Journal of Experimental Botany, Vol. 54, No. 383, pp. 845–849, February 2003
DOI: 10.1093/jxb/erg068

Journal of
Experimental
Botany

RESEARCH PAPER

The effects of air flow and stem flexure on the mechanical and hydraulic properties of the stems of sunflowers *Helianthus annuus* L.

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Received 22 July 2002; Accepted 8 October 2002

Abstract

Many studies have shown that wind affects plant development, causing them to develop shorter and usually stronger stems. Many of these effects have been shown to be due to a response to mechanical flexing of the stem which is known as thigmomorphogenesis. However, it is not known how wind affects the hydraulic properties of stems, nor have the effects of air flow past leaves been examined in isolation from mechanical flexing. This study, therefore, used a factorial experiment to distinguish between the effects of stem flexing and air flow, and examined the morphology, hydraulics and mechanics of developing sunflowers *Helianthus annuus.* It was found that flexure and air flow had opposite effects on several aspects of development; air flow increased plant height and length-specific stem hydraulic conductivity, k_h, and reduced stem rigidity and strength, while flexing did the reverse. There was also a clear trade-off between hydraulic and mechanical capability: as one increased the other decreased. A plant's response to wind must, therefore, be a complex response to at least two different stimuli and this might help explain why it varies with species and environment.

Key words: Hydraulic conductivity, mechanics, plant development, thigmomorphogenesis, wind.

Introduction

Wind has many effects on plants (see Grace, 1977; Van Gardingen and Grace, 1991; Ennos, 1997, for reviews). The short-term effects on leaf photosynthesis have been well studied and found to be extremely variable. A gentle breeze will usually increase the photosynthesis of a leaf compared to dead calm conditions, because low winds reduce the thickness of its boundary layer. The resistance to movement of carbon dioxide into the leaf will, therefore, fall. However, strong winds may actually reduce photosynthesis both because of direct and indirect effects; wind will cool the leaves and reduce their effective area by causing them to curl up; and the stomata may shut to reduce water loss, so *increasing* resistance to entry of carbon dioxide into the leaf. The precise effect, therefore, depends on the morphology of the leaves, the optimal temperature of the photosynthetic enzymes, and the wind speed as well as other environmental factors. Scaling up to the level of the whole plant, wind tunnel experiments have shown that relative growth rate is often maximized at wind speeds below 1 m s^{-1}, falling in still air or at higher speeds (Wadsworth, 1959).

Over the longer term, wind can also affect the development of plants and alter their morphology. Wind-exposed plants generally develop fewer, smaller leaves which contain a higher proportion of mechanical tissues (Martin and Clements, 1935; Niklas, 1996; Grace and Russell, 1977). Most wind-exposed plants also exhibit reduced shoot extension (Whitehead, 1962; Lawton, 1982) and changes in the morphology and mechanics of their stems and roots, but the effects vary with species. Many herbs develop stiffer stems containing more mechanical tissue (Grace and Russell, 1977), while trees show increases in the amount of secondary wood they lay down, producing thicker trunks and roots (Jacobs, 1954; Lawton, 1982; Telewski and Jaffe, 1986; Stokes *et al.*, 1995). This 'flexure wood', though, is more flexible than

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normal wood, having high microfibrillar angles and spiral grain (Telewski, 1989). Most of these changes make adaptive sense as they should reduce the plant's susceptibility to mechanical damage. One might also expect that, in the wind, the conductivity of the stem should increase as this would help maintain water flow to the leaves, but the effect of wind on the hydraulic properties of the stems of plants has not been specifically studied.

A major difficulty with understanding the effects of wind on plants is that it acts not as a single stimulus, but has two quite different effects: it increases the air flow past the leaves and it mechanically stimulates the plant, in particular flexing the stem. Little effort has been made to look at the effect of air flow in the absence of mechanical stimulation, but many studies in recent years have isolated the second, mechanical effect, by either flexing plants in the absence of wind (Jaffe, 1973, 1976; Jaffe *et al.*, 1980; Patterson, 1992; Gartner, 1994; Goodman and Ennos, 1996, 1998) or comparing free-standing with supported plants (Jacobs, 1954; Holbrook and Putz, 1989; Crook and Ennos, 1996; Goodman and Ennos, 1997). The results of both types of studies have shown that many of the effects of the wind may be ascribed to a response to mechanical stimulation called thigmomorphogenesis (Jaffe, 1973). This seems to reduce extension growth at a whole plant level (Coutand and Moulia, 2000) but to locally stimulate secondary thickening (Mattheck, 1991; Goodman and Ennos, 1998). The effect on the hydraulic conductivity of stems and roots has, however, been largely ignored.

This paper outlines an investigation which sought to make up for some of the gaps that had been identified on the effect of wind on plant development. A factorial experiment was designed which would determine separately the effects of both air flow and stem flexure on the development of sunflowers. Their effects, not only on plant morphology and the mechanical properties of the stem, but also on its hydraulic properties were then investigated.

Materials and methods

The plants

Eighty seeds of sunflower *Helianthus annuus* L., var. Giant Yellow Sunflower, were sown in January 2002, one each in 13 cm diameter pots filled with well-watered John Innes No.3 compost. They were then transferred to a glasshouse which was heated to an average daytime temperature of 26 °C, falling to 12 °C at night. Supplementary lighting was also supplied to give a 16 h day. After 28 d, 60 plants of a similar size were chosen and divided randomly into four treatment groups, of 15 plants each.

The treatments

The four treatment groups were evenly spaced within the glasshouse and subjected to contrasting conditions in a 2×2 factorial experiment, to investigate separately the effects of air flow past them and mechanical flexing of the stem. To investigate the effects of air flow, two of the groups were continuously blown by a Sona 30W fan, giving wind speeds within the stand, measured using a hot wire anemometer, of 0.3–1.7 m s^{-1}, while the other two were grown in 'still' air (a wind speed of less than 0.2 m s^{-1}). To investigate the effects of mechanical stress, the stems of two groups of plants were flexed through 45° from side to side 40 times each day over a period of 1 min; the stems of the other two groups were not only left unflexed, but were supported by being tied to wooden canes. Plants were therefore grown with or without airflow and with or without stem flexure.

Each day pots were rotated by 45° to ensure that plants received air flow or flexure evenly from all directions. Similarly, plants were moved within their rows to ensure that each wind-blown plant was subjected to a similar mean wind speed.

Harvesting

Harvesting and measuring plants began on day 52, 23 d after the treatments were first applied, and continued over the next 7 d. To remove the potential confounding variable of age, therefore, equal numbers of plants from each group were harvested and processed each day.

Morphological measurements

The total height of each plant was measured using a ruler and the diameter of the first internode was measured at its midpoint using calipers. The leaf area of each plant was then measured by photocopying all of its leaves, cutting out the photocopies, and weighing the paper.

Stem hydraulic conductivity

The hydraulic conductivity of the first internode of each plant was measured using an apparatus similar to that described by Sperry *et al.* (1988). This measures the rate at which a perfusing solution was forced through the internode by a given gravity-induced pressure.

First, a 15 cm length of the internode was cut from the plant using a razor blade. The cuts were carried out under 10 mM oxalic acid solution to prevent air entering the stems. The segment was then connected to the conductivity apparatus, rubber tubing being used to ensure a leak-proof fit. Oxalic acid was used throughout rather than distilled water to ensure consistent conductance measurements (Sperry *et al.*, 1988). Next, a crop sprayer developing a pressure of 200 kPa was used to force oxalic acid through the stem for 10 min to dissolve and expel any emboli present in the stem. A 0.22 μm in-line filter downstream of the pump prevented the accumulation of particles and stopped microbes entering the stem. Negative pressure was then applied from the other end of the stem using the vacuum pump to remove any remaining air. The vacuum pump was then removed and replaced by a Pasteur pipette. For the actual tests of conductance the solution was re-routed using a 3-way tap to allow the flow of solution from a 20 l aspirator containing solution with a pressure head 45 cm above the level of the stem. This applied a gravity-induced pressure, ΔP, of 4.41 kPa. After an adjustment period of 5 min, the flow rate through the stem was measured by measuring the time taken for 5 drops of solution to fall into a small preweighed test tube. The tube was then reweighed and the volume flow rate calculated.

The length-specific conductivity, k_h, of the stem could then be calculated using the formula

$$k_h = FL/\Delta P \qquad (1)$$

where F is the flow rate in m^3 s^{-1} and L the length of the internode segment.

Stem mechanical properties

The internode was then removed from the conductance apparatus and subjected to a 3 point bending test in a universal mechanical testing machine (Instron model 4301). The internode was placed on

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two supports which were set 14 cm apart. A pushing probe of radius 20 mm was attached to the load cell and lowered until it just touched the mid-point of the sample. The crosshead was then lowered at a rate of 20 mm min^{-1}, bending the sample until it eventually buckled. A computer with an interface to the testing machine was used to produce a graph of force versus displacement, permitting calculation of the mechanical properties of the sample (Ennos *et al.*, 1993).

These were two structural properties: the bending rigidity, *R*, and bending strength, *S*, of the internode; and two material properties of the stem, its bending stiffness, *E*, and maximum stress, $\sigma_{\max}$ (Gordon, 1978).

Anatomical examination

Finally, sections of several internodes were taken, as near as possible to the centre, stained with toluidine blue to show up lignified tissue, and examined under a compound microscope to look for the stage of development and for any gross differences in anatomy between the four treatments.

Statistical analysis

The results of all aspects of the study were subjected to two-way ANOVA in SPSS to determine the effects of each of the main factors, air flow, and mechanical flexure, and to investigate whether there were any interactions between the two.

Results

Morphological measurements

The treatments had a significant effect only on plant height (Table 1). The two-way ANOVA showed that both air flow ($F_{1.56}$=4.86, P=0.032) and flexing ($F_{1.56}$=60.40, P <0.001) had significant effects; air flow increased height by about 7%, while flexing decreased it by about 22%. No significant two-way interaction between wind and flexing was observed. Neither stem diameter nor leaf area was significantly affected by the treatments.

Stem hydraulic conductivity

Both treatments had a significant effect on the conductivity of internode 1 (Table 1). Air flow increased conductivity by about 8% ($F_{1.56}$=8.05, P=0.006) whereas flexing decreased it by about 16% ($F_{1.56}$=33.5, P <0.001). No significant two-way interaction between wind and flexing was observed.

Stem mechanical properties

The results for the mechanical tests are shown in Table 2. The mechanical properties of the internodes were all affected in the opposite way to conductance by the treatments. Rigidity was reduced by about 23% by air flow ($F_{1.56}$=12.05, P=0.001) and increased by 12% by flexing ($F_{1.56}$=5.01, P=0.029). Strength was similarly reduced by about 23% by air flow ($F_{1.56}$=12.53, P=0.001) and increased by 26% by flexing ($F_{1.56}$=16.62, P <0.001). No significant two-way interaction between wind and flexing was observed.

The material properties of the internodes was also affected in the same manner. Stiffness was reduced by about 31% by air flow ($F_{1.56}$=17.89, P <0.001) though not significantly affected by flexing. Maximum stress was reduced by about 29% by air flow ($F_{1.56}$=27.22, P=0.001) and increased by 27% by flexing ($F_{1.56}$=12.13, P=0.001). No significant two-way interaction between wind and flexing was observed.

Anatomical examination

None of the internodes showed any sign of secondary growth at the interfascicular cambium; the vascular bundles were clearly separated and there were no obvious differences in their size and shape, nor in the relative amounts of fibres and vessels.

Discussion

As a method to distinguish between the two effects of wind, air flow and stem flexure, the factorial experiment described here appeared to work well and showed clear results. There were some flaws in the separation of the two effects. The plants which were supported but which were placed in the wind would have received some mechanical stimulation to their leaves and petioles which the simply supported plants would not. Similarly, the flexed plants which were placed in the wind would have received more mechanical stimulation to their stems than the flexed plants grown in still air since the wind would also have flexed their stems. However, the effect would probably have been small because the wind flexed the plants by much less than the 45° that the stems were flexed experimentally.

The results clearly show that the two aspects of wind stimulation, air flow and flexing, had directly opposite effects on the plants. Air flow increased height and stem conductivity, while reducing the strength and rigidity of

Table 1. *The results of the morphological and hydraulic measurements on plants subjected to the four different treatments, showing means ±SD for height, first internode diameter, leaf area and length specific conductivity* k_h

Asterisks show measures that were significantly affected by treatment.

	No wind/no flex	No wind/flex	Wind/no flex	Wind/flex
Height (cm)*	66.8±10.8	52.9±7.0	72.3±8.9	56.4±5.1
Stem diameter (mm)	8.4±0.4	8.2±0.6	7.9±0.8	8.5±0.7
Leaf area (cm)	725±93	703±61	635±139	654±108
k_h ($\text{m}^4\ \text{Pa}^{-1}\ \text{s}^{-1}\times10^{-15}$)*	10.8±1.3	9.6±0.9	11.5±0.7	10.2±1.0

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Table 2. *The results of the mechanical measurements on the first internode of plants subjected to the four different treatments, showing means ±SD for rigidity, strength, stiffness and maximum stress*

Asterisks show measures that were significantly affected by treatment.

	No wind/no flex	No wind/flex	Wind/no flex	Wind/flex
Stem rigidity (N m^2)*	0.63±0.15	0.71±0.20	0.46±0.16	0.58±0.17
Stem strength (N m)*	0.33±0.06	0.42±0.11	0.24±0.09	0.34±0.10
Stiffness (MPa)*	297±100	295±109	185±52	225±49
Maximum stress (MPa)*	6.2±1.3	7.2±2.1	4.1±0.8	5.6±1.0

the stem. Stem flexure reduced height and stem conductivity, while increasing the strength and rigidity of the stem. Neither air flow nor stem flexure would, therefore, have had much effect on the overall hydraulic resistance of the stem, because the changes in conductivity and stem length they caused tended to cancel each other out. The results also suggest that there was a clear trade-off between the mechanical and hydraulic functions of the stem; as conductivity increased, strength decreased and vice versa. Neither stimulus affected stem diameter, however, so they must have altered the relative investment *within* the stem between mechanical and hydraulic tissue. There was no clear visible difference in stem anatomy, but the relatively small changes in conductivity and mechanical properties that were observed would only require very moderate alterations. A small increase in the number of fibres or an increase in the thickness of their cell walls would be enough to strengthen the stem. Similarly, a small increase in the number of vessels or in vessel diameter would be enough to increase stem conductance, particularly as the conductivity of vessels increases with the fourth power of their diameter.

Closer anatomical study would clearly be a subject for future investigations and it might also shed light on the cellular mechanism by which the developmental changes were produced. The effects are unlikely to be due solely to reorientation of cellulose microfibrils in the primary cell walls of fibres and vessels. Mechanical stimulation is thought to reduce fibre angle relative to the long axis of the cell, and this would indeed result in the reduced extension growth observed in flexed plants. However, it would also result in an increase in diameter of the vessels, which would increase conductivity, the opposite of what was observed. Similarly, air flow could not just have increased fibre angle; this would have resulted in the increased extension growth that was observed, but the diameter of the vessels would have been reduced, lowering conductivity. The effect of both stimuli must, therefore, be more complex; it might include changes in the size and relative numbers of young fibre and vessel cells, or in the extent of secondary thickening of their cell walls.

The results shown here are not all novel. It has already been seen in the introduction that shaking plants often increases the strength and rigidity of their stems, and there have been suggestions that mechanical stimulation can reduce hydraulic conductivity; Gartner (1991) found that the stems of self-supporting plants of poison oak, which would be more heavily mechanically stressed, have lower conductivity than those of supported vines of the same species. Similarly, the increase in height caused by the relatively slow air flows produced by the fan in this experiment is not unexpected given the positive effects of low winds on plant growth rate found by Wadsworth (1959). However, the fact that air flow has the opposite effect from mechanical stimulation on both mechanics and hydraulics *is* new. The responses of plants to wind, therefore, would seem to be the sum of two separate responses: a (possibly physiological) response to air flow past the leaves; and the response of the stem to flexure.

In this experiment, plants subjected to both air flow and stem flexure tended to have stems which were shorter, with lower conductivity and rigidity than those subjected to neither. However, these differences would have depended on the exact conditions. In real life the response of plants to the wind would depend on the relative importance of the effects of flexure and air flow, which in turn will depend on several factors: the area and size of leaves, the shape and drag coefficient of the canopy, the wind speed, and the relative sensitivity of the plant to the two forms of stimulation. This could help explain why the responses of plants to the wind can be so variable.

One thing the experiment failed to determine was the relative effect of flexing and air flow on the secondary growth of sunflowers, simply because the plants were harvested so young. No secondary growth had therefore occurred along the cambium in the first internode. A future experiment could usefully carry on the same procedure but harvest plants later. The results of such a study would be interesting because secondary cambial growth seems to respond in a different way, and at a local level, to mechanical stimulation (Mattheck, 1991; Goodman and Ennos, 1998) compared with primary growth which responds on a whole-plant basis (Coutand and Moulia, 2000). Thus there might be a different trade-off between the hydraulic and mechanical tissues.

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