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Effects of Vibration on Mechanical Properties and Biomass Allocation Pattern of *Capsella bursa-pastoris* (Cruciferae)

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The herbaceous dicot species *Capsella bursa-pastoris* (Cruciferae) was used to determine the influence of chronic mechanical perturbation on the biomass allocation pattern (i.e. dry weight distribution among roots, stems and reproductive structures) and the mechanical properties of roots and stems (i.e. tensile breaking stress and Young's modulus). It was hypothesized that mechanically stimulated plants would allocate more of their total biomass to root systems and less to shoots compared to control plants and that the breaking stress (a measure of strength) and Young's modulus (a measure of material stiffness) would increase for roots and decrease for stems because these responses would adaptively reduce the bending moment at the base of shoots and increase the anchorage strength of root systems. It was also hypothesized that mechanical perturbation would maladaptively reduce the relative fitness of individuals by reducing biomass allocation to their reproductive organs and the ability to broadcast seeds by means of elastic stem flexure. These hypotheses were tested by vibrating cultivated plants for 60 s every day during the course of growth to maturity and comparing their dry weight distributions and the mechanical properties of their body parts (measured in tension) to those of undisturbed control plants. Based on a total of 51 experimentally manipulated and 44 control plants for which mechanical properties were successfully tested, chronic organ flexure resulted in more massive root systems and less massive vegetative shoots, increased the magnitudes of root breaking stress and Young's modulus and had the reverse effect on stems, reduced the dry weight of reproductive structures at maturity, delayed the formation of the first mature flower and fruit, and accelerated the on-set of plant senescence compared to control plants. These responses to chronic organ flexure are interpreted to be vegetatively adaptive, since they reduce the probability of stem and root failure as a consequence of wind-pressure or foraging, and to be reproductively maladaptive, since they reduce reproductive effort and the ability to mechanically discharge seeds.

Key words: Adaptation, biomass allocation, biomechanics, elastic properties, roots, stems, thigmomorphogenesis.

INTRODUCTION

Many factors are known to influence the pattern of biomass allocation to different plant parts. For example, low availability of nitrogen, phosphorus and water enhances biomass allocation to roots, while low quantum flux densities promote allocation to leaves (see Brouwer, 1983; Lambers, 1983; Konings, 1989). Likewise, genotypic differences in biomass partitioning among leaves, stems and roots are correlated with differences in endogenous gibberellin (e.g. Rood *et al*., 1990) or abscisic acid levels (Saab *et al*., 1990) and with sensitivity to exogenous plant hormones (Jupe, Causton and Scott, 1988). Broad taxonomic differences also exist. Herbaceous monocot species typically invest relatively more biomass in roots and less in leaves compared to herbaceous dicot species with equivalent relative growth rates (Garnier, 1991). Biomass allocation patterns are thus 'plastic and variable' in the sense that they can be adjusted by a single genotype to respond to different ambient environmental conditions (especially for fast growing, weedy species; see Campbell and Grime, 1989; van der Werf *et al*., 1993) and they can differ significantly across even closely related species grown under similar conditions.

The influence of environmental factors on biomass allocation is made more complex by the fact that some factors are also known to influence the mechanical properties of plant structures and thus affect the biomechanical returns from the differential allocation of biomass to different organ types. One of the more extensively studied of these environmental factors is chronic mechanical stimulation. Much of the extensive literature dealing with this factor treats arborescent dicot species (e.g. Knight, 1811; Jacobs, 1954; Neel and Harris, 1971; Hathaway and Penny, 1975; Kellogg and Steucek, 1980; Telewski and Jaffe, 1986; Nicoll *et al*., 1995; Telewski, 1995; Teleski and Pruyn, 1998). Comparatively fewer studies have addressed the influence of this factor on both the material properties and the allocation of biomass to the body parts of herbaceous species, and typically emphasize commercially important plants that have been subjected to intense artificial selection (e.g. Ennos, 1989, 1991*a*, *b*, 1994; Ross, Ennos and Fitter, 1991; Crook and Ennos, 1993, 1994, 1996*a*, *b*; Ennos, Crook and Grimshaw, 1993*a*, *b*; Crook, Ennos and Sellers, 1994; Gartner, 1994; Goodman and Ennos, 1996).

By far the least well understood aspect of plant responses to chronic mechanical disturbance is the effect on reproductive success, both in terms of the allocation of biomass to flowers and seeds and the ability of plants to mechanically broadcast seeds. The literature indicates that, in general, chronically perturbed herbaceous plants invest

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more biomass in their root systems relative to their shoots and that they produce shorter shoots compared to control plants (Ennos, 1989, 1991*a*, *b*, 1994; Ross, Ennos and Fitter, 1991; Crook and Ennos, 1993, 1994, 1996*a*, *b*; Ennos, Crook and Grimshaw, 1993*a*, *b*; Crook, Ennos and Sellers, 1994; Gartner, 1994; Goodman and Ennos, 1996). Superficially, this suggests that chronic mechanical disturbance may reduce the biomass investment in reproductive structures and limit the ability of stems to mechanically broadcast seeds due to alterations in the mechanical properties and height of stems. If so, then mechanical stimulation may have a negative influence on relative fitness.

The objective of this study was to test this hypothesis for a herbaceous species that has not been the subject of intense artificial selection. The annual or biennial Shepherd's Purse, *Capsella bursa-pastoris* (L.) Medic., was selected for study because, in addition to being a wild relation of a number of commercially important crop plants, this species lacks the capacity to produce secondary tissues, which can unduly complicate the analyses of biomechanical and biomass allocation patterns among the different organ types. In this paper, I present data for the mechanical properties of roots and stems (strength and stiffness) as well as for the dry weight of reproductive organs, stems and roots. These data support the hypothesis that mechanical disturbance can alter both the chronology and the quantity of reproductive effort in potentially negative ways.

MATERIALS AND METHODS

Biological materials

Seeds of *C. bursa-pastoris* were harvested in summer from 20 randomly-selected field-grown plants, mixed in a container, and sorted according to size with a series of metal sieves. Approximately 200 seeds from the largest size-category in this sample were hydrated with distilled water in a Petri dish for 24 h at room temperature. Seeds were individually planted in cylindrical plastic pots measuring approx. 2 cm in diameter and 19 cm in length containing hydrated Cornell potting mix. The size and shape of pots and the composition of the potting soil were determined to foster the growth and development of taproot growth in preliminary experiments. These pots were placed in a cold frame where seed germination and the establishment of juvenile plants with a rosette growth habit were monitored throughout the autumn and winter months.

In the spring, the pots were removed from the cold frame and brought into the laboratory where plants were subsequently grown in a growth chamber to induce shoot bolting and flowering. Each pot was sub-irrigated by periodically adding water to a Petri dish placed beneath its perforated bottom. Plants were cultivated at a temperature of 25 °C with a day/night photoperiod of 15/9 h. The average light intensity measured at the level of the pots was 276 μmol photons m^{-2} s^{-1}. These growth conditions, which were selected on the basis of prior experience with this and other flowering plant species (e.g. Paolillo and Niklas, 1996), were judged to produce healthy and normal looking plants. Nevertheless, the data reported here cannot be extrapolated to encompass the mechanical properties and allometries of conspecifics grown under different ambient light conditions.

After seeds were planted, the 200 pots were randomly sorted into two groups of 100 pots each. These two groups were designated as the experimental and control groups. Both groups were cultivated in the cold frame and in the growth chamber in the same way.

Mechanical stimulation

Experimental and control plants were removed from the growth chamber and those belonging to the experimental group were vibrated for 60 s (at 250 Hz based on stroboscopic illumination of the vibrating tip) by applying the tip of a battery operated toothbrush (the vibrating tip was covered with a thin 'sock' of foam rubber to prevent abrasion of epidermal cells) to the base of the most proximal extended stem internode. Sufficient pressure was applied to ensure that the entire shoot vibrated; lateral displacements varied as a function of plant age and height, but ranged between 0·3 and 1·2 cm. Each shoot was subsequently gently pulled and pushed up and down ten times by hand to mechanically disturb root systems. Care was taken not to damage shoots, expose roots above the surface of the potting mix, or alter the contact point between the base of the shoot and the potting mix. Control plants were neither vibrated nor pulled. They were removed however from the growth chamber because, in theory, this could induce a thigmomorphogenetic response. (Control and experimental plants were both mechanically disturbed by air circulation in the growth chamber. This disturbance was considered modest based on visual inspection.) The pots were then returned to the growth chamber in a randomly selected order to minimize the potential effects on subsequent growth of variations in local light intensity resulting from the differential growth of neighbouring plants or the reflection of light from the white interior surfaces of the chamber. Plants were treated in this way from the first day of growth in the growth chamber to the end of this study, which spanned 49 d.

Plants bearing senescent leaves, ripened seeds or mature, drying fruits were observed to shed these parts when mechanically vibrated. Because the dry weights of the shoot or reproductive 'compartments' in plants could be underestimated if shed parts were not collected, a small paper cone was placed around the base of older plants before mechanical stimulation and shed parts collecting in the cone were added to the subsequently dissected parts of the plant which were then dried to determine biomass allocation patterns (see below).

Measurements of mechanical properties

Plants were harvested for mechanical testing and biomass measurements each day after they were placed in the growth chamber provided one or more internodes were extended sufficiently to mechanically test (i.e. $\geqslant 1{\cdot}5$ cm in length). Two biomechanical properties were measured for the stems

and taproots of plants: the breaking stress σ_b and Young's modulus E. Both of these properties were measured only in tension. Thus, as used throughout this study, the breaking stress is defined as the magnitude of the tensile force required to break a stem or taproot normalized with respect to the cross-sectional area of the organ. The breaking stress has units of newtons per metres squared (N m^{-2}). Likewise, as used here, the Young's modulus is the quotient of the tensile stress σ and strain ϵ measured within the elastic (proportional) limits of a stem or taproot (i.e. $E = \sigma/\epsilon$). Because strain is a dimensionless parameter, E has the same units as stress (i.e. N m^{-2}). The breaking stress was measured because this property defines 'strength', that is, the minimum mechanical force required to break either organ when placed in tension. The Young's modulus was measured because this property is a measure of organ stiffness and thus a measure of the ability of a taproot or stem to resist the tensile forces incurred by a bending or twisting force. In theory, there is no *a priori* correspondence between the breaking stress and the Young's modulus, nor is there any necessary relationship between the magnitudes of either of these two material properties when measured separately in tension and in compression for the same material. Thus, the data reported here for the ability of roots or stems to sustain tensile forces cannot be extended to infer the manner in which either organ type can cope with compressive or torsional forces, although relationships among organ stiffness measured in tension, compression and torsion may exist.

The (tensile) Young's modulus of taproots and stems was determined in the following way. Plants were removed from their plastic pots by submerging each container in tap water and gently washing the soil mix away from roots. Lateral roots, leaves and axillary branches (if any) were removed with a razor blade and stored in vials for subsequent dehydration to determine their dry weights. The cut surfaces of excised taproots and stems were coated with a thin layer of petroleum jelly to reduce the rate of tissue dehydration. Distilled water was also dripped on taproots during the course of experiments. The proximal end of an excised organ was held in place by a small clamp lined with a thin layer of foam rubber to reduce tissue crushing. The opposing distal end of each organ was vertically suspended and similarly clamped. A small rubber balloon was attached to this second clamp by means of a thin nylon thread. Liquid mercury was then injected into the balloon with a hypodermic needle to increase the tensile force exerted along the length of the organ. This force (expressed in units of N) was computed on the basis of the combined mass-force (weight) of the mercury, clamp, balloon and nylon thread. The tensile stress induced by this force was computed by normalizing the combined applied load with respect to the average cross-sectional area of the organ, which was subsequently measured from three free-hand cross sections taken at the mid length and near each end of the organ.

The longitudinal displacement of two biological or artificial markers (e.g. arbitrarily selected root hairs, leaf scars, or resin beads placed on the epidermis at convenient locations) resulting from the applied tensile load was measured with a microscope equipped with an ocular micrometer. The corresponding tensile strain was computed by dividing the longitudinal displacement by the original distance between the two markers which was previously measured with a microscope equipped with an ocular micrometer. The Young's elastic modulus was computed by dividing the tensile stress by the tensile strain.

Three magnitudes of tensile stress and their corresponding strains were used to determine E for each organ. This protocol was adopted to ensure that the linear elastic range of the organ's composite tissues was used to compute E. Data were rejected from organs whose linear elastic ranges had been exceeded. This was evident when organs failed to return to their original dimensions when they were unloaded. Different markers on the surface of an organ located at different distances from the two clamped ends were used to measure the tensile strains to determine if E varied significantly along the length of an organ. This was necessary because anatomical and morphological variations along the length of an organ may result in significant longitudinal variations in E which would go undetected if markers at two unique locations were used to measure strains. Data were rejected from organs that showed more than a 10% longitudinal variation in their elastic modulus determined on the basis of three different intensities of stress and strains measured at three different locations along their length. Despite these precautions, it cannot be assumed that the values reported for E do not represent tensile moduli measured for incipient non-linear elastic behaviour, nor can it be assumed that significant longitudinal variation in E did not exist at some locations for which strains were not measured. However, because all of the data presented here are from specimens that elastically retrieved their original inter-clamp lengths when unloaded, it is reasonable to assume that values for E were determined within or very near the elastic (proportional) limits of composite tissues.

The (tensile) breaking stress of each organ for which E was computed was determined in a similar manner to that described above. However, in these experiments, the tensile load was gradually increased above the maximum load used to compute E until the specimen broke. For this purpose, liquid mercury was injected into the balloon at the approximate rate of 0·02 N s^{-1} until the organ failed by breaking. The breaking stress was computed by dividing the combined mass-force (weight) of the clamp, balloon, mercury and thread by the average cross-sectional area of the two broken ends of the organ. These areas were measured from free-hand sections with the aid of a microscope. Data were rejected from organs that broke at or near either clamp because these organs may have failed due to unobserved tissue damage resulting from clamping their ends. Data were also rejected from organs that mechanically failed in part by the shearing of the vascular tissue system through the ground tissue. This was observed exclusively for taproots and typically took the form of vascular strand extension beyond the fracture plane of a broken root.

Longitudinal variations in the cross-sectional areas of roots and stems were evident for most of the specimens examined in this study. Because breaking stresses are computed on the basis of an average transverse area

TABLE 1. *Means (±s.e.m.) of the scaling (allometric) exponent and* y*–intercept of the regression curves (*α *and* β*, respectively) for various relationships between the physical properties and dry weights of* Capsella bursa-pastoris *roots and stems subjected to chronic mechanical disturbance ('stimulated plants'; n = 51) and not subjected to mechanical perturbation ('control plants'; n = 44) based on ordinary least squares regression analyses*

	Control plants			Stimulated plants		
Relationship	r^2	α	β	r^2	α	β
$\log M_R$ *vs.* M_F	0·990	5·32 ± 0·01	−5·32 ± 0·01	0·965	6·84 ± 0·02	−1·73 ± 0·01
$\log M_R$ *vs.* M_S	0·995	1·21 ± 0·02	−1·86 ± 0·01	0·982	1·55 ± 0·06	−1·82 ± 0·04
σ_b^S *vs.* M_S	0·961	7·74 ± 0·22	5·92 ± 0·17	0·953	7·71 ± 0·25	4·33 ± 0·15
σ_b^R vs. M_R	0·961	10·1 ± 0·29	5·49 ± 0·06	0·886	11·5 ± 0·63	6·89 ± 0·15
$\log E_S$ vs. $\log M_S$	0·986	0·41 ± 0·01	2·41 ± 0·00	0·972	0·40 ± 0·01	2·25 ± 0·01
$\log E_R$ vs. $\log M_R$	0·985	0·42 ± 0·01	2·29 ± 0·01	0·956	0·40 ± 0·01	2·44 ± 0·02
$\log \sigma_b^S$ vs. E_S	0·958	0·002 ± 0·00	0·62 ± 0·01	0·927	0·003 ± 0·00	0·48 ± 0·02
$\log \sigma_b^R$ vs. E_R	0·905	0·002 ± 0·00	0·66 ± 0·01	0·889	0·002 ± 0·00	0·75 ± 0·01

M_F, dry weight of reproductive structures; M_S, dry weight of stem; M_R, dry weight of taproot; σ_b^S, tensile breaking stress of stem; σ_b^R, tensile breaking stress of root; E_S, Young's modulus of stem measured in tension; E_R, Young's modulus of taproot measured in tension.

measured at the point of breakage and because organs failed at different points along their lengths, the breaking stresses reported here are undoubtedly idiosyncratic in the sense that they reflect the propensity of specimens to mechanical fail at certain locations owing to anatomical or morphological heterogeneity. Likewise, the breaking stresses of organs were undoubtedly over-estimated because most plant structures laterally contract when pulled and thus suffer an instantaneous reduction in cross-sectional area which was not directly measured (i.e. the cross-sectional areas used to compute breaking stresses were those of 'relaxed' unloaded broken organs).

After the breaking stress and Young's modulus were determined, the dry weights of reproductive organs (pedicles, flowers, seeds or fruits) (if any), root system, vegetative stems and foliar leaves were determined by dissecting each plant and dehydrating its organs in a drying oven for 72 h at 70 °C. Although the body parts shed from mature or senescent plants during vibration experiments were collected and added to each of these four categories (see above), the older parts of some plants may not have been completely retrieved from the growth chamber or may have been lost from plants growing in the cold frame or during the removal of plants from the chamber. Likewise, some abscised floral parts and shed pollen were undoubtedly not included in the measurements of dry weight.

The flexural stiffness *EI* was also computed for the basal most stem internode of mature shoots. This parameter, which measures the ability of a support member like a stem to resist bending, is the product of the Young's modulus and the second moment of area *I*. For a stem with a circular cross section with diameter *D*, *I* is given by the formula $0{\cdot}01563\pi D^4$ (Niklas, 1992). *EI* was measured for mature shoots to determine the combined effects of chronic mechanical perturbation on the contribution of stem materials properties (summarized by *E*) and cross sectional biomass investment (biomechanically summarized by *I*) on the ability of reproductive shoots to resist bending.

Allometry and statistical analyses

A total of 95 plants provided useful data to determine allometric relationships based on statistical analyses of dry weight and mechanical properties of body parts. A total of 20 seeds planted for the experimental group either failed to germinate or died before they were tested while data from a total of 29 surviving plants had to be rejected because their roots or stems either failed to return to their original dimensions when they were unloaded or broke at or near one of their clamped ends. Useful data were thus collected from only 51 plants arbitrarily assigned to the experimental group. Likewise, a total of 12 seeds assigned to the control group either failed to germinate or died before they were tested, while data from 44 surviving plants in the control group had to be rejected. Thus, data were collected from only 44 plants assigned to this group.

The dry weight of stems, taproots or entire shoots of the 95 successfully examined plants were used as measures of body size to determine the allometric relationship between mechanical properties and plant size and whether this relationship was affected by mechanical stimulation of shoots and roots (see Figs 1–3, 5). Ordinary least squares regression analyses were performed on untransformed or $\log_{10}$-transformed data to determine the means and the standard errors of means of the scaling (allometric) exponent and the *y*-intercept of the regression curve (α and β, respectively) providing the best fit for the data. Ordinary least squares regression analysis was judged adequate for this purpose because the coefficients of correlation determined for various relationships were uniformly high (see Table 1). The 95% confidence intervals of the scaling exponents and *y*-intercepts of regression curves were used to determine if the allometries of experimental and control plants statistically differed. ANOVA was used to determine whether the differences between mean values of morphometric or phenological parameters statistically differed in significant ways.

RESULTS

Chronic mechanical stimulation altered the biomass allocated to roots, vegetative shoots and reproductive structures but did not affect total biomass or growth rate with respect to control plants (Fig. 1). Root biomass increased exponentially with respect to either shoot or reproductive biomass for experimentally manipulated and control plants, but the increase in root biomass with respect to either of these biomass compartments was significantly greater for the mechanically disturbed plants (Fig. 1A). The slope of the regression curve fitting the linear relationship between $\log_{10}$-transformed root biomass and untransformed reproductive biomass was $6{\cdot}81 \pm 0{\cdot}03$ and $5{\cdot}32 \pm 0{\cdot}02$ for experimentally manipulated and control plants, respectively ($P < 0{\cdot}0001$). The slope of the regression curve fitting the linear relationship between $\log_{10}$-transformed root biomass and untransformed shoot biomass was $1{\cdot}55 \pm 0{\cdot}03$ and $1{\cdot}21 \pm 0{\cdot}02$ for experimentally manipulated and control plants, respectively ($P < 0{\cdot}0001$). Comparisons indicated no significant differences between the y-intercepts of the regression curves for comparable data from experimentally manipulated and control plants. Regression and statistical analyses of total plant biomass against time showed no difference in the rate of growth between mechanically perturbed and control plants (Fig. 1B). Thus, (1) both groups of plants initiated their growth with statistically indistinguishable allocations to each of the three biomass compartments (root, shoot, reproductive structures) but (2) the two groups of plants subsequently diverged in their allocation pattern such that (3) the proportion of root biomass increased relative to the rest of the plant body as a consequence of mechanical perturbation that nevertheless (4) affected neither total plant size nor the rate of dry biomass accumulation.

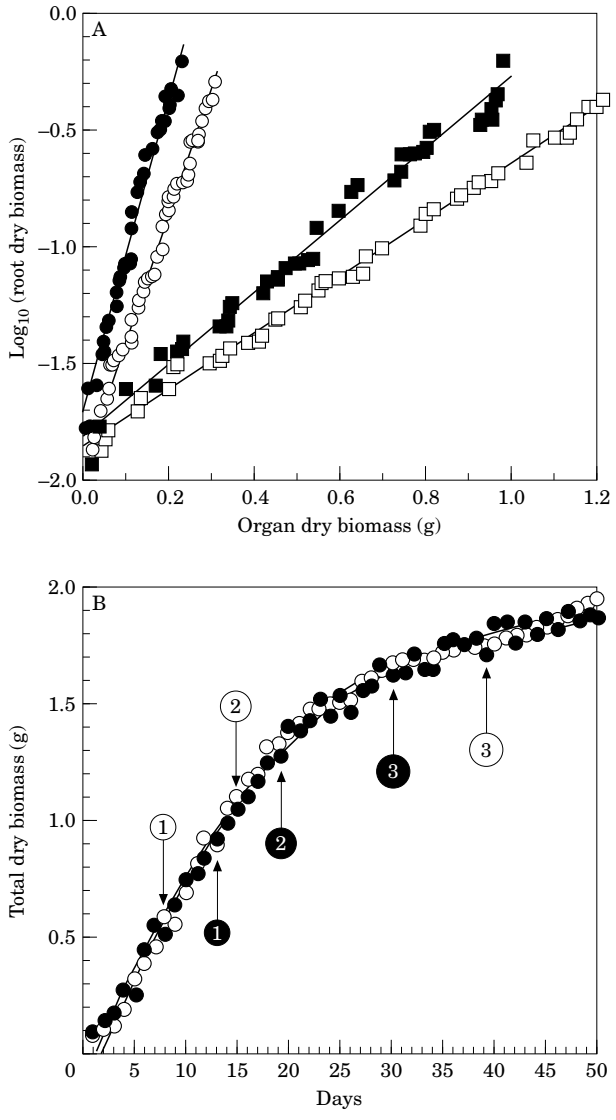

FIG. 1. Comparison of biomass allocation patterns and growth rates for mechanically stimulated and control plants. Ordinary least squares regression curves are shown for each relationship (see Table 1). A, Log_{10}-transformed root dry weight (biomass) plotted against shoot and reproductive biomass. Reproductive structures undisturbed (○); reproductive structures disturbed (●); shoot undisturbed (□); shoot disturbed (■). B, Total plant biomass and three developmental 'benchmarks' plotted against time: first mature flower (1); first mature fruit (2); onset of senescence (3) (diameters of circles = s.e.). Undisturbed (○); disturbed (●).

Morphometric and phenological differences were observed between experimentally manipulated and control plants. When mature, mechanically stimulated and control plants were $16{\cdot}1 \pm 2{\cdot}1$ and $11{\cdot}2 \pm 1{\cdot}4$ cm tall, respectively (i.e. experimental plants were, on average 30% shorter than control plants). Likewise, mechanically stimulated and control plants had basal stem diameters of $2{\cdot}21 \pm 0{\cdot}02$ and $1{\cdot}95 \pm 0{\cdot}01$ mm, respectively (i.e. the basal stem diameter of experimental plants was, on average, 12% thicker than that of control plants, and thus the average second moment of area measured at the base of control plant stems was 61% that of experimental plants). The tap- and lateral roots of manipulated plants were, on average, also 15% thicker (in diameter) compared to those of control plants. On average, mechanical disturbance delayed anthesis of the last flower by 5 d, the maturation of the first fruits by 3 d, and accelerated the on-set of plant senescence by 8 d with respect to control plants (Fig. 1B). Statistical comparisons of means (and their standard errors) indicated morphometric and phenological differences were significant between the 1 and 5% levels. Mechanically disturbed plants also produced, on average, 43% fewer seeds, which was statistically significant at the 1% level; no statistically significant difference in the average seed weight of experimental and control plants was detected.

Based on mean stem diameters and mean Young's modulus of mature shoots, the flexural stiffness of experimental plants was statistically significantly less than that of control plants: $1{\cdot}76 \times 10^{-4}$ N m^{-2} and $1{\cdot}99 \times 10^{-4}$ N m^{-2}, respectively. This difference indicated that the average increase in the girth of experimentally manipulated plants (which resulted in a significant increase in the second moment of area measured at the base of mature shoots) was not sufficient to compensate for the reduction in stem stiffness, and thus the mature shoots of experimental plants were, on average, significantly more flexible compared to the mature shoots of control plants.

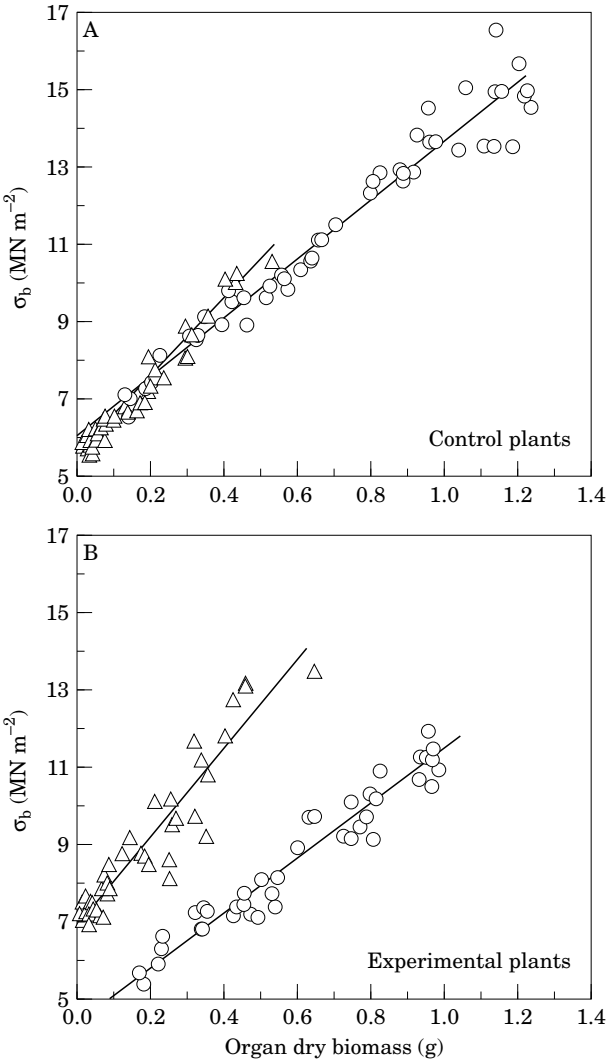

FIG. 2. Tensile breaking stress σ_b of stems (○) and roots (△) plotted against stem and root dry weights (organ dry biomass) for control (A) and mechanically stimulated (B) plants. Ordinary least squares regression curves are shown for each relationship (see Table 1).

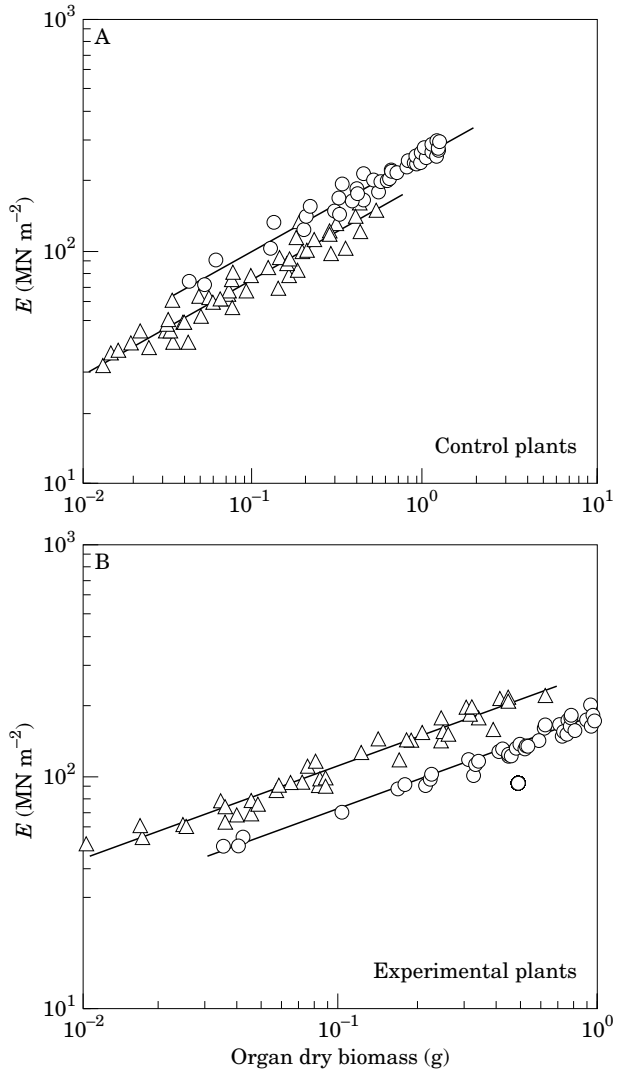

FIG. 3. Young's elastic modulus E measured in tension for stems (○) and roots (△) plotted against stem and root dry weights (organ dry biomass) for control (A) and mechanically stimulated (B) plants. Ordinary least squares regression curves are shown for each relationship (see Table 1).

The tensile breaking stress of taproots or the basal portions of stems was positively and significantly correlated with organ dry weight both for mechanically stimulated and control plants (Fig. 2). For each organ type, a simple linear regression curve provided the best fit for the relationship between the untransformed values for these variables (Table 1), indicating that the breaking stress increased in direct proportion to the allocation of biomass to these organs. Comparisons between the slopes of the linear regression curves for organ breaking stress *vs*. biomass indicated that the increase in the breaking strength relative to biomass investment was not significantly greater for taproots than for stems. Thus, mechanical stimulation did not significantly alter the manner in which the breaking stress of taproots or stems increased with respect to biomass increase. For example, even though the slope of the regression curve for breaking stress *vs*. dry weight was higher for the stems of control plants than for those of stimulated plants (i.e. 7·74 and 7·17, respectively), while the reverse was true for the taproots of these plants (i.e. 10·1 and 11·5, respectively), these differences were not statistically significant (Table 1).

The Young's modulus (stiffness) of taproots or stems was positively and significantly correlated with organ biomass both for mechanically stimulated and control plants (Fig. 3). However, in contrast to the simple linear relationship between organ breaking stress and biomass, a log-log linear regression curve provided the best fit for the relationship between these two variables (Table 1), indicating that the Young's modulus of the taproots or stems disproportionately decreased with increasing organ biomass (due to a scaling exponent less than unity). No difference between the slopes of the regression curves for the taproots and stems of control or stimulated plants was found. Thus, mechanical perturbation did not influence the manner in

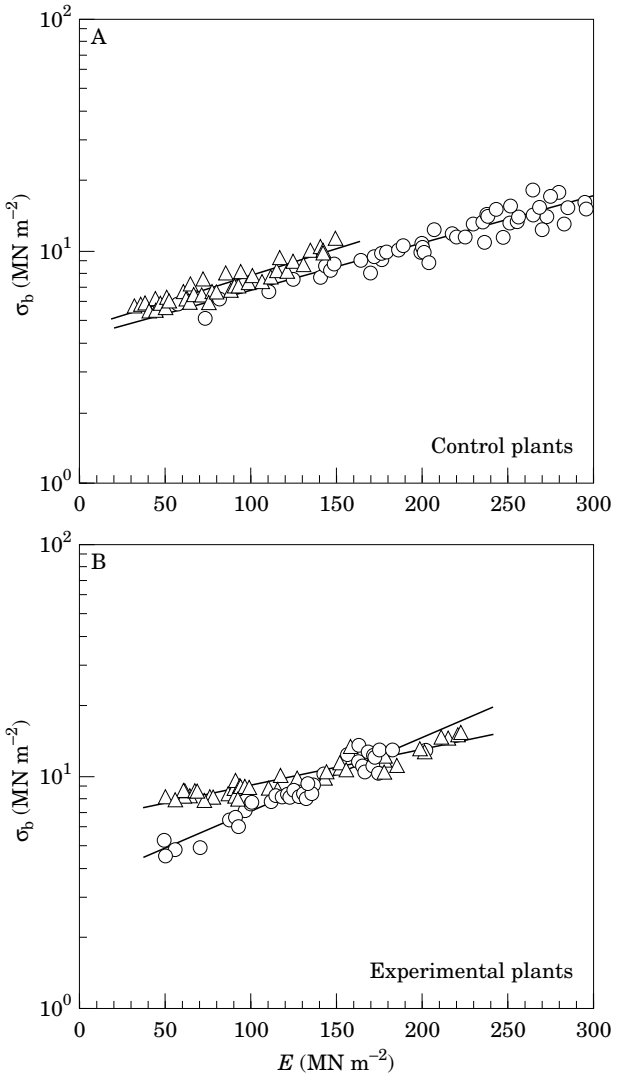

FIG. 4. Tensile breaking stress σ_b determined for stems (○) and roots (△) plotted against stem and root Young's elastic modulus E measured in tension for control (A) and mechanically stimulated (B) plants. Ordinary least squares regression curves are shown for each relationship (see Table 1).

which the stiffness of organs increased with respect to the allocation of biomass.

Significant differences in the absolute breaking stress and Young's modulus were found between control and stimulated plants (Table 1, Figs 2–3). For organs of equivalent biomass, mechanical stimulation significantly decreased the breaking stress and the Young's modulus of stems and had the reverse effect on taproots. Specifically, the y-intercept of the regression curve for stem breaking stress *vs.* biomass for control and stimulated plants was 5·92 and 4·33, respectively, while the y-intercept for the regression curve for stem Young's modulus *vs.* biomass for the control and stimulated plants was 2·41 and 2·25, respectively (Table 1). These data indicated that mechanical stimulation decreased absolute stem strength and concurrently increased absolute stem flexibility (i.e. the reciprocal of E) with respect to the mechanical properties of the stems of control plants. In contrast, the y-intercept for the relationship between taproot breaking stress and biomass for control and stimulated plants was 5·49 and 6·89, respectively, while the y-intercept for the relationship of Young's modulus and dry weight for the taproots of control and stimulated plants was 2·29 and 2·44, respectively (Table 1). Thus, for any equivalent organ biomass, the taproots of mechanically stimulated plants were stronger and stiffer (less flexible) than those of control plants.

The breaking stress and Young's modulus of taproots or stems were highly correlated with one another for both stimulated and control plants. The data indicated that mechanical stimulation decreased the strength of stems relative to their stiffness and had the reverse effect on taproots (Table 1). A log-linear regression curve provided the best fit for these relationships, indicating that the breaking stress increased as an exponential function of the elastic modulus of either organ type. Statistical comparisons indicated no significant differences existed for the manner in which the breaking stress increased with respect to the stiffness of control and experimental organs. However, comparisons among the y-intercepts of regression curves showed that stems of control plants had, on average, disproportionately higher breaking stresses with respect to their Young's moduli compared to stems of mechanically stimulated plants, while taproots of stimulated plants had, on average, disproportionately higher elastic moduli with respect to their breaking stresses compared to taproots of control plants.

Most of the aforementioned trends were summarized when the dimensionless quotient of the Young's modulus and breaking stress (i.e. E/σ_b) for taproots and stems was plotted against total shoot biomass (the sum of the dry weights of stems, leaves and reproductive organs). This dimensionless quotient quantifies the stiffness of an organ normalized with respect to its strength, and thus provides a measure of the ability of an organ to resist bending relative to the force required to break it. (Because both of these mechanical properties increased as a function of organ biomass, high values of E/σ_b cannot be interpreted to be a consequence of a reduction in the strength of an organ and must be a consequence of an increase in stiffness relative to an increase in organ strength.) The data for taproots indicated that the stiffness of these organs relative to their strength increased as a linear function of total shoot biomass both for stimulated and control plants. Based on statistical comparisons between the slopes of the linear regression curves affording the best fit for the data, mechanical stimulation unequivocally increased root stiffness relative to root strength (Fig. 5A). Specifically, the slope of the regression curve for E/σ_b *vs.* total shoot biomass was $8{\cdot}84 \pm 0{\cdot}49$ g^{-1} ($r^2 = 0{\cdot}849$) and $6{\cdot}00 \pm 0{\cdot}27$ g^{-1} ($r^2 = 0{\cdot}895$) for the experimental and control plants, respectively. In contrast to taproots, the relationship between E/σ_b for stems and total shoot biomass was non-linear and convex for both control and stimulated plants. A variety of regression curves were fit to these data. The most successful among those used was a second order polynomial regression curve, which indicated that stem stiffness relative

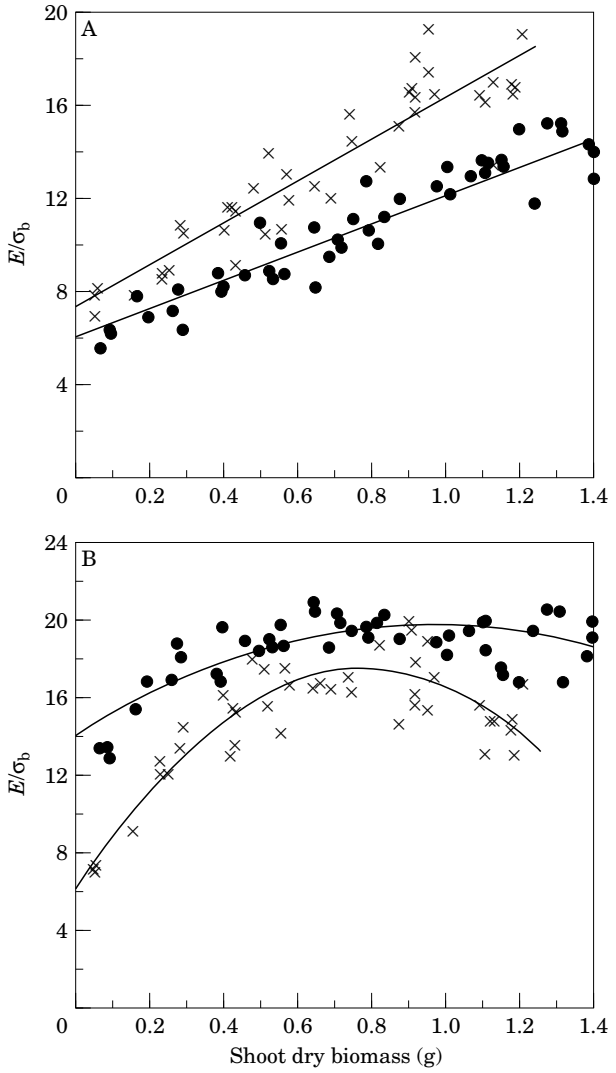

FIG. 5. The dimensionless quotient of the tensile Young's elastic modulus and the tensile breaking stress (E/σ_b) plotted against total shoot dry weight (shoot dry biomass) measured for the roots (A) and stems (B) of mechanically stimulated plants. Control plants (●); simulated plants (×). Ordinary least squares regression curves are shown for each relationship.

to stem strength increased and then decreased with increasing shoot size. Thus, the effect of mechanical stimulation was not uniform across the shoot size-range sampled here. Mechanical stimulation first amplified the relative stiffness of stems (as flowers developed and matured) and then decreased this parameter (at the end of the reproductive cycle, which was attended by plant senescence) (Fig. 5B).

DISCUSSION

The effects of mechanical perturbation on the material properties and the pattern of biomass allocation to roots and stems found for *C. bursa-pastori* are similar to those reported by previous studies of woody as well as herbaceous species. The stems of mechanically disturbed plants are generally thicker yet shorter and less stiff or strong compared to those of control plants (Knight, 1811; Venning, 1949; Turgeon and Webb, 1971; Jaffe, 1973; Grace and Russell, 1977; Kellogg and Steucek, 1980; Jaffe, Telewski and Cooke, 1984). Conversely, the roots of monocot and herbaceous dicot species are longer, stiffer and stronger than those of mechanically undisturbed plants (Ennos, 1991*a*; Goodman and Ennos, 1996). An increase in stem girth and a reduction in overall shoot biomass, length and stiffness are potentially advantageous because flexible and short shoots can reduce the maximum bending moment transmitted to anchorage systems by flexing under laterally applied external loads, and have a lower probability of snapping when subjected to external forces. Likewise, an increase in root (relative to shoot) biomass, stiffness and strength is advantageous because these responses to mechanical stimulation collectively increase the magnitude of the mechanical forces required to dislodge a plant from its substrate. Thus, from the perspective of survival of an individual plant, the responses to chronic mechanical perturbation are undoubtedly adaptive. In this respect the results reported for *C. bursa-pastori* are not novel, although empirical studies of the strength of herbaceous organs are generally taxonomically confined to monocot species (Silk, Wang and Cleland, 1982; Vincent, 1983; Ennos, 1991*a*, *b*; Crook and Ennos, 1994; Paolillo and Niklas, 1996; see, however, Ennos, 1989; Ennos and Fitter, 1992; Gartner, 1994; Ennos *et al.*, 1996*b*; Goodman and Ennos, 1996), which differ in their anatomy and development from herbaceous dicots.

By far the more interesting observation resulting from the present study is that mechanical stimulation delays the maturation of *C. bursa-pastori* flowers and fruits, shifts the allocation of biomass from reproductive to vegetative structures, and accelerates the onset of plant senescence. All of these responses to chronic mechanical perturbation have the potential to reduce relative fitness because individuals with shorter shoots bearing fewer reproductive structures produce, on average, fewer seeds and can mechanically discharge these seeds over a shorter distance compared to taller, reproductively more robust conspecifics. By the same token, a reduction in the time between the appearance of the first mature flower and the on-set of senescence reduces the window of opportunity for reproductive success. Thus, it is reasonable to argue that chronic mechanical perturbation can have negative effects on the relative fitness, here defined in terms of reproductive effort and the potential for long-distance colonization by seeds, of individuals compared to mechanically unperturbed conspecifics. This proposition, however, must be cast in terms of the fact that wind-induced organ flexure is a normal ecological event affecting plant growth and development, while reproductive success depends in part on the establishment and survival of vegetative structures. In this sense, the biomass allocation pattern observed for control plants is an artifact of withholding a normal environmental cue. The vegetative responses of plants like *C. bursa-pastori* to wind-induced flexure clearly provide advantages to survival because short and flexible shoots and comparatively massive and strong root systems help to resist large elastic displacements of shoots and dislodgment which could reduce subsequent

reproductive success. It must also be appreciated that herbaceous plants like *C. bursa-pastori*, which store and release wind-induced strain energy in stems to discharge seeds by means of rapid stem flexure, growing in protected sites and producing taller shoots may nevertheless broadcast seeds over shorter or equivalent distances compared to conspecifics growing in less protected sites because protected sites experience lower ambient wind speeds.

It is ill advised to extrapolate the results reported here for *C. bursa-pastori* to other herbaceous dicots. Even though the effects of chronic mechanical perturbation on vegetative organs are well known, comparatively few studies have focused on the effects on reproductive organs. By the same token, well reasoned arguments can be formulated suggesting that the tradeoff between the positive and negative effects on survival and growth, on the one hand, and reproductivd success, on the other, results in a stalemate. Clearly much more research is required before synoptic statements, if any regarding this tradeoff, can be made.

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LITERATURE CITED

Brouwer R. 1983. Some aspects of the equilibrium between overground and underground plant parts. *Mededelingen van het Instituut voor Biologisch en Scheikundig Onderzoek van Landbouwgewassen* **213**: 31–39.

Campbell BD, Grime JP. 1989. A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytologist* **112**: 261–267.

Crook MJ, Ennos AR. 1993. The mechanics of root lodging in winter wheat, *Triticum aestivum* L. *Journal of Experimental Botany* **44**: 1219–1224.

Crook MJ, Ennos AR. 1994. Stem and root characteristics associated with lodging resistance in four winter wheat cultivars. *Journal of Agricultural Science* **123**: 167–174.

Crook MJ, Ennos AR. 1996*a*. The effect of nitrogen and growth regulators on the stem and root characteristics associated with lodging in two cultivars of winter wheat. *Journal of Experimental Botany* **46**: 931–938.

Crook MJ, Ennos AR. 1996*b*. Mechanical differences between free-standing and supported wheat plants, *Triticum aestivum* L. *Annals of Botany* **77**: 197–202.

Crook MJ, Ennos AR, Sellers EK. 1994. Structural development of the shoot and root systems of two winter wheat cultivars, *Triticum aestivum* L. *Journal of Experimental Botany* **45**: 857–863.

Ennos AR. 1989. The mechanics of anchorage in seedlings of sunflower *Helianthus annuus*. *New Phytologist* **113**: 185–192.

Ennos AR. 1991*a*. The mechanics of anchorage in wheat *Triticum aestivium* L. I. The anchorage of wheat seedlings. *Journal of Experimental Botany* **42**: 1601–1606.

Ennos AR. 1991*b*. The mechanics of anchorage in wheat *Triticum aestivum* L. II. Anchorage of mature wheat against lodging. *Journal of Experimental Botany* **42**: 1607–1614.

Ennos AR. 1994. The biomechanics of root anchorage. *Biomimetics* **2**: 129–137.

Ennos AR, Crook MJ, Grimshaw C. 1993*a*. The anchorage mechanics of maize, *Zea mays*. *Journal of Experimental Botany* **44**: 147–153.

Ennos AR, Crook MJ, Grimshaw C. 1993*b*. A comparative study of the anchorage systems of Himalayan balsam *Impatians glandulifera* and mature sunflower *Helianthus annuus*. *Journal of Experimental Botany* **44**: 133–146.

Ennos AR, Fitter AH. 1992. Comparative functional morphology of the anchorage systems of annual dicots. *Functional Ecology* **6**: 71–78.

Garnier E. 1991. Above and below-ground resource capture in herbaceous plants: relationships with growth and biomass allocation. *Trends in Ecology and Evolution* **6**: 126–131.

Gartner BL. 1994. Root biomechanics and whole-plant allocation patterns: responses of tomato plants to stem flexure. *Journal of Experimental Botany* **45**: 1647–1654.

Goodman AM, Ennos AR. 1996. A comparative study of the response of the roots and shoots of sunflower and maize to mechanical stimulation. *Journal of Experimental Botany* **47**: 1499–1507.

Grace J, Russell G. 1977. The effect of wind on grasses. III. Influence of continuous drought or wind on anatomy and water relations in *Festuca arundinacea*. *Journal of Experimental Botany* **28**: 268–278.

Hathaway RL, Penny G. 1975. Root strength in some *Populus* and *Salix* clones. *New Zealand Journal of Botany* **13**: 333–344.

Jacobs MR. 1954. The effect of wind sway on the form and development of *Pinus radiata* D. Don. *Australian Journal of Botany* **2**: 35–51.

Jaffe MJ. 1973. Thigmomorphogenesis: the response of plant growth and development to mechanical stress. *Planta* **114**: 143–157.

Jaffe MJ, Telewski FT, Cooke PW. 1984. Thigmomorphogenesis: on the mechanical properties of mechanically perturbed bean plants. *Physiologia Plantarum* **62**: 73–78.

Jupe SC, Causton DR, Scott IM. 1988. Cellular basis of the effects of gibberellin and the *pro* gene on stem growth in tomato. *Planta* **174**: 106–111.

Kellogg RM, Steucek GL. 1980. Mechanical stimulation and xylem-production in Douglas fir. *Forest Science* **26**: 643–651.

Knight TA. 1811. On the causes which influence the direction of the growth of roots. *Philosophical Transactions of the Royal Society of London* **1811**: 209–219.

Konings H. 1989. Physiological and morphological differences between plants with a high NAR or a LAR as related to environmental conditions. In: Lambers H, Cambridge ML, Konings H, Pons TL, eds. *Causes and consequences of variation in growth rate and productivity of higher plants*. The Hague: SPB Academic Publishing, 101–123.

Lambers H. 1983. The 'functional equilibrium': nibbling on the edges of a paradigm. *Netherlands Journal of Agricultural Science* **31**: 305–311.

Neel PL, Harris RW. 1971. Factors influencing trunk growth. *Arborist's News* **36**: 115–138.

Nicoll BC, Easton EP, Milner AD, Walker C, Coutts MP. 1995. Wind stability factors in tree selection: distribution of biomass within root systems of Sitka spruce clones. In: Coutts MP, Grace J, eds. *Wind and trees*. Cambridge: Cambridge University Press, 276–292.

Niklas KJ. 1992. *Plant biomechanics: an engineering approach to plant form and function*. Chicago, IL: University Chicago Press.

Paolillo DJ Jr, Niklas KJ. 1996. Effects of *Rht*-dosage on the breaking strength of wheat seedling leaves. *American Journal of Botany* **83**: 567–572.

Rood SB, Buzzell RI, Major DJ, Pharis RP. 1990. Gibberellins and heterosis in maize: quantitative relationships. *Crop Science* **30**: 281–286.

Ross SJ, Ennos AR, Fitter AH. 1991. Turf strength and root characteristics of ten turfgrass cultivars. *Annals of Applied Biology* **118**: 433–444.

Saab IN, Sharp RE, Pritchard J, Voetberg GS. 1990. Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth of maize seedlings at low water potentials. *Plant Physiology* **93**: 1329–1336.

Silk WK, Wang LL, Cleland RE. 1982. Mechanical properties of the rice panicle. *Plant Physiology* **70**: 460–464.

Telewski FW. 1995. Wind induced physiological and developmental responses in trees. In: Coutts MP, Grace J, eds. *Wind and trees*. Cambridge: Cambridge University Press, 237–263.

Telewski FW, Jaffe MJ. 1986. Thigmomorphogenesis field and laboratory studies of *Abies frazei* in response to wind or mechanical perturbation. *Physiologia Plantarum* **66**: 211–218.

Telewski FW, Pruyn ML. 1998. Thigmomorphogenesis: A dose response to flexing in *Ulmus americana* seedlings. *Tree Physiology* **18**: 65–68.

Turgeon R, Webb JA. 1971. Growth inhibition by mechanical stress. *Science* **174**: 961–962.

Venning FD. 1949. Stimulation by wind motion of collenchyma formation in celery petioles. *International Journal of Plant Sciences* (formerly *Botanical Gazette*) **110**: 511–514.

Vincent JFV. 1983. The influence of water content on the stiffness and fracture properties of grass leaves. *Grass and Forage Science* **38**: 107–114.

Van der Werf A, Visser AJ, Schieving F, Lambers H. 1993. Evidence for optimal partitioning of biomass and nitrogen at a range of nitrogen availabilities for a fast- and slow-growing species. *Functional Ecology* **7**: 63–74.