternative view". Geobiology. 7 (1): 1–7. doi:10.1111/j.1472-4669.2009.00188.x. PMID 19200141.

38. Steemans, P.; Herisse, L.; Melvin, J.; Miller, A.; Paris, F.; Verniers, J.; Wellman, H. (Apr 2009). "Origin and Radiation of the Earliest Vascular Land Plants". Science. 324 (5925): 353. Bibcode:2009Sci...324..353S. doi:10.1126/science.1169659. hdl:1854/LU-697223. ISSN 0036-8075. PMID 19372423. S2CID 206518080.

39. Rubinstein, Claudia; Vajda, Vivi (2019). "Baltica cradle of early land plants? Oldest record of trilete spores and diverse cryptospore assemblages; evidence from Ordovician successions of Sweden". GFF (Journal of the Geological Society of Sweden). 141 (3): 181–190. doi:10.1080/11035897.2019.1636860.

40. Gray, J.; Chaloner, W. G.; Westoll, T. S. (1985). "The Microfossil Record of Early Land Plants: Advances in Understanding of Early Terrestrialization, 1970–1984". Philosophical Transactions of the Royal Society B. 309 (1138): 167–195. Bibcode:1985RSPTB.309..167G. doi:10.1098/rstb.1985.0077. JSTOR 2396358.

41. Tomescu, A. M. F. (2006). "Wetlands before tracheophytes: Thalloid terrestrial communities of the Early Silurian Passage Creek biota (Virginia)". Wetlands Through Time (PDF). doi:10.1130/2006.2399(02). ISBN 9780813723990 http://www.humboldt.edu/biosci/docs/faculty/TomescuRothwell2006.pdf. Retrieved 2014-05-28. Missing or empty |title= (help)

42. Tomescu, A. M. F.; Honegger, R.; Rothwell, G. W. (2008). "Earliest fossil record of bacterial–cyanobacterial mat consortia: the early Silurian Passage Creek biota (440 Ma, Virginia, USA)". Geobiology. 6 (2): 120–124. doi:10.1111/j.1472-4669.2007.00143.x. PMID 18380874.