Pith Autolysis in Herbaceous, Dicotyledonous Plants: Experimental Manipulation of Pith Autolysis in Several Cultivated Species

SUSAN M. CARR* and MORDECAI J. JAFFE†

Biology Department, Wake Forest University, Winston-Salem, North Carolina 27109, USA

Pith autolysis, a condition in which dicotyledonous herbaceous plants have a hollow stem, results from the autolysis of a plant's storage pith. Our central hypothesis concerning the aetiology of pith autolysis states that the carbon from the pith is transported to the growth regions of the plant and used at times when the plant cannot meet its carbon needs by photosynthesis alone. According to this hypothesis, accelerated growth should increase pith autolysis. We here provide supporting evidence for the central hypothesis. More pith autolysis was found in faster growing tomato varieties than in dwarf varieties. More pith autolysis was found in both beans and tomatoes treated with GA_3 than in controls. More pith autolysis was found in leggy bean plants grown in low light than in normal plants grown under normal light conditions. Pith autolysis decreased in both beans and tomatoes when mechanically perturbed or sprayed with paclobutrazol, both treatments that reduced growth. The stems of buckwheat plants that were flowering showed greater pith autolysis and therefore were more hollow than plants which were not flowering or which had the incipient flowers pinched off. This indicated that carbon from the storage pith may also be used in the formation of reproductive structures which require extra carbon. Also in support of the central hypothesis is the prevention of pith autolysis by the addition of extra carbon to the plant, in the form of an increased CO_2 concentration of the surrounding air.

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INTRODUCTION

Pith autolysis (Sachs, 1882; Sayer, 1929) is a syndrome in many dicotlydonous herbaceous plants where the storage pith of the stem, petiole or flower stalk is autolysed by the plant's cell wall-degrading enzymes, leaving a hollow stem (Aloni and Pressman, 1981). In the past, pith autolysis has been studied in cultivated plants both as field crops and in the laboratory (Aloni and Pressman, 1981; Sayer, 1929). More recently, it has also been studied in wild plants in the field (Carr *et al.*, 1995).

There have been several suggestions about the role of pith autolysis in plants and about what causes it. In general, it has been thought that pith autolysis represents a pathological condition and that it weakens plants (Sayer, 1929). Conversely, we have presented preliminary evidence that the development of pith autolysis is part of the natural growth and development of the plant and that it is a response to fluctuations in various environmental factors (Jaffe and Lineberry, 1989; Carr *et al.*, 1995). From these considerations of the plants that have been studied, we have developed a central hypothesis of pith autolysis which states that if there is a greater demand for carbon than can be satisfied by photosynthesis, the plant utilizes its own storage pith (Jaffe and Lineberry, 1989). In particular, during death

of the pith cells, the cell walls of the pith may be degraded to their component monomers which then are transported to the growing point to form new structures. Therefore, stages of the life cycle during which growth accelerates or new growth occurs, as well as environmental conditions which cause the growth rate to increase, might be expected to increase pith autolysis. Conversely, conditions which inhibit growth, such as mechanical perturbation (MP) or treatment with gibberellin inhibitors such as paclobutrazol, should decrease pith autolysis. Increased pith autolysis might also be expected at the onset of the production of reproductive structures which act as carbon sinks. Other conditions expected to increase pith autolysis are stresses, such as drought, or low light intensity, which might reduce the ability of the plant to fix carbon. Thus, one of the aims of this study was to test the central hypothesis with several different kinds of treatments and the use of different genetic material and species.

MATERIALS AND METHODS

Plant material

Bean (*Phaseolus vulgaris* cv. Cherokee Wax) was planted in vermiculite. Tomato (*Lycopersicon esculentum* cvs Patio, Super Bush and Better Boy) and Buckwheat (*Fagopyrum esculentum*) were planted in a soil mixture (2 parts sandy loam, 1 part vermiculite and 1 part perlite) and the plants

* Present address: Biology Department, Yale University, New Haven, Connecticut, USA.
† For correspondence.

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were subirrigated. The tomatoes were fertilized twice with 20:20:20 fertilizer.

Treatments

Pith autolysis was induced in tomato by drought stress (Aloni and Pressman, 1981; Pressman *et al.*, 1983). Drought stress was applied by leaving the plants in the soil mix for 5–7 d without irrigation. When a plant was visibly wilted for 24 h, it was re-irrigated by putting the pot into a tray containing water. Forty-eight hours after the beginning of re-irrigation, the plants were cut open and assayed for pith autolysis.

Mechanical perturbation (MP) was given to bean (once each day for 4 d) and tomato (once each day for the 2 weeks preceding drought stress) by rubbing the appropriate internode (1 and all, respectively) as previously reported (Jaffe and Lineberry, 1988, 1989; Pressman *et al.*, 1983). Paclobutrazol (5 mM), GA_3 (10 μM), or control solution, were made up in 0·015 M-phosphate buffer, pH 6·5, containing 5% DMSO, and sprayed to runoff once daily for 4 d (beans) and for 2 weeks prior to drought stress (tomatoes). In each case, treatment was started when the bean plants were 15 cm high and the first (only) internode was 1 cm long; the spray treatment or the MP of the tomato plants was started when each plant had five to six internodes. Observations of buckwheat were made on plants having six to eight internodes. Plants were divided into flowering samples and samples which were not yet flowering. In all cases, three to six replicates of each treatment containing five to nine plants were performed. Measurements were made of all internodes.

Injection experiments

The effect of exogenous sucrose (0·05 M) on pith autolysis was tested by injecting the sucrose or control solution into the hypocotyl in bean. The beans were injected daily for 5 d and then pith autolysis measurements were made. The solution was 0·015 M phosphate buffer, pH 6·5, containing the antibiotics carbenicillin (0·115 g per 200 ml) and cefotaxime (0·0198 g per 200 ml) (Sigma Chem. Co., St. Louis, Mo., USA). The effect of the antibiotics was to block the development of infection which was observed as darkening of the tissue in samples injected in their absence.

Carbon dioxide treatments

Bean seeds were germinated and then planted in soil mix in plastic pots. The pots were placed in large glass chambers (60 cm high × 30 cm wide × 30 cm deep) with an inlet tube running down to the bottom of the chamber and an outlet tube vented out of the greenhouse. The lucite top was sealed with vacuum grease and held down with bricks. The inlet tube of the control tank was connected to an air pump, so that the normal greenhouse air could be passed through the chamber. The inlet tube of the other chamber was connected to a tank of compressed air having 2·5% CO_2. The two tanks were completely flushed twice each day, once at 0900 h and once at 1630 h. When the first internode of a

plant was 40–45 mm long, the plant was removed and the percent pith autolysis of the hypocotyl and the first internode was determined.

Measurements of pith autolysis

The objective method of estimating pith autolysis involved the development of an equation based on measured parameters of the hollow region and of the internode (Carr *et al.*, 1995).

$$V_p = 0·75\pi r^2 L$$

where V_p is the volume of the hollow region, r is the radius of the hollow region and L is the length of the hollow region. The value of the hollow region was expressed as the percentage of the total volume of the internode occupied by the volume of the hollow region (i.e. percent pith autolysis).

RESULTS

According to the central hypothesis, any treatment that decreases growth should also lessen the development of pith autolysis. In this report, growth is defined as elongation or changes in thickness in the given length of time. Bean plants grown under lower light levels grew more rapidly, and exhibited more pith autolysis in both the hypocotyl and first internode (Table 1). For example, in the first internode pith autolysis was 73% greater in plants grown exposed to light

TABLE 1. *The effect of different light levels on length and pith autolysis of bean stems grown for 7 d under different light levels (4·8–75 μmol m^{-2} s^{-1}) in the greenhouse or in total darkness in the darkroom. Each datum $\pm$ s.e. is the average of three replicates of six plants each*

Measurement	Radiant flux (μmol m^{-2} s^{-1})	Hypocotyl[∥]	Internode 1[**]
Length (mm)[*†]	0	180 ± 13^a	152 ± 13^a
	4·8	126 ± 9^b	105 ± 4^b
	8·1	113 ± 7^b	79 ± 7^c
	39·8	72 ± 4^c	47 ± 3^d
	75·0	69 ± 3^c	40 ± 4^d
Pith autolysis (%)[‡§]	0	39 ± 5^a	$14 \pm 4^{a, c}$
	4·8	$31 \pm 3^{a, d}$	26 ± 3^b
	8·1	$22 \pm 2^{b, d, e}$	$24 \pm 4^{a, b}$
	39·8	$18 \pm 2^{c, e}$	9 ± 1^c
	75·0	15 ± 2^c	7 ± 1^c

* All hypocotyl lengths followed by different superscript letters are significantly different at $P < 0·002$ or better, by t-test.

† All internode lengths followed by different superscript letters are significantly different at $P < 0·009$ or better, by t-test.

‡ All hypocotyl percent pith autolysis values followed by different letters are significantly different at $P < 0·041$ or better by t-test.

§ All first internode percent pith autolysis values followed by different superscript letters are significantly different at $P < 0·019$ or better, by t-test.

∥ The correlation coefficient, r, for length *vs.* pith autolysis of the hypocotyl is 0·971, significant at $P < 0·01$.

** The correlation coefficient, r, for length *vs.* pith autolysis of the first internode, when the value obtained in the darkroom is omitted, is 0·961, significant at $P < 0·05$.

TABLE 2. *The effect of exogenous GA_3, paclobutrazol (PAC) or mechanical perturbation (MP) on length and pith autolysis of bean hypocotyls or first internodes after 7 d of treatment following emergence. Each datum is the average of three replicates of at least three plants each. Data points $\pm$ s.e. in the same row followed by different superscript letters are significantly different from each other by at least P < 0·05 (hypocotyl lengths), P < 0·003 (first internode lengths), P < 0·01 (hypocotyl pith autolysis) or P < 0·004 (first internode pith autolysis)*

Stem part	Measurement	Control	MP	GA_3	PAC
Hypocotyl*	Length (mm)	$91+8^a$	71 ± 3^a	115 ± 0^b	38 ± 3^c
	Pith autolysis (%)	17 ± 2^a	12 ± 2^a	19 ± 3^a	2 ± 2^b
First internode†	Length (mm)	49 ± 4^a	35 ± 4^b	87 ± 3^c	7 ± 0^d
	Pith autolysis (%)	13 ± 2^a	4 ± 1^b	20 ± 3^c	0 ± 0^d

* The correlation coefficient, r, for length $vs.$ pith autolysis of the hypocotyl is 0·971, significant at $P < 0·02$.

† The correlation coefficient, r, for length $vs.$ pith autolysis of the first internode is 1·000, significant at $P < 0·001$.

of 3·7 μmol m^{-2} s^{-1} than in plants grown at 75·7 μmol m^{-2} s^{-1}. In both the hypocotyl and the first internode, there were significant correlations between increasing growth due to lower light and increasing pith autolysis in the stem.

We treated bean plants with MP, the growth retardant paclobutrazol or GA_3. The complete growth of the first internode occurred during the period of the experiment. Mechanical perturbation and paclobutrazol retarded both growth and the development of pith autolysis, whereas GA_3 promoted both properties (Table 2). In the first internode, pith autolysis was decreased 69% by MP, 100% by paclobutrazol, and was increased 54% by GA_3.

A more slowly growing variety of a species should, according to the central hypothesis, develop less pith autolysis than a rapidly growing variety. In our hands, the tomato cultivars used had five to six internodes at the start of the experiment and eight to twelve at the end. During this time the most pith autolysis was observed in internodes 2, 3, 6 and 7. Pith autolysis seems to develop from the middle of the stem (Aloni and Pressman, 1981; Pressman *et al.*, 1983). The dwarf cultivar, Patio, had shorter internodes and less hollow internodes than the pole cultivar, Better Boy (Fig. 1). In addition, both MP and paclobutrazol decreased pith autolysis, whereas GA_3 increased pith autolysis in the previously mentioned cultivars, as well as in the Superbush cultivar (Table 3). This was true of all the internodes that had the potential to become hollow.

According to the central hypothesis, the production of reproductive structures might act as a sink for carbon (Jaffe and Lineberry, 1989). Buckwheat, which is an indeterminate species, might be expected to have an even greater need for carbon, since it would need it for new vegetative growth as well as flowering. When flowering plants were compared to plants that were not yet flowering, it was found that there was consistently more pith autolysis in the flowering plants than in the non-flowering plants (Fig. 2). In addition, when
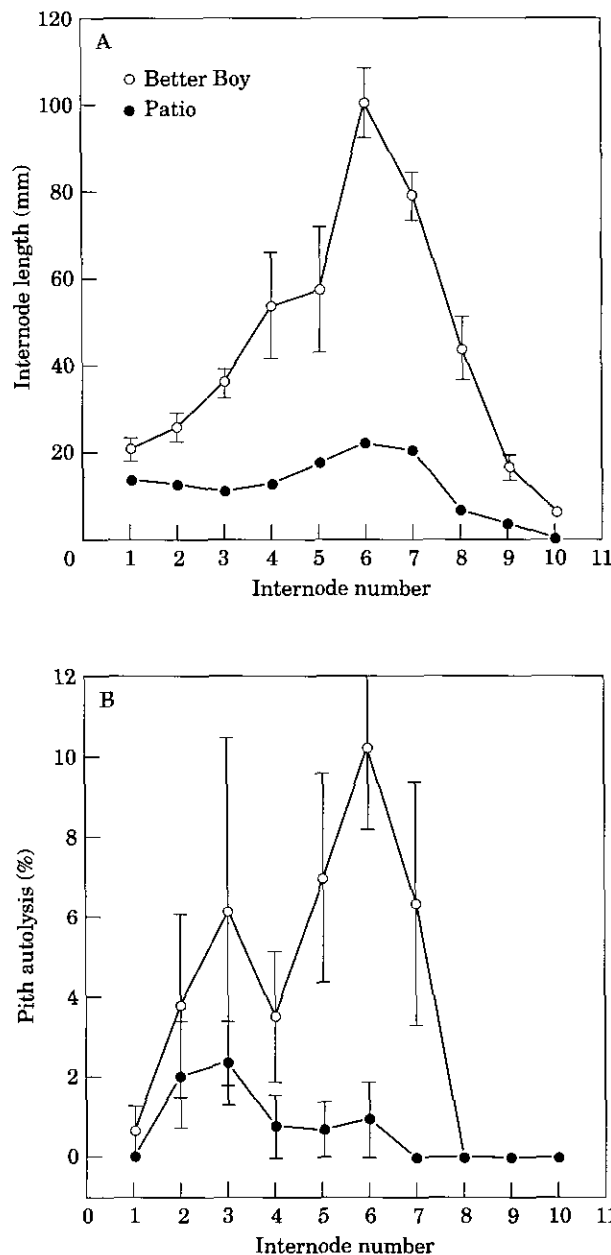

FIG. 1. A comparison of lengths (A) and pith autolysis (B) of the first 10 internodes (internode 1 = bottom) of tomato cultivars: Better Boy (pole, or normal variety, ○) and Patio (bush, or dwarf variety, ●).

floral buds were pinched off as soon as they became apparent, the pith autolysis was no greater than that observed in the non-flowering plants (Fig. 2).

We tested the effect of sucrose injections on bean. The sucrose treatment caused a decrease in internodal pith autolysis as we have previously shown (Jaffe and Lineberry, 1989). As an additional test of this hypothesis, bean plants were grown under normal or high levels of CO_2. Table 4 shows that with access to a surfeit of CO_2, pith autolysis was decreased by 50% in the hypocotyl and by 78% in the first internode, even though there was no significant change in elongation.

TABLE 3. *The effects of mechanical perturbation (MP), GA_3 or paclobutrazol (PAC) on the length and pith autolysis of the sixth internode of Superbush tomato plants grown in the greenhouse (for details see Materials and Methods). Each datum ±s.e. is the average of three replicates of at least three plants each. Data points in the same row followed by different superscript letters are significantly different from each other by at least P < 0·05 (length measurements) or P < 0·007 (pith autolysis measurements) by t-test. The correlation coefficient of length vs. pith autolysis is 0·99, significant at P < 0·01*

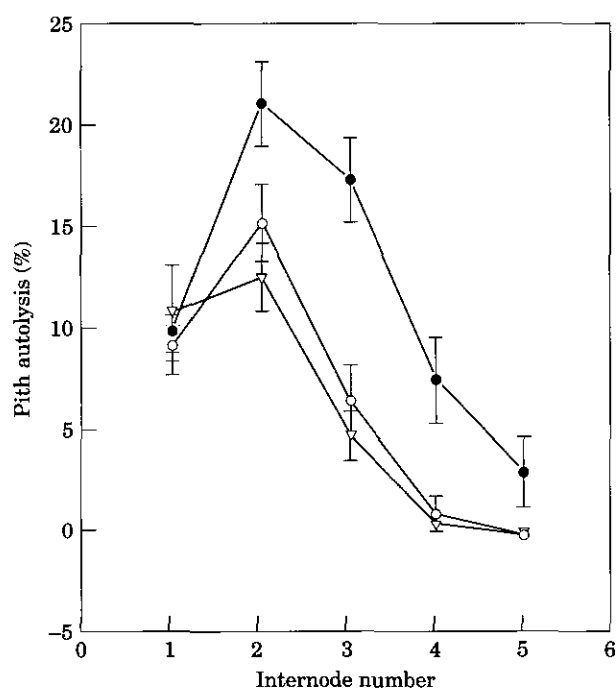| Measurement	Control	MP	GA_3	PAC
Length (mm)	28 ± 4^a	21 ± 3^b	37 ± 2^c	18 ± 3^b
Pith autolysis (%)	8 ± 1^a	1 ± 1^b	17 ± 2^c	1 ± 1^b

FIG. 2. The amount of pith autolysis in the first five internodes (Bottom internode = 1) of buckwheat control plants, flowering plants or plants with the floral buds pinched off as soon as they were visible on the plant. ●, Flowering; ○, not flowering; △, flowers removed.

TABLE 4. *The effect of a high CO_2 atmosphere (25% CO_2) compared to normal air (0·05% CO_2), on the growth and pith autolysis of bean stems. Each datum ±s.e. represents the average of three replicates of three plants each. Numbers on a given line are significantly different from one another when the second number is followed by one or more asterisks. P < 0·5 (*) or P < 0·004 (***) by t-test*

Stem part	Measurement	0·05% CO_2	2% CO_2
Hypocotyl	Length (mm)	73 ± 8	77 ± 6
	Pith autolysis (%)	12 ± 3	$6\pm2^*$
First Internode	Length (mm)	40 ± 2	40 ± 6
	Pith autolysis (%)	9 ± 2	$2\pm0^{***}$

DISCUSSION

The central hypothesis of pith autolysis (Jaffe and Lineberry, 1989), can be stated as: 'Pith autolysis results when the programmed growth rate of a plant exceeds its ability to fix the carbon to support that growth, so that it digests its own pith's carbon reserves in that effort'. One consequence of this principle is that pith autolysis should be expected to increase when the growth rate is stimulated and to decrease when it is retarded. The experiments described in this report have supported this prediction.

If we assume that the untreated control plants of the various species grow at the normal rate, then treatments that increase or decrease that rate should enhance or retard pith autolysis. This has been shown to be true in every case. Treatment with GA_3 (tomato and bean) or low light intensities (bean) increased both the growth and the amount of pith autolysis in every case (Tables 1, 2 and 3). This corroborates and extends experiments by Pressman *et al.* (1984) who showed that treating celery with GA_3 promotes both elongation and the development of pith autolysis in the petioles. There was also a significant correlation between increasing growth and increasing pith autolysis under lower and lower light levels (Table 1). These data support field observations made with wild plants. For example, *Hypericum* sp. growing in a shady environment was moderately hollow, but was not hollow in a sunny field (Carr *et al.*, 1995).

Situations which retarded growth always decreased pith autolysis. Both MP and the application of paclobutrazol significantly retarded stem growth in both tomato and bean (Tables 2 and 3). Both MP and GA_3 caused only apparently lesser and greater pith autolysis in the bean hypocotyl (Table 2), because by the time the treatments started, the hypocotyl was already one half to two thirds grown and the treatments did not have an opportunity to have a significant effect. However, the treatments were begun before the growth of the first internode, and so significantly affected both its growth and its pith autolysis. In addition, a slow growing 'dwarf' cultivar of tomato was significantly less hollow than a more rapidly growing 'pole' cultivar (Fig. 1).

In nature, MP often impacts plants in the form of wind. Observations at the Atlantic shoreline with *Chrysopsis gossypina, Hydrocotyle bonariensis* and *Gaillardia* sp. support this phenomenon. Plants of these species, growing in front of the coastal dune, and directly exposed to the onshore wind, were short and not hollow. Those growing behind the dune were much taller and very hollow (Carr *et al.*, 1995).

In order to summarize the results of these experiments, the growth of the controls were normalized to 100%, and those of all the other treatments in all of the experiments similarly adjusted. When this was done, the correlation coefficient, r, for $n = 14$ was +0·941, a value significant at P < 0·001. A t-test performed on the two sets (i.e. length and pith autolysis) of normalized data produced a probability of 0·414, indicating that they followed the same pattern and therefore were not significantly different from one another. Thus, we may conclude that for different kinds of treatments which either decrease or increase the amount

of stem growth, there is a significant positive correlation between growth and pith autolysis, and the central hypothesis of pith autolysis is upheld.

The production of reproductive organs plays a role in the development of pith autolysis (i.e. the development of flowers in buckwheat increases stem pith autolysis). This observation is comparable to that made of field grown tomatoes (Aloni, Pressman and Jaffe, unpubl. res.). In that study, the removal of very young fruit, before enlargement, significantly decreased the development of pith autolysis in the stems. One of the most commonly observed types of pith autolysis is in rapidly growing flower stalks. Common ornamental plants such as daffodil, amaryllis and daylily all produce flowerstalks by very rapid growth, and by the time they mature, these stalks are hollow. Indeed, the dandilion (*Taraxicum officinalis* Weber) produces a flower stalk in one night, and the following night produces seeds and a hollow stem. It is likely that the carbon and perhaps other nutrients from the pith of the flower stalk are utilized by the developing seeds.

We have previously shown that when radioactively labelled sugar is fed to bean plants, through the roots or by injection to the hypocotyl, the radioactive label becomes concentrated at the growing point of the stem (Jaffe and Lineberry, 1989). Thus, it seems that sugars released due to the digestion of the pith cell walls would go to the growing point and be used there for the continuation of new stem growth. Further, if enough carbon is fed to the stem in the form of sugar, pith autolysis is inhibited (Jaffe and Lineberry, 1989). These observations support the current findings that enriching the atmosphere with a high level of CO_2 prevents pith autolysis from developing. It is of special interest to note that when exposed to high levels of atmospheric CO_2, the plants not only do not become hollow, but also maintain a normal growth rate. In all of the experiments that we have done, this is the only case in which pith autolysis was inhibited without growth being retarded. The plants do not have to have their growth inhibited to keep from getting hollow, since carbon (as CO_2) is no longer the limiting factor.

The effects of high levels of CO_2 on plants have been known for a long time. High levels of CO_2 can have an inhibitory effect. For example, Kidd and West (1917) found that the narcotic effect of 2–4% CO_2 inhibited the germination of mustard seeds. In our hands, two treatments per day with 2·5% CO_2 had no apparent deleterious effect on the bean plants. Contrary to its inhibitory effects, high levels of atmospheric CO_2 are well known to provide substrate for increasing the growth of plants (Rabinowitch, 1956). In fact, CO_2 often may be the limiting factor in plant growth (Rabinowitch, 1956). Krizek and his co-workers have demonstrated that high levels of CO_2 increase the growth rate of many vegetable crops to a great extent. For example, when the temperature was held constant, and the CO_2 levels were either 0·04 or 0·2%, cucumber elongation after 15 d averaged 93 and 174 mm, respectively, while tomato elongation averaged 87 and 150 mm, respectively (Krizek *et al.*, 1974). Thus, it is not surprising that 2·5% CO_2 increased biomass production in beans. Although we have not worked out all of the relationships between

photosynthesis and pith autolysis, it is clear that the fixation of carbon is a rate limiting step in the development of pith autolysis.

Other workers have suggested that the development of pith autolysis is a morbid syndrome, capable of harming the plant by making it weaker. However, we have shown in work to be published elsewhere, that this is not the case. It is well known that the strength of a structural member is a function of its outer layer and not its central region (Wainwright *et al.*, 1976; Fung, 1981). This is why bones can be hollow and steel girders are fabricated in the form of I-beams and not solid beams. Similarly, hollow stems or flower stalks retain their flexural stiffness even when they reach quite large sizes (Niklas and O'Rourke, 1987). Thus, pith autolysis does not weaken the plant and is therefore not a morbid condition.

On the contrary, pith autolysis is necessary to the plant and is part of the natural development of the life cycle. We may view the life of the plant in terms of a balance of catabolism and anabolism. When there is a surfeit of carbon fixation, the plant stores the excess in the form of starch in the pith cells and of cellulose in the cell wall matrix of the pith tissue. When the time comes, however, due to stress, low light, fructification, etc., that it is utilizing carbon faster than it can fix it by photosynthesis, it calls on its reserves, as has been demonstrated by the mobilization of ^{14}C-sugar, to support new growth at the growing point (Jaffe and Lineberry, 1989). First, it uses its stored starch, and then if that is not enough, the plant kills the pith cells and calls on the carbon stored in the cell walls. It probably also uses the water and other nutrients released from the cells during autolysis, for nutrients for the newly formed cells at the growing point. Finally, it is probably significant that the vascular tissue exists in an outer ring in the stem, and is not distributed throughout the stem. Thus, after autolysis of the pith, the released nutrients can still be transported via the outer ring of vascular bundles, which have the added advantage of contributing structural strength to the thin remaining layer.

If the amount of stem pith autolysis is determined by the rate of growth of the stem, what effect might seasonally changing growth rates have on pith autolysis? This is a phenomenon that has been documented for a number of dicotyledonous plants, many of them woody. For example, *Dalhergia sisoo* has been observed to change its pith diameter and length with the season: the diameter decreases by 20% from Apr. to May and then increases again in Jun. (Agarwal, 1981). Others have observed similar effects, with up to three growth flushes occurring in a given year (Tukey 1933, 1934; Coombe, 1976). Both seasonal and diurnal stem shrinkage, such as those described above, have been shown to be due to transient water deficits (Kozlowski, 1971*a, b*). This was nicely demonstrated by spraying plants with the antitranspirant phenylmercuric acetate. This caused the plants to transpire 10% less water, and concomitantly, to increase in stem diameter by at least 50% more than the controls (Turner and Waggoner, 1968). In no instance has the amount of pith autolysis been examined in relation to these phenomena. However, from the point of view of the plant's water status, both drought stress (Pressman *et al.*,

1983) and flooding stress (data not shown) can induce pith autolysis. Thus, it is unlikely that transient, non-stressful changes in water status might inhibit pith autolysis.

It is useful to consider the role of stem pith autolysis in relation to the whole, growing plant. In addition to occurring in stems, autolysis causing hollow organs has been reported in celery leaves (Pressman et al., 1984) and corn roots (i.e. aerenchyma) (Konings, 1982). Thus, it is at least theoretically possible that organs other than the stem can also undergo complete or partial pith autolysis. Pith autolysis has been shown to be caused by high levels of ethylene, but inhibited by lower levels (Jaffe and Lineberry, 1988, 1989; Huberman et al., 1993). The same low levels of ethylene that block pith autolysis in the stem, induce aerenchyma formation in roots (Atwell, Drew and Jackson, 1988; Drew, He and Morgan, 1989). This does not necessarily mean that the two organs have opposite mechanisms of pith autolysis, although that is of course possible. It is well known that root growth usually occurs when shoot growth is minimized. However, it is also possible that both organs might respond to the same hormonal signal, but at different concentrations. One further point is worth examining in this regard. Although we have not yet made systematic observations, we have never seen pith autolysis in the root at the same time that it was evident in the shoot. Similarly, we have not observed increased root growth correlated with pith autolysis, but the development of leaves is positively correlated with pith autolysis. The relationships of the different organs of a plant in terms of stem pith autolysis is an important subject that will be addressed in the future.

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