Original article

ABA, IAA and cytokinin concentrations in developing hazelnut fruits and their relation with blanks

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Received 9 December 1999
Accepted 21 March 2000

Fruits, 2000, vol. 55, p. 283–291

RESUMEN ESPAÑOL, p. 291

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Abstract — Introduction. Hazelnut (*Corylus avellana* L.) is grown world wide. Production is reduced by the occurrence of blank fruits; this problem is cultivar dependent and results in substantial yield losses. Since abcisic acid (ABA), indole acetic acid (IAA) and cytokinins have been implicated in the regulation of fruit set and development, this study aimed to analyse the concentrations of these plant growth regulators (PGR) in blank and normal fruits of two cultivars (Butler and Merveille de Bollwiller). **Materials and methods**. The analysis of plant growth regulators was made on the fruit tissues (shell, kernel and inner tissues) collected on three specific dates of the growth curve of the fruit. IAA and cytokinins were analysed by immunoassay and ABA by radioimmunoassay. **Results and discussion**. PGR concentrations varied between blank and normal fruits. There were significant differences in ABA content between the blank and normal fruits only for cv. 'Merveille de Bollwiller'. This indicates alterations in ABA mobilization from the shell to the inner tissues in blank fruits. IAA levels were lower in blank than in normal fruits at the end of cell division, enlargement, and accumulation of reserves (third sampling date). Cytokinin concentration was higher in blank fruits than in normal fruits at the start of embryo growth (second sampling date). This coincides with the highest cell division rates. © Éditions scientifiques et médicales Elsevier SAS

Portugal / *Corylus avellana* / hazelnuts / growth substances / functional disorders / malformations / fruit

Concentrations en ABA, AIA et en cytokinine dans les noisettes en formation et relations avec les anomalies de formation de l'amande.

Résumé — Introduction. Le noisettier (*Corylus avellana* L.) pousse dans le monde entier. Sa production est réduite par l'occurrence de coques vides ; ce problème, lié au cultivar, aboutit à des pertes substantielles de rendement. Puisque l'acide abscissique (ABA), l'acide indolacétique (AIA) et les cytokinines ont été impliqués dans la régulation de la formation du fruit et de son développement, cette étude a cherché à analyser les concentrations de ces régulateurs de croissance de plantes (RCP) dans des noisettes plus ou moins bien formées de deux cultivars (Butler et Merveille de Bollwiller). **Matériel et méthodes**. Une analyse des RCP a été faite sur des tissus du fruit (coquille, amande et tissus intérieurs) prélevés à trois dates spécifiques de la courbe de croissance du fruit. L'AIA et les cytokinines ont été analysés par immunoassay et ABA par radioimmunoanalyse. **Résultats et discussion**. Les concentrations en RCP n'ont pas été analogues dans les fruits normaux et anormaux. Seul le cv 'Merveille de Bollwiller' a montré des différences significatives de teneur en ABA entre fruits normaux et anormaux. Cela indiquerait des changements de la mobilisation d'ABA de la coquille vers les tissus intérieurs des fruits anormaux. Les niveaux d'AIA ont été plus faibles dans les fruits anormaux que dans les fruits normaux en fin de division, d'accroissement et d'accumulation des cellules de réserves (troisième date de prélèvement). La concentration en cytokinine a été plus élevée dans les fruits anormaux que dans les fruits normaux en début de croissance des embryons (deuxième date de prélèvement). Cela coïncide avec le taux de division des cellules, le plus élevé. © Éditions scientifiques et médicales Elsevier SAS

Portugal / *Corylus avellana* / noisette / substance de croissance végétale / trouble fonctionnel / malformation / fruit

1. introduction

In hazelnut (*Corylus avellana* L.) the occurrence of seedless nuts, also called blanks, is universal. Studies in several countries showed genotypic differences in the frequency of blanks and year-by-year variation of more than 25 % [1]. Studies on nut and kernel abnormalities in Oregon [2] indicated that the most frequent problems are blanks (13.6 %), poorly filled nuts (10.6 %), mouldy kernels (4.5 %), shrivelled kernels (3.7 %) and black tips (2.9 %).

The causes of blanks are unknown. Several explanations such as genetic constitution of the cultivar, alternate bearing habit, pollen source, water and mineral nutritional status of the trees, and environmental conditions have been suggested [1–5]. Blanks are of several types [6, 7] and follow fruit set. Although the ovules have formed, their growth has stopped at various stages of fruit development [8]. A reduction of empty fruits in hazelnut would bring great economic benefits, not only by increasing yield but also by reducing harvesting costs.

Plant growth regulators (PGR) have been reported as playing a crucial role in the way plants grow and develop, in the regulation of growth rhythms of the individual parts of the plant, and in the control of the reproductive processes [9, 10]. Therefore, alterations in the hormonal control of fruit growth could be the cause of blanks in hazelnut.

In hazelnut, the formation of fruit encompasses embryo development with various physiological processes, particularly the arrest of tissue growth and development, the accumulation of nutritive reserves, and the ability to withstand dissection. Plant hormones are capable of influencing these processes and changes in hormone levels or activity have been correlated with changes in embryo growth [11, 12].

Cytokinins, generally involved in promoting cell division and affecting the number of endosperm cells in seeds, are present in large amounts during seed development at early stages of seed growth [13].

The maximum concentration of PGR occurs when dry matter accumulation is most rapid [13]. High auxin levels are found during active seed growth and are coincident with cell expansion and fruit growth. PGR concentrations vary between fruit tissues as in seed legumes which show a different evolution of indole acetic acid (IAA) between pods and seeds. Maximum levels were found at different time periods in the two parts, and probably a similar situation might occur between the shell and kernel of hazelnut.

Abscisic acid accumulates during the middle and late periods of seed development in woody plants, coinciding with the accumulation of reserves and seed maturation. Abscisic acid (ABA) helps to cause normal embryogenesis and formation of seed-storage proteins [14]. At the beginning of seed dehydration, levels of endogenous ABA decrease and are low in the dry seed [12].

ABA moves at a higher velocity than auxin, being translocated from the roots to shoots via the xylem stream, the leaves responding to variations in ABA levels. The dynamic movement of ABA is also evident when moving from mature leaves to any other vegetative parts whereas it generally accumulates in sink tissues [13]. We questioned if reproductive organs also represent sink tissues for this plant hormone and if turnovers of ABA occur within nut fruits.

The major objective of this study was to quantify the levels of IAA, ABA and cytokinin throughout the growth and development of normal and blank fruits in two hazelnut cultivars. Our goal was also to establish if a correlation existed between the occurrence of blank fruits and some difference in the hormonal levels in nut tissues.

2. materials and methods

2.1. plant material

Two hazelnut cultivars, cv. 'Butler' and 'Merveille de Bollwiller' were selected from a 12-year-old experimental orchard con-

taining 11 cultivars. These cultivars had the least and the largest percentages of occurrence of blank fruit, respectively. Trees were planted in March 1984, at Vila Real in northern Portugal at 470 m above sea level, 41° 19' N and 7° 44' W, on a typical Dystrochrept silt loam soil [15]. The climate is characterized as a transition from Csb to Csa (mesothermic climate with a dry season in the summer) of Köpen [16]. A plot of 75 plants representing 11 cultivars was planted at 5 m × 3 m spacings in a completely randomized design and left unpruned. The trees developed in a natural growth habit.

2.2. harvest and preparation of plants extracts

From the onset of the fruit growth, at the beginning of May, and every 4 d up to harvest, ten typical nuts were sampled per tree, from each cultivar, for volume and weight determinations, according to Thompson et al. [17]. A cumulative growth curve was constructed for fruit growth. Using this growth curve (*figure 1*), three dates were selected for the quantification of IAA, ABA, and cytokinin levels. The first date (9 June) corresponded to the beginning of fruit development. At this time, no differences between blanks and normal fruits were detected. The second date (10 July) coincides with the start of embryo growth when abnormalities between the two fruit types begin to become apparent, while the third date (1 August) is at the end of fruit growth. To minimize fruit-by-fruit variability, ten fruits from each tree were collected, which were divided into shell and inner tissues, frozen in liquid nitrogen, powdered and freeze-dried separately. From this material, two samples of 100 mg each were weighed and analysed three times for every plant hormone. This procedure was done for each sampling date and applied to blank fruits when detected (second sampling date). The shell terminology refers to the outer hard part of the fruit. For the inner part of the fruit two terms are used: kernel for the normal fruits and inner tissue for all the inside in blank fruits.

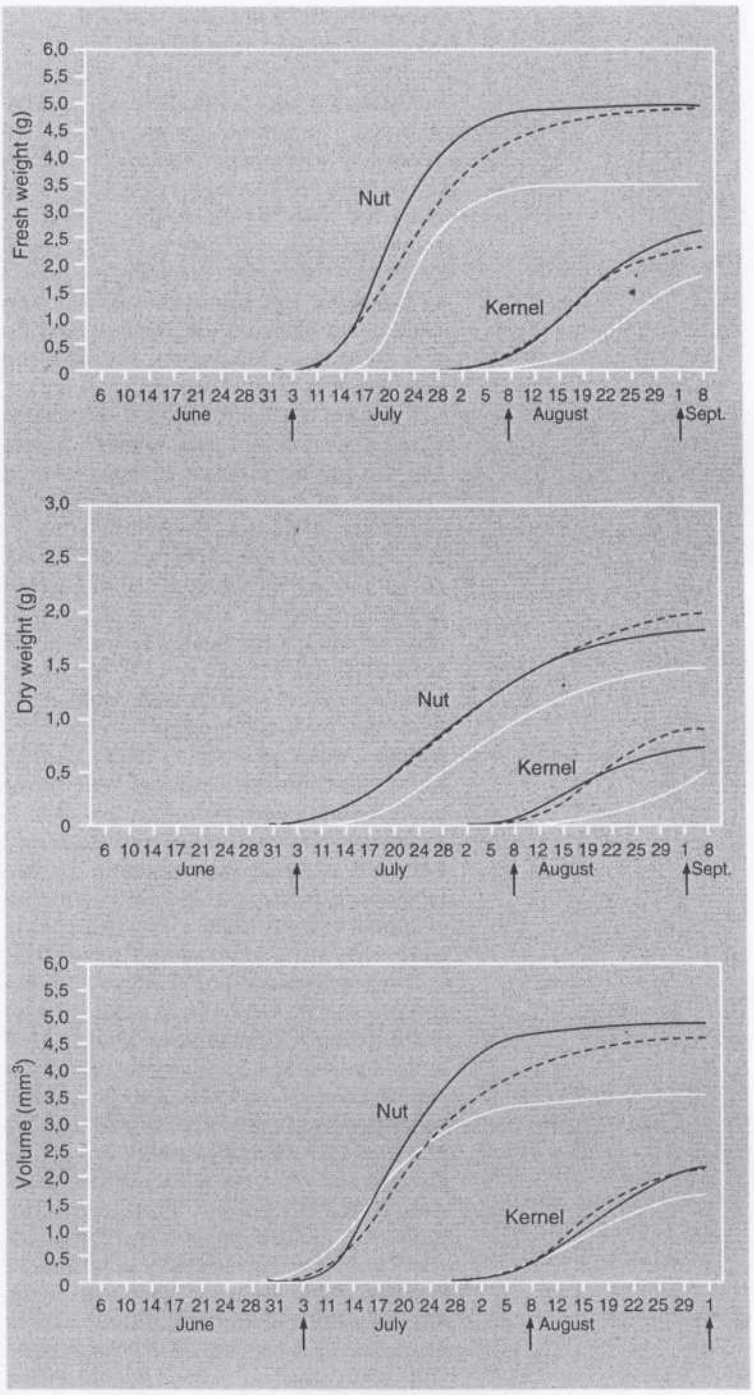

Figure 1.
Annual growth curves for nut and kernel of hazelnut fruits cvs. 'Butler' and 'Merveille de Bollwiller', sampled at 4 d intervals. The arrows represent the three sampling dates chosen to do fruit analyses regarding plant growth regulator concentrations.

2.3. extraction and purification of plant growth regulators

Extraction and purification of free IAA, ABA and cytokinins were performed according to Fernández et al. [18]. Powdered tissues (100 mg dry weight) were extracted twice by thoroughly mixing for more than 14 h at 4 °C with 25 mL of 80 % (v/v) cold methanol containing 10 mg·L^{-1} of butylated hydroxytoluene (BHT). The extract was filtered through GF/A glass filters (Whatman, Maidstone, UK) and the solid residues re-extracted with this extraction solvent for 7 h. Combined methanolic extracts were evaporated under vacuum (30 °C), and the resultant aqueous solution taken to 5 mL in distilled water. Radiolabelled standards 2[^{14}C]-IAA (53.8 mCi·mmol^{-1}), 2[^{14}C]-ABA (35.0 mCi·mmol^{-1}), and 8[^{14}C]-BA (54 mCi·mmol^{-1}) were added at the start of this step to identify losses during purification. Samples were cleared by centrifugation (10 000 *g* for 15 min at 4 °C), and supernatants adjusted to pH 3 with dilute acetic acid and purified through Sep-Pak cartridges (Waters Associates Inc., Madrid, Spain). The Sep-Pak cartridges were previously equilibrated with 5 mL of 100 % methanol and 2 × 5 mL of distilled water. Retained plant growth regulators were eluted with 2 × 5 mL of 70 % (v/v) aqueous methanol. Subsequently, combined extracts were reduced to dryness and redissolved in 2 mL phosphate buffer saline solution (PBS) (10 mM, pH 7.4) and applied to an immunoaffinity column against zeatin-type and isopentenyl adenine-type cytokinins [18]. To elute IAA and ABA, the column was washed with 15 mL of PBS, 10 mM, pH 7.4. Resultant PBS eluate was acidified to pH 3.0 with diluted HCl and extracted four times with diethyl ether at 4 °C in darkness. The eluate was divided into two equal volumes and the ether removed under a N_2 stream. Retained cytokinins were eluted with 30 mL of pure methanol and reduced to dryness by speed-vac concentration (Savant SC-200) and redissolved in acetonitrile of HPLC grade.

Separation of cytokinins was achieved by reverse-phase HPLC using a Varian 5 000 liquid chromatograph connected to a UV-Vis Varichrom detector and a Gilson 230 fraction collector. The method of Horgan and Scott was used [19]. This requires a Spherisorb ODS-2.5 µm (150 mm × 4 mm) reverse-phase column and a mobile phase of acetonitrile and water (pH 7 with triethylammonium bicarbonate) in a linear gradient from 5 to 20 % (V/V) over 40 min and a flow rate of 1.5 mL·min^{-1}. Eluates were monitored at 265 nm, 1.5 mL fractions collected and dried using a speed-vac concentrator.

2.4. quantification of plant growth regulators

Samples for IAA quantification were methylated by the method of Neill and Horgan [20] prior to enzyme-linked immunoassay (ELISA) (Sigma Chemical Co.). Abscisic acid samples were redissolved in distilled water, and quantified by radioimmunoassay (RIA) (Sigma Chemical Co.). Cytokinins were quantified by ELISA following the method of Centeno et al. [21].

2.5. statistical analysis

PGR means and standard errors were calculated for each cultivar and sampling date. Since normal and blank fruits were indistinguishable at the first sampling date, data from this date are represented by a single value.

3. results and discussion

Trees of cv. 'Butler' produced 8 % blank fruits and 'Merveille de Bollwiller' 20 %. These values are consistent with previous studies [2].

3.1. ABA levels

There were significant differences ($p < 0.001$) in ABA levels between the two cultivars. Levels varied between 0.22 and 1.16 nmol·g^{-1} dry weight in 'Merveille de Bollwiller' and between 0.29 and 0.46 nmol·g^{-1} dry weight in 'Butler' (*table I*

Table I.
Concentrations (nmol·g^{-1} dry weight) of abscisic acid (ABA), indole acetic acid (IAA) and cytokinins in shell and kernel of normal and blank hazelnut fruits of cvs. 'Butler' and 'Merveille de Bollwiller', at three dates corresponding to the fruit development (9 June: beginning of fruit development, 10 July: start of embryo 1 August: end of fruit growth). The values correspond to mean of two biological and three analytical replications (± $S_{\bar{x}}$).

Date	Type	Part	ABA[1]		IAA[2]		Cytokinins	
			Butler	Merveille	Butler	Merveille	Butler	Merveille
9 June[3]	–	kernel[4]	0.36 ± 0.062	0.46 ± 0.086	3.98 ± 0.822	2.42 ± 0.155	2.13 ± 0.138	1.92 ± 0.102
		shell	0.33 ± 0.088	0.51 ± 0.001	4.31 ± 0.25	5.34 ± 0.859	1.59 ± 0.06	0.59 ± 0.034
10 July	normal	kernel	0.29 ± 0.057	0.46 ± 0.017	0.40 ± 0.019	0.41 ± 0.017	1.59 ± 0.228	1.73 ± 0.101
		shell	0.45 ± 0.073	0.37 ± 0.025	0.63 ± 0.007	0.34 ± 0.004	2.47 ± 0.391	1.85 ± 0.095
	blank	inner tissue	0.41 ± 0.085	0.25 ± 0.045	0.23 ± 0.008	0.30 ± 0.046	2.45 ± 0.599	2.88 ± 0.310
		shell	0.43 ± 0.079	0.46 ± 0.004	0.31 ± 0.002	0.36 ± 0.016	3.92 ± 0.596	2.60 ± 0.190
1 August	normal	kernel	0.36 ± 0.100	0.88 ± 0.025	3.48 ± 0.425	3.81 ± 0.355	0.56 ± 0.030	4.02 ± 0.507
		shell	0.41 ± 0.064	0.22 ± 0.014	1.47 ± 0.329	3.91 ± 0.394	0.45 ± 0.020	2.94 ± 0.292
	blank	inner tissue	0.46 ± 0.044	0.52 ± 0.04	1.70 ± 0.007	1.59 ± 0.093	0.70 ± 0.032	4.46 ± 0.477
		shell	0.32 ± 0.085	1.16 ± 0.053	0.44 ± 0.019	1.45 ± 0.016	2.41 ± 0.282	3.57 ± 0.292

[1] ABA: abscisic acid.
[2] IAA: indole-3-acetic acid.
[3] At this time, no differences between blanks and normal fruits were detected.
[4] For the inner part of the fruit two terms are used: kernel for the normal fruits and inner tissue for all the inside in blank fruits.

and *figures 2a–2d*). On average, between the sampling dates there were also significant differences ($p < 0.001$) between concentrations of 0.387 nmol·g^{-1} dry weight at sample date 2 and 0.541 nmol·g^{-1} dry weight at sample date 3.

In cv. 'Merveille de Bollwiller', the ABA concentrations of kernel and shell (*figures 2c, 2d*) were similar at the first sampling date. In the kernel of normal fruits, there was a tendency for ABA to accumulate, but to decrease in the shell. In normal fruits, a turnover in ABA seems to be designed within the two parts: in the kernel, ABA content increases significantly from 0.46 to 0.88 nmol·g^{-1} dry weight between harvest two and three, while, in the shell, ABA level decreases from 0.37 to 0.22 nmol·g^{-1} dry weight. These data may indicate that ABA moves from the shell to the inner tissues during the active growth of the kernel. The kernel appears to be the 'sink' whereas the 'source' could be the shell as well as other parts of the plant with chloroplasts which are considered to be the site of synthesis [22]. More research is needed to specifically study the transport and sites of synthesis of ABA within nuts. In blank fruits of cv. 'Merveille de Bollwiller', ABA movement from shell to inner

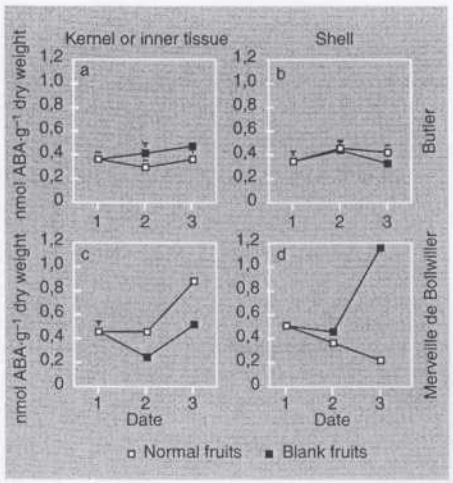

Figure 2.
Absicic acid concentrations in kernel or inner tissue and shell of normal and blank hazelnut fruits of cvs 'Butler' and 'Merveille de Bollwiller'. When $S_{\bar{x}}$ bars are not shown, $S_{\bar{x}}$ is smaller than the symbols.

tissues failed since an increase was noted in both parts of the fruit (*figures 2c, 2d*). Thus, the amount of ABA in the inner tissues (0.52 nmol·g^{-1} dry weight) could not be higher enough to induce an enlargement of the kernel in blank fruits with respect to the normal ones (0.88 nmol·g^{-1} dry weight); indeed, it is known that ABA plays an important role in the deposition of reserves in the endosperm, particularly being responsible for promoting the synthesis of storage proteins in the late stages of embryogenesis as suggested in other seed types [23].

The fruits of cv. 'Butler', (*figures 2a, 2b*) showed smaller variations in ABA concentration during fruit growth as cv. 'Merveille de Bollwiller', both in the shell and inner tissues.

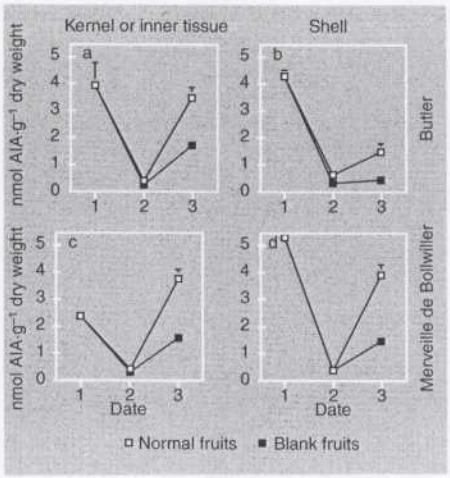

Figure 3.
Indole acetic acid concentrations in kernel or inner tissue and shell of normal and blank hazelnut fruits of cvs 'Butler' and 'Merveille de Bollwiller'. When $S_{\bar{x}}$ bars are not shown, $S_{\bar{x}}$ is smaller than the symbols.

3.2. IAA levels

Indole acetic acid concentration throughout fruit growth (*figure 3*) did not differ between cultivars, shell or kernell tissues but differed between blank and normal fruits (*table II*). Sampling date induced high differences ($p < 0.001$). IAA concentration decreased from the first to the second sampling date (3.98 to 0.40 nmol·g^{-1} dry weight in cv. 'Butler' and from 2.42 to 0.41 nmol·g^{-1} dry weight in cv. 'Merveille de Bollwiller'), and then increased between the second and third sampling dates (to 3.48 nmol·g^{-1} dry weight in the cv. 'Butler' and to 3.81 nmol·g^{-1} dry weight in the cv. 'Merveille de Bollwiller'). The last increase was greater in normal fruits than in blank

Table II.
Summary of analyses of variance for testing plant growth regulator concentrations in two parts (kernel and shell) of hazelnut fruits, cvs. 'Butler' and 'Merveille de Bollwiller', at three dates corresponding to the fruit development.

Source of variation	Abscisic acid	Indole acetic acid	Cytokinins
Cultivar	***	ns	***
Date	***	***	***
Cultivar × date	***	**	***
Type	*	***	***
Cultivar × type	ns	ns	ns
Date × type	*	***	**
Cultivar × date × type	*	ns	ns
Part	ns	ns	ns
Cultivar × part	ns	***	***
Date × part	ns	***	***
Cultivar × date × part	ns	*	ns
Type × part	***	ns	ns
Cultivar × type × part	***	ns	ns
Date × type × part	***	ns	ns
Cultivar × date × type × part	***	ns	ns

ns, *, **, ***, Non-significant or significant at $p = 0.05$, 0.01 or 0.001, respectively.

ones, mainly in the seeds of cv. 'Merveille de Bollwiller' which had the highest incidence of blanks. Thus, it seems that blank fruits of hazelnut are characterized by low IAA levels during late embryogenesis (1.70 nmol·g^{-1} dry weight in cv. 'Butler' and 1.59 nmol·g^{-1} dry weight in cv. 'Merveille de Bollwiller'). According to our results on the IAA and ABA levels, we suggest that the higher number of blanks in the cv. 'Merveille de Bollwiller' when compared to the cv. 'Butler' could be due to the presence of major hormonal differences between normal and blank fruits in the first cultivar. Alternatively it could be that the kernel died and lost its ability to synthesize the hormone. Therefore, instead of being a cause, it could be an effect. However, to confirm this hypothesis it would be made recommendable to analyse the ABA and IAA in fruits of other cultivars with a range of percentages of blanks.

The low IAA levels measured in the second sampling are likely to be due to the use, and further catabolism, of almost all IAA during the shell growth processes, since this harvest date coincided with the maximum shell enlargement and expansion. At this stage, embryo growth started to show a marked increase due mainly to cell division; in this process, other hormones such as cytokinins are more involved than IAA. As soon as cells finish the first step of multiplication and enter the process of enlargement, IAA begins to play a major role. This is supported by the large increase of IAA levels in normal fruits from stage 2 to stage 3 of kernel growth, as well as by the lack of this IAA enhancement in the blank fruits. In the kernel of blanks, little or no tissue was formed in contrast to the high number of cells formed in normal fruits; therefore no hormone is requested or needed for cell enlargement on blank fruits.

3.3. cytokinins levels

The cytokinin concentrations differed between the two cultivars ($p < 0.001$) and showed different trends (*table I*). In the normal fruits of cv. 'Merveille de Bollwiller', cytokinin concentrations increased throughout the growth period of fruit, mainly in the shell (from 0.59 to 3.57 nmol·g^{-1} dry weight), whereas, in the cv. 'Butler', there was a ten-

Table III.
Plant growth regulators (PGR) ratios in shell and inner part of normal and blank fruits of hazelnut cvs. 'Butler' and 'Merveille de Bollwiller', at two dates corresponding to the fruit development (10 July: start of embryo,1 August: end of fruit growth).

Cultivar	Part[1]	Type	[Cytokinin / IAA[2]]		[IAA / ABA[3]] at 1 August
			at 10 July	at 1 August	
Merveille	kernell	normal	4.2	1.1	4.3
	inner tissue	blank	9.5	2.8	3.1
	shell	normal	5.4	0.8	17.9
		blank	7.2	2.5	1.3
Butler	kernell	normal	3.9	0.2	9.8
	inner tissue	blank	10.9	0.4	3.7
	shell	normal	3.9	0.3	3.6
		blank	12.7	5.5	1.4

[1] For the inner part of the fruit two terms are used: kernel for the normal fruits and inner tissue for all the inside in blank fruits.
[2] IAA: indole-3-acetic acid.
[3] ABA: abscisic acid.

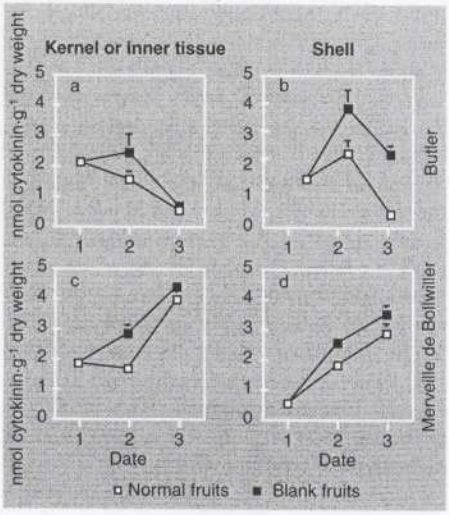

Figure 4.
Cytokinins concentrations in kernel or inner tissue and shell of normal and blank (g) hazelnut fruits of cvs 'Butler' and 'Merveille de Bollwiller'. When $S_{\bar{x}}$ bars are not shown, $S_{\bar{x}}$ is smaller than the symbols.

dency to decrease in the kernel (from 2.13 to 0.56 nmol·g^{-1} dry weight) and the shell (from 1.60 to 0.45 nmol·g^{-1} dry weight). Nevertheless, in both cultivars, the cytokinin levels measured in blank fruits were always higher than in normal fruits ($p < 0.001$) (*figures 4a, 4d*). Moreover, this difference between blank and normal fruits was more evident on the second sampling date (1.59 vs 2.45 nmol·g^{-1} dry weight in cv 'Butler' and 1.73 vs 2.88 nmol·g^{-1} dry weight in cv 'Merveille de Bollwiller'), coinciding with the moment of maximum cell division in the seed (*figure 1*). Thus, another hormonal characteristic of blank fruits was the excess of cytokinin content at the beginning of kernel growth.

The [cytokinin / IAA] ratio, which emphasizes the relationship of cell division with cell enlargement, reached an extremely high value on the second harvest date, being higher in blank fruits than in normal ones for both cultivars (*table III*). On the third harvest date, in which cell division is likely to have stopped, and therefore, the process of cell enlargement be predominant, the [cytokinin / IAA] ratio decreased. Nevertheless, this balance was again higher in blank fruits. At this stage the [IAA / ABA] ratio was also the lowest in blank fruits, mainly in the shell of cv. 'Merveille de Bollwiller' due to the increase in ABA concentration in the outer tissues.

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Concentración en ABA, AIA y en citoquininas en avellanas en formación y relaciones con las anomalías de la formación de la almendra.

Resumen — Introducción. El avellano (*Corylus avellana* L.) crece en el mundo entero. Su producción está reducida por la ocurrencia de las cáscaras vacías. Este problema, ligado al cultivar, conlleva a pérdidas substanciales de rendimiento. Debido a que el ácido abscisico (ABA), el ácido indolacetico (AIA) y las citoquininas han estado implicados en la regulación de la formación del fruto y de su desarrollo, este estudio ha buscado a analizar la concentración de esos reguladores de crecimiento de plantas (RCP) en avellanas más o menos bien formadas de dos cultivares (Butler y Merveille de Bollwiller). **Material y métodos**. Un análisis de los RCP se realizó en tejidos de frutas (cáscara, almendra y en tejidos interiores), tomados en trés fechas específicas de la curva de crecimiento del fruto. El AIA y las citoquininas fueron analizados por inmunoassay y por ABA por medio de radioinmunoanálisis. **Resultados y discusión**. Los concentraciones en RCP no han sido análogas en frutas normales y anormales. Solamente el cultivar 'Merveille de Bollwiller' ha mostrado significancias en cuanto al contenido en ABA entre las frutas normales y anormales. Esto indicaría cambios de la mobilización del ABA de la cáscara hacia los tejidos de frutas anormales. Los niveles de AIA han sido más débiles en las frutas anormales que en las frutas a fines normales de la división de las células de reserva (tercera fecha de la toma de muestras), del aumento y de la acumulación de las mismas. La concentración en citoquininas ha sido más alta en las frutas normales a principio de crecimiento de los embriones (segunda fecha de toma de muestras). Esto coincide con la tasa de división más elevada de las células.

Portugal / *Corylus avellana* / avellana / sustancias de crecimiento vegetal / trastornos funcionales / malformación / fruto