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Internode or Stem Unit: A Problem of Terminology

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IN RECENT YEARS the term *stem unit* (SU) has increasingly supplanted *internode* in the literature of conifer shoot growth, especially since the adoption of SU in a collection of papers titled "Tree Physiology and Yield Improvement" (Cannell and Last 1976). In standard botanical terminology, a *node* is the point on a stem where one or more lateral appendages (foliage or scale leaves) are attached, and an *internode* is the portion of stem between two successive nodes. The original meaning of SU was more inclusive than *internode,* and the current practice of using SU and *internode* interchangeably has had two negative effects. It makes SU unavailable for use in its original sense, and it creates an obstacle to communication among students of shoot growth.

SU was introduced by C. C. Doak (1935) in his monograph on the morphology and evolution of the pine shoot. *Pinus* is unique among the genera of Pinaceae in its compound shoot, and Doak coined SU to refer to the homologous serial elements of this complex structure. These elements make up the entire plant shoot, not just the stem, and some of the present confusion in terminology may be due to Doak's naming them *stem units* rather than *shoot units.* The same shoot components were named *phytons* or *phytomers* in the 19th century (Arber 1930, Galinat 1959), but only the latter term is still used in this sense.

As defined by Doak (1935), the pine SU has four components, and the first three are always present: (1) a node, (2) the internode proximal to (below) it, (3) a lateral appendage (usually a scale leaf) at the node, and (4) structures in the axil of the lateral appendage. Doak described the SU as fertile or sterile depending on the presence or absence of one of the following axillary structures: a short shoot with fascicled needle leaves (usually one to five), a long shoot, a pollen cone, or a seed cone. By far the most common type of SU in pines past the seedling stage is a short internodal segment of a long shoot, with a scale leaf at its distal (upper) end and a needle fascicle in the axil of the scale leaf. The homologous element of the pine seed-cone, as Doak interpreted it, is a short internodal segment of the cone axis, with a bract at its distal end and a seed-bearing scale in the axil of the bract.

SU was revived by Lanner (1968) to describe pine shoots, and reappeared in print when Van den Berg and Lanner (1971) used both it ("*sensu* Doak 1935") and *internode* in describing the vegetative buds of *Pinus contorta.* Cannell and Last (1976) introduced SU to a wider audience and initiated its current dual usage. In a chapter on variations in pine shoot development (p. 223–243), Lanner quoted and carefully adhered to Doak's definition of SU. In another chapter analyzing conifer shoot growth (p. 173–205), Cannell and others defined SU as "needle internodes" (p. 175), and used SU synonymously with *internode* as well as in its original, broader sense. An appended discussion (p. 521–523) applied SU

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terminology to both coniferous and broad-leaved trees, but this extended usage has not been accepted.

Between 1976 and 1983 at least a dozen papers employed SU terminology. All dealt with the Pinaceae, mostly pines but also species of *Picea* and *Pseudotsuga*. The use of SU varies widely in these papers, and where definitions are obscure or lacking the reader must infer whether SU means *internode* or retains its original meaning. An example of inconsistent usage is a series of papers on shoot growth of *Pinus banksiana* seedlings (Kremer and Larson 1982, 1983; Kremer 1984). In the first paper, SU is defined as "an internode plus the node and its nodal appendage," and in the second as "a node plus its internode." In the third paper (Kremer 1984), SU is not used, and stem growth is described in terms of internodes.

The terms *node* and *internode* have another meaning in forestry, and this may account for the ready acceptance of SU in the limited sector of the scientific literature dealing with conifer shoot growth. In descriptions of the crown architecture of pines and other conifers, *node* refers to a cluster or whorl of branches and *internode* is the part of the stem between successive branch whorls. Van den Berg and Lanner (1971) proposed that this usage be abandoned, but no satisfactory substitutes are available. Misunderstanding can be avoided if these terms are modified to *branch node* and *branch internode* in the context of crown architecture.

To summarize, the usage of SU has evolved in different directions since the term was revived. It is no longer restricted to pines, and could eventually enter botanical terminology as another collective designation for internode/node/lateral appendage/axillary structure. At the same time, SU has been carelessly substituted for *internode* to designate the linear components of the stem. This use erodes the original meaning of SU and introduces an unnecessary source of confusion into the literature on shoot growth.

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