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DETERMINING THE GERMINATION DATE OF WOODY PLANTS: A PROPOSED METHOD FOR LOCATING THE ROOT/SHOOT INTERFACE

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ABSTRACT

A method for determining the germination dates of trees is based on wood anatomical characteristics and dendrochronology. This procedure requires destructive sampling of the tree for an extensive analysis of the zone between the roots and the trunk of the tree (root/shoot interface). The method is applicable to forest ecology and woody plant life history studies.

Die Methode zur Bestimmung des Keimzeitpunkts bei Bäumen basiert auf der Charakteristik der Holzanatomie und der Dendrochronologie. Das Verfahren erfordert ein destruktives Sammeln von Baumproben für eine umfassende Analyse der Zone zwischen Wurzel und Baumstamm ("root/shoot interface"). Diese Methode ist in der Waldökologie und bei geschichtlichen Studien über Holzpflanzen anwendbar.

La méthode destinée à déterminer la date de germination des arbres est basée sur des caractéristiques anatomiques du bois et sur la dendrochronologie. Cette procédure exige un échantillonnage destructif de l'arbre pour réaliser une analyse complète de la zone située entre les racines et le tronc (interface racine - pousse aérienne). La méthode est applicable en écologie forestière et pour l'étude de l'histoire de la vie des plantes ligneuses.

INTRODUCTION

The increased interest in and use of dendrochronological procedures in forest ecology and woody plant life history studies has led to a need for a procedure to accurately determine the date of tree germination. A pith date obtained at dbh (1.37 m) only represents the age of the tree at that height, not necessarily the absolute age of the tree or the year of germination (Telewski and Lynch 1991). In many cases, suppressed understory trees can grow for 100 to 150 years before attaining a height of 1.37 m (Morris 1948; Tucker et al. 1987).

Telewski and Lynch (1991) state that the germination date of a woody plant can be determined by locating the boundary between the root and the shoot (tree trunk), and determining the pith date in the trunk at this location. To apply this method in ecological studies, a working knowledge of plant morphology and anatomy is necessary to interpret the boundary between shoot and root structure. The boundary between the shoot and root (root/shoot interface) occurs in the primary structure of the embryonic tissues, between the radicle (embryonic root) and hypocotyl (embryonic shoot below the cotyledons or embryonic leaves). The primary xylem structure remains intact within the xylem tissues of a mature tree. All subsequent primary tissues are produced by apical meristems above the cotyledons (epicotyl) and at the tips of roots. The subsequent secondary growth originates from the lateral meristems or cambial tissues, resulting in the formation of growth rings and bark. It is the formation of these rings that is necessary for assigning a calendar year to the germination date using the established methods of dendrochronology (Fritts 1976; Stokes and Smiley 1968). For a review of primary and secondary growth in the stems of woody plants, see Esau (1965, 1977).

COMPARATIVE ANATOMY IN THE STEMS AND ROOTS OF VASCULAR PLANTS

In 1886, Van Tieghem and Douliot (1886) published the Stelar Theory to interpret the evolutionary sequence represented by differences in morphology of the primary vascular and associated tissues (collectively referred to as the stele) between different groups of plants. A review of the concept of the stele can be found in Esau (1965, 1977) and Foster and Gifford (1974). Very primitive vascular plants possess a relatively simple vascular system in both shoots and roots. The protostele is characterized a by a solid core of primary xylem surrounded by an outer layer of primary phloem. More advanced vascular plants developed a more complex primary vascular system in their shoots. The siphonostele contains a central column of pith and a primary tissue composed of thin, nonlignified, isodiametric cells and is considered phylogenetically more advanced than the protostele. This type of stele is characteristic of the shoots of many ferns.

Coniferous and dicotyledonous trees possess a stele within the shoot that appears, in transverse section, as a ring of more-or-less discrete vascular bundles separated by parenchyma tissue with a central core of pith. Brebner (1902) named this vascular configuration the eustele. A clearer understanding of the structure and function of the eustele, and associated phyllotaxy, must include a three-dimensional view of the primary vascular system. Fortunately, for the purpose of this paper, an in-depth analysis and comparison of stele types and function is not necessary. A detailed description of stelar structure is presented by Beck et al. (1983).

In plants with a eustele, the transition from primary growth to secondary growth is marked by the development of a vascular cambium within and between the primary vascular bundles. Development begins first between the primary xylem and phloem of the vascular bundles (fascicular cambium) and then in the spaces between the vascular bundles (intrafascicular cambium). Over a relatively short period of time, the vascular cambium forms a sheath in the shoot. Further development of this tissue results in the formation of secondary phloem (to the outside) and secondary xylem (to the inside). If phenological and developmental conditions favor growth ring development within a species of tree, this first layer of primary and subsequent secondary xylem produced during the first year of growth will represent the first tree ring. All subsequent growth rings are then produced by the vascular cambium.

As the vascular plants evolved increasingly complex primary vascular organization within the shoots, the stelar configuration of the root remained primitive. The protostele is the functional vascular architecture in the roots of conifers and dicotylenous woody plants. A three-dimensional reconstruction of the xylem in the transition zone from shoot to root, would approximate the structure of a narrow champagne glass. The solid glass wall would represent both the primary and secondary xylem while the hollow portion, which holds the liquid, represents the pith. The point where the glass constricts to form the solid 'stem of the glass' is analogous to the xylem of the shoot constricting at the base of the tree trunk, excluding the pith from the root. This position is the root/shoot interface and represents the oldest tissues of the plant. The pith date in the shoot (tree trunk), or the xylem core date in the root at this position represents the date of germination.

It should be noted that this date can not be used to infer the exact age of the seed that produced the tree. The seeds of many tree species can remain dormant for several years before germinating. Only after germination and the subsequent development of growth rings can the trees be dated. Therefore, germination dates may not reflect the exact timing of seed mast years.

METHOD

The clear anatomical distinction between the structure of the root (protostele) and the shoot (eustele) is the basis for determining the germination date of trees (Figure 1). The first step is to locate the root collar. The actual location of the root collar, and therefore the root/shoot interface, may be obscured by erosion or sedimentation (Telewski and Lynch 1991). In cases where the base of the tree has been buried by sediments or the soil eroded from around the roots, it will be more difficult to locate the interface zone. These conditions will require analysis of larger sections of the trunk to locate the germination date.

After the section of the tree containing the transition zone between root and shoot tissue has been identified, the next step is identification of shoot tissue with a pith (Figure 1a) and root tissue without a pith (Figure 1b). Locating the exact transition requires a systematic approach of very careful serial sectioning or sanding the root collar using an abbreviated method identical to that employed in stem analysis (Duff and Nolan 1953). It is not necessary to produce histological thin sections of the stem; however, it is necessary to produce a finely polished wood surface so the tissue types can be properly identified under magnification.

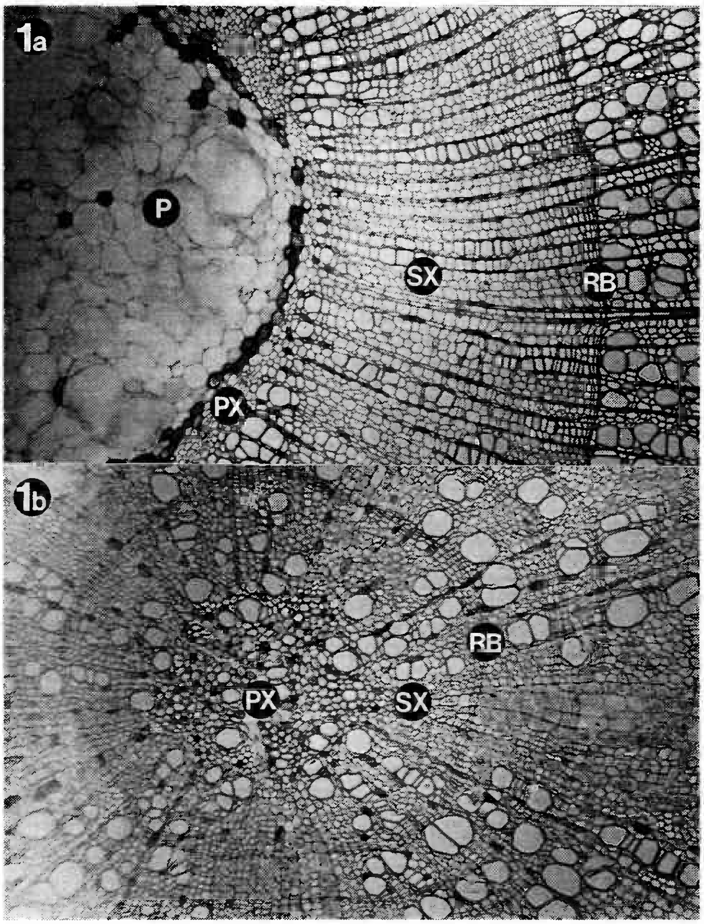

Figure 1. Transverse section of the stem (a) and root (b) of *Tilia americana* showing the pith (P), primary xylem (PX), secondary xylem (SX), and associated growth ring boundaries (RB).

The distance between the top of the last growth increment and the root/shoot interface depends on the amount of extension growth of the epicotyl (stem growth above the cotyledons) that occurred during the first year of growth and the extension of the hypocotyl. Conifers and small-seeded dicotylenous angiosperms, such as *Acer* and *Fraxinus*, produce an extended hypocotyl of up to two cm. Dicotylenous angiosperms with large nut-like seeds, such as *Quercus* and *Juglans*, do not produce an extended hypocotyl, only epicotyl growth during the first year. The height growth can be extensive in fast growing seedlings (in excess of one meter) or quite short in suppressed seedlings (Telewski and Lynch 1991). Some species of pine that possess a "seedling grass stage", such as *P. palustrus* (longleaf pine) and *P. arizonica* (Arizona longleaf pine), produce very little epicotyl extension growth for several years. The first several years of growth occur in the roots, favoring establishment of the young seedlings. Several years of height growth could be lost within a single chain saw cut.

At the first evidence of an absence of pith (or the first occurrence of a pith, if working from the bottom up) the section should be crossdated to verify the exact calendar date of the innermost growth ring. The distortion of growth rings at the root collar may complicate this analysis. It may be necessary to work only with the innermost series of concentric growth rings, produced prior to the tree attaining a large size and compression of the root collar by radically enlarging lateral roots.

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