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Grain yield of the sunflower capitulum promoted by surgical removal of the involucral bract primordia

Luis F. Hernández

Departamento de Agronomía-CERZOS, Universidad Nacional del Sur. 8000, Bahía, Blanca, Argentina

ABSTRACT

This paper reports the effect on the sunflower capitulum development and seed yield of removing the involucral bract (IB) primordia and upper leaf primordia during early growth of the capitulum. Plants of sunflower cv. Dekalb G100, were used grown in a controlled environment and in the field. As a result of IB and/or upper leaves removal, the rate of floral development and the size of the treated capitula, increased significantly in both experiments. The total number of disc floret primordia also increased significantly by up to 21.5%. The absence of IB during capitulum formation produced a significant increase in capitulum size and promoted grain yield measured on per plant basis. It is concluded that the growth of the receptacle in the sunflower capitulum is highly dependent of the supply of photoassimilates coming from older mature non-growing leaves and that the younger leaves which are expanding at the time of capitulum formation and the involucral bract primordia can produce strong competition for assimilates that can result in a reduction in the potential size of the capitulum.

FS: floral stage; IB: Involucral bracts: CER: CO_2 exchange rate; DFE: days from emergence; LD: Long-day photoperiod

INTRODUCTION

The involucral bracts (IB), botanically known as *phyllaries*, play an important role in the protection of the structure and physiology of the developing inflorescence in Compositae. In a young capitulum of sunflower (30-

35 DFE) the IB comprise 78-82 % of its total dry matter (Hernández, 1988). It has recently been shown that in the early stages of capitulum growth (from 20 DFE to 35 DFE) the IB compete for photoassimilates with the rest of the capitulum structures, particularly floret primordia (Hernández and Palmer, 1992).

It is also known that a large active meristematic surface in the young receptacle before floret primordia differentiation, is important to maximize the number of florets generated by the capitulum and hence, the potential grain yield per plant (Hernández, 1988; Palmer and Hernández, 1988). Although the mature IB contribute to the total plant CER during the grain filling period (Patil *et al.*, 1976; Rawson and Constable, 1980), the IB competition for photoassimilates in early stages of capitulum development could exert an overall negative effect on dry matter accumulation in the capitulum and on floret primordia growth and consequently affecting the plant's grain yield potential.

The procedure of organ removal in crop plants at the vegetative or reproductive stage has generally been used to evaluate the relative capacity of organs to import or export photoassimilates. In the sunflower mature leaves has been removed to access their effect on plant growth or yield (i.e. Sackston 1959; Rodriguez Pereyra, 1978; Hernández and Orioli, 1992) but this technique has not been used on young plants, during the incipient differentiation of reproductive organs.

This paper reports the effect on the sunflower capitulum development and seed yield of removing the involucral bract primordia and upper leaf primordia during early growth of the capitulum.

MATERIALS AND METHODS

Controlled environment trial (**Experiment 1**). Plants of sunflower

cv. Dekalb @100, were used. Plants were grown in 1.5 L plastic pots containing a mixture of compost and soil (Petrocalcic haplustol) appropriately fertilized. The light source supplied 350 µmol $m^{-2}s^{-1}$ (PPFD-PAR) at the top of plants and an 18 h LD photoperiod. The temperature in the controlled environment chamber ranged between 28°C and 30°C.

The onset of reproductive growth and capitulum formation was recorded by frequently sampling and scoring the appearance of the shoot apex using the 10-stage classification of Marc and Palmer (1981) for floral stages (FS) in the development of the sunflower capitulum. Plants with apices at FS 3 were used(22-24 days from emergence) when the dome was differentiating and the first set of IB were forming at the incipient receptacle rim. Under a dissecting microscope the leaves in the apical bud were carefully displaced with a pair of fine forceps to expose the involucral bract primordia which were removed using a fine suture needle (Ethilon, Johnson & Johnson, USA). Although care was taken to avoid damage to the capitulum surface, when this occurred, the plant was discarded. In other plants, only the 18-23 last formed leaves in the apical bud were removed. Controls comprised intact plants.

Treated plants were maintained in the controlled environment cabinet and samples were taken at intervals of 2-3 days to assess the progress through the stage of capitulum development and to measure capitulum dimensions. Final samples were made 45 days from emergence and at maturity. The samples were used for floret row counting, determining grain yield and recording the final number of involucral bracts and leaves which developed in each treatment. Fifteen plants were used in each treatment and the experiment was replicated once.

Field trial (**Experiment 2**). The

same sunflower cv. used in Experiment 1 was sown in the field in a sandy soil (Typic upstipsament) in early spring (20.9.91). The plant population was set at a density of 5.6 plants m^{-2} and the plot consisted of 10 6-m rows with a 0.60 m row spacing. Floral development in the apical bud was recorded by periodically sampling and scoring the state of the apex as in Experiment 1. On attainment of FS 3 twenty plants were randomly chosen from the plot and the surgical removal of IB or leaf primordia was done *in situ* using the procedure described in Experiment 1. The plot was irrigated and appropriately fertilized to minimize soil moisture deficits and optimal availability of nutrients. The control comprised intact plants randomly selected into the plot.

Measurements.The reproductive growth rate (RGR) was defined as the slope of the linear regression equation obtained of the evolution of floral development against time, and expressed as units of $FS.day^{-1}$. Receptacle diameter was measured with an ocular micrometer attached to a stereoscopic microscope and the capitulum receptacle area calculated. At maturity the plants were harvested to measure grain yield components. Differences between the means of the same sampling time for different treatments were compared by the LSD test at $P < 0.05\%$.

RESULTS AND DISCUSSION

The percentage of upper leaves removed, compared with the controls, ranged between 35.8 and 37.1 % for plants grown in the controlled environment (Exp. 1, Table 1) and between 40.5 and 41.7% for plants in the field (Exp. 2, Table 2).

The reduction in the final number of leaves counted in mature plants, indicated that the treatment to remove only the upper leaves also resulted in the removal of between 7.3 and 10.0% of the IB

Table 1: Exp. 1. Number of leaves, involucral bracts and floret primordia present at FS 8 in plants growing in a controlled environment after the surgical excision of involucral bracts in FS 3 (21 days after emergence). Values are the mean of 15 plants.

Treatment	Nº of remaining leaves in FS 8	Var (%)	Nº of Inv. Bracts in FS 8	Var (%)	Number of floret primordia in FS 8	Var(%)
Control	31.0 ± 4.9 a	----	79.8 ± 7.6 a	----	585 ± 97 a	----
Upper leaves removed*	19.9 ± 1.7 b	-35.8	71.8 ± 7.2 a	-10	623 ± 76 ab	+ 6.5
Upper leaves * and involucral bracts removed	19.5 ± 1.5 b	-37.1	54.6 ± 3.7 b	-31.6	711 ± 54 b	+ 21.5

***: Leaves Nº 23 to 31; Var(%): variation percent compared with the control. Values in the same column followed by the same letter do not differ significantly (P<0,05) according to Duncan's multiple range test.**

Table 2: Exp. 2. Yield and number of leaves, involucral bracts and floret primordia present at FS 8 in plants growing in the field after the surgical excision of involucral bracts in FS 3 (23 days after emergence). Values are the mean of 20 plants.

Treatment	Nº of remaining leaves in FS 8	Var (%)	Nº of Inv. Bracts in FS 8	Var (%)	Number of floret primordia in FS 8	Var(%)	Yield (g plant^{-1})	Var(%)
Control	32.1 ± 3.5 a	----	75.8 ± 5.1 a	----	987 ± 85 a	----	71.6 ± 10.1 a	----
Upper leaves* removed	18.7 ± 2.1 b	-41.7	70.3 ± 3.0 a	-7.3	1061 ± 48 ab	+ 7.5	77.5 ± 11.0 a	+ 8.0
Upper leaves * and involucral bracts removed	19.1 ± 1.2 b	-40.5	52.7 ± 4.9 b	-30.5	1198 ± 91 b	+ 21.4	83.3 ± 9.7 b	+ 14.0

***: Leaves Nº 23 to 32; Var(%): variation percent compared with the control. Values in the same column followed by the same letter do not differ significantly (P<0,05) according to Duncan's multiple range test.**

(Table 1 and 2). This was attributed to the difficulty of identifying the IB in their early primordial stages. When both the IB and upper leaves were removed, a subsequent development or differentiation of new IB was observed, leaving the level of IB removal at 31.6 and 30.5% respectively (Tables 1 and 2). It is not clear whether this increased new development of IB was due to dedifferentiation of rim cells or that incipient IB primordia were activated into growth.

As a result, of IB and/or upper leaves removal the rate of floral development (Fig. 1) and the size of the treated capitula (Fig. 2), increased significantly in both experiments. Then, the RGR for plants growing without IB or without upper leaves significantly increased both in Experiment 1 & 2 (Fig. 1). The increase ranged from 0.231 units of FS.day^{-1} to 0.396 units of FS.day^{-1} between the control and IB removed (in Exp. 1) and 0.215 units of FS.day^{-1} to

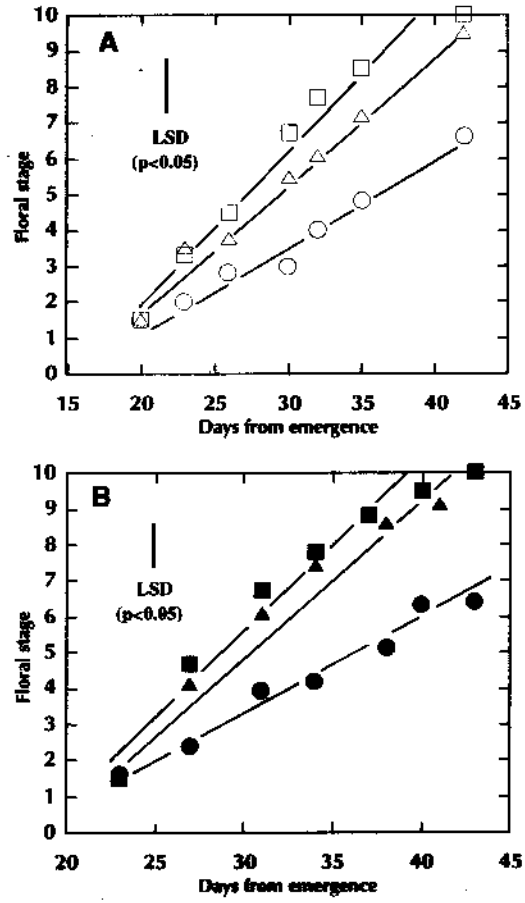

Figure 1: Effect of involucral bract removal on the rate of progression through floral stages in plants grown in controlled environment (A) or in the field (B). (○ , ●): Control; (△ , ▲): Upper leaves removed; (□ , ■): Upper leaves and involucral bracts removed. Values of RGR (Units FS. day^{-1}):
Figure 1a = ○ :0.231; △ 0.351; □ ;0.396.
Figure 1b = ● :0.251; ▲ 0.404; ■ :0.412.

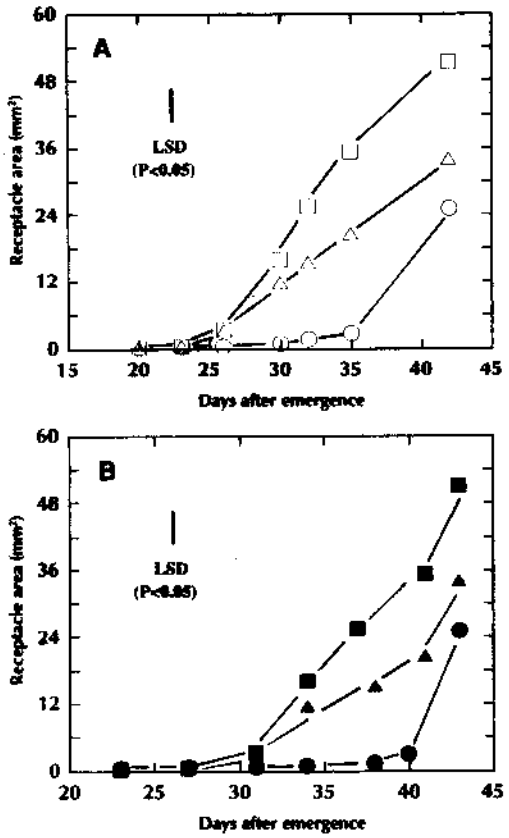

Figure 2: Increaase in receptacle area in plants grown in controlled environment conditions (A) or in the field (B). The same notation as in Figure 1.

0.412 units of FS.day^{-1} between control and IB removed plant in Exp. 2. This response could be because there is competition for nutrients between the upper shoot leaves and the capitulum early in the development of the capitulum.

Although in Exp. 2 all the visible IB were removed, a late development of IB occurred (Tables 1 and 2). This response could account for the plateau observed in the curves of receptacle expansion starting from 35-45 days after emergence (Fig. 2).

In both experiments the total number of disc floret primordia increased significantly by up to 21.5% (Tables 1 and 2). This could be the result of an enlarged receptacle surface induced by the treatments (Fig. 2). Modeling receptacle and disc floret primordia growth in the sunflower (Hernández and Palmer, 1988) has shown that there is a linear relationship between the area of the meristematic surface of the receptacle at FS 5 and the total number of disc floret primordia which differentiate in the capitulum. This finding leads to the generalization that factors which promote receptacle size maximize disc floret numbers in

the sunflower. Larger receptacle surfaces have proved to be crucial in the maximization of floret primordia number in sunflower (Palmer and Hernández, 1988; Hernández and Palmer, 1988). This conclusion is supported by a 14.0% increase in grain yield in field grown plants (Table 2).

A recent report (Hernández and Palmer, 1992) has shown that the incorporation of labeled assimilates into the capitulum in the early stages is preferentially directed towards the IB and the peripheral capitulum tissue. On the other hand, organogenesis of leaves has been associated with vascular development at the apex (Larson, 1983; Roberts, 1987). The central region of the young capitulum are frequently deprived at that stage of a significant availability of nutrient or photoassimilates. This phenomenon has been explained by a deficient or well-developed vascular system into the receptacle base (Durreiu *et al.*, 1985; Hernández and Palmer, 1992).

As is well known removal of growing or storage organs as well as restricting physiological activity slows the import of assimilates toward it (Kursanov, 1984). While the nature of this mechanism of organ inhibition is not understood it should not be forgotten that the manipulation of photosynthate supply by removing competitive sinks may be confounded by changes in correlative hormonal signals (Patrick, 1988).

CONCLUSIONS

The final size of any specific organ is affected by the rate of incorporation of assimilates and by the partitioning of assimilates within its own tissue. It is possible that the effect of IB removal was to alter assimilate partitioning, so that more assimilates flowed to the remaining primordia and parenchymatic tissue.

The absence of IB during capitulum formation produced a

significant increase in capitulum size and promoted grain yield measured per plant. It appears clear that the growth of the receptacle in the sunflower capitulum is highly dependent of the supply of photoassimilates coming from older mature non-growing leaves and that the younger leaves which are expanding at the time of capitulum formation and the involucral bract primordia can produce strong competition for assimilates that can result in a reduction in the potential size of the capitulum.

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