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Understanding Indeterminate Soybean Leaf Appearance Dynamics

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Maximizing canopy cover at the beginning of pod setting is key to maximizing soybean yield; canopy cover depends on the number of leaves and their size. This article explains the process of leaf formation and appearance in indeterminate soybean, from seed germination until the end of leaf appearance at the beginning of seed filling. Understanding these processes can help soybean producers in Nebraska and other production areas optimize their management practices to ensure proper canopy cover and to help maximize seed yield.

Key Terms

Phyllochron: rate at which successive new leaves visible to the naked eye appear at the main stem apex

Primordium: clump of cells (invisible to naked eye) that will form into visible leaves

Shoot apical meristem (SAM): located in the main stem tip where successive primordia develop

Plastochron: rate at which successive new primordia develop at the SAM

Determinate: growth habit in which main stem tip node accrual ceases at beginning of flowering

Indeterminate: growth habit in which main stem tip node accrual ceases at beginning of seed filling

Most soybean cultivars grown in the north-central United States are indeterminate in growth habit. In indeterminate soybean, a new main stem node is created at the main stem apex in a cyclic manner. Botanically, the rate at which new leaves visible to the naked eye appear at the stem apex is called the **phyllochron**. Most producers and crop consultants are familiar with the **phyllochron**-based soybean staging system developed by **Fehr and Caviness (1977)**. In the **F&C** system, main stem node accrual is assessed with a **Vn** code (i.e., cotyledon node is **V0**, unifoliolate leaf node is **V1**, and the trifoliolate leaf nodes thereafter are coded **V2** on up). Plants whose uppermost leaflets are just unfolding are assigned a **Vn** based on the **n**th main stem node just below the node with the unfolding leaflets. For more details on soybean staging, please refer to the following:

- *A Visual Guide to Soybean Growth Stages*, **published by University of Wisconsin–Madison Extension, at https://ipcm.wisc.edu/download/pubsGuides/UW_SoybeanGrowthDev.pdf**
- *Nebraska Soybean & Corn Pocket Field Guide, 2019 Edition*, **published by Nebraska Soybean Checkoff, Nebraska Corn Board, and University of Nebraska–Lincoln, at https://nebraskasoybeans.org/wp-content/uploads/2019/06/58960–25_NE_SoybeanGuide_NoCrops-1.pdf**

Maximizing leaf number in indeterminate soybean requires an understanding of the cellular basis of the **phyllochron**. Invisible to the naked eye, each new leaf begins as a clump of cells (known as a **primordium**) that sequentially develop at the periphery of the shoot apical meristem (**SAM**). The

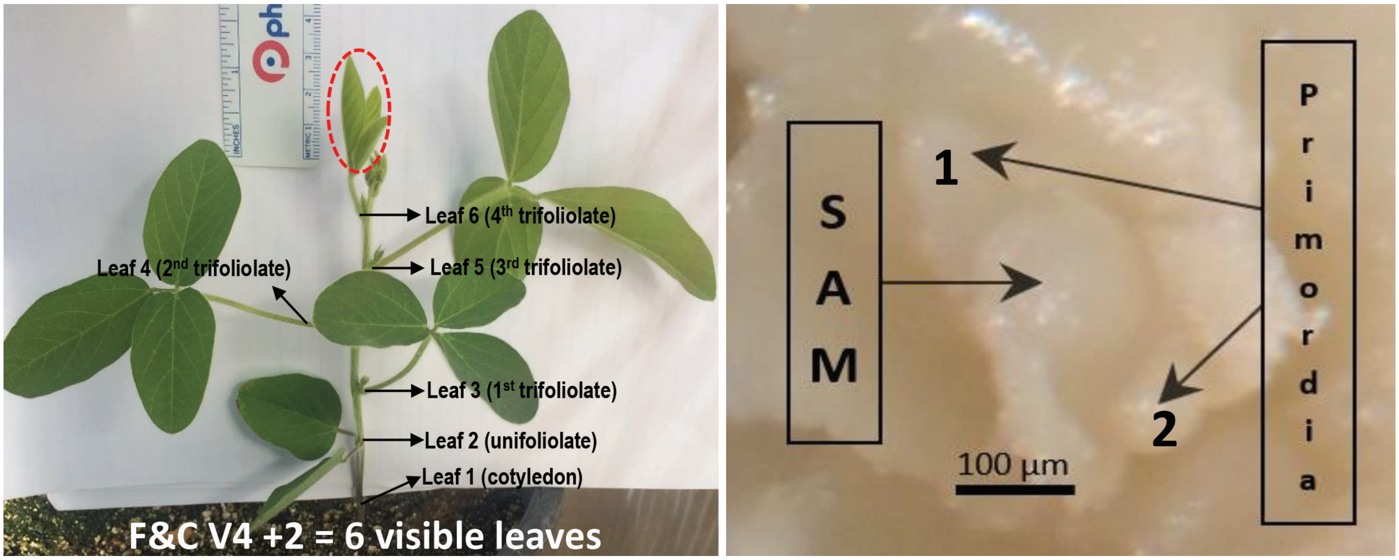

Figure 1. Left: A soybean plant at the **Fehr and Caviness (1977) F&C V4** stage, where **V0** is the cotyledon node. **Tenorio et al. (2017)** counted as "visible leaves" the cotyledons (**1**), unifoliolates (**2**), and the next four trifoliolates (**3**, **4**, **5**, **6**), which leads to the Tenorio node count of **six** being equivalent to **F&C V4** + **1** cotyledon + **1** visible trifoliolate whose three leaflets have unfolded to no longer touch. **Right**: Leaf primordia are evident in this microscopic image as two cellular clumps ("bumps 1 & 2") on the peripheral circumference of the shoot apical meristem (**SAM**). The lower right primordium 2 is the more recently developed of the two "bumps".

rate at which new primordium develop at the **SAM** is called the **plastochron**. Recognizing the factors that could affect the developed **primordia** at **SAM** to potentially appear as visible leaves can help producers optimize their management practices to increase yield. In addition, understanding **plastochron** and its relationship with **phyllochron** provides a convenient way for producers to know the total number of leaves (visible and invisible to naked eye) at any given **F&C Vn** stage. For example, **if a hail storm occurs at V7 and damages the SAM where primordia are already developed, how many future leaves have been lost?** Being able to answer such questions will provide a more accurate estimate of yield loss, in this case from hail damage.

The **plastochron** (days between successive microscopic leaf primordia) was known to be faster than the **phyllochron** (days between successive leaves that are visible to the naked eye) in the indeterminate soybean, based on 70-year-old reports by **Miksche (1961)** and **Johnson et al. (1960)**. However, only recently were the two rates quantified in a comprehensive way (**Tenorio et al., 2017**). The difference in the two rates is important to know, given that soybean stem node accrual, at any given **F&C Vn** stage, will not only reflect the number of main stem nodal leaves that are currently visibly evident to the crop scout, but will also be reflective of the number of leaf primordia that are not visible (except microscopically) at the stem tip. The latter number is a key component, because it is predictive of future main stem nodal leaves that have yet to fully develop into visible leaves. **Tenorio et al. (2017)** provide the pictorial and microscopic evidence of this coordination. In this study, the indeterminate main stem nodes were numbered differently than in the **F&C** system, with the cotyledon node numbered by Tenorio as **1** (not zero) and the last stem node counted being a visible leaf (not the node below an unfolding leaf as in the F&C system). For that reason, the "visible" node count discussed in the **Tenorio et al. (2017)** paper will be **two** main stem nodes greater than the equivalent **Vn** stage in the **F&C** staging system.

Displayed in **Figure 1** (**left**) is an indeterminate soybean plant that is in the **F&C V4** stage (i.e., cot node **0**; uni node **1**, 1st tri node **2**, 2nd tri node **3**, 3rd tri node **4**, with the 4th tri node **5** showing just unfolding leaflets). **Tenorio et al. (2017)** numbered these six visible leaf nodes as **1 thru 6**. Keep this nodal count difference in mind as you view the remaining figures. A microscopic view of the main stem apex of the same plant (**Figure 1**, **right**) shows the stem tip, including the **SAM** along with two recently developed "bumps" of leaf primordia at periphery of the **SAM**. The lower right one is the most recently developed primordium 2 and the upper left one has been the prior developed primordium 1.

Given the information provided in Tenorio et al. (2017), we can ask and answer four major questions.

1. **How many leaf primordia does a dormant seed have?**

Figure 2 displays microscopic images of a dormant soybean seed that has undergone a 3-day germination period. Prior to germination, the dry seed possesses

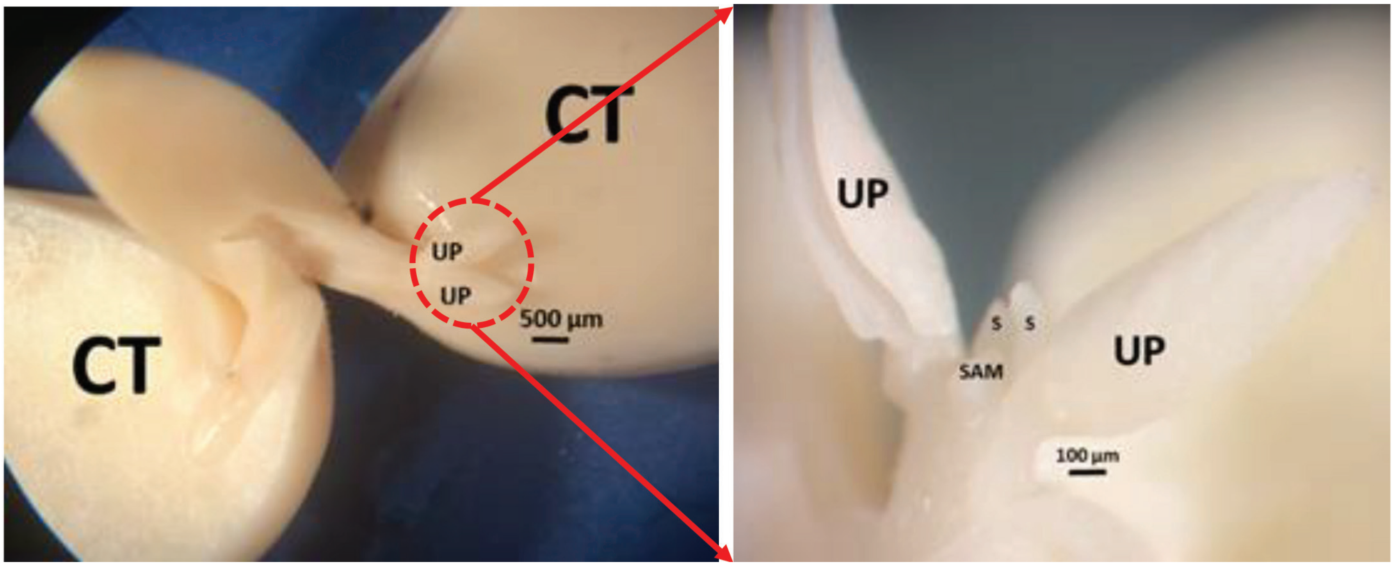

Figure 2. Microscopic images of a **3-day pre-germinated soybean seed** showing the cotyledons (**CT**) in the **left** image, and with the cotyledons removed in the **right** image. Evident are the two unifoliolate primordia (**UP**), and the shoot apical meristem (**SAM**). The stipules (**S**) are also shown.

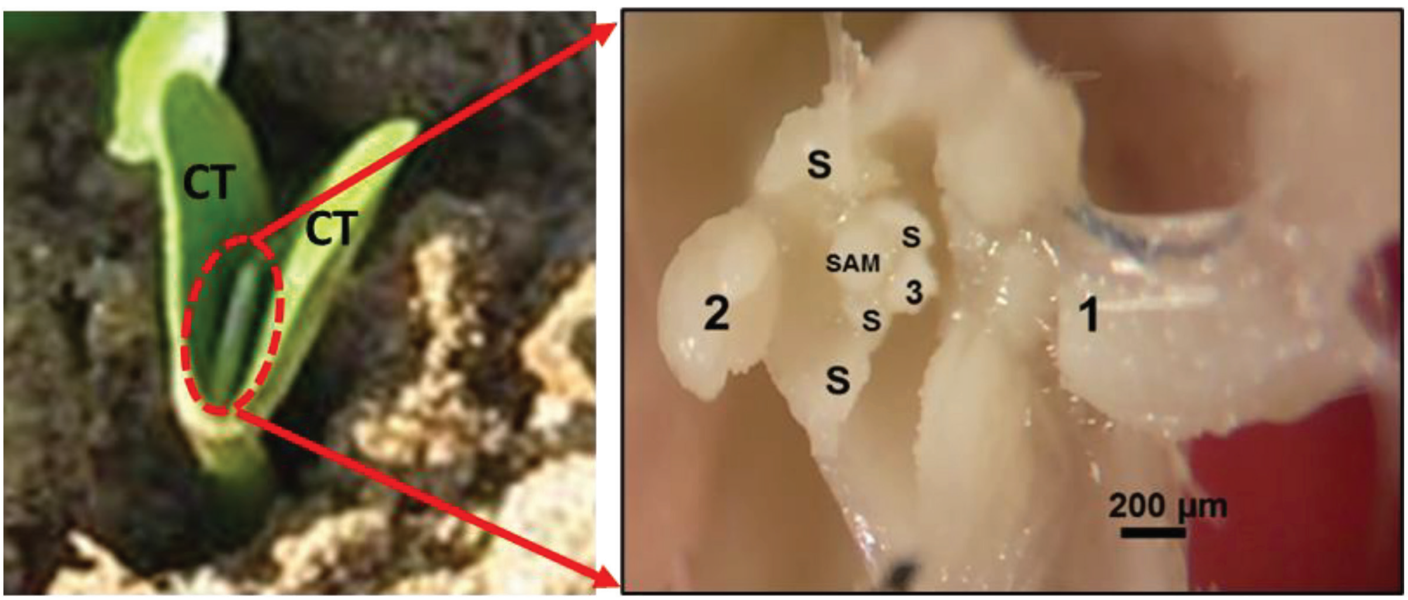

Figure 3. Left: A soybean at the emergence stage (**F&C VE**) showing the pair of cotyledons (**CT**). **Right**: Zoomed microscopic image showing the emerged seedling main stem tip, but with cotyledons and unifoliolates removed to better show the first (**1**), second (**2**), and third (**3**) formed trifoliolate primordia (**TP**) that have developed in that chronological order. Also shown are the **SAM** and stipules (**S**).

cotyledons (which originated from primordia developed when that seed was forming on the mother plant during the **F&C R5** to **R6** seed development stage). In the same dry seed, the unifoliolate leaflets are still in an initial primordial stage as shown here. Soon after the onset of germination, two **unifoliolate primordia (UP)** rapidly develop.

2. **How many primordia are present at the shoot apex of an emerged soybean seedling (F&C VE stage)?**

At **emergence**, aside from the visible pair of cotyledons and pair of unifoliolate leaflets (**Figure 3, left**), the primordia for the first three trifoliolates (numbered **1**, **2**, & **3**) are now microscopically evident at the **SAM** periphery (**Figure 3, right**).

3. **Leaf primordia and visible leaves develop concurrently, but when does each cease?**

Initiation of new primordia at the periphery of the **SAM** continues until the **F&C R3** stage (beginning of pod set) (**Figure 4**). In contrast, the appearance of new visible leaves stops around the **F&C R5** stage (begin-

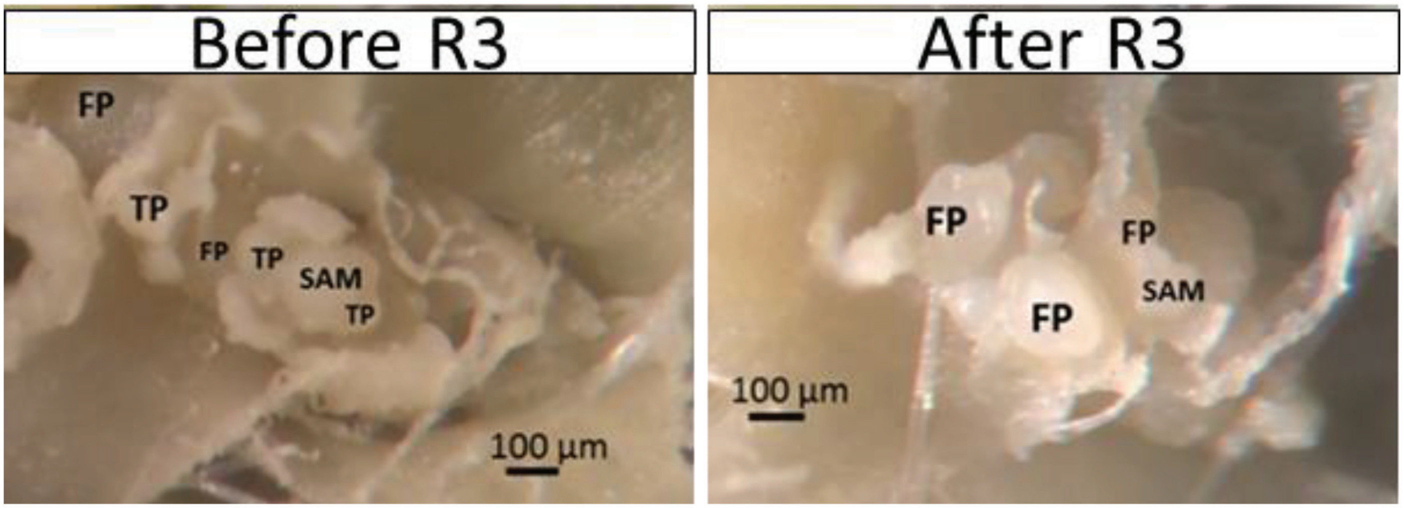

Figure 4. A microscopic image of soybean terminal bud before the beginning of **R3** pod set stage (**left image**) showing the trifoliolate primordia (**TP**) on the flanks of a **SAM**. Before **R3**, axillary buds in each main stem node have already formed floral primordia (**FP**). After **R3** (**right image**), differentiation of **FP** in the axillary bud adjacent to the **SAM** is shown, which is coincident with the end of leaf primordium initiation at the stem apex.

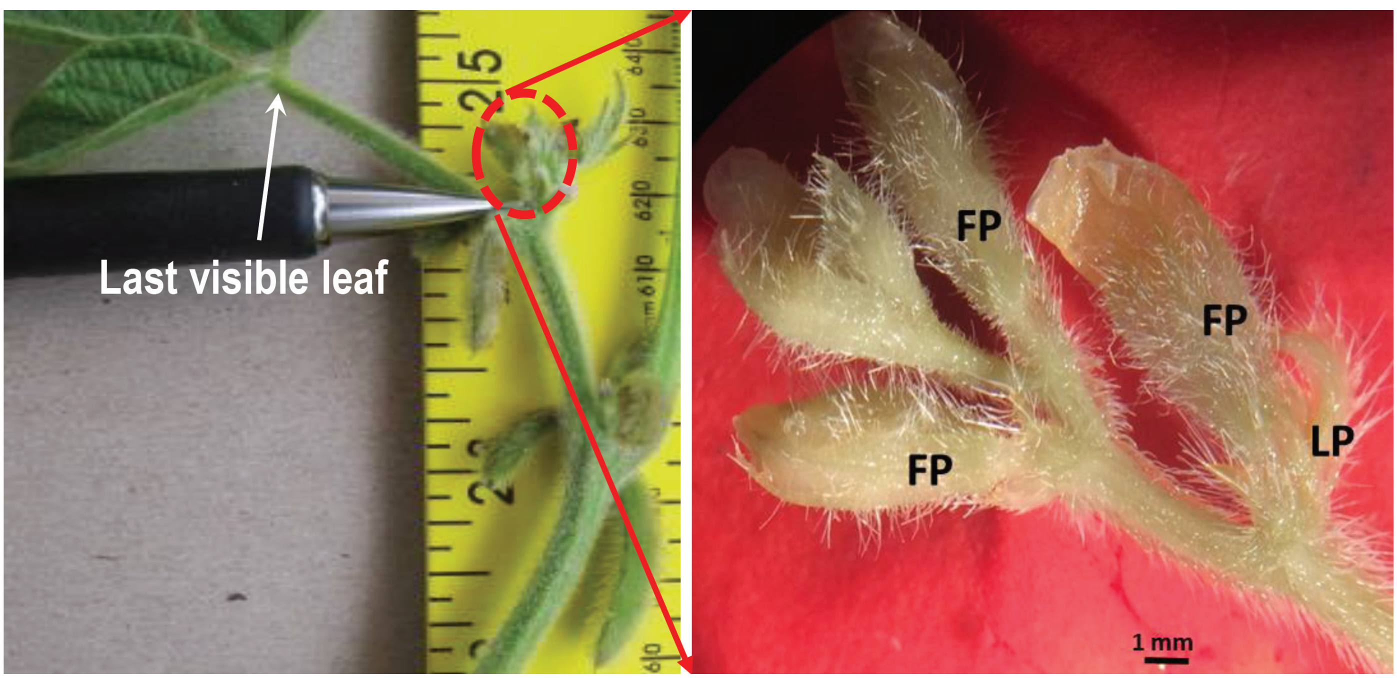

Figure 5. Left: A soybean plant at beginning of seed filling (**F&C R5**) showing the last visible leaf, with the pencil pointing to, and red circle enclosing, the main stem tip. **Right**: Zoomed image showed a microscopic image of main stem tip at **F&C R5** with the floral primordia (**FP**) and a leaf primordium (**LP**) that, because of diversion of all new photosynthate to developing seed after **R5**, will lead to that **LP not** developing further into a fully visible leaf.

ning of seed fill) (**Figure 5**). In indeterminate soybean, the visible leaflets at the stem apex become noticeably smaller and smaller near the end of **R5** stage, and eventually become only microscopically detectable. So, the degree to which initiated primordia will appear as developed visible leaves depends on thermal time between **emergence** and **R5** as determined by **cultivar maturity group** and **latitudinal group**. That said, one can expect to see a higher number of visible leaves on the main stem in scenarios that favor a long seasonal cycle such as a later maturity group and/or an earlier planting date.

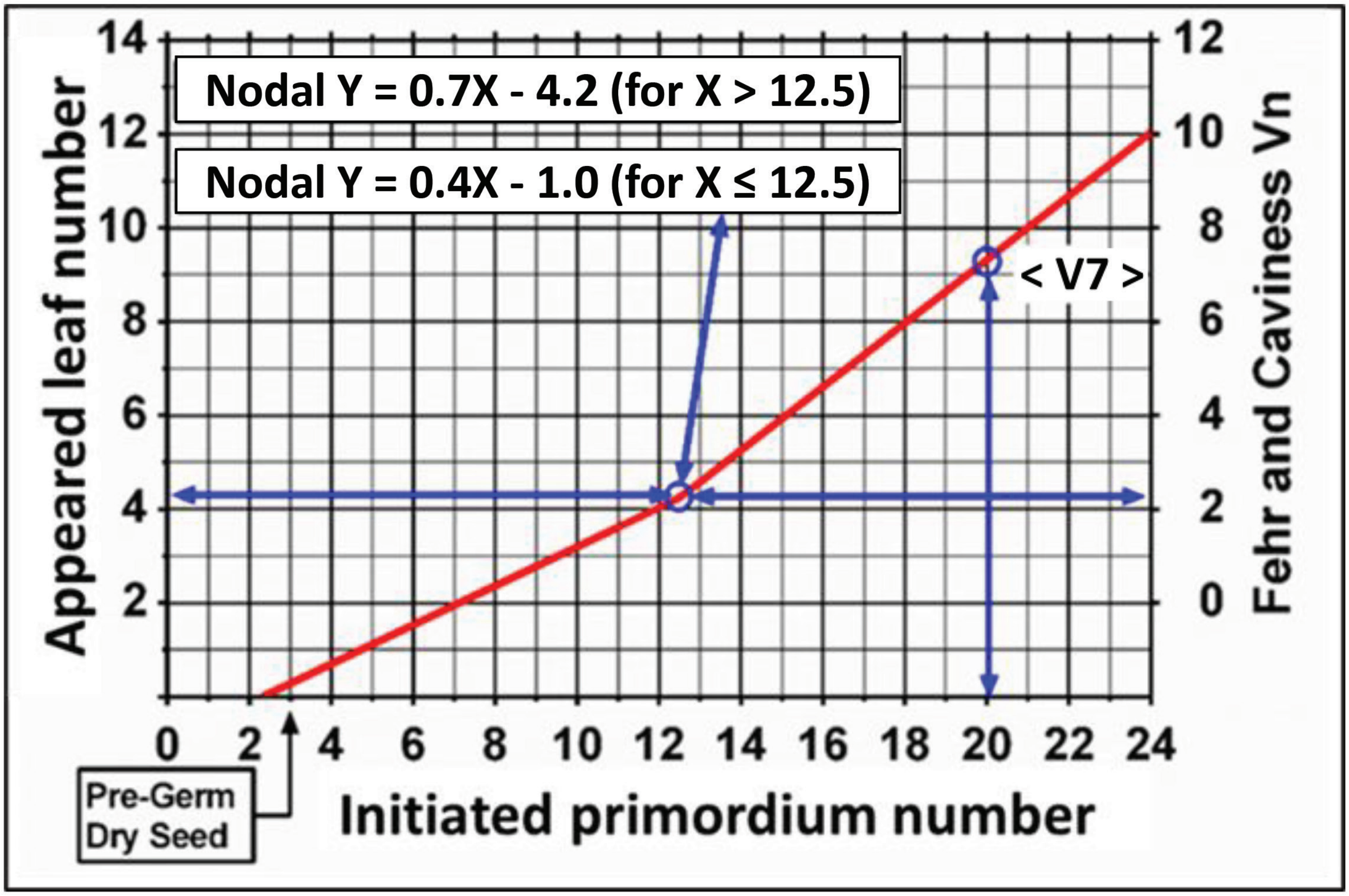

Figure 6. Relationship between appeared leaf number and initiated primordium number in indeterminate soybean. Appeared leaf number = Fehr and Caviness Vn + 2 (cotyledon + last leaflet with edges not touching).

4. **How fast does primordia initiation occur in relation to leaf appearance?**

Figure 6 summarizes the answer to this question based on the results of **Tenorio et al (2017)**. In this chart, the bottom axis is the main stem nodal designation for leaf primordia that are numbered from node **1** (cot node—Tenorio) on up to **24**. The right axis displays the **F&C Vn** nodal stages (**V0**=cot node) while the left axis shows the total visible nodal leaf count (as noted previously equivalent to **Vn + 2**). The red line denotes the two-segment linear regression model that best explains the relationship between "appeared" (visible to the naked eye) leaf number (left axis) and "microscopic" leaf primordia number (bottom axis). From sowing to **F&C V2**, the indeterminate soybean shoot apex produces about **2.5** (=1÷0.4) **new primordia per each new leaf that appears**. Thereafter, **1.4** (=1÷0.7) **new primordia are produced per appeared leaf**. Note that the regression line breakpoint occurs at about leaf primordium number **12.5**, which is concordant with **F&C** stage **V2** and appeared leaf number **4**.

Layperson Bottom-Line

The implication of these findings is that if a producer or crop consultant uses the **F&C** staging system to scout a given indeterminate soybean field grown in the north-central US region, they can then use the scout-date-specific detected **Vn** stage (shown on the right axis in chart) to find the concurrent total number of leaf primordia accumulated as of that date. For example, if the scout reported a **F&C** stage **V7** (blue circle on chart) for the given soybean field, then they could expect that the soybean plants, on that scout date, would likely have accumulated **20** leaf primordia by then (blue line arrow from V7 to 20 in chart). Of those **20**, **nine** would have developed into visible leaves as per **Tenorio** (left axis), so the other **11** would not yet be visible in the stem apex. Thus, if a hail storm occurred at

V7, the hail stones could injure or remove the **11** primordia in the stem apex that would ordinarily have the potential to be future appeared leaves.

Understanding leaf dynamics—both at the macroscopic (**phyllochron**) and microscopic (**plastochron**) level—is important to guide management practices. For example, optimizing practices (e.g., late maturity group or early planting date) that extend the duration to **R5** stage (in thermal time) could increase the possibility for developed primordia at the **SAM** to eventually appear as visible leaves. Finally, the relationship between **phyllochron** and **plastochron** provides a way for producers and crop consultants to determine, at any given crop stage, the number of leaves that can potentially become visible later on.

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