Stem lodging in sunflower: Variations in stem failure moment of force and structure across crop population densities and post-anthesis developmental stages in two genotypes of contrasting susceptibility to lodging

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ABSTRACT

Stem lodging is a risk to sunflower production in Argentina, and may contribute to fixing the upper limit to commercially viable crop population density, since yield is known to increase up to densities higher than those currently used. Reputedly, crops are particularly susceptible to stem lodging during grain filling and at harvest maturity, but the temporal and spatial unpredictability of lodging events under field conditions has hampered systematic research on this issue. In this study we used mechanical lodging to examine the relationships between stem failure moment of force and stem structure in plants of two sunflower hybrids of contrasting susceptibility to stem lodging grown at each of three crop population densities (5.6 plants m^{-2}, 10 plants m^{-2} and 16 plants m^{-2}). Measurements were performed at mid- and near-end of grain filling and at harvest maturity in crops grown in three separate seasons at two locations. Stem failure moment of force at all three developmental stages was significantly ($p < 0.05$) greater in the lodging-resistant hybrid than in the lodging-susceptible hybrid used in these experiments at 5.6 plants m^{-2}, and fell with increasing crop population density and between 90% grain filling and harvest maturity in both hybrids. At harvest maturity differences in stem failure moment of force between hybrids were significant ($p < 0.05$) at all three crop population densities. Stem flexural rigidity (ability of the stem to resist bending) and stem deformation (horizontal displacement from the vertical of the stem immediately prior to breakage) exhibited responses to hybrid, crop population density and developmental stage that were broadly consistent with those of stem failure moment of force. Stem diameter at the breakage point fell with crop population density, but there was little difference between hybrids except at the harvest maturity, when the susceptible hybrid at the two highest crop population densities had smaller diameters than the resistant hybrid. Measured at the breakage point, the thickness of the epidermis plus cortex tissues (i.e., the effective thickness of the stem wall) which surround the friable stem pith fell with crop population density and between end of grain filling and harvest maturity in both hybrids. Differences in effective thickness of the stem wall between hybrids were small and often not significant, but there was a tendency for the susceptible hybrid to exhibit greater thickness of the effective stem wall, particularly at the two higher population densities. Stem failure moment of force was linearly related to thickness of the effective stem wall in both hybrids, the slope of the relationship being significantly greater for the resistant hybrid. We conclude that, within limits, the thickness of the effective stem wall may prove to be useful as a guide to genotype susceptibility to stem lodging in breeding programs and may offer a simple approach to modelling susceptibility. This work has also served to highlight the need to investigate the origins (presumably related to stem anatomy and/or cell wall properties) of the genotypic effects on the stem failure moment of force/the effective stem wall relationship. Finally, the demonstration of the existence of genotype differences in tolerance to stem lodging should encourage the execution of a broader survey aimed at identifying sources of tolerance to stem lodging at high crop population densities in sunflower.

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1. Introduction

Stem and root lodging constitute a significant risk to sunflower (*Helianthus annuus* L.) production in Argentina, with about 10% of the annual cropped area being affected, for an estimated yield loss

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equivalent to US$ 40 million (Bragachini et al., 2001). Because current hybrids, when protected from lodging and disease, show increases in yield potential with crop population density up to densities that are almost three times the current commercial density of 5 plants m^{-2} (López Pereira et al., 2004), it seems very likely that propensity to lodge at high crop population densities also plays a part in reducing realizable yield potential in this crop.

The unpredictable occurrence of lodging across time and space has hampered the establishment of a clear and quantitative picture of the effects of genotype, crop population density and crop developmental stage on the likelihood of lodging, and of the links between these effects and plant mechanical and structural properties. Sposaro et al. (2008) have conducted a detailed study on the impact of these factors on root lodging. This paper presents a complementary study of the effects of these factors on key stem mechanical and structural properties involved in determining plant susceptibility to stem lodging. The measurements and observations reported in both papers have used the lodging model of Baker et al. (1998) as a reference framework. The overall aim of this work is to lay the foundations for adapting the lodging models developed for wheat and barley (Berry et al., 2003a, 2006; Sterling et al., 2003) to sunflower.

Observations by farmers and breeders tend to agree that sunflower is most susceptible to stem lodging between flowering and harvest maturity (Abelardo de la Vega, pers. comm.; INTA, 2003). A study on the effects of source/sink relationships on the force required to produce stem breakage (Polack, 1992) also indicated a reduction in the value of this force between flowering and harvest maturity. In other species, e.g. pea (Beeck et al., 2006), wheat and barley (Crook and Ennos, 1994; Berry et al., 2003a,b, 2006; Kelbert et al., 2004), Miscanthus (Kaack and Schwarz, 2001) differences between genotypes in susceptibility to stem lodging have been shown to exist. In sunflower there is anecdotal evidence of intra-specific variability in susceptibility to stem lodging, and de la Vega et al. (2004) have shown that hybrids exhibiting stay-green characteristics were less susceptible to stem lodging than those exhibiting a fast-dry-down pattern of leaf senescence, and that the force required to produce stem breakage was greater in the former group. High crop population densities can be expected to give rise to thinner and weaker stems given the frequently observed effects of the shade avoidance syndrome on stem thickness and the partitioning of biomass to the stem (e.g., Ballaré, 1994). However, little work has been focussed on this aspect of the problem, whether in sunflower or in other species. A feature common to many of the studies cited above for species other than sunflower, has been the limited way in which the effects of crop population density and crop development on susceptibility to stem lodging have been explored, although the effects of genotype have received some attention. In sunflower, studies have been much fewer and far less systematic.

Studies on stem lodging in several species (e.g., wheat [*Triticum aestivum*], barley [*Hordeum vulgare*], pea [*Pisum sativum*], *Miscanthus × giganteus* and *M. sinensis*) have shown that the thickness of the wall of the hollow, approximately cylindrical, stems are more closely related to lodging susceptibility than stem diameter (e.g., Crook and Ennos, 1994; Kaack and Schwarz, 2001; Berry et al., 2003a,b, 2006; Kelbert et al., 2004). Sunflower stems are solid, although the pith parenchyma cells tend to lose turgor and the pith tissue becomes friable as development proceeds. Whether or not the pith contributes to stem resistance to lodging is not known. If some simple relationship between stem morphology at the breakage site and stem failure moment of force can be established, then this relationship could inform modelling of the stem lodging process. Equally, a simple relationship of this nature could be helpful to breeders seeking to improve cultivar tolerance to stem lodging.

Work described herein aimed to describe and quantify the effects of genotype, crop population density, and crop developmental stage during the flowering to harvest maturity phase on the stem failure moment of force and the structural properties of the stem at the site of stem breakage. To do this, the force required to artificially produce stem lodging was measured and the stem structure at the site of breakage was examined at three developmental stages between anthesis and harvest maturity in plants of crops of two hybrids of contrasting susceptibility to stem lodging. In one experiment crops were grown at a crop population density of 5.6 plants m^{-2}, in two other experiments the crops were grown at three population densities from 5.6 plants m^{-2} to 16 plants m^{-2}.

2. Materials and methods

2.1. Experimental design and crop treatments

Three experiments (E) were carried out at two different locations: in 2004/5 (E1) and 2006/7 (E3) crops were grown on a silty clay loam soil (Typic Argiudoll) at the Faculty of Agronomy, University of Buenos Aires (FAUBA) (34°35′S, 58°29′W); in 2005/6 (E2), the crops were established on a deep coarse loam soil (Typic Hapludoll) at the Advanta Semillas Research Centre, Venado Tuerto (VT), Argentina (33°41′S, 61°57′W). In all trials two hybrids of contrasting susceptibility to stem lodging were used (Advanta V70597, resistant to stem lodging, Advanta Semillas, Argentina; and Zenit, susceptible to stem lodging, Sursem, Argentina). Putative ranking for hybrid susceptibility to stem lodging was provided by Abelardo de la Vega (pers. comm.). Advanta V70597 is a stay-green hybrid, and the canopies of crops of this hybrid senesce more slowly during grain filling and after physiological maturity of the grain than in Zenit, which has canopies which exhibit a fast-dry-down syndrome over the same developmental phase. Crops were sown by hand in rows spaced at 0.7 m and thinned at the V4 stage (Schneiter and Miller, 1981) to 5.6 plants m^{-2} (E1) and to 5.6 plants m^{-2} (D1), 10 plants m^{-2} (D2) and 16 plants m^{-2} (D3) (E2 and E3). Plots were six rows (including two border rows) wide by 6 m long, and were set out as a randomized complete block design with three replications. Crops were protected against weeds, insects and diseases as needed and were irrigated and fertilized to prevent water and nutritional stresses.

2.2. Measurements of stem failure moment of force and stem structure at the breaking point

When the grain on each crop was estimated to have reached each of: (a) 50% of its final dry weight (Stage R7, on the Schneiter and Miller, 1981 scale), (b) 90% of its final dry weight (R8), and (c) harvest maturity (HM), three contiguous plants per treatment replicate were artificially lodged. These three stages cover the developmental phase during which sunflower crops are reportedly most susceptible to stem lodging. Crop population densities in the row-section selected for measurement (including at least one border plant at each end of the sampled row-section) and in the flanking row-sections to either side of the sampled row were the nominal ones for the treatment involved. Artificial lodging was effected using the instrument described by Sposaro et al. (2008) (basically, a horizontal push-bar attached to two vertical arms that had pivots anchored to the soil on the axis of the row-section). Measurements were only performed when the surface soil was sufficiently dry as to provide the plants with a firm anchorage and to avoid root lodging. After removal of the leaves and the capitulum, the instrument push-bar was set at 60% of the plant height (h) in contact with the stem. In preliminary experiments using the lodging instrument we found that if the push-bar was set
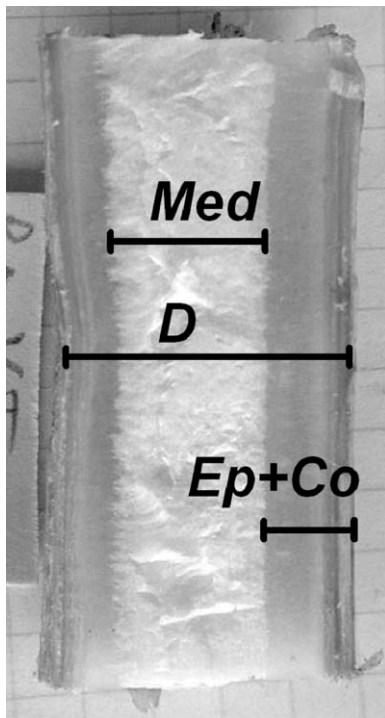
Fig. 1. Longitudinal section of a stem close to the point of breakage. *D*: external diameter; *Ep + Co*: thickness of epidermis plus cortex (or effective stem wall thickness); *Med*: diameter of pith.

higher than 70% of total plant height stem lodging did not occur, because the upper portion of the stem is flexible and the push-bar slipped over it. We therefore chose to set the push-bar at 60% of total plant height. Force was applied to the push-bar at the point it came into contact with the stem by means of steel cable attached to a windlass and pulley system linked to a balance (Model HEC, Balanzas Electrónicas Torres, Venado Tuerto), and the stem was displaced in 5° steps from its vertical position until stem breakage occurred. At the end of each incremental displacement, the force at the balance (F_B, kg), the angle between the cable and the push-bar (α_P), and the angle of displacement of the stem from the vertical were registered (see diagram in Sposaro et al., 2008). When the stem broke, the unbroken stem closest to the point of breakage was sectioned vertically and the thickness of the epidermis plus cortex ($Ep + Co$) (effective stem wall thickness) and that of the pith (Fig. 1) were measured. The height of the breakage point from the soil surface and the diameter of the stem at that point were also measured.

Forces registered at the balance at each incremental step were transformed, using standard decomposition of forces procedures, to estimate the force (F_P, in the units of Newton [N]) acting perpendicular to the stem:

$$F_P = F_B \times \cos \alpha \qquad (1)$$

where $\alpha = 90 - \alpha_P$, and the highest F_P obtained in each run was taken to be the force needed to induce stem lodging for the plant.

The stem failure moment of force (B_S, N m, i.e., the moment of force needed to induce stem lodging) was obtained as the product of F_P (N) by 0.6h (plant height, m).

Stem deformation (i.e., the horizontal displacement, at the point of application of the force, of the stem from the vertical, as measured immediately prior to breakage, Def_T, in the units of m) was estimated as:

$$De f_T = 0.6h \times \sin \alpha_d, \qquad (2)$$

where α_d is the angle between the initial (quasi vertical) position of the stem and that achieved immediately prior to breakage.

Stem flexural rigidity (also referred to as flexural stiffness, Niklas (1992), a measure of the ability of a structure to resist bending or, more precisely, the force couple required to bend a rigid structure to a unit curvature, El_T, in the units of N m^2) was estimated using the usual engineering approximation for a hollow circular tube (Beléndez et al., 2001; Niklas, 1992):

$$El_T = \frac{(F_P \times 9.80665 \times (0.6h \times 0.01)3)}{3 \times De f_T} \qquad (3)$$

where 9.80665 and 0.01 are constants needed to transform kg into N and cm into m, respectively.

2.3. Statistical analyses

A Linear Mixed Model Analysis using REML (residual maximum likelihood) was implemented on GenStat® for WindowsTM (VSN International, 2007) to establish the significance of treatment effects and their interactions. The fixed effects were G (genotype), D (density), S (developmental stage) and the double and triple interactions between these factors. Random effects were E (experiments) and the E × replicate interaction. For the fixed effects the analysis generates the Wald Statistic which, divided by the appropriate degrees of freedom, has an F distribution. Resulting F values and their probabilities (p) are similar to those generated by the ANOVA analysis, and can be interpreted in the same fashion. This approach permits the handling of unbalanced data bases (i.e., only one crop population density was used in E1 vs. three in E2 and E3). Linear regressions between variables were fitted using the iterative optimisation technique of TableCurve V 3.0 (Jandel Scientific, 1991).

3. Results

Genotype, crop population density and developmental stage all had significant effects on stem failure moment, while the double and triple interactions between factors were non-significant with the exception of the G × D interaction for stem failure moment (Table 1). Stem failure moment (B_S) values for both hybrids decreased with crop population density at all three developmental stages (Fig. 2). Genotype had a large effect on stem failure moment at 5.6 plants m^{-2} and a consistent, albeit small, effect at the highest crop population density at all three development stages. At the intermediate crop population density, genotype effects were only

Table 1
F-values and significance levels thereof for the indicated response variables obtained using REML analysis with genotype (G), crop population density (D), and development stage (S) as fixed factors. REML analysis was applied to data obtained in experiments E1, E2 and E3. Values in brackets next to each *F*-value indicate the proportion of non-error variances in each response variable explained by the fixed effects and their interactions. B_S, stem failure moment; $Ep + Co$, thickness of epidermis plus cortex; El_T, stem flexural rigidity; Def_T, stem deformation from the vertical; *Diam*, stem diameter at the breaking point. NS: non-significant.

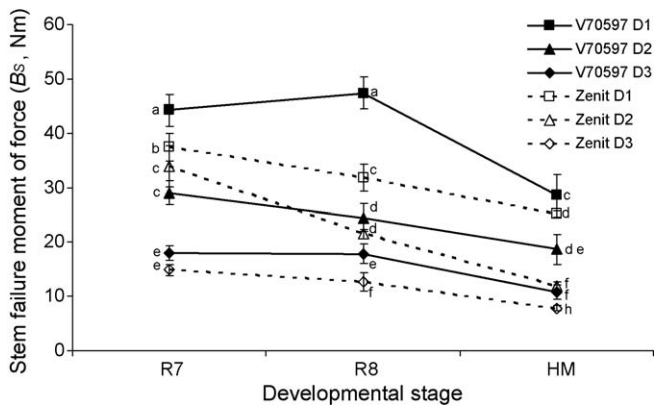| Fixed factors	F				
	B_S	$Ep + Co$	El_T	Def_T	Diam
G	8.1**(3)	32.4***(19)	6.8**(3)	29.1***(53)	0.2 NS(0.1)
D	99.9***(67)	20***(12)	87.3***(73.4)	10.2***(37)	54.05***(71)
S	30.8***(21)	113.7***(67)	17.7***(15)	0.7 NS(2.6)	1.32 NS(1.7)
G × D	4.1*(3)	1.3 NS(1)	3.5*(3)	0.1 NS(0.2)	2.19 NS(2.9)
G × S	2.5 NS(2)	1.6 NS(1)	1.2 NS(1)	0.1 NS(0.2)	4.82 NS(6.3)
D × S	2.5 NS(3)	0.4 NS(0.2)	1.9 NS(3.2)	0.7 NS(5.2)	2.65 NS(7)
G × D × S	1.3 NS(2)	0.5 NS(0.3)	0.9 NS(1.6)	0.3 NS(2.4)	4.09 NS(10.8)

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Fig. 2. Stem failure moment of force (B_S) measured at R7 and R8 (Schneiter and Miller, 1981 scale) and at harvest maturity (HM) for V70597 and Zenit hybrids grown at three crop population densities (5.6 plants m^{-2} [D1], 10 plants m^{-2} [D2] and 16 plants m^{-2} [D3]). Each point is the overall mean of data from the three experiments, obtained using REML analyses. Error bars indicate ±1 standard error ($n = 3$). Different letters next to symbols indicate significant ($p < 0.05$) differences across hybrids, crop population densities and developmental stages.

Fig. 4. Stem flexural rigidity (El_T) immediately prior to breakage measured at R7 and R8 (Schneiter and Miller, 1981 scale) and at harvest maturity (HM) for V70597 and Zenit hybrids grown at three crop population densities (5.6 plants m^{-2} [D1], 10 plants m^{-2} [D2] and 16 plants m^{-2} [D3]). Each point is the overall mean of data from the three experiments, obtained using REML analyses. Error bars indicate ±1 standard error ($n = 3$). Different letters next to symbols indicate significant ($p < 0.05$) differences across hybrids, crop population densities and developmental stages.

significant at the harvest maturity stage. Stem failure moment fell with advancing development, across the three developmental stages in Zenit and between the R8 and the harvest maturity stages in V70597.

Effects of genotype and crop population density on stem deformation (Def_T) were significant, with deformation being greater (relative to Zenit) for V70597 at the two higher crop population densities and all developmental stages (with the sole exception of plants sown at 10 plants m^{-2} at harvest maturity) (Table 1, Fig. 3). With the latter exception, no effect of developmental stage on stem deformation was found. Within each hybrid, the effects of crop population density on Def_T were almost never significant.

Stem flexural rigidity was greater for V70597 than for Zenit at the lowest crop population density across all three development stages, but this difference disappeared at the mid and high crop population densities (Table 1, Fig. 4). The overall picture that emerges is that genotype differences in Def_T and El_T that are clear at 5.6 plants m^{-2} tend to become diluted at higher crop population densities and, to a lesser extent, with advancing development. Greater values of Def_T and El_T for V70597 are consistent with the greater values of B_S for this hybrid (Fig. 2). Treatment effects on the

elastic modulus of the stem (E, in units of N m^{-2}) were significant ($p < 0.05$) for crop population density (333×10^7 N m^{-2} vs. 302×10^7 N m^{-2} for V70597 at 5.6 and 16 plants m^{-2}, respectively; 248×10^7 N m^{-2} vs. 203×10^7 N m^{-2} for Zenit at 5.6 plants m^{-2} and 16 plants m^{-2}, respectively), but effect of genotype and developmental stage were not significant (data not shown). A significant ($p < 0.01$) crop population density by genotype interaction for E was traceable to the fact that V70597 at 5.6 plants m^{-2} had high values across all three developmental stages while values of E for Zenit at 16 plants m^{-2} were consistently lower than those of other treatment combinations across the three developmental stages (data not shown).

Effective stem wall thickness (i.e., $Ep + Co$) decreased with crop population density in both hybrids; and also decreased quite markedly between R8 and harvest maturity stages in both hybrids (Table 1, Fig. 5). Genotype effects on this variable were significant at mid- and high crop population densities, with Zenit exhibiting greater thickness at these densities. Stem diameter at the breakage point fell with increasing crop population density in both hybrids (Fig. 6), and this factor explained a major proportion of the non-error variance (Table 1) for this variable. There was also an indication of stem shrinkage between R8 and HM in Zenit at the
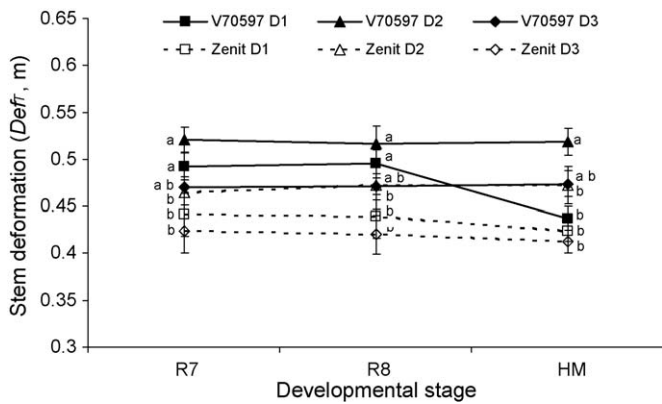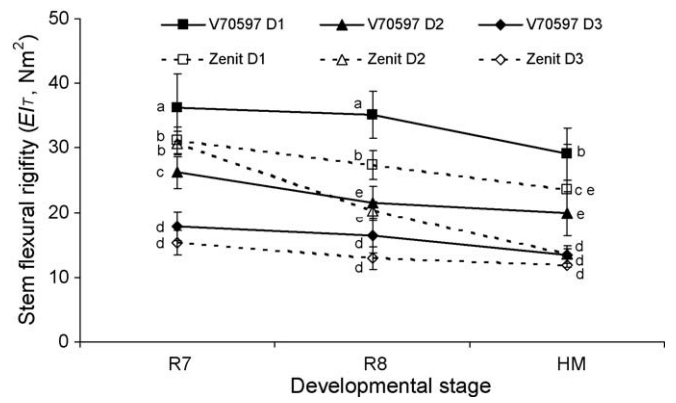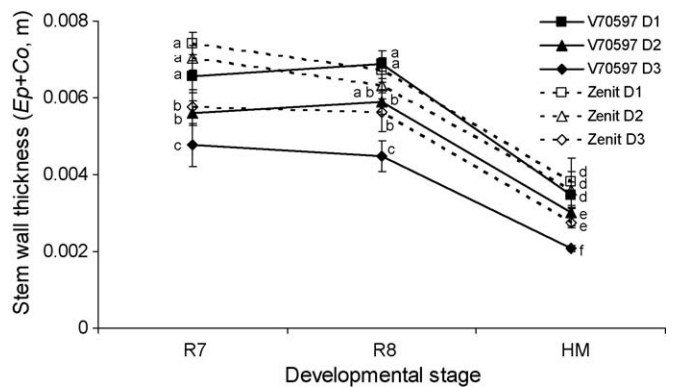

Fig. 3. Stem deformation (Def_T) immediately prior to breakage measured at R7 and R8 (Schneiter and Miller, 1981 scale) and at harvest maturity (HM) for V70597 and Zenit hybrids grown at three crop population densities (5.6 plants m^{-2} [D1], 10 plants m^{-2} [D2] and 16 plants m^{-2} [D3]). Each point is the overall mean of data from the three experiments, obtained using REML analyses. Error bars indicate ±1 standard error ($n = 3$). Different letters next to symbols indicate significant ($p < 0.05$) differences across hybrids, crop population densities and developmental stages.

Fig. 5. Thickness of $Ep + Co$ measured at R7 and R8 (Schneiter and Miller, 1981 scale) and at harvest maturity (HM) for V70597 and Zenit hybrids grown at three crop population densities (5.6 plants m^{-2} [D1], 10 plants m^{-2} [D2] and 16 plants m^{-2} [D3]). Each point is the overall mean of data from the three experiments, obtained using REML analyses. Error bars indicate ±1 standard error ($n = 3$). Different letters next to symbols indicate significant ($p < 0.05$) differences across hybrids, crop population densities and developmental stages.
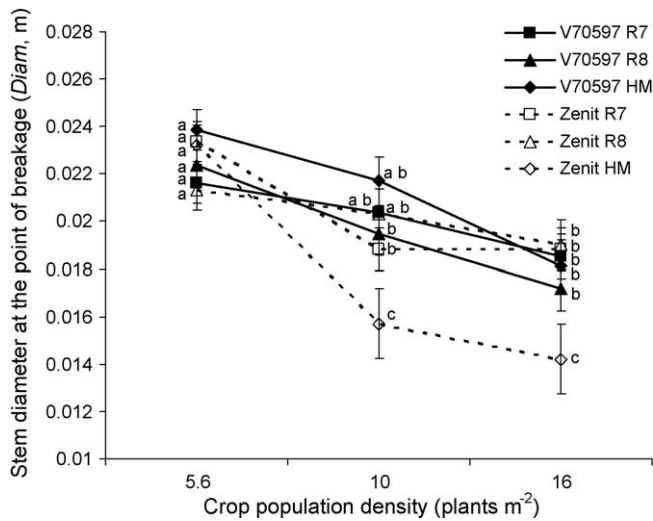
Fig. 6. Changes in stem diameter (*Diam*) at the point of breakage with crop population density, developmental stage and genotype. Each point is the overall mean of data from the three experiments, obtained using REML analyses. Error bars indicate ±1 standard error (*n* = 3). Different letters next to symbols indicate significant (*p* < 0.05) differences across hybrids, crop population densities and developmental stages.

two highest crop population densities. No association was found between stem failure moment and either the diameter of the stem or that of the pith (data not shown). Although both crop population density and developmental stage had significant effects on the height of the breakage point, the absolute variations were small, with all treatment means falling in the 9–23 cm range, with an overall mean of 15 cm (data not shown).

Stem failure moment in both hybrids was linearly related to the thickness of the summed epidermis and cortex across the range of observed values, with V70597 exhibiting a significantly (*p* < 0.05) steeper response to *Ep* + *Co* (Fig. 7) than Zenit. The *y*-axis intercepts
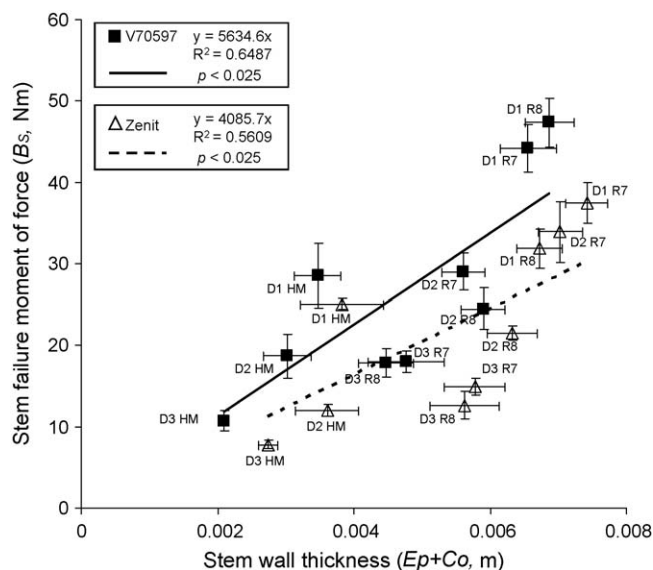

Fig. 7. Relationships between stem failure moment of force (*B_S*) and thickness of epidermis plus cortex (*Ep* + *Co*) for V70597 and Zenit hybrids grown at three crop population densities (5.6 plants m^{-2} [D1], 10 plants m^{-2} [D2] and 16 plants m^{-2} [D3]). Each point represents the overall mean of data from the three experiments, obtained using REML analyses, for each combination of hybrid, crop population density and crop developmental stage. Letters next to symbols indicate population density/developmental stage combinations. Fitted functions are forced through the origin. Vertical and horizontal error bars indicate ±1 standard error (*n* = 3).

of the fitted functions did not differ from zero nor between hybrids, so were functions shown in Fig. 7 forced through zero.

4. Discussion

Stem failure moment (B_S) was strongly and significantly altered by the three factors (genotype, crop population density and developmental stage) explored in these experiments (Table 1 and Fig. 2). In both genotypes, there was an almost 2.7-fold reduction on B_S between extreme population densities (Fig. 2). Differences between hybrids for B_S were strongly expressed at the lowest crop population density, with V70597 achieving significantly greater values across all three developmental stages (Fig. 2, Table 1). These differences disappeared or became slight at higher crop population densities, although they remained significant at the highest crop population density. The observed genotype by crop population density interaction (Table 1) can be traced to these response patterns. The relatively modest effect of genotype on B_S at the higher crop population densities indicates the need for a much broader survey of intra-specific variability for stem lodging susceptibility at high population densities, if sources for resistance to stem lodging at high population densities are to be identified. B_S for Zenit fell continuously with the advance in development at all crop population densities, while that for V70597 stayed unchanged between R7 and R8, falling only toward harvest maturity, suggesting (in agreement with de la Vega et al., 2004) that the stay-green trait may reduce the risk of stem lodging in this species. It is possible there may be some connection between canopy senescence patterns and lodging susceptibility, because stems become brittle more slowly after physiological maturity in stay-green types, but we are unable to demonstrate the generality of this association on the basis of a contrast between only two hybrids.

Estimated stem flexural rigidity (EI_T) exhibited similar factor response patterns to those of B_S (Table 1, Fig. 4), but the genotypic difference at the highest crop population density disappeared (Fig. 4). Interestingly, the flexural rigidity of V70597 at 5.6 plants m^{-2} measured at harvest maturity (i.e., its lowest value) was indistinguishable from that of Zenit at the two earlier stages of development (Fig. 4). With the exception of the harvest maturity measurement in V70597, stem deformation remained stable across development in both hybrids, with V70597 exhibiting greater deformation (Fig. 3). A fuller interpretation of the effects of genotype, crop population density and development on whole stem flexural rigidity and stem deformation would require measurement and analysis of the variations in stem mechanical properties along the whole of its length. Nevertheless, the data shown in Figs. 3 and 4 indicate that V70597 at 5.6 plants m^{-2} had more rigid stems and underwent greater deformation before breaking than Zenit.

The thickness of the apparent stem wall (i.e., *Ep* + *Co*) was reduced by almost one-third between extreme crop population densities and fell between R8 and harvest maturity in both genotypes, while genotype effects were more muted (Fig. 5 and Table 1). Interestingly, Zenit, the hybrid with lower stem failure moments, exhibited similar or greater *Ep* + *Co* values to those of V70597. Values of *Ep* + *Co* fell strongly between R8 and harvest maturity, indicating rapid changes in stem structural properties after physiological maturity of the grain. The linear association between B_S and *Ep* + *Co* (Fig. 7) is particularly interesting, both because *Ep* + *Co* is a fairly simple property to measure (something which could be helpful to breeders, at least at currently used crop population densities) and because the relationships shown in Fig. 7 should be fairly simple to use in modelling the stem lodging process. Given the small effects of the factors explored in this work on the height of the breakage point, measurement of *Ep* + *Co* for

crop improvement purposes could be made at 15 cm from the soil surface.

The comparison between Figs. 2, 5 and 6 indicates that genotype susceptibility to stem lodging must include some other components in addition to the thickness of $Ep + Co$. This additional component is likely to reflect genotype effects on stem tissue composition and properties, as has been found for other species such as barley and *Miscanthus* (Kokubo et al., 1989; Kaack et al., 2003). This topic merits further investigation. It seems clear from our data (Fig. 6) that it is unlikely that genotype differences in stem diameter are involved in determining genotypic variations in B_S, with the possible exception of the observations for Zenit at harvest maturity and mid- to high crop population densities. Equally, the lack of association between B_S and the diameter of the pith, in contrast to the association between B_S and $Ep + Co$ (Fig. 7), suggests that sunflower stem functions, in mechanical terms and during the grain filling phase, somewhat like a hollow cylinder. In this, sunflower appears to be similar to species with true hollow stems (e.g., Crook and Ennos, 1994; Kaack and Schwarz, 2001; Berry et al., 2003a,b, 2006; Kelbert et al., 2004).

In summary, the experiments and analysis presented here have served to establish, for the first time in sunflower, the effects of genotype, developmental stage during the grain filling to harvest maturity phase, and crop population density on susceptibility to stem lodging. They have also served to show that, within limits, the thickness of $Ep + Co$ may prove to be useful as a guide to susceptibility to stem lodging in breeding programs. Further, and as shown by previous work in cereals (e.g., Berry et al., 2003a, 2006; Sterling et al., 2003), stem failure moment/stem wall thickness relationships such as those shown in Fig. 7 constitute a key component of models which can predict stem lodging as a function of wind loading and stem attributes. This work has also served to highlight the need to investigate the origins (presumably related to stem anatomy and/or cell wall properties) of the genotypic effects on the $B_S/[Ep + Co]$ relationship. Finally, the demonstration of the existence of genotype differences in tolerance to stem lodging should encourage the execution of a broader survey aimed at identifying sources of tolerance to stem lodging at high crop population densities in sunflower.

Acknowledgements

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