DE GRUYTER HELIA 2021; 44(75): 155–165

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Phyllody in sunflowers; 44 years to explain the appearance of aberrant flowers

https://doi.org/10.1515/helia-2021-0004
Received March 4, 2021; accepted May 11, 2021; published online July 2, 2021

Abstract: Phyllody in sunflowers (*Helianthus annuus* L.) is characterized by the appearance of bracts and ray flowers in the centre of the heads. It has been discussed for decades among the sunflower plant breeders and experts without a clear "unique" explanation for it. The erratic appearance of the phenomena has led to consider it either a disease or hybrid defect and the plants with Phyllody as off-types, raising several farmers claims to seed producers. However, the auxins gradient, in the growing *Asteraceae* heads, determines the differentiation pathway of the undifferentiated cells. i.e., bracts and ray flowers at the border and disk flowers in the centre of the head. Disruption of the natural auxin gradient alters the cell differentiation in the growing heads and causes bracts and ray flowers to grow where only disk flowers should grow. The disruption of the natural head bottom auxin gradients may be caused by small injures in the fast-growing head receptacle. The most common causes of Phyllody are hormonal herbicide damage and Boron (B) deficiency, even temporary. Plants growing with B deficiency have brittle cell wall and membranes while a plant with high B levels produces plastic or elastic cell wall and membranes. Brittle cell walls are susceptible to breaks during growth. Sunflowers genotypes may react to crack or small damages in the sunflower bud in two ways. Some tend to repair the damages by regrowing new organs such as ligules or bracts and forming Phyllody. Others do not regrow and only heal the wound creating the funnel hole head shape.

Keywords: auxins; Boron deficiency; hormonal herbicides; Phyllody; sunflower.

Introduction

Phyllody in sunflowers (*Helianthus annuus* L.), often referred to as a sunflower disease, is characterized by the appearance of bracts and ray flowers in the centre of the heads of certain plants. It has been discussed for decades among the sunflower plant breeders and experts without a clear "unique" explanation for it other

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than this is a Genotype-Environment interaction to a certain extent unpredictable because there is not a single factor triggering it. The percentage of plants with Phyllody in commercial fields is in most cases below 1% but being aberrant, it is not unusual to receive unjustified compensation claims from farmers. But the yield impact is often neglectable.

Mycoplasma infection was suggested (Signoret et al. 1976) based on the presence of Mycoplasma-like bodies in tissues of diseased plants but not in healthy ones. However, the disease was not transmitted using crude sap extracted from infected sunflowers leaves or modified flowers. Boron deficiency was soon associated with sunflowers head deformations and in some cases ray flowers or bracts growing in the middle of the head (Bergmann 1986; Blamey 1976). Different aetiology damages, at the sunflowers, head growing point, followed by plant reparation was suggested as a cause of Phyllody in sunflowers. Among these: Climatic induced damages, such as cold, physical or chemical damages, nutritional deficiencies and genetic susceptibility. During the 1980s a sunflower inbred line showed different degrees of Phyllody and plants with a hole in the centre of the head resembling a funnel shape, indicating these symptoms were different reactions to the same inducing factor (Alonso 1988). In a recent publication (Zoulias et al. 2019) (Figure 1) concerning the causes of Phyllody in the *Asteraceae* (the sunflower and daisies family), showed that the plant hormones auxins are involved in the deformation of the head in all the sunflower family and imply an external factor causing this aberrant head types. Several types of daisies aberrant flowers, with bracts and ligules in the centre of the head, were induced applying different rates of auxins. In this article the authors conclude:

> During capitulum development, a temporal auxin gradient occurs, regulating the successive and centripetal formation of distinct florets and phyllaries**. Disruption of the endogenous auxin gradient led to homeotic conversions of florets and phyllaries in the capitulum**. Furthermore, auxin regulates floral meristem identity genes, such RAY2 and LFY, which determine floret and phyllary identity.

Thus, the auxins gradient in the growing *Asteraceae* heads determines the differentiation pathway of the undifferentiated cells. i.e., bracts and ray flowers at the border and disk flowers in the centre of the head. Disruption of the natural auxin gradient alters the cell differentiation in the growing heads.

Material and methods

In this article, the causes of Phyllody in sunflowers will be reviewed. Observations made since the 1980s (Alonso 1988), the publication on daisies (Zoulias et al. 2019) and recent field observations in two sunflower fields during 2019 have helped to understand better this abiotic disorder.

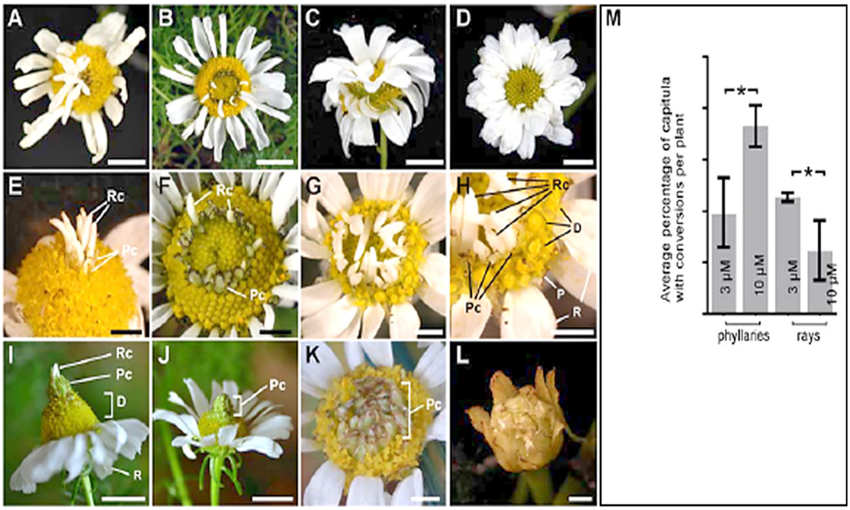

Figure 1: Auxin application induced homeotic conversions in the capitulum. Phenotypes of capitula sprayed with 3 µM (A–I) and 10 µM (J–L) IAA, showing conversion of disc florets into both ray florets and phyllaries (A–I) or solely into phyllaries (J–L). A–D, Capitula with fully developed converted phyllaries and ray florets. E–H, initial developing stages of converted phyllaries and ray florets post IAA treatment. H, Close-up of (G) showing the order of converted phyllaries and ray florets. Scale bars = 5 mm (A–D, I and J), 2 mm (E–H, K and L). Pc; converted phyllary; Rc; converted ray floret. M, Quantification of phyllary and ray floret conversion post-IAA treatment. Each error bar represents the mean ± SEM. Values marked by an asterisk are significantly different ($P = 0.04$ for ray florets and $P = 0.04$ for Phyllaries; Two-tailed *t*-test analysis) (With the approval of the Editor, Retrieved from Zoulias et al. 2019, www.plantphysiol.org/cgi/doi/10.1104/pp.18.01119. (Copyright American Society of Plant Biologists).

Filed 1: observation made on August 15th, 2019 in Syngenta's Agro-Center Barayevo – Northern Kazakhstan

General:

- Sunflower Demo field included several different Syngenta hybrids.
- Field affected by Hormonal herbicide damage coming from neighbours fields.

In North Kazakhstan, there is frequent sunflower damage caused in this way. Wheat Hormonal herbicides are auxins that can fly away several Km as micro-drops and cause damage to dicot crops such as sunflowers. The degree of damage may vary from very light symptoms, difficult to see by inexpert eye, to severe damage in the sunflower bottom stage.

Field 2: observation made in Mato Grosso Brazil, May 21st, 2019: production farms from Campo Novo do Parecis

General: In the area where Parecis, a cooperative of farmers that own an oilseed crushing industry along with Celena. Farmers grow sunflowers as second crop after Soybeans. The yields in the area are very variable year by year from 2 to 3 t/ha. One of the most frequent blamed causes of lower yields was the “lack of pollination” due to very high temperatures. In 2019 there were many fields with aborted seeds. But this explanation did not fit with my experience, as we have in Spain very high temperatures and never observed the types of seed set failures found there. The area had suffered a short drought during the early stages of sunflower growth to receive rains during the floral bottom stage.

The agronomist from ¨Campo Novo do Parecis¨ had also fertilization trials including several combinations of macro and micronutrients.

Results and discussion

The same sunflower genotype can produce aberrant sunflower heads with a hole in the centre, funnel shape, or with bracts and ligules in the centre, Phyllody (Alonso 1988), suggesting these two aberrant head types are a reaction to the same cause.

Field observation in Bayarevo (North Kazakhstan)

- All the sunflower hybrids in the strip test were affected by the hormonal herbicide though plants have recovered well.
- There were differences in the reaction of different hybrids.
- There were a few hybrids showing head Phyllody with different degrees (Figure 2(A)).
- Some hybrids did not show Phyllody but had a “funnel head shape” with a hole in the centre (Figure 2(B)).
- Hybrids that showed Phyllody had recover better from the herbicide damage than those showing no Phyllody.

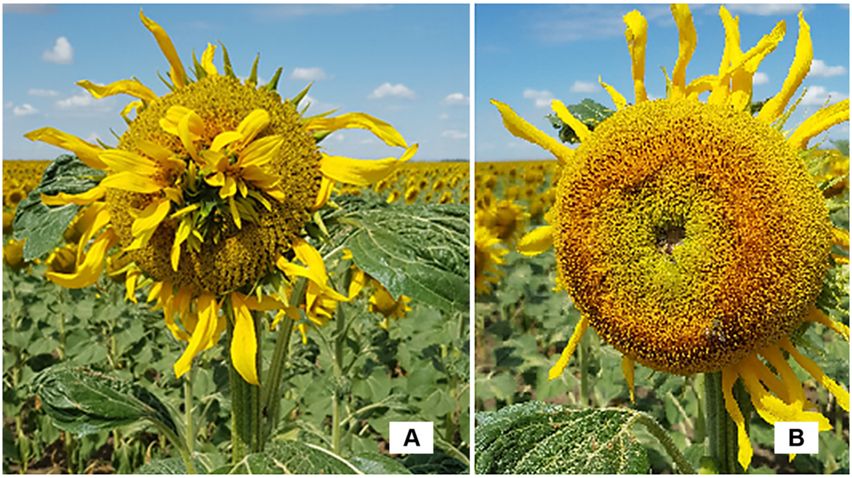

Figure 2: Phyllody (A) and Funnel shape (B) sunflower heads in North Kazakhstan caused by wheat hormone herbicide application.

Insights from this field

- Hormonal wheat herbicides can cause sunflower damage even when the treated fields are several Km away from the sunflower field.
- The typical hormonal wheat herbicide damage in sunflowers include the deformed leaves, easy to be recognized.
- Hormonal wheat herbicides can also cause damage to the growing organs of sunflowers such as the sunflower head in the bottom stage. The artificial auxin causes in the sunflower bottom a disruption of the endogenous auxin gradient. The sunflower plant can react to this in two ways.
  a) Led to homeotic genes, that regulate the development of anatomical structures, to change the development of tubular florets to bracts and ligules in the capitulum. i.e., Phyllody.
  b) Not being able to repair the damage and creating a hole in the growing point. i.e., Funnel shape.

Field observation made in Campo Novo do Parecis, Mato Grosso Brazil

- There were many plants with a very good canopy development but showing many empty seeds.

- The plants did not show the typical Boron (B) deficiency symptoms described on the Borax web page. i.e., deformed heads with bracts and phyllodes inside, young leaves with bronze colour malformed and necrotic, head drop resembling insect cuts and puffy and wrinkled leaves.
- However few plants showed some less known B deficiency symptoms such as Aborted seeds (Figure 3(A)), Longitudinal injures or cracks in the stem (Figure 3(B)), Longitudinal break in the upper part of the petiole (Figure 3(C)) leading to nutrient disruption to the leaf resembling a fungal disease (Figure 3(D)) and funnel shape heads with an empty hole in the centre (Figure 3(E)).
- In a fertilization trial run by Celena's technical team, foliar B application showed plants without B deficiency symptoms in the upper part of the plant while they showed symptoms in the lower part that had grown before the treatment.

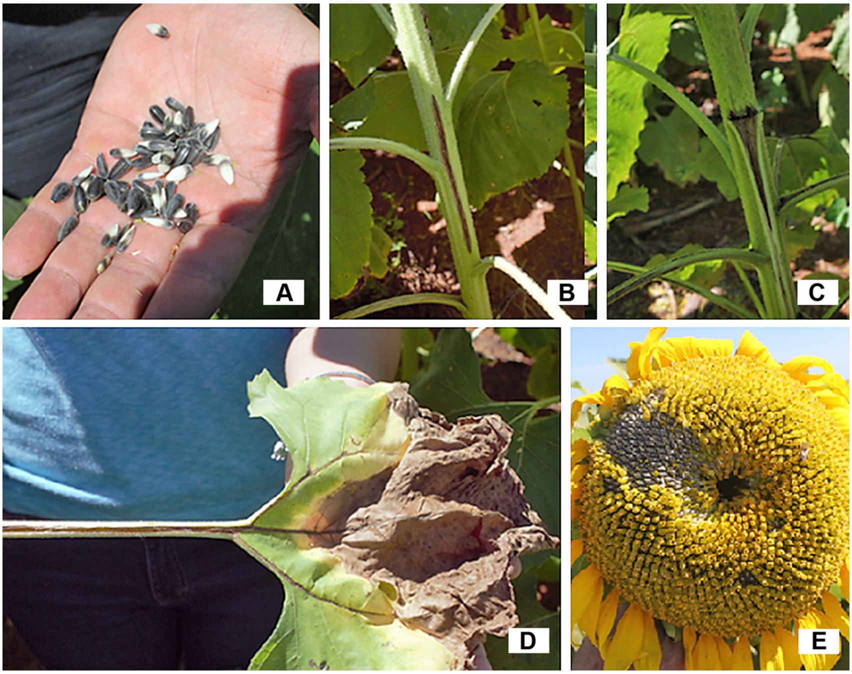

Figure 3: Little known B deficiency symptoms in sunflowers. Aborted seeds (A), Longitudinal injures or cracks in the stem (B), Longitudinal break in the upper part of the petiole (C)) leading to nutrient disruption to the leaf resembling a fungal disease (D) and funnel shape heads with an empty hole in the centre (E).

Insights from these fields

- The drought period during vegetative growth of sunflowers dried the upper part of the soil, where B is available but sunflower plants were unable to take it.
- After the rains, rapid sunflower growth was induced but the plants could not supply B fast enough creating a temporary deficit and the B deficiency symptoms including funnel shape heads.
- When foliar B was applied in trials just before the rains, the plants did not show the B deficiency symptoms.

Sunflower is one of the most sensitive crops to low B supply developing characteristic B deficiency symptoms on leaves, stems and reproductive parts (Asad et al. 2003). B deficiency in plants includes abnormalities in the cell wall and middle lamella organization. Plants membranes flexibility is B dependent. Plants growing with B deficiency have brittle cell wall and membranes while a plant with high B levels produces plastic or elastic cell wall and membranes (Pandey 2013). Thus, the observed symptoms in Campo Novo do Parecis in 2019 were B deficiency symptoms. These are caused by the fast growth of the sunflower plant with a mild or temporary B deficiency. The sunflower tissues become brittle and under the growth tension break causing vertical wounds in the stems and longitudinal on the leaf's petioles.

Figure 4 illustrates a drawing recreation of a sunflower transversal section showing a break in the outer epidermis (1) due to lack of cell walls and membrane plasticity. When the stem grows in diameter the break becomes a wound (2) with a vertical appearance as in stem as shown in Figure 3(B)–(D).

A very fast and vigorous growth after a period of slow or no growth can also cause small cracks in the apical growing meristem and the natural auxin gradient is altered. Different events can cause cracks and auxin gradients in the growing head receptacle but b) and c) in the below list are probably the most frequent.

a) Day/night temperature difference

If during the night the temperature falls below the biological needs for sunflowers, the growth stops. The next morning, if the temperature rises to favourable growth the plant restarts growing at a fast rate. These "Stop/grow" changes may alter the natural auxin gradients within the floral button and cause the Phyllody or the funnel hole damage.

b) The presence of hormonal herbicides

As shown in the example from Kazakhstan, the wheat hormonal herbicides (auxins) can damage sunflowers even when the crop is planted many Km apart

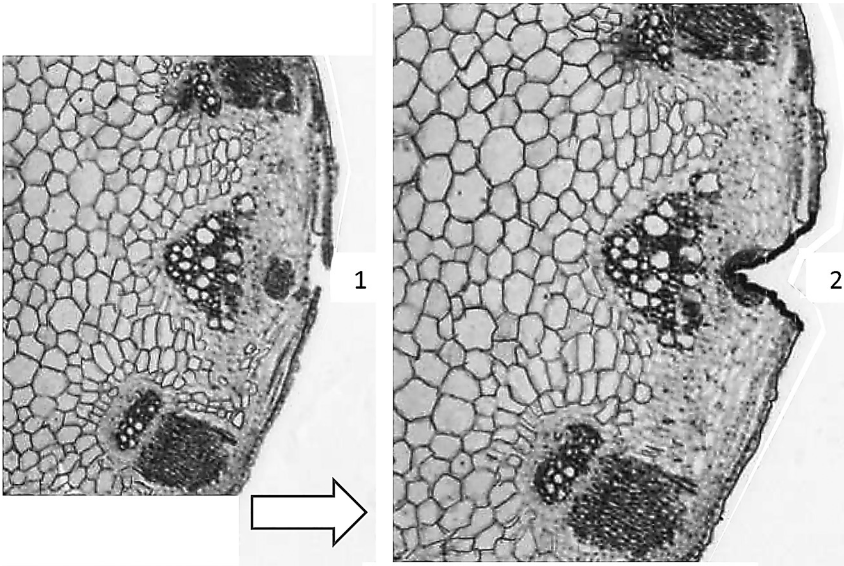

Figure 4: The drawing illustrates a sunflower transversal section showing a break in the outer epidermis (1) due to a lack of cell walls and membrane plasticity. When the stem grows in diameter the break becomes a wound (2) with a vertical appearance as in sunflower stem.

from the treated field. This hormonal herbicide damage, as in the example of daisies, can alter the natural gradients of auxins in the growing sunflower floral botton and cause either phyllodies or funnel hole type heads.

c) Boron deficiency

This is the most frequent cause of growing heads damages, as sunflowers is a very sensitive plant to B deficiency and there are some considerations.

1. Boron is only available in the upper layer of the soil. If this layer dries in certain periods, leaves the sunflower plant with a B deficit.
2. Boron does not move from lower to upper leaves of sunflowers. I.e., If during the season, there is enough water in the soil during the early part, the sunflower plant may have enough B. But drought can cause the sunflower plant to take nutrients from deep soil layers where B is not available. Thus the plant may enter a fast-growing period without enough B supply and being unable to mobilize it from already developed leaves.
3. If after a dry period, the rains arrive, sunflowers may react to growing very fast. Vigorous hybrids compensate faster the water deficit period and grow very fast. If during a certain period, there is a B deficit, the cell walls and membranes

become brittle and susceptible to breaks during growth. i.e., vertical injuries in the stem, break of leave petioles and some damage in apical meristems. Thus, vigorous growth causes the breaks. These breaks disrupt auxins gradients in the growing head.

4. The boron deficiency may be temporary, as the rains also make the upper soil B available to the plant. Thus, the yield may not be affected whereas in soil with strong B deficiency the plant will abort seeds too.
5. Hybrids or inbreds with little vigour may not grow vigorously when they receive rains after a dry period, thus may not show any head deformation but this may reflect the incapacity of these hybrids to compensate and recover good yield after a dry period.

d) Pathogens and insect damages

The possibility of pathogens and insects damaging the growing point of the sunflower head cannot be discarded. The sunflower reaction would be the same once the natural auxins gradients are altered.

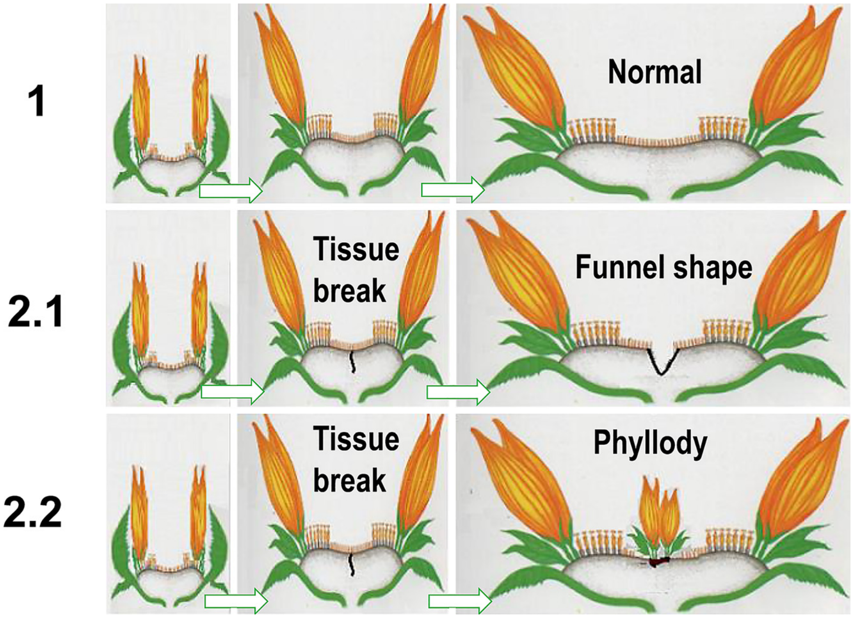

Figure 5: Sunflowers flowering head growth may follow the normal pattern (1) or have cell breaks in the head receptacle. The breaks disrupt the endogenous auxin gradient. In some cases, the plant only repairs the damage leaving a funnel head shape (2.1) while in others the plant regenerates the injured tissues producing Phyllody.

Sunflowers reaction to crack or small damages in the sunflower bud varies from hybrid to hybrid. Some vigorous hybrids tend to repair the damages by regrowing new organs such as ligules or bracts and forming phyllodies. Other, less vigorous genotypes, do not regrow and only heal the wound creating the funnel hole shape. Figure 5 illustrates these two possible pathways to repair the head damage in sunflowers.

Hybrids that tend to produce phyllodies are often the highest in yield potential. This may be due to their genetic "extra vigour" to grow fast when the water and temperature conditions are ideal. But this "extra vigour" has a penalty. If there is some B deficit, even temporary, the plants may receive some damage in the growing points and produce aberrant flowers. Phyllody may result in alarming or ugly, but the impact on comparative yield/ha of hybrids having phyllodies vs those not having it is often in favour of those having it. if the yield expectation is above 2 t/ha it is recommendable to apply soluble B before or at the very early bottom stage to secure the plants have enough B during the fast-growing period avoiding not only Phyllody but also other B deficiency symptoms.

Conclusions

The appearance of aberrant sunflower capitula with ligules and bracts in the centre (Phyllody) have caused multiple complaints from farmers who consider it a genetic defect or lack of varietal purity. By associating this reaction with some genotypes more than others, breeders tend to select against these genotypes. However, there is no adequate explanation for this phenomenon. In this review we have been able to verify:

- That Phyllody is caused by a disruption of the auxin gradient in the growing heads as occurs in daisies.
- Various external factors can damage the growing flower bud and these cause disruption of the auxin gradient.
- Some genotypes react by repairing the damage in the growing flower bud by simply leaving a hole in the centre of the capitulum and this ends in a funnel shape.
- Other genotypes repair the damage by considering the cells in the vicinity of the cracks as if they were button border and producing bracts and ligules.
- The most common causes of Phyllody are hormonal herbicide damage and Boron (B) deficiency, even temporary.
- The boron deficiency, even temporary, produces inelastic tissues that break as they grow. These breaks can be seen in the stems and petioles as longitudinal wounds.

- The formation of tissues without elasticity in the flower bud also produces cracks in the centre and these induce Phyllody.
- Some herbicides from cereals, such as hormonal ones, can cause Phyllody in sunflower and funnel-shaped heads.
- Hybrids that form Phyllody tend to recover better than those that form funnel-shaped strands when exposed to the hormonal herbicide.

Author contributions: All the authors have accepted responsibility for the entire content of this submitted manuscript and approved submission.
Research funding: None declared.
Conflict of interest statement: The authors declare no conflicts of interest regarding this article.

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