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Mechanism of photoregulation of carotenoid biosynthesis in plants

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Abstract - It is a well known phenomenon that in plants both development and metabolism are highly dependent on external factors, in particular on light. Biosynthesis of various compounds starts only after illumination; such a regulation has been reported also for carotenoids in different groups of plants.

The main problem in the photoregulation of carotenoid biosynthesis is - like in the photoregulations of other processes - how can the organism translate the physical signal "light" into a biochemical signal and finally into physiological and biochemical events. The sequence of reactions involved includes the photoreception by a receptor pigment, the signal transduction and the regulatory level of the activity of carotenogenic enzymes.

This review concentrates on the elucidation of these problems. The present state of knowledge is reported and discussed for three groups of plants - algae, higher plants and fungi - which might represent different mechanism types.

INTRODUCTION

For plants one of the most important environmental factors is light. It serves as a source of energy for photosynthesis in all chlorophyll containing plants. Besides this function, it is also an important regulating factor in plant development, not only in green but also in non-photosynthetic organisms, for instance fungi. Since development is based on specific alterations of metabolism, such as the formation of enzymes and their products, photoregulation of biosyntheses is also a common phenomenon; the most striking example is the obligatory light-dependence of chlorophyll formation in higher plants. Besides this effect on chlorophyll formation, photoregulation of carotenoid biosynthesis has also been reported not only in higher plants, but also in algae, fungi and non-photosynthetic bacteria.

Why do many plants produce carotenoids only as a response to illumination? Has this photoregulation any ecological meaning? During the development it may be very economical for the organism to form structures and compounds only when they are needed. The main functions of carotenoids in plants, i.e. their role in photosynthesis and protection of the organism against the potentially harmful effects of irradiation, are related only to growth of the plant in the light. Consequently, the bulk of carotenoids is needed when e.g. the seedling emerges from the ground or fungal mycelia grow into illuminated areas. Therefore, photoregulation acts quite clearly as a "saving mechanism" to avoid waste of both material and energy and may provide the organism with an ecological advantage.

The photoregulation of carotenoid biosynthesis and its characteristics have often been reviewed previously, and from various points of view (Refs. 1-6). Therefore, it is not the intention of this paper to give a further survey of the literature relevant to this topic, but rather to concentrate on progress in elucidating the photoregulatory mechanism of carotenoid biosynthesis.

GENERAL PROBLEMS IN PHOTOREGULATION

The main problem in the photoregulation of carotenoid biosynthesis is - as in the photoregulation of other processes - how can the organism translate the physical signal "light" into a biochemical signal and finally into physiological and biochemical events? The sequence of reactions involved, beginning with the reception of the light signal and ending up with the final response - biosynthesis of of carotenoids - is usually termed the "mechanism" of the photoregulation. For convenience we may divide the regulatory chain into several steps.

Photoreception - Signal transduction - Level of regulation - Synthesis

Although it is difficult to separate the reaction completely, some general principles of the different steps shall be described briefly.

Photoreceptor pigments. The usual approach to discovering the photoreceptor that is responsible for a certain response, is a comparison of the action spectrum of the response with the absorption spectra of putative pigments. However, besides action spectroscopy further investigations using other methods are necessary for an unequivocal identification of the acting photoreceptor. At least three of the photoreceptors, discussed as being responsible for light-mediated carotenogenesis - chlorophyll, phytochrome and a "blue/UV-photoreceptor" designated "cryptochrome" - are also very important for other photoresponses in plants.

Signal transduction. In signal transduction two different types of regulation are important which also have implications for the level of regulation. In the first situation accumulation of carotenoids proceeds only during illumination, that is the permanent presence of the inducing factor "light" is essential for the response or, in the second, light is needed only as a trigger whereas the response takes place also in darkness. The latter case is the so-called classical "induction" mechanism.

Level of photoregulation. Considering the biochemical background of all known photoregulations of biosynthetic processes, in particular the molecular machinery for the formation of enzymes, in principle there are four possible levels for the action of light, for all of them well documented examples analogous to photoregulation of carotenogenesis are known:

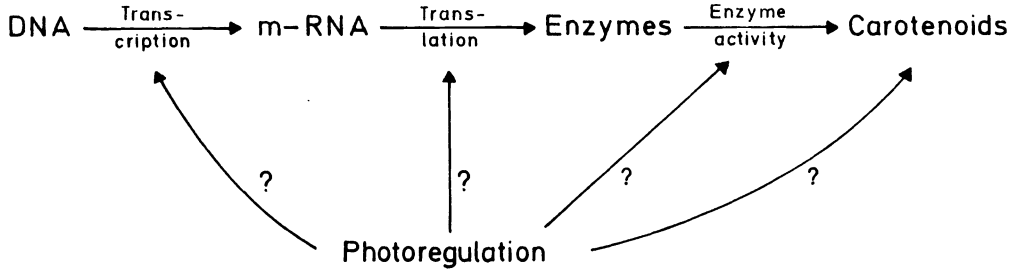

Fig. 1 Possible levels for the action of light in photoregulation of carotenoid biosynthesis.

1. A direct transformation of a light-absorbing compound - a certain carotenoid - which then facilitates subsequent biosynthetic steps; 2. photoinduced changes in the activity of carotenogenic enzymes already presented; 3. de novo synthesis of carotenogenic enzymes from messenger-RNA already present by regulation of translation or 4. de novo synthesis of the enzymes via regulation of transcription, that is de novo synthesis of the appropriate messenger-RNA's.

In the following report on and discussion of the present state of knowledge on the mechanism for 3 groups of plants - algae, higher plants and fungi - it will be demonstrated that they represent different types of mechanism with respect to photoreceptors, signal transduction and level of photoregulation.

ALGAE

Algae form intact chloroplasts and the usual plastid carotenoids when grown in the dark; this indicates that carotenoid biosynthesis in algae exhibits no light-requirement, although variations in the carotenoid pattern induced by illumination have been reported for some species. The only case of photoregulation of carotenogenesis in wild-type strains appears to be that of the phytoflagellate Euglena gracilis. Although dark-grown cultures have the capacity to synthesize all carotenoids that are present in light-grown cultures, the amount of carotenoids is greatly enhanced by illumination (reviewed in Ref. 7).

However, in mutants of Euglena, as well as in mutants of the green algae Chlorella and Scenedesmus, strong photoregulation has been detected and investigated in more detail by the groups of Schiff, Claes, Britton and Senger. Some of these mutants are green but others have lost the capacity for chlorophyll synthesis. The carotenoid pattern in some representative mutants grown either in the dark or in the light are compiled in Table 1.

TABLE 1. Contents of carotenoids in algal mutants in the dark or under illumination (representative data only).

		Carotenoids (units reported by each of the authors)					
Organism	Conditions	ζ - Carotene	Neuro-sporene	Lyco-pene	α + β-Carotene	Xantho-phylls	Ref.
Chlorella vulgaris	dark	1122	266	?	-	18	48
(mut. 5/520)	light	886	170	?	55	304	
Scenedesmus	dark	401	-	-	8	+	
obliquus (mut. PG1)	light	+	-	-	276	536	49
Scenedesmus	dark	250	34	20	10	-	
obliquus (mut. 1 E)	light	+	-	-	272	332	49
Scenedesmus	dark	156	57*	66*	-	-	
obliquus (mut. C-6D)	light	10	+	3	92	326	10,11

?, not determined; -, absent; +,present in trace amounts; *, mainly cis isomers.

The data clearly show that - neglecting some leakage - dark-grown cells of all mutant strains are unable to synthesize cyclic carotenes and xanthophylls, present in cultures of the wild-types from which the mutants were derived; such carotenoids are synthesized only in the light and under this condition in Scenedesmus acyclic carotenoids are present in trace amounts only. The data suggest that the photoregulated biosynthetic step may be the cyclisation of carotenes.

Photoreceptors

From an action spectrum for this photoregulation determined for Euglena (Ref. 12) it has been concluded that a protochlorophyllide is the acting photoreceptor. An action spectrum obtained by Claes (13) for the Chlorella-mutant listed in Table 1 and the result that the red light effect could not be nullified by simultaneous illumination with far-red light were taken as evidence that chlorophylls are the photoreceptor in this organism.

In chlorophyll-free mutants from Scenedesmus, only the blue part of the spectrum is effective; from the action spectrum and additional results (Ref. 14) it can be assumed that the blue-light photoreceptor which has recently been designated "cryptochrome" and which will be discussed later in more detail is responsible in this case.

In a bleached mutant strain from Euglena which is deficient in protochlorophyllide in dark-grown cultures blue light minus dark difference spectra indicated a photoisomerisation of cis- to trans- ζ-carotene (Ref. 15). Since additional results (Ref. 16) have shown that no compound other than cis- ζ-carotene is the photoreceptor responsible for its own isomerisation one might speculate that this is the rate-limiting step for the subsequent biosynthesis of more unsaturated carotenes and xanthophylls.

Level of photoregulation

From the data shown in Table 1 one might consider that, in the dark, only enzymes for the formation of acyclic carotenoids are present; that means such carotenoids are formed independently of light, and illumination triggers the formation of cyclases and hydroxylases. However, kinetics of the changes in pigment composition during illumination, some of which are shown in Fig. 2,

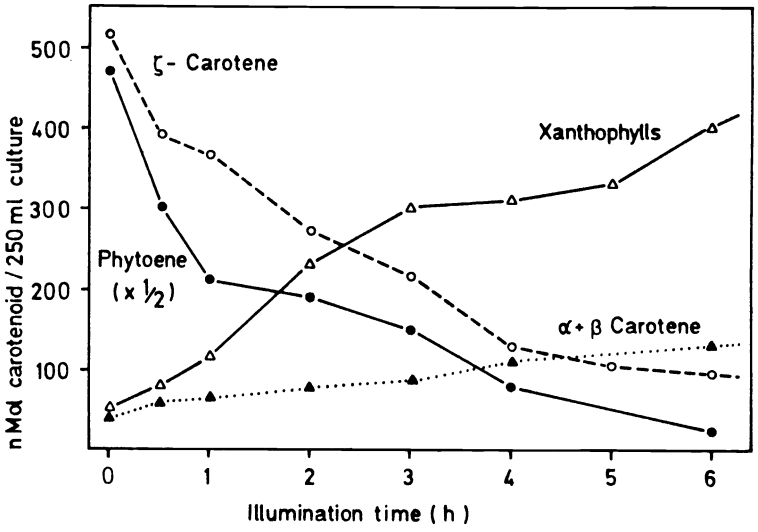

Fig. 2 Pigment changes following illumination of a dark-grown culture of Scenedesmus obliquus mutant PG 1 (calculated from Powls and Britton, Ref. 17).

have been published by Powls and Britton (17) for a mutant of Scenedesmus. They show a rapid fall in phytoene and ζ-carotene concentrations immediately after the onset of light, that is without any lag-period. Furthermore, they also show a concomitant and immediate increase of ß-carotene and xanthophylls. Similar results have been obtained in studies by Senger and Straßberger (11) who used a different mutant strain of Scenedesmus, as well as by Claes (8) with Chlorella mutants.

In summary, a common characteristic of each of the 3 cases is the absence of any lag-phase in the photoinduced pigment transformation. Furthermore, the results obtained with Chlorella mutants and Euglena show that pigment transformation operates only during illumination. Consequently, photoinduction of de novo formation of the carotenogenic enzymes via protein synthesis can very likely be ruled out. Instead, it might be considered that light acts as "modulating" factor like in some cases of photomorphogenesis of higher plants or similarly to the photoregulation of carotenoid accumulation in higher plants which will be dealt with later. Whether such a modulation might be caused by a light-mediated change of enzyme activity - like in flavin-containing enzymes as reviewed in Ref. 18 - is at the moment a mere speculation. In this case a quantitative change would not be sufficient to explain the results, but a qualitative change has to be assumed.

HIGHER PLANTS

Seedlings of higher plants grown in the dark have some capacity for carotenoid biosynthesis but only angiosperms show a light-dependent stimulation of carotenoid production during the development of the young plant. In investigations on photoregulation in angiosperm seedlings one has to consider that the complete transformation of proplastids or etioplasts to photosynthetically active chloroplasts, including the synthesis of chlorophyll, is completely light-dependent. As a consequence, the stimulation of carotenoid synthesis is only a part of the photomorphogenetic transformations and therefore is not entirely independent of them. It is a well-documented phenomenon, though, that light-grown plants contain higher

levels of carotenoids than do dark-grown plants (reviewed in Ref. 19). Photoregulation of carotenoid biosynthesis during the ripening of fruits has been reported but only in tomatoes and in paprika (Refs. 20,21).

Photoreceptors and signal transduction

There is no doubt that in higher plants an acting photoreceptor for the photoregulation of carotenoid accumulation is phytochrome. Phytochrome is a blue-green chromoprotein containing a linear tetrapyrrole as chromophore. It is specific for plants and exists in two interconvertible light-absorbing forms - a red-light and a far-red-light form. Since phytochrome is an important photoreceptor in photomorphogenesis of higher plants its structure, photochemical reactions and its mode of action have been intensely discussed (for reviews see Ref. 22).

Goodwin and his co-workers (Refs. 23,24) were the first to find that total carotenoid formation in seedlings is stimulated by a brief illumination with red light and that this effect can be nullified by a subsequent exposure to far-red-light; further investigations confirmed these results (e.g. Refs. 25,26). Although an action spectrum determined for carotenoid accumulation in etiolated wheat leaves indicate protochlorophyll rather than phytochrome as the photoreceptor (Ref. 27), further characteristics of this photoinduction closely resemble those of other photoregulations mediated by phytochrome (e.g. Ref. 28). Therefore, by analogy, the mechanism in this case, that is pulse illumination, is that of a classical induction - reversion phytochrome reaction in which the far-red absorbing form of phytochrome produced on exposure to red light acts as an inducer.

A different type of mechanism appears to be involved when dark-grown seedlings are exposed to continuous far-red light (Refs. 25,29). Only prolonged illumination increases the rate of carotenoid accumulation after a lag-period; soon after the light is turned off, pigment production is reduced to the dark rate. Such so-called "high irradiance reactions" are characteristic of other developmental responses of seedlings which are continuously illuminated. Action spectra of such responses exhibit, in addition to a peak in the far-red region, effectiveness of light in the blue and near UV region of the spectrum (reviewed e.g. in Ref. 30). It is discussed, in the context of whether high irradiance reactions are mediated by two photoreceptors, phytochrome and the blue light photoreceptor, cryptochrome (reviewed in Ref. 31)

The level of photoregulation

The shape of the accumulation kinetics during continuous far-red light (Ref. 25) shows that carotenoid formation is dependent on continuous illumination. Obviously, this type of photoregulation is different from that of an "induction" mechanism mediated by phytochrome via pulse illumination or by blue light as described later for fungi. Consequently, for the level of photoregulation it might be considered that as in the case of the algae some kind of "photomodulation" is involved (reviewed in Ref. 35) the mechanism of which has yet to be elucidated.

Further evidence for such a type of regulation comes from the following results: As long as illumination operates only via phytochrome without a concomitant biosynthesis of chlorophyll (red-light pulses, continuous far-red light), accumulation of carotenoids is enhanced to a moderate extent only. Furthermore, the carotenoid pattern virtually unchanged compared to that in complete darkness (Ref. 32). This effect seems to be due to a stimulation of early step(s) in the biosynthetic pathway (Ref. 26). If, however, seedlings are illuminated with white or continuous red-light leading to the synthesis of large amounts of chlorophyll and to the transformation of etioplasts to chloroplasts carotenoids production is increased drastically (Refs. 28,29; reviewed in Refs. 33,34). A distinct change in the carotenoid pattern was found concomitantly (Ref. 32). The authors explain this effect with the suggestion that during plastidal grana formation large amounts of carotenoids are incorporated into the chlorophyll/carotenoid/ protein-complexes in the thylakoid membranes (reviewed by Cogdell, this issue). As level of photoregulation some kind of "modulation" through a negative feedback regulation is discussed (Ref. 28).

FUNGI

Photoregulation of carotenoid biosynthesis in fungi has been detected in only a few species as we have compiled earlier (Ref. 6); detailed investigations have been carried out on only 4 species: Neurospora crassa, Phycomyces blakesleeanus, Fusarium aquaeductuum and Verticillium agaricinum. The organisms synthesize carotenoids characteristic of the particular species. Wild-type Phycomyces produces ß-carotene as the main pigment, intermediates are found in only trace amounts. In contrast, in Fusarium, Neurospora and Verticillium these intermediates which can

be arranged according to the desaturation sequence first proposed by the late Prof. Porter (Ref. 36) are accumulated to some extent.

Whereas in Verticillium carotenoids accumulate only during illumination (Ref. 37) the kinetics of photo-induced accumulation in Fusarium (Fig. 3) and also in Neurospora show different characteristics:

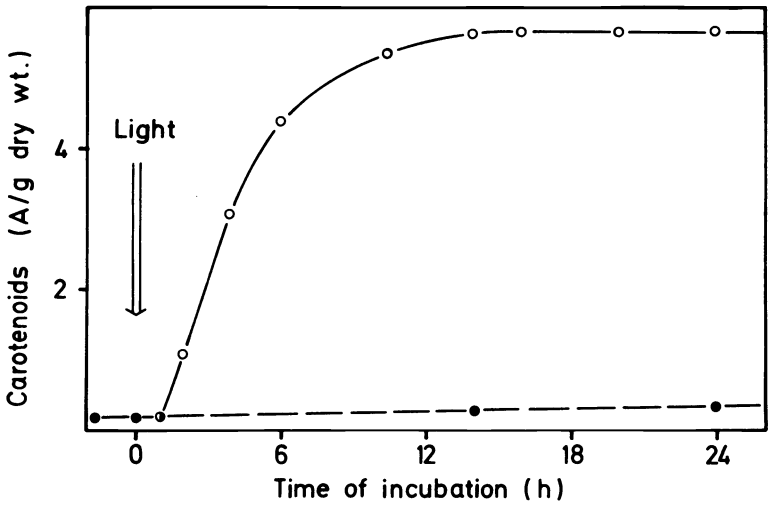

Fig. 3 Accumulation of carotenoids in young mycelia of Fusarium aquaeductuum in the dark (closed circles - •) and following a brief illumination (open circles - o). The arrow indicates the period of brief illumination.

Following a lag-period after a brief illumination the amount of pigments increases rapidly for a certain time, and thereafter net pigment synthesis ceases; only continuous illumination leads to a prolonged accumulation. The data gathered from experiments with brief illumination periods clearly show that the dark reactions are a strict consequence of photoreactions indicating that in the sequence of events (see Fig. 1) a very early "point of no return" exists. This type of regulation exhibits all features of a "classical" induction mechanism.

Photoreceptors

Besides earlier reports on the spectral dependence, Zalokar (38) was the first to determine an action spectrum of carotenogenesis in Neurospora. A more detailed action spectrum for this fungus described by DeFabo, Harding and Shropshire (39), as well as ours for Fusarium (Ref. 40) are shown in Ref. 4 together with a spectrum from a non-photosynthetic bacterium. They all show the following characteristic features: a maximum at 370 - 380 nm and three peaks or at least shoulders between 400 and 500 nm. Light of wavelengths greater than appr. 520 nm is ineffective. The shapes of the action spectra for carotenoid biosynthesis resemble those for a variety of developmental and movement responses in plants (Ref. 3). The most prominent among these is the phototropic reaction of coleoptiles and fungal sporangiophores. Action spectra of this type have been related to a photoreceptor designated "Cryptochrome", but there is no evidence for a single cryptochrome (Ref. 41). The chemical nature of cryptochrome is the subject of continuing discussion, which shall not be repeated here. Two candidates, flavins and carotenoids are taken into consideration.

A different type of action spectra has been found Verticillium (Ref. 42) and in Leptosphaeria (Ref. 43). For Leptosphaeria, it was suggested that the photoreceptor is a porphyrin. Although the spectral effectiveness in Verticillium is not very different, Valadon (42) considered a yet unknown photoreceptor pigment since no porphyrins have been identified in the mycelium of this fungus. In Verticillium, Valadon and his co-workers (Refs. 37, 44) found, in addition to the effect of UV-blue light some effect also by light in the red region of the spectrum. The photoreaction shows the typical induction by red light and subsequent reversion by the far-red. However, since additional spectroscopic data and further results (Ref. 45) cannot fully be explained in terms of phytochrome transformations, the involvement of phytochrome needs further clarification. In the fungi Fusarium and Neurospora, in which cryptochrome is the photoreceptor, we could not find any additional effectiveness of light from the red part of the spectrum (Ref. 46).

Signal transduction

The following results which we have gathered mainly from experiments using Fusarium led us to the conclusion that signal transduction is mediated by redox-reactions (reviewed in Ref. 4).

For optimal photo-induction the presence of oxygen during illumination is essential. However, a minor induction is possible in the absence of oxygen. Moreover, when mycelia were illuminated in an atmosphere of nitrogen with saturating fluences the photoreceptor system can be reactivated by oxygen in the dark. We therefore concluded that oxygen is not involved directly in the photochemical reaction of the photoreceptor but rather functions as an electron acceptor in keeping the photoreceptor - we consider a flavoprotein - in a proper state of oxidation. The reducing agent dithionite applied to mycelia immediately after illumination prevents photoinduction. On the other hand incubation of the mycelia with buffered hydrogen peroxide solution in the dark can mimic, to a certain extent, the effect of light in inducing carotenoid synthesis. Biosynthesis of carotenoids is also induced when mycelia are incubated with methylene blue and then illuminated with red light which is not effective in photoinduction via the natural photoreceptor (Ref. 3). Photoinduction by red light was found to be triggered only in the presence of photodynamically active redox dyes.

From these results and on consideration of results from other blue-light mediated phenomena, we have drawn a hypothetical scheme illustrating the events during photoinduction via the cryptochrome photoreceptor (see Ref. 4). In this scheme we assume that irradiation of the photoreceptor causes, by its own redox-reactions, an oxidation of a yet hypothetical substance which acts as a "trigger" for subsequent induction steps.

Level of photoregulation

In contrast to the phytochrome-mediated regulation of carotenoid accumulation in seedlings (Ref. 25), in mycelia of Fusarium and Neurospora pigment production after a first illumination (see Fig. 3), and renewed synthesis after a second light treatment, starts only after a lag-phase (Ref. 47). The occurrence of a lag-phase always points to time-consuming events intercalated between photoinduction and the final events. Earlier results, using several fungal species, have shown that photoinduced carotenoid accumulation is completely blocked by cycloheximide - a potent inhibitor of protein synthesis - when applied prior to or immediately after illumination of the mycelia (reviewed in Ref. 4). From these results it has been concluded that light induces a de novo synthesis of carotenogenic enzymes which are absent or present only in minor amounts in dark grown cultures.

We found earlier that an inhibitor of transcription in fungi - Distamycin - and an antimetabolite of adenosine in RNA-synthesis - Tubericidin - blocked light-induced pigment formation in Fusarium (Ref. 4). Recent investigations show that the inhibition of carotenoid synthesis is reduced gradually with the time elapsing between illumination and application of the inhibitor. Moreover, the time course of the decrease of inhibitory power is different for the inhibitors of messenger-RNA synthesis and protein synthesis. This might indicate that synthesis of carotenogenic enzymes is preceded by the synthesis of the messenger-RNA's coding for the synthesis of these enzymes. These results led us to the hypothesis that the synthesis of the carotenogenic enzymes is regulated at the level of transcription.

However, the involvement of light-induced gene expression remains speculative unless specific photoregulated messenger-RNAs have been identified. As a first step towards such direct evidence, Schrott (48) some years ago found that, shortly after photoinduction, there is an increase in the relative amount of polyadenylated RNA being synthesized. Mitzka-Schnabel reports in her paper on carotenogenic enzymes in Neurospora (see this issue), the presence of polypeptides in which radioactivity after in vivo-labeling with ^{35}S-methionine was increased in response to photoinduction.

Therefore, we started to extract messenger-RNAs and to investigate their capacity for translation in an in vitro-translation system from rabbit reticulocytes. Cellular poly(A)-RNA extracted from dark grown and illuminated mycelia of Neurospora and Fusarium revealed high translational capacity in vitro reflected by the stimulation of ^{35}S-methionine incorporation (Ref. 49). The amount of poly(A)-RNA is increased in illuminated mycelia in both fungal species; this might indicate a higher biosynthetic activity during carotenogenesis.

The products of the in vitro translation were then separated by two-dimensional electrophoresis on polyacrylamid gels (Ref. 49). Fluorographs show that some in-vitro translated polypeptides increased in response to photoinducation. However, whether these polypeptides are connected with the carotenogenic enzymes has to be proved by further investigations.

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