Dormancy: Toward a Reduced, Universal Terminology

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In observing the growth phases of a plant's many structures, a paraphrasing of J.L. Harper (7), and later Sussman and Douthit (13), comes to mind: "Some structures are born dormant, some achieve dormancy, and some have dormancy thrust upon them". Indeed, the dormancy phenomena can be associated with essentially all meristematic regions of the plant. Accordingly, a wealth of terminology has arisen to describe various plant dormancy phenomena. While recently discussing seasonal growth processes, our use and misuse of current and historic dormancy terms led us to conclude that a simplified, descriptive dormancy terminology would be of benefit to the plant science community. Our purpose here is to review briefly the terminology now in use, critically examine dormancy phenomena and reduce terminol-



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ogy to a minimal number of descriptive terms, and consequently to stimulate discussion of this terminology scheme by our peers.

The unwieldy literature. The dormancy literature is littered with a variety of descriptive terms. These may be grouped around 2 general dormancy phenomena. The first of these is predominantly termed "rest" (2, 12, 13, 15, 16, 19; S.A. Weinbaum and T.M. DeJong, personal communication), but also has been called "dormancy" (4, 8), "true dormancy", "main rest", "middle rest" (15), "innate dormancy" (10, 13), "correlative dormancy", "correlative inhibition", "midrest" (12), "winter rest" (5), "winter dormancy" (5, 8, 11), "internal dormancy", "autogenic dormancy", "physiological dormancy", "spontaneous dormancy", "permanent dormancy", "autonomic dormancy"



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(S.A. Weinbaum and T.M. DeJong, personal communication,) "physiodormancy" (19), "deep dormancy" (10), "primary dormancy", "endogenous dormancy", "constitutive dormancy", and "constitutional dormancy" (13). In relation to this phenomenon, Vegis (15) and others (12, 13) also use the terms "early rest", "after rest", "predormancy", "postdormancy", "after-ripening", "secondary dormancy", "preliminary rest", and "induced dormancy". Briefly, the dormancy phenomenon usually described by "rest" is that plant organ condition "characterized by an *internal* (innate) inhibition of growth resulting from physiological factors and having certain distinct features such as onset, intensity, and duration . . . (such that) a given species cannot be induced to grow even if suitable condi-

Fig. 1. Dormancy: a simple, descriptive terminology applied to regulatory factors and examples of plant dormancy.

tions prevail" (19).

The 2nd major dormancy phenomenon is predominantly termed "quiescence" (9, 12, 13, 16; S.A. Weinbaum and T.M. DeJong, personal communication), but it also has been called "imposed dormancy" (15, 16), "external dormancy" (S.A. Weinbaum and T.M. DeJong, personal communication), "relative dormancy", "conditional dormancy" (15), "exogenous dormancy", "environmental dormancy", "enforced dormancy", and "imposed rest" (13). Briefly, the dormancy described by "quiescence" is that plant organ condition "wherein development is delayed because of unfavorable chemical or physical conditions of the environment" (13).

At this point in our discourse, one may ask: if these are the 2 major dormancy phenomena, why not simply pick one of the terms given for each, discard the others, and consider the matter clarified? There are 2 reasons we feel we cannot do this. First, even if the 2 dormancy categories described were all-encompassing, the literature is not free from juxtaposition of terms for one dormancy type with the other. For example, one recent review (10) began by defining strictly the difference between "dormant" buds and "quiescent" buds, then proceeded to refer to "dormant buds" throughout the discussion of "quiescence". As recently as 1984, the term "quiescent" was used synonymously with "correlative inhibition" (8), "correlative dormancy", and "summer dormancy" (10). It also is used in at least one other area of plant physiology which has nothing to do with dormancy phenomena: the histological zonation within the apex, e.g., the "quiesent zone". Also, the term "rest" (modified with various prefixes or adjectives) has been used for both phenomena, as previously shown. Strictly speaking, the word "rest" denotes a general state of inactivity and, as such, lacks specificity in describing a distinct type of dormancy. Second, we feel, as do Samish (12) and others, that a 3rd dormancy phenomenon warrants description.

Dormancy phenomena. Exactly what is meant by dormancy? Dormancy, by definition, is a state of reduced activity or development (1). Broadly speaking, plant dormancy has been defined as "any rest period or reversible interruption of the phenotypic development of an organism . . ." (13); "a period of markedly reduced growth rate with few, or in some cases no, cell divisions in the terminal or lateral meristems \ldots '' (11); the condition in which ''a seed or bud (is) without visible growth \ldots '' (17); ''a period of inactivity in bulbs, seeds, buds, and other plant organs \ldots '' (18). Some definitions have been so analytical as to consider dormancy in terms of changing biochemical parameters, such as rates of protein and nucleic acid synthesis or respiration (10).

For practical reasons, we consider "dormancy" to be a universal term for "no visible growth" of meristematic regions; as such, the term "dormancy" may be used without regard to its cause (12). Specifically, we have chosen the term dormancy to describe the following condition: no visible growth of any structure containing a meristem, e.g., shoot or root apices, vegetative buds, cambium, floral buds, developing leaves, and developing fruit. Regarding the determinant meristems of the latter 3 structures, we note that upon completion of cell division, these structures are no longer meristematic and consequently may only undergo "dormancy" prior to cell division completion. For example, suspension of Stage III cell elongation growth in a peach fruit would not be considered "dormancy". The above description of meristematic structures also encompasses the case of dormancy as it applies to seeds (see 'Application of Scheme to Plant Growth' section).

In developing our terminology, we have used a simple systems analysis approach, focusing on the putative "regulation" of the dormancy phenomena; that is, what event triggers or alleviates dormancy, and where is this trigger perceived? Note that we are not addressing the *final* biochemical event which precludes growth in the structure of interest, but rather where the first signal is perceived or generated, ultimately leading to the final growth-inhibiting reaction. Classifying types of dormancy in terms of regulation leads to 3 distinct phenomena (Fig. 1). The first is regulated by factors external to the plant, environmental in nature, e.g., water, temperature, or nutrients. We term this ecodormancy; by definition, dormancy having to do with habitat or environment.

The 2nd phenomenon is regulated by factors which are within the plant, but which are external to the dormant structure, e.g., apical dominance or certain cases of photoperiodic control. We term this *ecto-dormancy*; by definition, dormancy having to do with an external part. This type of dormancy is analogous to that described by Samish (12) and Chouard (3) as "correlative inhibition", by Fuchigami et al. (5) as "summer dormancy", and by Weinbaum and DeJong (personal communication): as "reversible dormancy" in buds.

The 3rd phenomenon is regulated by factors which are within the dormant structure itself, e.g., chilling or some instances of photoperiodic control. We term this endodormancy; by definition, dormancy having to do with factors inside the affected structure. Our description of these dormancy phenomena is in agreement with others who, while acknowledging 3 probable regulatory points, tended to group the phenomena into only 2 main categories: regulation internal or external to the plant (12), or regulation internal or external to the dormant structure (10). We consider our terminology to be more scientifically descriptive, yet simpler and easier to use, than the plethora of historic terms which are, by and large, imprecise and confusing.

Application of scheme to plant growth. Reviews of dormancy mechanisms generally focus on single plant structures, e.g., seeds or vegetative buds of temperate zone plants (12, 16). We wish to examine several plant structures and apply our dormancy terminology to a number of major examples. We invite contributions of examples we may have omitted or tenuous cases which the reader may feel need further explanation in light of our scheme.

Beginning with the vegetative bud, the cessation of growth due to unfavorable environmental factors, such as drought, temperature extremes, nutrient deficiencies, or air pollution, would classify the structure as *eco-dormant*. Upon supplying the plant with an environment containing the necessary basic growth factors (i.e., adequate water, nutrients, and growing temperatures), eco-dormancy is broken, and the plant resumes growth.

The prevention or cessation of bud growth from physiological factors arising elsewhere in the plant would classify the structure as *ecto-dormant*. A lateral vegetative bud is ectodormant if the apex or the subtending leaf is correlated with suppression of the bud's



Fig. 2. The relative contribution of the various types of dormancy during a hypothetical dormant period for an apical bud.

growth. The ecto-dormancy classification also is applied to changes in cambial activity which are regulated by perception of photoperiod in the apex (14). Terminal buds may become ecto-dormant as day length decreases if the change in photoperiod is perceived by a structure other than the bud, such as leaves (16) or bud scales (11). We differ here from Wareing (16), who considers bud scale inhibition of growth to be "rest" (equivalent to endo-dormancy in our context). We consider the bud scales to be separate from the bud, just as subtending leaves are, and therefore a factor causing ecto-dormancy. Only when the perception of the photoperiodic change (or other regulatory factors, such as chilling) is in the bud itself (11) would the bud be classified as endo-dormant.

We realize, however, that the phases of dormancy may represent a continuous gradient of regulatory events (see Fig. 2); for example, buds may enter eco-dormancy in late summer due to drought, shifting to ectodormancy or endo-dormancy as a result of photoperiod-induced changes in endogenous growth factors. Although the bud entered dormancy due to an unfavorable environment, it is now under the control of endogenous physiological factors that prevent growth even if returned to favorable environmental conditions. Buds which begin growth after having been chilled would be classified as breaking endo-dormancy. When the chilling requirement has been met (terminating endo-dormancy if the plant has no other regulatory requirement), but the temperature is not high enough for growth metabolism, the bud would no longer be classified as endo-dormant, but as eco-dormant. Thus, classifying the type of dormancy imposed upon a single bud over a developmental season is still a trifle tedious with our terminology, but that is a necessity of the science of dynamic systems. We find it far more descriptive than terms such as "prerest, rest, postrest", ad infinitum, all of which merely describe a bud which exhibits no growth, giving no clue as to the hypothesized regulatory event. If the regulatory event is unknown, simply using the term dormant confers the necessary information.

Classification of bud dormancy in nonwoody plants, such as the "eyes" of a potato tuber, would follow similar lines as above. Evergreens and tropical zone plants which display growth on an endogenous rhythm basis (6) would be classified as ecto-dormant or endo-dormant during periods of no growth, depending upon where, in relation to the dormant meristem, the cyclic growth-controlling substance originates.

Regarding roots, Samish (12) has stated "Roots are not thought to have a rest period, and Harris has shown that under favorable conditions root growth continues all year around . . .". This is not to say, however, that roots never exhibit dormancy. Whereas roots may have no internal dormancy mechanism (i.e., no endo-dormancy), they may exhibit eco-dormancy if the environment lacks adequate water, oxygen, nutrients, or suitable temperatures for growth. We can think of no root dormancy cases which would be classified as ecto-dormancy.

The classification of seed dormancy/germination depends upon one's interpretation of seed structure relationships to dormancy regulation. If water and temperatures suitable for growth exist, yet an excised embryo will not germinate without a treatment (i.e., stratification, light, dry storage), it is classified as endo-dormant. However, if it is the seed coat which is preventing germination, the phenomenon may be eco-dormancy or ecto-dormancy. If the seed coat is acting to maintain an unfavorable environment (i.e., an impermeable seed coat provides a situation analogous to water or oxygen stress), seed dormancy would be classified as ecodormancy. This would also be the case if temperatures were too low. However, if the seed coat inhibits growth via production of an inhibitor, which is removed upon chilling or light treatment, the seed would be classified as ecto-dormant. Our line of reasoning for ecto-dormancy in seeds is derived from consideration of the seed coat as a separate structure (genetically and physically) from the dormant embryo; consequently, dormancy-regulating physiological factors originating in the seed coat are analogous to control of bud growth by leaves, apices, or bud scales.

We realize our terminology is ambiguous with regard to time of year. This is deliberate, for as Figure 2 depicts, description of a dormant structure by seasonal terms (i.e., "summer dormancy") confers only the information that the structure lacks growth during a 3-month period of time. Of what use is this term in comprehending *why* no growth is observed? If cause is unknown, "summer dormancy" suffices, but if one or more factors involved are known or hypothesized, "time-of-year" dormancy terms are inadequate for scientific description. We should leave such terms behind and set about to investigate and categorize dormancy phenomena more precisely, and look forward to the day a totally descriptive definition may be stated once plant dormancy regulation has been fully elucidated.

We invite testing of this dormancy scheme across all stages of plant development, and request your criticism and suggestions for improvement. Comments may be sent directly to us or to the *HortScience* Science Editor, who will oversee printing of responses to encourage further evaluation. In addition, we propose to collate your suggestions into our terminology format for possible adoption in the ASHS Publication Manual.

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LETTERS

SPECIFIC LEAF WEIGHT EQUALS 1.0—ALWAYS!

At a recent meeting on the regulations of sources and sinks in crop plants in York, England, frequent references were made to "specific leaf weight", and this quantity appeared on the axes of many figures, frequently with the dimension of mg cm⁻².

Within the Système International d'Unités (SI), "specific" has a very particular use. I quote from the Royal Society's "Little Red Book" (*Quantities, Units and Symbols,* 1975), p. 10:

The word "specific" before the name of an extensive physical quantity should be restricted to the meaning "divided by the mass". For example, specific volume is the volume divided by the mass. When the extensive quantity is represented by a capital letter, the corresponding specific quantity may be represented by the corresponding lowercase letter. Examples: heat capacity, C_P ; specific heat capacity, C_P/m .

The similar use of the work ''molar'' also may be of interest (''Little Red Book'', p. 11):

The word "molar" before the name of an extensive quantity should be restricted to the meaning "divided by amount of substance". For example, molar volume is the volume divided by the amount of substance. The subscript *m* attached to the symbol for the extensive quantity denotes the corresponding molar quantity. Examples: volume, V; molar volume, $V_m = V/n$.

Clearly, "specific leaf weight" is a nonsensical quantity: the weight of a leaf divided by its mass will usually be unity.

The quantity to which the name "specific leaf weight" seems generally to be given is, in fact, the reciprocal of the specific leaf area. "Specific leaf area" is the correct name for the quantity leaf area divided by leaf weight, so that a quantity leaf weight divided by leaf area is (specific leaf area) $^{-1}$. I suppose by analogy with the proper usage of 'specific'' and ''molar'' indicated above, this quantity might be called the "area leaf weight", but I know of no precedent for this. More conventionally, the quantity (leaf weight/leaf area) should be defined as such when it is used and given an appropriate symbol such as W_z . In many instances it will be adequate to refer to this quantity simply as "leaf weight" when the area is unchanging.

How has this misnomer arisen? "Specific leaf weight" does not appear in the earlier, classic papers on growth analysis by V.H. Blackman & G.E. Blackman, G.E. Briggs, R. Kidd & C. West, or R.A. Fisher, and is not to be found in more recent texts like *The Quantitative Analysis of Plant Growth* (G.C. Evans, 1972), *Plant Photosynthetic Production: Manual of Methods* (Z. Sestak, J. Catsky, & P.G. Jarvis, 1971), or *Plant Growth Curves* (R. Hunt, 1982). It seems to be a recent invention of agronomists and plant physiologists. It has, unfortunately, already become rather widespread, particularly in the United States. I hope this note will encourage those who have taken it up, to put it down, as fast as possible.

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RADIATION ENERGY TERMINOLOGY

A bouquet to Holmes, Klein, and Sager for their paper "Photon, Flux, and Some Light on Philology" [*HortScience* 20(1):29–31, Feb. 1985]. As a humble biologist I had almost given up trying to keep up with the changes in fashion of terminology in this field. I had resolved that my inability to comprehend the logic behind "flux density" was that I do not have the mind of a physicist. Now I know that, as I suspected deep down inside, the term really is illogical. I feel much better. Thank you! I could also easily understand their explanation of "fluence rate" and "flux". Well done!

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WHAT IS 30% SHADE?

Many ornamental crops have optimum light levels below the full-sun level for many parts of the country during much of the year. In production, shading compounds are applied to the greenhouse glass or the plants are grown under a polypropylene fabric available in several weave densities to provide different shade levels. The industry commonly refers to shade level as the percentage of shade; e.g., 30% shade. This terminology has carried over to the scientific literature and it is not unusual to read in the Journal of the American Society for Horticultural Science or HortScience that research plants were grown under 30% shade, or some other level. This causes 2 problems for the reader:

1) If one is not familiar with industry practices, it is not known if the light level was 30% of full sun or if 30% of the light was excluded. In industry terminology, 30% shade means the plants were grown at 70% of full sun.

2) Full-sun light level varies with time of year and geographic location, so the reader does not know the actual amount of light the plants were receiving. This could be a significant problem if one tries to duplicate the conditions of the experiment.

I suggest that we give light level in appropriate Système International d'Unités (SI) when it is important to give the light level under which plants are grown. When shade levels are used, we should adopt the more descriptive terminology "light exclusion" (e.g., 30% light exclusion).

This is not the biggest problem facing our publications but it is one that we can improve.

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Letters to the editor, with the writer's name and address, should be sent to: ASHS Editorial Office, Lincoln C. Peirce, Science Editor, Dept. of Plant Science, Nesmith Hall, Univ. of New Hampshire, Durham, NH 03824. Letters may be edited for purposes of clarity or space.