
Growth-Differentiation Balance vs. Carbohydrate-Nitrogen Ratio


It has been nearly 30 years since Klebs (4) published his “Wirk- 
kürliche Entwicklungshemmnisse bei Pflanzen,” in which he 
summarized his earlier work on the behavior of plants in varying 
environments, and proposed the principle that the course of plant 
development is determined by internal conditions, but that these 
internal conditions may in turn be altered by external factors. 
Klebs’ proposal remained largely a matter of academic interest 
until Kraus and Kraybill (5) showed the applicability of his prin- 
ciple to the control of fruiting in commercial crops. It is safe to 
venture that nothing has more influenced horticultural investiga-
tions of the last decade than Oregon Bulletin No. 149. On page six of this bulletin moisture, mineral nutrients, and available carbo-
hydrates as well as total nitrogen and total carbohydrates are 
spoken of as factors affecting the fruiting responses of plants.

The relatively great importance of nitrogen in the field fertiliza-
tion of perennial fruit plants has led some workers to the assump-
tion that the mathematical ratio of total nitrogen to total carbo-
hydrates is a determining factor in plant development although the 
experiments of Work (10), Nightingale (7), Potter and Phillips 
(8), and others clearly indicate that there is no simple or con-
sistent relationship between the ratio of nitrogen to carbohydrates 
and the growth response of the plant. On the other hand the ex-
perience of growers and research workers is adequate evidence that 
there is a relationship between the nitrogen fertilization of an apple 
orchard and its fruiting.

The suggestion is here advanced that the unquestioned progress 
which has resulted from the use of the carbohydrate-nitrogen con-
cept in horticulture has been due to its inclusion of two of the 
important Growth-Differentiation Balance factors, and that its fa-

rises have been due to the omission of other essential factors.

The Growth-Differentiation Concept

Following common practice we divide the development of plants 
into three, overlapping, but reasonably distinct, phases, namely, (1) 
the cell division phase, (2) the cell enlargement phase, and (3) the 
phase of maturation or cell differentiation. The first two of these 
can be grouped together as increase in size, or growth. Differentia-
tion, we are accustomed to think of as morphological in nature, but 
our knowledge of the general course of plant metabolism and of 
the specific responses of plants to varying conditions, makes it 
equally logical to consider observed morphological changes as an 
expression of pre-existing chemical conditions within the cell or 
tissue. For the purposes of the Growth-Differentiation Balance

we define differentiation as the sum of the chemical changes which 
occur in maturing cells, and of the morphological changes which 
arise as the result of these chemical conditions. Qualitatively, 
differentiation is dependent upon genetic factors, but wide quanti-
tative variations are possible.

The recent work of Priestley (9) and others on the growth of 
plants makes it possible to classify some of the more important in-
ternal factors affecting plant development. A tentative classification 
of factors affecting the Growth-Differentiation Balance is given in 
the following tabulation:

Factors Affecting the Development of Plants

I. Growth

A. Cell Division

1. Protoplast. The building of new protoplasts in cell division depends upon 
(a) sugars; (b) nitrogen; (c) sulfur and phosphorus, and probably mag-
nesium, potassium, iron, boron, and other nutrients; (d) the necessary enzyme 
complex; and (e) in some plants, apparently, upon radiation factors not covered 
in the usual concept of photosynthesis.

2. Moisture. According to Priestley (9), cell division is dependent upon a 
liberal moisture supply at the growing point. Drought limits growth directly 
and moisture is a major factor in the growth balance.

3. Temperature. Cell division involves many biochemical changes which are 
accelerated by rising temperatures over a limited range and inhibited by ex-
cessively high temperature.

4. Oxygen. Available oxygen is essential but its concentration apparently 
and not be high.

B. Cell Enlargement

1. Moisture. The enlargement of the newly divided, plastic walled cells ap-
pers to depend almost alone on available moisture. Higher osmotic pressure will 
increase the force with which water is absorbed, but they commonly mean higher 
sugars and a rapid thickening and decrease in the extensibility of the cell wall.

II. Differentiation

1. Sugars. The maturation of enlarged cells is primarily a series of chemical 
processes for which available carbohydrates (probably sugars) serve as the raw 
material. These changes may be in (a) the cell wall, as lignification, sub-
erization, etc.; (b) the chemical composition of the cell contents, as the accumu-
lation of alkaloids, essential oils, gums, etc.; (c) the structure of the protoplast, 
as seems probable in cold and drought resistance and possible in dormancy; or, 
(d) the type of development, as the changes from vegetative buds to flower 
bulbs or from somatic cells to spore mother cells.

2. Temperature is obviously important in a process as dependent upon chemi-
ical reactions as is differentiation.

If we omit oxygen, which is seldom directly limiting for plant 
growth, and temperature, which accelerates reactions on both sides 
of the balance, growth is found to be dependent upon available 
moisture and the synthesis of protoplasm, and differentiation de-
pendent upon available carbohydrates. The carbohydrate-nitrogen 
balance has been modified by raising the water supply from an 
incidental to a major and frequently determining factor, and by
including with nitrogen all of the other complex, and in many cases unknown, factors which affect the synthesis of protoplasm.

Kraus and Kraybill (5) suggest, and Work (10) and Potter and Phillips (8) emphasize, that accumulations of insoluble carbohydrates are a better measure of the past history of the plant than of its present responses. It is felt that if analyses could be made at the instant of the initiation of a particular carbohydrate response that soluble materials and probably sugars would be the active substances. For this reason sugars rather than total carbohydrates are given as the important factor affecting differentiation.

**Applications of the Growth-Differentiation Balance**

If plants are grown at moderately high temperatures with liberal supplies of moisture and nutrients and with favorable illumination, the rapid vegetative growth obtained is characteristic of the Class II plants of Kraus and Kraybill (5). Under these conditions the sugars produced by the plant are used in the synthesis of proteins and to supply the high energy requirements of active meristematic tissues. Differentiation approaches a minimum for the species, and flowering may be suppressed. At the same time the shoots produced are succulent and their cell walls thin and poorly lignified. The leaves are large with little or no cuticle and with poorly developed conducting tissues. The accumulation of gums, alkaloids, or essential oils, etc., is reduced to a minimum and the plant is non-dormant and non-hardy to cold and drought. All of these conditions are according to our definition, expressions of the dominance of growth over differentiation.

If the growth of such a rapidly growing and relatively undifferentiated plant is checked in a manner which does not appreciably reduce the photosynthetic activity of the plant, for example, by gradually reducing the moisture or nutrient supply available to the top, the carbohydrates formerly used in growth now accumulate and serve at once as the stimulus and as raw materials for differentiation. Cuticle and cork develop, cell walls are thickened, fibers and conducting elements are more abundant in the new tissues, resins, gums, alkaloids, etc., accumulate, the protoplasts become more resistant to drying and cold, and flowering may result.

Numberless examples could be given to illustrate differentiation resulting from increased carbohydrate concentrations. The best tobacco for cigar wrappers is grown under shade in humid climates with minimum differentiation, but the best tobacco for insecticides is grown in hot, dry sections with brilliant sunshine. Rubber and camphor producers choose sections in which the climate alternates from conditions favorable to growth and the production of a large photosynthetic area to conditions which favor the accumulation of sugars and the differentiation of the commercial product desired. Plants grown in bright sun on dry soil are more differentiated than shade plants growing in moist soil. Plants whose roots are injured may flower heavily but plants which have lost portions of their photosynthetic area commonly show a growth response, and so on.

An interesting and important subphase of the general G/D Balance is the root-top ratio. Although growth and differentiation in the roots is not essentially different from the same processes in the top, the interdependence of the roots and tops for their supplies of materials necessary for growth has been shown by Chandler (1) and by Loomis (6) to result in an equilibrium between the growth of these organs. When moisture and nutrient conditions are favorable for top growth the organic foods are used in this process and root development suffers. With differentiation conditions and sugar accumulations in the top, as the result perhaps of dry or infertile soil or of deficient root development, organic materials are translocated to the roots, and root development is stimulated.

**The Growth-Differentiation Balance and Reproduction**

Within our definition of differentiation, sexual reproduction in seed plants consists of alternating cycles of differentiation and growth. The flower bud is initiated by differentiation; it grows into the flower. The gametes are differentiated; the fruit and fertilized ovules grow. With this rapid swing from one type of development to the other it is commonly impracticable to alternate the G/D Balance and we compromise by growing fruiting plants under intermediate conditions so that differentiation and growth can occur simultaneously; Class III of Kraus and Kraybill (5). The differentiation nature of flower bud initiation and the importance of relatively high sugars at this point is generally recognized. The work of Howlett (3) and common experience in orchard practice indicates the importance of protoplasm synthesis and water supply in flower and fruit growth.

**The Growth-Differentiation Balance and Hardiness**

The recent work of Graber (2) and his associates indicates that winter hardiness is dependent upon a high carbohydrate supply in the tissues and suggests that hardiness is a differentiation process. In a private communication Dr. J. N. Martin states that the appearance of the protoplasts in hardened alfalfa and sweet clover plants is distinctly different from that of the unhardened plants of the same variety. Future research may show that hardiness is the result of a structural differentiation of the protoplast which makes it more resistant to precipitation, such differentiation being dependent upon and in part initiated by a high sugar concentration in the tissues.

**The Growth-Differentiation Balance and Photoperiodism**

Our knowledge of the nature of the photoperiod response is so meager as to make generalizations on the topic somewhat danger-
ous, but the observations of Nightingale (7) that nitrate and starch accumulate together in short-day, flowering, salvia plants suggests an explanation of this interesting and important phenomena. Nightingale's data can be interpreted as indicating that the synthesis of protoplasm in short-day plants is dependent upon the length of the daily illumination period. Under short-day conditions protoplasm synthesis, and therefore growth, is checked, carbohydrates accumulate in spite of the short period for photosynthesis and differentiation results. The nature of the photochemical reactions involved can of course be determined only by further research.

In long-day plants these factors necessary for protoplasm synthesis may be produced more rapidly so that long light exposure which reduces available moisture and increases photosynthesis is the factor checking growth and resulting in the sugar accumulation necessary for flower bud differentiation.

**Summary**

Plant development is divided into two phases, namely, growth and differentiation; and variations in the form, chemical composition, and growth behavior of a genotype are explained on the basis of variations in the Growth-Differentiation Balance within the plant.

Growth is defined as increase in size due to cell division and cell enlargement, and differentiation as the sum of the chemical and morphological changes which start during cell enlargement and end with the death of the cell.

At moderately high temperatures growth in plants is dependent upon the moisture supply at the growing point and upon the supply of synthesizable, protoplasm building materials. Differentiation, under the same conditions, is assumed to be dependent upon the sugar concentration of the cell sap of the differentiating cells or upon substances closely correlated with this concentration.

Growth-Differentiation Balance differs from the Carbohydrate-Nitrogen Balance as commonly stated in (a) assigning an independent and major role to moisture, (b) including with nitrogen the other equally essential if not so commonly limiting factors concerned in the synthesis of protoplasm, (c) recognizing the effects of temperature, and (d) emphasizing the importance of active carbohydrates as opposed to storage forms.

The concept of Growth-Differentiation Balance is not offered as a complete and final statement of the developmental processes in plants, but as a convenient and simplified scheme for predicting or explaining plant behavior.

**Literature Cited**