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Changes in Endogenous Gibberellins and the Metabolism of [^{3}H]-GA_4 after Geostimulation in Shoots of the Oat Plant (*Avena sativa*)[1]

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ABSTRACT

The recovery from "lodging," or bending over, by shoots of 42-day-old *Avena sativa* plants is controlled primarily by a negatively geotropic differential growth of the lower halves of the p-1 node-pulvinus and the base of the p-1 internode, relative to the upper halves. Although geostimulation causes a significant reduction in p-1 internode length, dry matter accumulation in the p-1 node-pulvinus is increased, apparently at the expense of the sheath. Recovery to an angle of 30° is associated with changes in endogenous gibberellin-like substances (GAs), and in differential metabolism of applied [^{3}H]GA_4 (1.4 Curie per millimole). Although geostimulation depressed total GAs (relative to upright plant parts) to 0.40 and 0.13 for node-pulvini and sheaths, respectively, it increased them 2-fold for internodes. Within the plant part geostimulation increased GAs (relative to upper halves) 29- and 7-fold in lower halves of node-pulvini and internodes, respectively, but reduced GAs to 0.3 in lower halves of sheaths. At age 42 days a $GA_{4/7}$-like (nonpolar) substance predominates, with lesser amounts of a GA_3-like (polar) substance. Native GAs of *Avena* include GA_3, GA_4, and GA_7. Geostimulation enhanced the ratio of nonpolar to polar GAs for both halves of internodes, but tended to depress it for sheaths and node-pulvini.

The disposition and metabolism of applied [^{3}H]GA_4 confirmed the above trends for endogenous GAs regarding localization (*e.g.* up to 2-fold increases in [^{3}H]GA_4 and acidic ^{3}H-metabolites in the lower halves, relative to upper halves). Also, metabolism into highly water-soluble ^{3}H-metabolites (biologically inactive conjugates?) was greater (up to 1.8-fold) in upper than in lower halves. The end result of such metabolic trends would be to reduce acidic (biologically active?) GAs in the upper half, while retaining them for a longer time in the lower half.

Geotropically stimulated *Avena* shoots thus increase, within 24 hours, the levels of acidic GAs in the lower halves of the p-1 node-pulvinus and p-1 internode, the two plant parts responsible for the geostimulated growth.

Previous investigations on the negative geotropic response in geostimulated shoots of dicots and monocots have shown that the response is markedly stimulated by exogenously supplied auxin and that auxin becomes asymmetrically distributed to the lower side of the corresponding tissue (6, 13, 24). Most of what is known about the possible roles of gibberellins (GAs) in geotropic movements of plant shoots is based on the exogenous application of GAs, or GA antagonists to the plant. Thus, exogenous GA_3 can enhance hyponasty, even counteracting positively geotropic growth of lateral branches and the main stem of intact conifers under certain conditions (18–20), and GAs are implicated in the growth habit of the shoot of peanut (10) and a number of plant species (references cited in 10, 18). It has also been reported (21) that the activity of GA-like substances diffusing from the lower halves of geotropically stimulated sunflower buds was almost 10 times that of upper halves, and a similar redistribution was noted for the lower halves of geotropically stimulated maize coleoptiles (22).

Shoots of grasses respond to geotropic stimulus at specialized pulvini located at the base of the leaf sheath in festucoid grasses, and also at one located at the base of the internode in panicoid grasses (5, 7). When *Avena* shoots are geostimulated, one, and usually two node-pulvini respond by negative geotropic curvature over a period of 20 min to 48 h (6, 7). This growth in the node-pulvinus which results in negative geotropic curvative can be enhanced by, and is very sensitive to, auxin application in *Avena* (13), and in *Poa pratensis* to Ethephon, and especially Ethephon plus GA_3, but not to GA_3 alone (25). In *Avena,* a festucoid grass, the leaf sheath pulvinus (termed node-pulvinus hereafter) is a significant source of GAs, as are elongating internodes and inflorescences (15). During transition from lag to log phases of internodal extension there is a significant increase in more polar GAs (15). One of the major polar GAs in the inflorescence is GA_3 (15), as is probably the case for the node-pulvinus and internode. An optimal internodal extension response of excised shoots to exogenously supplied GA_3 is strongly dependent upon the presence of the primary sources of native GAs: the two leaves associated with the internode, the two node-pulvini at top and bottom of the internode, and the inflorescence (16). These observations imply that GAs, as well as auxin and ethylene, may be involved in shoot geotropic movement, and specifically in the growth by both node-pulvini and internodes of grasses that causes the negative curvature response to geotropic stimulation.

The present study investigates the correlation between endogenous GAs and the curvature response to geotropic stimulation in *Avena* shoots. Additionally, since the metabolic conversion of the nonpolar GA_4 to the more polar GA_1 is closely correlated with GA_4-induced growth in the hypocotyl of lettuce (8), the disposition

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and metabolism of high specific activity [^{3}H]GA_4 was followed after geostimulation of *Avena* shoots. This was done to obtain additional insight into how the node-pulvinus and the internodal intercalary meristem distribute and metabolize a nonpolar GA (which may be expected to undergo rapid metabolism) as recovery to lodging takes place.

MATERIALS AND METHODS

Plant material of *Avena sativa* cv. 'Victory' was grown, treated, harvested, immediately frozen in liquid N_2, and lyophilized in Ann Arbor before shipping to Calgary for analysis of GAs. Plants were grown in flats in a cooled greenhouse (21.5 C day, 15.5 C night) under natural photoperiod from September to December. Plant parts sampled and their dry weights are given in Table I and the technique of sampling illustrated in Figure 1, a and b.

At time of treatment (age 42 to 45 days) the p-1 internode averaged 2 to 3 cm. For experiments with [^{3}H]GA_4 40 plants were carefully removed from the flat, soil particles washed free of the roots, and the plants placed in plastic trays filled to 2 cm with 1 liter of Hoagland solution. Half (20 plants) remained upright (shoots were held vertically by wire support frames), half were geostimulated (lodged), in which case the shoots at time zero (t_0) were bent horizontally to about a 5° angle, and held there with large glass plates placed on top of the "root area" (Fig. 1a). Geostimulated plants were allowed to respond geotropically to a 30° angle (reached 44 to 48 h after t_0). [^{3}H]GA_4 [about 1.4 Ci/mmol; 10^7 dpm in 3.2 ml of ethanol:H_2O (95:5)] was added to the Hoagland solution 24 h prior to t_0 to allow for reasonable uptake prior to the lodging. Shoots were harvested at 44.5 h after t_0, when they had attained 30° curvature.

The grouped appropriate plant parts from 300 to 600 plants (Fig. 1b, Tables I, II) were analyzed for endogenous GA-like substances as previously noted (15) for *Avena* tissue. While upper and bottom halves were analyzed separately, left and right halves were grouped after cutting, and extracted together, the absolute values being divided by two. This procedure was utilized, not only for convenience, but also because preliminary results which compared "left" and "right" halves of upright maize tissue had shown a variability (±20%) which would have required a large number of replicates to rationalize (Pharis, unpublished results). Such variability may be due to the continual "corrections" in movement from left to right that take place during normal, upright growth of all plant shoots. Quantitation of GAs was based on bioassays

Table I. *Dry Weight of Avena Shoot Parts Sampled*

Plant Part	Upright				Geostimulated			
	Replicate no.				Replicate no.			
	1[a]	2	3	4[a]	1[a]	2	3	4[a]
	g/1,000 half-plant parts							
p-1 Node-pulvinus								
Either half	0.89	0.88	1.20					
Upper half					0.94	1.38	1.36	
Lower half					1.27	1.46	1.56	
p-1 Internode								
Either half			2.04	3.16				
Upper half							3.48	3.05
Lower half							3.48	3.20
Sheath								
Either half	8.32							
Upper half					6.13			
Lower half					6.13			

[a] Used for analyses of GA-like substances (Table II).

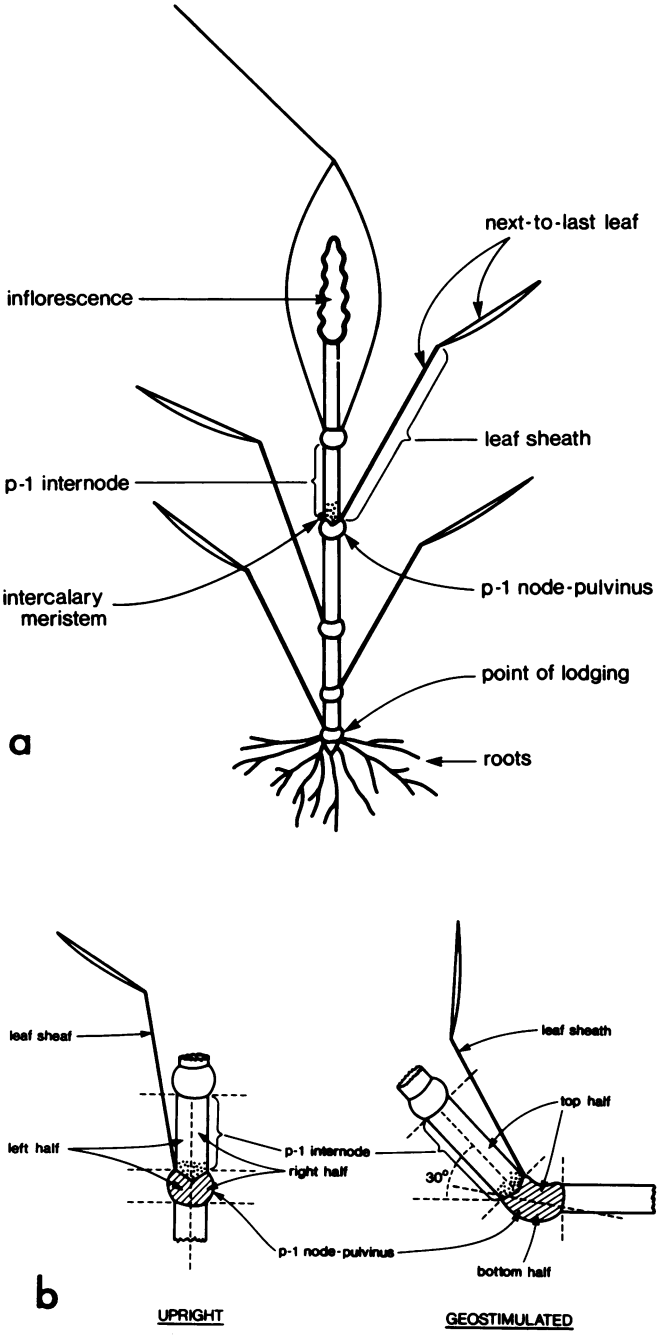

FIG. 1. a, Diagrammatic representation of *Avena* plants at time of geotropic stimulation and/or harvest of plant parts. b, Diagrammatic representation of plant parts harvested for the *Avena* shoot p-1 node-pulvinus and p-1 internode in upright (left) or geostimulated (right) shoots.

performed on each of 26 fractions eluted from a SiO_2 partition column (9) as noted earlier (15). The amount of radioactivity retained by the 40 node-pulvini, internodes, and leaf sheaths during the 68.5 h incubation period with [^{3}H]GA_4 was quite low (9,519 and 12,169 dpm for upright and geostimulated plant parts, in sum, respectively). Since the dry weight was also low, the 80% methanolic extract of grouped plant part halves was subjected directly to SiO_2 partition column chromatography (9) without further purification. Acidic, ethyl acetate soluble dpm were eluted in the first 26 fractions and the "highly water-soluble" dpm (probably glucosyl esters and glucosides of the [^{3}H]GA_4 precursor and/or its metabolites) were eluted by washing the column with absolute methanol. Estimates of dpm were made by liquid scintil-

Table II. *Levels of GA-like Substances*[a] *in Upright and Geostimulated Avena Plant Parts*

Plant Part	Fr. 1-11 (GA_4, GA_7 R_F) (μg)[b]	Fr. 12+ (GA_3, GA_8 R_F) (μg)[b]	Total	Ratio Fr. 1-11/ 12+
Sheaths[c]				
Either half	2.55	0.16	2.71	16/1
Node-pulvini[c]				
Either half	1.81	0.05	1.86	36/1
Internodes[d]				
Either half	0.21	0.14	0.35	1.5/1
Sheaths[e]				
Upper half	0.49	0.04	0.53	12/1
Lower half	0.11	0.04	0.15	3/1
			$\Sigma = 0.68$	
Node-pulvini[e]				
Upper half	0.03	0.02	0.05	1.5/1
Lower half	1.39	0.05	1.44	28/1
			$\Sigma = 1.49$	
Internodes[f]				
Upper half	0.18	0.01	0.19	18/1
Lower half	1.04	0.26	1.30	4/1
			$\Sigma = 1.49$	

[a] For one replicate for each of nine treatments/plant parts. Based on the significance of growth differences (mm of sheath length) between vials of 10 dwarf rice (cv. Tan-ginbozu) bioassay plants per serial dilution (1/75, 1/150, 1/300, 1/600) on each of the 26 fractions from three nine SiO_2 partition columns (measured over the assay range of 0.0005 to 0.02 μg GA_3 equivalents per rice plant), a conservative estimate of accuracy (but not precision) for any one treatment amount in Table II would be: within 0.02 μg: 0.01 to 0.099 μg GA_3 equivalent range; within 0.05 μg: 0.1 to 0.49 μg GA_3 equivalent range; within 0.1 μg: 0.5 to 0.99 μg GA_3 equivalent range; within 0.2 μg: 1.0 μg or greater GA_3 equivalent range.

[b] GA_3 equivalents (μg) per 1,000 plant-part halves.

[c] Replicate 1, Table I, 300 and 400 plants for nodes and sheaths, respectively.

[d] Replicate 4, Table I, 402 plants.

[e] Replicate 1, Table I, 308 and 298 plants for nodes and sheaths, respectively, geostimulated 24 hours to 30° to 40° curvature.

[f] Replicate 4, Table I, 402 plants, geostimulated 24 h to 30° to 40° curvature.

lation spectrometry of aliquots in 1 ml of methanol and 10 ml of cocktail (4).

RESULTS

Effects of Geostimulation on the Distribution of Dry Matter Between and Within Plant Parts. Dry weights of the various plant parts and their halves were measured for upright and geostimulated (about 30°) *Avena* shoots in several experiments (Table I). Geostimulation for 24 h increased the dry weight of the node-pulvinus (1.2 to 1.6 times), appeared variable in its effect on internode dry weight, and decreased dry weight of the leaf sheath (0.8 times) relative to dry weights of equivalent fractions in upright plants. Trends evident in Table I were confirmed in subsequent tests. Within the plant parts geostimulation tended to increase the distribution of dry weight toward the bottom half of the node-pulvinus (1.1 to 1.3 times) with no apparent effect on the leaf sheath and internodes relative to the upper half (Table I).

Effects of Geostimulation on the Distribution of Water Content of and Within the Node-Pulvinus, and on Elongation of Internodes. When geostimulated (about 30°), fresh weight of node-pulvini tended to increase (2.6%, to a value of 88.6% water) above that of upright node-pulvini. Curvature to either 30° or 60° also tended to increase fresh weight of bottom halves (3%, to values of 90 and 83% water, respectively) relative to top halves.

In two experiments geostimulation to 37.2° and 37.8° depressed internode elongation to 0.34 and 0.23 cm, respectively, relative to the 1.06 and 1.00 cm for upright internodes.

Effects of Geostimulation on Total Endogenous GA-like Substances Between Plant Parts. In an initial experiment (Replicate No. 1, Table I), we examined the endogenous acidic, ethyl acetate soluble GA-like substances (GAs) of the node-pulvinus and leaf sheath under normal (upright) conditions and after geostimulation (Fig. 2). Geostimulation to 30° decreased GAs to 0.4 and 0.13 of the upright parts in the node-pulvini and leaf sheaths, respectively (Table II).

In another experiment (replicate No. 4, Table I), we attempted to examine the endogenous GAs of internodes and node-pulvini from the same plants, the problems during the extraction and purification procedure caused extensive losses for extracts of the node-pulvini. However, the internodes were successfully assayed for GAs (Fig. 2), and geostimulation to 30° increased the total GAs four times relative to upright internodes (Table II).

Effects of Geostimulation on Total Endogenous GA-like Substances Within Plant Parts. Geostimulation resulted in very pronounced changes in distribution of GAs between upper and lower halves (Figs. 2, 3, Table II). Total GAs were 29 and 7 times greater in the lower halves of node-pulvini and internodes, respectively, relative to upper halves, but were 0.3 times less in the lower halves of leaf sheaths, relative to the upper halves. Amounts of endogenous GAs in geostimulated plants, relative to upright plants, decreased for the lower halves of node-pulvini (0.78 times), sheaths (0.06 times), and upper halves of node-pulvini (0.003 times), shealths (0.2 times), and internodes (0.54 times). Only the lower halves of internodes increased (3.7 times) relative to upright plants (Table II).

Effects of Geostimulation on Polar *Versus* Nonpolar Endogenous GA-like Substances Between Plant Parts. In age 42 day *Avena* plants there was a preponderance of nonpolar (Fr. 1-11) GAs relative to more polar (Fr. 12+) GAs (Figs. 2, 3, Table II). This is in contrast to age 50 and 55 day plants (15) when polar GAs (probably mainly GA_3) predominated. Subsequent work has shown that node-pulvinus plus internode tissue contains large amounts of nonpolar GAs when harvested at day 42, as does the inflorescence at day 47, and two of the GAs from each tissue sample were characterized as GA_4 and GA_7 by GC-MS (Noma, Ogiyama, Pharis, and Kaufman, unpublished).

One can take as an indication of "normality" the ratios of nonpolar (Fr. 1-11) to polar (Fr. 12+) GAs from upright plant parts, and these are 36:1, 16:1, and 1.5:1, for node-pulvini, sheaths, and internodes, respectively (Table II). Geotropic stimulation decreased this ratio for both node-pulvini and sheaths, especially for the upper half of the node-pulvinus and lower half of the sheath. However, geostimulation increased the ratio of nonpolar to polar GAs for internodes, especially upper internode halves (Table II).

The decreased ratios in nonpolar to polar GAs come about primarily by decreases in nonpolar GAs, whereas the increased ratios (internodes) are brought about by an increase in nonpolar GAs (5 times) for lower halves, and a decrease in polar GAs (0.07 times) for upper halves.

The end result of the above changes is that lower halves of geostimulated node-pulvini and internodes have, respectively, 46 and 6 times the amounts of nonpolar GAs, and 2.5 and 2.6 times the amounts of polar GAs of the upper halves. In sheaths, the lower halves have, respectively, 0.23 and 1.0 times the amounts of nonpolar and polar GAs, relative to upper halves.

Effects of Geostimulation on Disposition of [^{3}H]GA_4 and Its

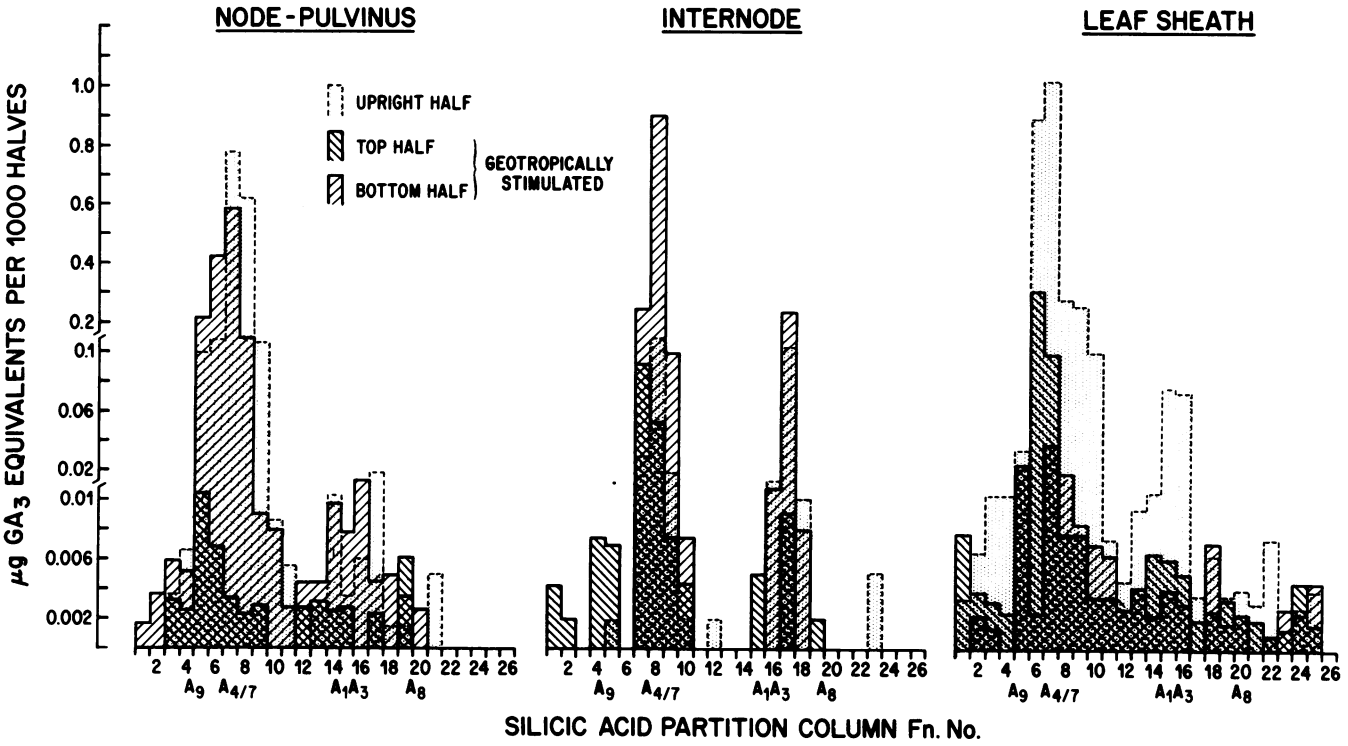

FIG. 2. Elution pattern of standard GAs (shown below the fraction numbers) and GA-like substance present in *Avena* plant parts, as assayed on dwarf rice Tan-ginbozu in serial dilution, for each of 26 fractions from a gradient-eluted SiO_2 partition column. Node-pulvinus and leaf sheath tissue from replicate 1, internode tissue from replicate 4 (Table I). A quantitative estimate for fraction groupings is shown in Table II.

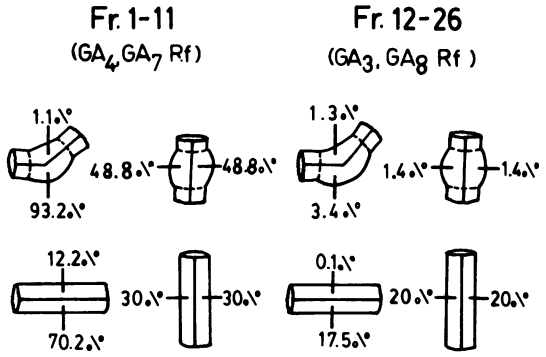

FIG. 3. Diagrammatic representation of endogenous acidic, GA-like substances in *Avena* upright and geostimulated plant parts. Data adapted from Table II. 100% equals upper + lower halves (or left + right halves) for Fr. 1-11 + Fr. 12-26 for each plant part.

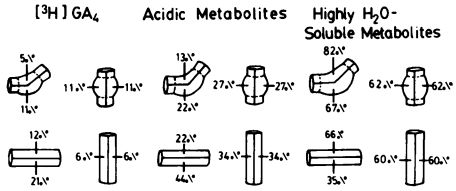

FIG. 4. Diagrammatic representation of percentage distribution of ^{3}H-dpm in node-pulvinus and internode halves after SiO_2 partition column chromatography of 20 upright or 20 geostimulated plants (30° curvature) incubated in 10×10^6 dpm of [^{3}H]GA_4 (1.4 Ci/mmol) for 24 h prior to geostimulation (t_0) of 20 plants, and 44.5 h after t_0. The 80% methanolic extract was chromatographed without further purification and the highly H_2O-soluble metabolites (probably glucosides and/or glucosyl esters) were eluted from the column with absolute methanol after the completion of the hexane to ethyl acetate gradient. Actual dpm present were 945 (node-pulvini) and 4918 (internodes) for left plus right halves, and 3774 (node-pulvini) and 3938 (internodes) for upper plus lower halves. For plant parts from geostimulated shoots the sum of all bottom halves for each plant part = 100%, as does the sum of top halves. Left halves were within 8% of right halves for node-pulvini, but the 4918 dpm value for internodes may be anomalous since the left halves contained 1226 dpm, right halves 3692 dpm. Hence, since there is no reason to believe that left halves should not equal right halves, the sum of left + right ÷ 2 is shown for vertical plant parts. Lower halves of geostimulated plant parts contained 1927 and 2027 dpm and upper halves 1847 and 1811 dpm for each of node-pulvini and internodes, respectively. Data for leaf sheaths are given in "Results."

Metabolites. The distribution of total radioactivity between and within node-pulvini and internodes is shown in the legend to Figure 4. Geostimulation increased total dpm found in node-pulvini by almost five times, but anomalous counts in the upright internode halves prevented a similar comparison for internodes. Geostimulated leaf sheaths tended to have more dpm than upright sheaths (4,557 *versus* 3,656, respectively). Within the plant part more dpm tended to accumulate in the lower halves of node-pulvini and internodes (Fig. 4) as well as sheaths (2,604 dpm on bottom, 1,953 dpm on top). This represents about 6 to 15 pg of GA_4 carrier per plant part, compared with endogenous levels of 100 to 1,300 pg of GA_4/A_7-like substance (Table II) for the lower halves. These latter values may, in turn, represent two to four times the actual levels in *Avena* shoots since they probably represent GAs which are quickly metabolized in the bioassay plant, but are compared with GA_3 standards, and hence expressed in GA_3 equivalents. Thus, the exogenously applied GA_4 should not have unduly perturbed the geotropic response system of the *Avena* shoot.

Of more interest, however, is the distribution of acidic, ethyl acetate-soluble dpm ([^{3}H]GA_4 and [^{3}H]GA_4 metabolites) and highly water-soluble dpm (probably glucoside or glucosyl ester conjugates of precursor [^{3}H]GA_4 and its acidic metabolites). Upright node-pulvini and internodes, within the 68.5 h incubation

period, put most of their dpm in highly water-soluble form, with very little left as [^{3}H]GA_4 (Fig. 4). However, upright sheaths retained 34% of their dpm as [^{3}H]GA_4, conjugating only 44% (22% went to acidic metabolites).

Geostimulation had pronounced effects on distribution of [^{3}H]GA_4 and its metabolites between halves (Fig. 4). Geostimulation skewed the majority of dpm to the lower half of the node-pulvini and internodes for five out of the six acidic radioactive peaks (*e.g.* [^{3}H]GA_4 and acidic metabolites). The trend for sheaths was similar, except for precursor [^{3}H]GA_4, where approximately equal amounts were present for upper and lower halves.

If one assumed that [^{3}H]GA_4 and its acidic metabolites represent biologically active GAs, then their disposition, as was noted for endogenous GA-like substances (Table II, Figs. 2, 3), indicates that lower halves of geotropically stimulated node-pulvini and internodes again possess larger proportions of acidic GAs than do upper halves (Fig. 4). Further, if one assumes that highly water-soluble dpm represent an increased ability to "remove" acidic GAs from an "active form," then the analogy with data presented in Table II and Figure 3 (*e.g.* reduced GA-like substances in upper halves) also holds true for radioactivity distribution [*e.g.* more of "highly water-soluble dpm" in upper halves (Fig. 4)].

DISCUSSION

Geostimulation results in rapid and marked changes in the p-1 node-pulvinus, internode, and sheath. These changes involve water content, dry matter accumulation, endogenous GAs, and GA_4 metabolism. All occur in the lower halves of the p-1 node-pulvinus and basal portion of the p-1 internode in a way that is consistent with the differential and negative geotropic growth in these plant parts. At these meristematic loci the growth response occurs as a result of accelerated cell elongation (6, 7). Upward growth starts within 20 min in *Avena* node-pulvini and continues at a rate of 1.5°/h (at 30 C) until the shoot has reached an angle of 90° from its initial horizontal position at the time of geostimulation.

Past work (15, 16) has shown that GAs, primarily a GA_3-like substance from the inflorescence and p-1 node-pulvinus, regulate internodal elongation in *Avena* at around 55 days of age. The data presented herein imply that GAs (especially $GA_{4/7}$-like substances) in the node-pulvinus are closely associated with negatively geotropic growth in the *Avena* shoot at age 42 to 45 days. The qualitative difference in GAs appears to be associated primarily with plant age, since inflorescences harvested at about day 47 have very high levels of nonpolar GAs [including GA_4 and GA_7 (Noma, Ogiyama, Pharis, and Kaufman, unpublished)] compared to harvests at day 55 where polar GAs (including GA_3) predominate (15). However, upright internodes, even at day 45 have appreciable amounts of a GA_3-like substance present (Table II, Fig. 2). Geostimulation tends to maintain a preponderance of nonpolar GAs in the lower halves of the node-pulvini, and increases this preponderance in both halves of internodes (Table II, Fig. 3). Of interest here is the fact that exogenous application of GAs will enhance (1.5-fold) the upward movement of geostimulated *Avena* shoots during the first 20 h of curvature, relative to control plants, a $GA_{4/7}$ mixture being more effective than GA_3 (Kaufman, Pharis, and Reid, unpublished results). A similar situation occurs with regard to GA_3 for conifer shoots and lateral branches, both in intact and decapitated plants (3, 18–20).

It also appears that the increase in dry matter for the p-1 node-pulvinus and relative changes in GAs (*e.g.* bottom *versus* top) may take place at the expense of sheath tissue where dry weight (Table I) and especially GA content (Table II) are reduced as a result of geostimulation.

Excised *Avena* stem node-pulvinus-sheath segments treated with GA_3 exhibit increases in the fresh weight of the internode with no significant change in fresh weight of the sheath and node-pulvinus (1). In contrast, GA_3 causes an increase in dry weight of the internode at the expense of the sheath and node-pulvinus (the latter drops to one-third the weight of vertical controls) (1). Application of GA_3 results in acidification of the medium by excised stem segments (11) and also blocks silica deposition in the basal portion of the internode [part of which is geosensitive (23)]. The node-pulvinus is also relatively unsilicified (7, 14). The node-pulvinus and the internode base are also relatively free of lignin (except in tracheary elements) (7). Further investigation of a possible causal relationship between the unsilicified and unlignified states of these geosensitive plant parts and elevated GA levels would appear warranted.

How do the very large changes in endogenous GAs between and within plant parts come about in such a relatively brief period of time? The drop in both polar and nonpolar GAs in the upper half of the node-pulvinus and the very large increase for p-1 internode lower halves, coupled with the large drop in nonpolar GAs and virtual disappearance of polar GAs in the upper internode half (Table II, Figs. 2, 3) suggest that movement of preexisting GAs of all polarities into the lower half may occur. Additionally, GAs have been reduced 4-fold in the leaf sheaths (Table II). Finally, data from the use of [^{3}H]GA_4 suggest that lower halves of all plant parts tend to produce/retain less ^{3}H highly water-soluble substances than upper halves, and vice versa (Fig. 4). This latter tendency implies increased conjugation in upper halves, and vice versa for lower halves. If it was applicable to endogenous GAs, and if it represented a homeostatic system [see (2) for discussion of such a system for IAA and its conjugates], it would certainly help explain the final differences within plant parts (Table II, Figs. 2, 3). A similar tendency of endogenous IAA and its esterified conjugates is also shown for geostimulated node-pulvini of *Avena* shoots relative to upright node-pulvini, and for lower halves of geostimulated node-pulvini relative to upper halves (13).

Evidence for increased synthesis of GAs upon geostimulation, is not compelling, although increases in the ratio of nonpolar to polar GAs are evident in lower halves of internodes, and absolute amounts of nonpolar GAs have also increased in internodes with geostimulation (Table II).

The results presented herein confirm earlier reports for a number of herbaceous plant systems (*cf.* 10), including peanut shoots (10), sunflower buds (21), maize coleoptiles (22), and for conifer shoots (3, 18, 19), which indicate that increased levels of GAs, present endogenously, or applied exogenously, are associated with, and indeed appear to control, the differential growth that allows plant shoots to respond to geostimulation by growing upright. Auxins are also implicated in many of these systems, including the *Avena* shoot system (12, 13), as is ethylene (3, 17, 26), the latter perhaps being the first growth regulator involved in sensing the environmental stimulus and/or signaling the receptor tissue [secondary cambial meristem (3) and p-1 node-pulvinus/internode (Kaufman, Reid, and Pharis, unpublished)].

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