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Effect of growth temperature on lipid fatty acids of four fungi (*Aspergillus niger, Neurospora crassa, Penicillium chrysogenum*, and *Trichoderma reesei*)

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Abstract The effect of growth temperature on the lipid fatty acid composition was studied over a temperature range from 35 to 10° C with 5° C intervals in four exponentially growing fungi: *Aspergillus niger, Neurospora crassa, Penicillium chrysogenum,* and *Trichoderma reesei*. Fatty acid unsaturation increased in *A. niger, P. chrysogenum*, and *T. reesei* when the temperature was lowered to 20–15, 20, and 26–20° C, respectively. In *A. niger* and *T. reesei*, this was due to the increase in linolenic acid content. In *P. chrysogenum*, the linolenic acid content increased concomitantly with a more pronounced decrease in the less-unsaturated fatty acid, oleic acid, and in palmitic and linoleic acids; consequently, the fatty acid content decreased as the temperature was lowered to 20° C. In *T. reesei*, when the growth temperature was reduced below 26–20° C, fatty acid unsaturation decreased since the mycelial linolenic acid content decreased. In *A. niger* and *P. chrysogenum*, the mycelial fatty acid content increased greatly at temperatures below 20–15° C. In contrast, in *N. crassa*, fatty acid unsaturation was nearly temperature-independent, although palmitic and linoleic acid contents clearly decreased when the temperature was lowered between 26 and 20° C; concomitantly, the growth rate decreased. Therefore, large differences in the effects of growth temperature on mycelial fatty acids were observed among various fungal species. However, the similarities found may indicate common regulatory mechanisms causing the responses.

Key words Temperature · Fatty acids · Fungi · *Aspergillus niger* · *Neurospora crassa* · *Penicillium chrysogenum* · *Trichoderma reesei*

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Introduction

In fungi, the major fatty acids that typically occur in membrane phospholipids and storage triacylglycerols are palmitic and stearic acids and their unsaturated derivatives palmitoleic, oleic, linoleic, and linolenic acids. The saturated long-chain fatty acids are elongated by the type I multienzyme complex fatty acid synthetase; coenzyme A (CoA) derivatives of the acids may thereafter be desaturated to palmitoleic and oleic acids. The latter can then be desaturated to linoleic acid, and further to linolenic acid by desaturases that use either CoA derivatives of the acids or phospholipid-bound acids as a substrate (Okayasu et al. 1981; Ferrante and Kates 1983; Chopra and Khuller 1984; Kamisaka et al. 1990). *Penicillium chrysogenum* produces linolenic acid by elongation of hexadecatrienoic acid (Richards and Quackenbush 1974). The composition of mycelial fatty acids varies greatly depending on growth conditions, such as nutritional factors, oxygen, and the environmental temperature. In general, fatty acid unsaturation increases as the temperature decreases, although opposing reports exist (Sumner et al. 1969; Wilson and Miller 1978; Chavant et al. 1981; Lösel 1988; Suutari et al. 1990; Suutari and Laakso 1994). In the technologically interesting Ascomycotina *P. chrysogenum, Aspergillus niger* (Plectomycetes), and *Neurospora crassa* (Pyrenomycetes), and in *Trichoderma reesei*, a representative of the Deuteromycotina, fatty acid profiles have been determined (Bennett and Quackenbush 1969; Martin and Johnston 1983; Vokt and Brody 1985; Lösel 1988; Radwan and Soliman 1988; Brown et al. 1990). However, there is little information on absolute amounts of fatty acids in these fungi and on changes in their composition in response to variations in the external temperature. This paper reports on changes in the fatty acid composition in *P. chrysogenum, A. niger, N. crassa*, and *T. reesei* when these fungi are grown over a temperature range from 35 to 10° C, with 5° C intervals.

Materials and methods

Strains and growth conditions

The fungi *Aspergillus niger* VTT-D-77020 (VTT, Technical Research Centre of Finland), *Neurospora crassa* VTT-D-75017, *Penicillium chrysogenum* VTT-D-74021, and *Trichoderma reesei* VTT-D-74068 were stored as spores in 10% (v/v) glycerol (Merck, Darmstadt, Germany) at –60° C. Spores (10^5/ml) were inoculated into at least four parallel Erlenmeyer flasks (250 ml) containing 100 ml of wort broth base (Merck), pH 4.5. The flasks were shaken at 240 rpm in a Gallenkamp (Leicestershire, UK) orbital shaker/incubator (model INR 200-010V) at each of the following growth temperatures: 10, 15, 20, 26, 30, and 35° C. On the basis of the mycelial dry weight, fatty acids were analyzed in the early exponential (dry wt < 1.0 g/l), exponential (1.5–2.5 g/l), late exponential (3.0–4.0 g/l), and stationary (> 4.0 g/l) growth phases. In the exponential-growth-phase samples (mycelial dry wt 1.5–3.5 g/l) that were used for studies on the dependence of fatty acid composition on growth temperature, the pH of the growth medium was as follows: *A. niger*, pH 2.9–3.9; *N. crassa*, pH 3.8–4.1; *P. chrysogenum*, pH 3.9–4.2; *T. reesei*, pH 3.9–4.9.

Fatty acid analyses

To determine the mycelial dry weight and fatty acid content, the fungi were separated from the medium by centrifuging the cultures for 10 min at 4° C (8,000 × *g*). The supernatant was removed, and the mycelium was washed with 50 ml of tap water. The centrifugation was repeated, water was removed, and the mycelium was frozen under a nitrogen atmosphere. The sample was lyophilized, and the mycelial dry weight was determined. After the addition of an internal standard (methylheptadecanoate, Sigma, St. Louis, Mo., USA) to the sample, fungal fatty acid esters were saponified, converted to methyl esters, extracted as fatty acid methyl esters, and analysed by GLC, as described previously (Suutari et al. 1990).

Calculations

The relative fatty acid composition was estimated as a percentage of the total peak area on the GLC chromatogram. Absolute amounts of individual fatty acids in a mycelial sample (mg/g dry wt) were calculated by dividing areas of the acids on the GLC chromatogram with that of the standard and multiplying by the amount of the standard. The total fatty acid content of the mycelium was calculated as a percentage of fatty acid methyl esters of the cell dry weight. The final value was the mean of two determinations from mycelium (dry weight 1.5–3.5 g/l), in which the growth phase did not affect the mycelial fatty acid profile. The standard deviation (n = 8) of the fatty acid analysis was < 0.9%. The degree of fatty acid unsaturation (Δmol^{-1}) in lipids was calculated as Δmol^{-1} = [Σ(% monoene + 2 × % diene + 3 × % triene)]/100. The growth rate was determined from the slope of the growth curve during the exponential growth.

Results

Fatty acid composition

The major fatty acids present in *A. niger, P. chrysogenum, T. reesei*, and *N. crassa* were palmitic, palmitoleic, stearic, oleic, linoleic, and linolenic acids. These acids accounted for over 95% of total fatty acids at all growth temperatures (Table 1) and phases studied. Their composition was nearly unaltered in the exponentially growing fungi; however, the proportion of saturated fatty acids decreased as the stationary growth phase approached. In addition, the total amount of fatty acids esterified to lipids of the exponentially growing fungi changed 1.7–5.5%, with the exception of the high fatty acid content found in *A. niger* and *P. chrysogenum* at temperatures of 15–10° C.

Within the growth-temperature ranges studied, the amount of palmitic acid varied from 20 to 24% and 7.8 to 13.1 mg/g dry wt in *T. reesei* and *N. crassa*, and was clearly higher than in *A. niger* and *P. chrysogenum* (13–18% of total fatty acids; 3.3–5.7 mg/g dry wt), except at temperatures below 20° C (Table 1). The monounsaturated derivative of palmitic acid, palmitoleic acid, was detected in small amounts (< 3% of total fatty acids; < 1.8 mg/g dry wt) in all fungi studied. In contrast, stearic acid and its monounsaturated derivative, oleic acid, were clearly present in higher amounts in *A. niger* and *P. chrysogenum* (stearic acid: 5–14%, 2.0–3.2 mg/g dry wt; oleic acid: 16–28%, 3.8–11.4 mg/g dry wt) than in *T. reesei* and *N. crassa* (stearic acid: 1–3%, 0.3–2.0 mg/g dry wt; oleic acid: 3–10% and 2.0–4.9 mg/g dry wt). In addition, stearic and oleic acid contents also greatly increased in *A. niger* and *P. chrysogenum* at temperatures below 20° C. Furthermore, the amount of the major fatty acid of the fungi, linoleic acid, varied from 33 to 55% and 7.3 to 27.0 mg/g dry wt in relative and absolute amounts, respectively, and its content also increased in *A. niger* and *P. chrysogenum* at temperatures below 20° C. Finally, the most unsaturated fatty acid, linolenic acid, was detected in fungi from trace amounts to up to 29% of total fatty acids (16.2 mg/g dry wt).

The effect of temperature on fungal fatty acids

The temperatures used in this study broadly covered the growth temperature ranges of the fungi. On approaching the lower growth temperature extreme, growth rates decreased nearly to zero (< 0.02 g l^{-1} h^{-1}) at 10° C (Table 1). Towards the upper temperature extreme, *P. chrysogenum* did not grow at 35° C, and the other fungi did not grow at 40° C. Within these broad growth temperature ranges studied, significant differences in fatty acid content of the exponentially growing fungi, depending on the fungal species and temperature range considered, were observed.

In *A. niger*, the mycelial linolenic acid content mainly increased when growth temperature was lowered to 20–15° C (Table 1). Consequently, the degree of fatty acid unsaturation increased due to the increase in the proportion of linolenic acid and the decrease in linoleic acid. Concomitantly with the reduction in the temperature to 20–15° C, the relative amount of stearic acid slightly increased, and that of palmitic and oleic acids decreased. However, when the growth temperature was further reduced from 20–15 to 10° C, the cellular palmitic, palmitoleic, stearic, oleic, and linoleic acids contents greatly increased, whereas the amount of the most unsaturated fatty acid, linolenic acid, decreased. *A. niger* accumulated lipids in connection with visible sporulation. As a result, the degree of fatty acid unsaturation decreased as the external temperature

was lowered from 20–15 to 10° C because of the increase in proportion of the less-unsaturated fatty acids, palmitic and oleic acids, whereas the amount of polyunsaturated linoleic and linolenic acids decreased. The growth rate of *A. niger* decreased over the entire decreasing temperature range between 35 and 10° C.

In *P. chrysogenum*, the mycelial fatty acid content slightly decreased when the growth temperature was reduced from 30 to 20° C; an increase in the most unsaturated fatty acid, linolenic acid, was accompanied by a more pronounced decrease in oleic and linoleic acids (Table 1). Hence, the degree of fatty acid unsaturation increased as the temperature was lowered to 20° C because of the increase in the linolenic acid proportion and the decrease in oleic acid. However, when the growth temperature further decreased from 20 towards 10° C, the cellular fatty acid content also significantly increased in *P. chrysogenum*. At lower temperatures between 20 and 15° C, the contents of palmitic, palmitoleic, oleic, and linoleic acids increased, whereas that of linolenic acid decreased similarly as above in *A. niger* when the temperature was lowered from 15 to 10° C. Consequently, fatty acid unsaturation decreased in *P. chrysogenum* at lower temperatures between 20 and 15° C because of the increase in the proportion of oleic acid and the decrease in linoleic and linolenic acids. However, when the temperature was further reduced to 15–10° C, absolute amounts of palmitic, palmitoleic, stearic, linoleic, and linolenic acids increased, while that of oleic acid decreased. Therefore, the degree of fatty acid unsaturation increased since the proportion of oleic and linoleic acids decreased, while the amount of the most unsaturated fatty acid, linolenic acid, increased. The growth rate of *P. chrysogenum* increased when the temperature was lowered from 30 to 26° C, and decreased thereafter as the temperature was lowered towards 10° C.

In *T. reesei*, the temperature mainly affected the mycelial linolenic acid content, which increased as temperatures were reduced to 26–20° C, and decreased as temperatures neared 10° C (Table 1). Thus, the proportion of linolenic acid increased and that of linoleic acid decreased; consequently, fatty acid unsaturation increased as temperature was lowered to 26–20° C. At temperatures below 26–20° C, opposite changes occurred: the relative amount of linolenic acid decreased and that of linoleic acid increased, and hence, fatty acid unsaturation decreased. Similarly, in *A. niger*, the linolenic acid content increased at lowered temperatures above 20–15° C. The growth rate of *T. reesei* decreased over the entire decreasing temperature range from 20 to 10° C.

In *N. crassa*, the major change in fatty acids that occurred was the decrease in the cellular palmitic and linoleic acids content when the growth temperature was lowered to 26–20° C (Table 1). Above and below this temperature range, only minor alterations were observed in the myceliar fatty acid profile. Consequently, the proportion of linoleic acid decreased and that of linolenic acid increased as the temperature was lowered from 26 to 20° C, in such a manner that the degree of fatty acid unsaturation remained nearly unaltered over the entire temperature range studied. Concomitantly with the decrease in the temperature from 26 to 20° C, the growth rate decreased.

Discussion

This study clearly showed that temperature-dependent alterations in mycelial fatty acids, and consequently fatty acid unsaturation, greatly differed in the fungal species tested and depended on the growth temperature range considered (Fig. 1), as has been observed in yeasts (Suutari et al. 1990). The changes that occurred in the mycelial fatty acid profile at varying environmental temperatures did not linearly correlate with alterations in the oxygen solubility or growth rate. When the temperature was lowered, the degree of fatty acid unsaturation in total lipids increased, decreased, or remained unaltered (Fig. 1), and cannot, therefore, be unambiguously related to the increasing oxygen solubility, and thus, desaturation efficiency, although a correlation may exist. Similarly, studies on *Candida utilis* support the idea that effects of the growth temperature and dissolved oxygen tension are separate (Brown and Rose 1969). Nevertheless, results such as the nearly constant fatty acid unsaturation observed in *N. crassa* over the growth temperature range studied (Table 1) support the presence of an exact temperature control for fatty acid unsaturation in total lipids. Similarly, in *Saccharomyces cerevisiae*, fatty acid unsaturation is main-

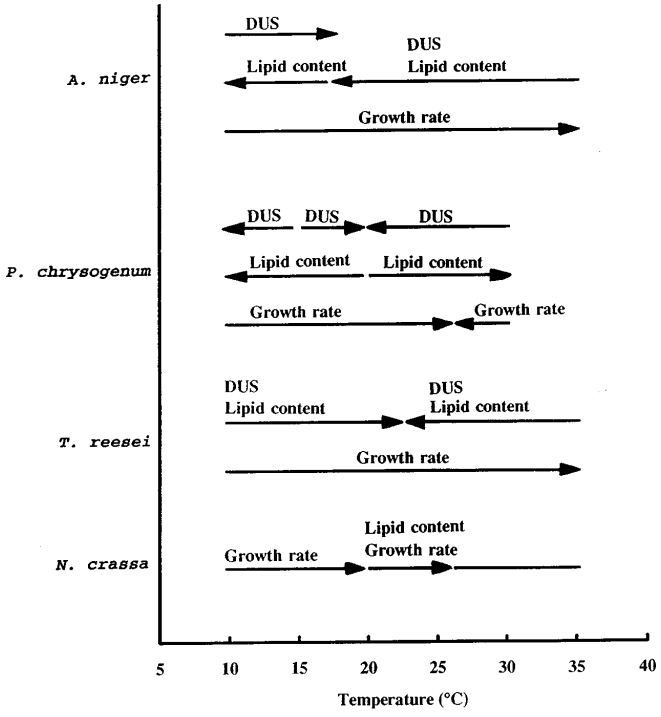

Fig 1 Summary scheme of changes that occur in lipids and growth rates of the fungi *Aspergillus niger*, *Penicillium chrysogenum*, *Trichoderma reesei*, and *Neurospora crassa* as a response to alterations in environmental temperatures. *Arrows* show increases in trends within temperature ranges presented in the horizontal axis (*DUS* degree of fatty acid unsaturation)

Table 1 The effect of growth temperature on relative and absolute amounts of fatty acids, the mycelial fatty acid content, the degree of fatty acid unsaturation, and the growth rate of *Aspergillus niger, Penicillium chrysogenum, Trichoderma reesei,* and *Neurospora crassa*

Fungi	Temperature (°C)	Growth time (h)	Growth rate (g l^{-1} h^{-1})	Fatty acid content (% dry wt)	Relative fatty acid composition (%)						Absolute amounts of fatty acids (mg/g dry wt)						Degree of unsaturation
					16:0	16:1	18:0	18:1	18:2	18:3	16:0	16:1	18:0	18:1	18:2	18:3	(Δmol^{-1})
Aspergillus niger	10	550	0.01	25.2	21	1	13	45	17	3	54.6	1.3	31.9	113.1	43.4	7.7	0.88
	15	214	0.02	5.0	12	1	12	14	35	24	6.0	0.2	6.5	7.0	18.1	12.5	1.57
	20	88	0.08	2.5	13	1	14	16	33	20	3.6	0.1	3.2	4.3	8.7	5.1	1.44
	26	38	0.22	2.1	17	1	10	16	39	12	3.9	0.1	2.7	3.8	8.1	2.4	1.32
	30	30	0.37	3.6	18	1	11	20	43	6	5.0	0.2	2.5	5.0	11.4	2.0	1.23
	35	35	0.39	1.7	17	1	8	21	50	4	3.3	0.1	2.0	4.5	7.3	0.2	1.31
Penicillium chrysogenum	10	273	0.02	6.3	13	2	9	23	38	13	10.5	1.8	6.6	6.3	29.6	7.9	1.40
	15	164	0.10	5.9	14	2	8	26	44	4	8.3	1.0	4.9	16.1	26.7	2.2	1.27
	20	59	0.11	3.3	13	1	5	16	49	13	4.7	0.1	2.3	5.4	16.6	4.0	1.53
	26	38	0.16	4.0	14	1	5	19	50	8	5.7	0.2	2.5	8.2	20.1	3.0	1.43
	30	37	0.09	4.0	14	1	5	28	46	3	5.6	0.2	2.0	11.4	19.3	1.1	1.30
Trichoderma reesei	10	214	0.01	4.2	21	2	2	5	52	15	9.1	0.7	0.9	2.0	22.5	6.7	1.55
	15	128	0.04	4.8	20	1	2	3	48	22	10.2	0.4	0.9	2.6	23.6	10.6	1.66
	20	62	0.07	5.5	20	1	2	5	40	29	11.2	0.6	1.1	2.9	22.9	16.2	1.73
	26	32	0.11	5.3	20	1	1	3	47	26	11.4	0.4	0.8	2.2	24.2	13.7	1.77
	30	34	0.15	4.5	22	1	1	5	52	15	10.4	0.3	0.6	2.3	24.0	7.0	1.54
	35	24	0.16	4.6	21	1	2	8	55	10	9.1	0.3	0.3	4.9	27.0	4.1	1.48
Neurospora crassa	10	214	0.02	4.1	22	2	2	7	44	19	9.2	1.0	0.9	3.1	18.4	8.0	1.56
	15	129	0.03	3.4	23	3	3	10	42	17	8.3	0.7	1.2	3.5	14.9	5.8	1.47
	20	76	0.08	3.8	20	2	3	9	38	22	7.8	0.8	2.0	3.4	15.1	8.8	1.54
	26	26	0.30	5.2	24	2	3	6	47	14	13.1	1.0	1.6	3.4	25.2	7.2	1.42
	30	23	0.26	5.1	21	2	3	9	49	13	11.3	0.9	1.4	4.8	25.9	6.7	1.45
	35	24	0.21	5.0	21	2	2	8	49	15	10.8	0.9	0.9	3.9	25.6	7.7	1.50

tained at all growth temperatures and rates (Suutari et al. 1990). Furthermore, despite the fact that temperature-induced changes in fatty acids often did not linearly correlate with alterations in the growth rate, these two factors may be related (Fig. 1). For example, in *N. crassa*, the cellular palmitic and linoleic acids content significantly decreased when the temperature was lowered to 26–20° C, and concomitantly, the growth rate decreased (Table 1). Interestingly, within this same growth temperature range (at 22° C), the fatty acid chain-elongation mutant (*cel*) of *N. crassa* loses its ability to keep the time of sporulation temperature independent (Coté and Brody 1987). However, for example in *T. reesei*, the growth rate decreased over the entire decreasing temperature range, whereas fatty acid unsaturation increased when the temperature was reduced to 26–20° C and decreased thereafter because of changes in the linolenic acid content (Table 1, Fig. 1).

Despite the diversity in responses, similarities were found in modes of the alterations of the total fatty acid content in several fungi and were similar to that of yeasts. Fatty acid unsaturation increased in *A. niger* and *T. reesei* when the temperature decreased to 20–15 and 26–20° C, respectively, because of an increase in the linolenic acid content up to 16.2 mg/g dry wt (Table 1). Hence, the biosynthesis of linolenic acid via stearic, oleic, and linoleic acids (Chopra and Khuller 1984) seemed to increase when the temperature was lowered. Similarly, when the external temperature decreases, the content of the most unsaturated fatty acid (linoleic acid) of *Candida lipolytica* increases (Kates and Paradis 1973), caused by the increased desaturation of oleyl-CoA to linoleyl-CoA (Chopra and Khuller 1984). In *P. chrysogenum*, fatty acid unsaturation also increased when the temperature was lowered to 20° C (Table 1), but this occurred because the less-unsaturated fatty acids, oleic and linoleic acids, decreased more than the most-unsaturated fatty acid, linolenic acid, increased; consequently, the cellular fatty acid content decreased. Therefore, the increased biosynthesis of linolenic acid via stearic, oleic, and linoleic acids (Chopra and Khuller 1984) seems to be related to the reduction in the cellular oleic and linoleic acids content. The latter mode of temperature-dependent alteration of the total mycelial fatty acid content is the same as that observed in *Candida utilis* at decreasing temperatures above 20° C (Suutari et al. 1990). The lowering of the growth temperature below 20–15° C greatly increased the mycelial fatty acid content in *P. chrysogenum* and *A. niger* (Table 1).

Generally, lipid accumulation is related to growth conditions restricting protein biosynthesis (Brennan et al. 1974), and hence the low growth temperature could have

induced the same mechanism. Similarly, the accumulation of lipids at low growth temperatures occurs at least in *Lipomyces starkeyi* (Suutari et al. 1990, 1993) and *Humicola lanuginosa* (Crisan 1973). In *A. niger*, the fatty acid content increases in connection with sporulation, the phenomena occasionally observed to be related (Lösel 1988). Moreover, the fatty acids accumulated (palmitic, stearic, oleic, and linoleic acids) were the same in *P. chrysogenum* and *A. niger* when the temperature was lowered from 20–15 to 10° C, and from 20 to 15° C, respectively (Table 1). These fatty acids can be synthesized before their incorporation with phosphatidic acid, which is the precursor of major phospholipids and also triacylglycerols via diacylglycerols (Chopra and Khuller 1984). Since fatty acids acylated to major phospholipids may be further desaturated (Chopra and Khuller 1984), the degree of fatty acid unsaturation often is lower in triacylglycerols than in phospholipids (Lösel 1988). Indeed, here fatty acid unsaturation also decreased to 0.88 Δmol^{-1} in *A. niger* when the fatty acid content greatly increased at 10° C, although values generally varied between 1.23 and 1.77 Δmol^{-1} (Table 1), which is typical or slightly higher than the values determined earlier for mesophilic fungi (Mumma et al. 1970). In contrast, the most unsaturated fatty acid, linolenic acid, also accumulated at temperatures below 15° C in *P. chrysogenum*, which contains two pathways for the biosynthesis of linolenic acid (Richards and Quakenbush 1974). Therefore, the observed large alterations in the linolenic acid content at 15–10° C may be related to differences in the temperature regulation of the two pathways, as temperature-dependences of desaturases forming linoleic acid from a CoA-derivative and phospholipid-bound oleic acid differed in *C. lipolytica* (Kates and Paradis 1973). On the other hand, the similarities presented may indicate that the same biosynthetic routes are temperature-regulated. Moreover, although factors that determine the fatty acid profile of polar and neutral lipids are known to differ (Chopra and Khuller 1984; Lösel 1988), the sum of temperature-induced changes in these lipids appears to be similar in several fungi within certain growth temperature ranges, supporting the presence of common regulatory mechanisms.

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