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Roenneberg, Till; Merrow, Martha

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Seasonality and Photoperiodism in Fungi

Till Roenneberg¹ and Martha Merrow

Institute for Medical Psychology, University of Munich, Goethestr. 31, 80336 Munich, Germany

Abstract This review gives a retrospective of what is known about photoperiodism in fungi, which is largely based on reports about seasonal spore concentrations. Relatively few species have been investigated under laboratory conditions, so that our knowledge whether seasonal reproduction in fungi is mainly a direct response to environmental conditions or whether it involves a photoperiodic machinery with memory capacities and a relationship to the circadian system is extremely limited. To form a basis for further experimental endeavors into fungal photoperiodism, we review the reports about endogenous rhythms and photobiology. Finally, we will look at the possibilities of using the fungal circadian model system of *Neurospora crassa* for future work on photoperiodism.

Key words circadian, photoperiodic timer, photoperiodic memory, night length, *Neurospora*

Three chronobiologists were having beer and *Schwammerl* and *Knödel** in the famous Munich Schneiderbräu. Their conversation focused on rhythms and seasonality—how different the Bavarian beers were throughout the year: Starkbier in spring, Weißbier in summer, Wiesenbier in autumn, and Weihnachtsbier for the short days. Soon, the debate turned to yeast and the possibility of it also being different at different times of the year. But when one of them pointed out that yeast, at least the captive one used for brewing, had a lousy—if any—photobiology—“well, except for the odd photolyase with a transduction cascade for fixing up some UV-damaged gene”—the three scientists gave up the idea of explaining the differences in beers with the help of yeast photoperiodism. Yet, the stage was set, and after several silent minutes, the microbiologist among them came back to the basic question inherent in the earlier conversation. “What do we know about photoperiodism in fungi?” When there was no answer for some time, the microbiologist added, “And why would they need a photoperiodic

response in the first place?” This time, the answer was prompt, “S’pose, for the same reason as other organisms—to anticipate seasonal changes—mainly for reproduction.” “So, why do we know so little about it?” Except for mumbled remarks by the animal and plant representatives, going in the direction of fungi having no testes to weigh and no leaves to count, the conversation moved to other matters.

It is quite surprising how little is known about photoperiodism in fungi. There are several reports of seasonality in fungi (see Seasonality and Photoperiodism in Fungi), but are they passive adaptations to seasonal changes or do they involve a photoperiodic mechanism? The circadian domain distinguishes between synchronization and entrainment, the former being a biological rhythm that is passively driven by environmental changes, the latter involving the active process of repetitive phase shifts resulting in a specific phase angle between an endogenous oscillation and a rhythmic environment. By analogy, seasonality can also be a driven process—a direct consequence of

* Bavarian mushroom dish with dumplings.

1. To whom all correspondence should be addressed.

environmental qualities: day or night length, temperature, and other climatic parameters such as humidity and rainfall, or even triggered by other organisms in the form of food and, in the case of pathogens, host availability. Alternatively, seasonality can be a consequence of an active process, or rather of two "interrelated processes" (Nunes and Saunders, 1999): (a) a timer that measures night length (rarely day length; see Saunders, 1982, 1987) and (b) some kind of memory that integrates the seasonal changes over time.

To approach the possibility of photoperiodism in fungi, we will review their photobiology, circadian systems, and seasonality of reproduction. Finally, we will integrate the details of the *Neurospora* system into possible molecular and genetic research on photoperiodism in fungi. The different fungi mentioned in the text are systematically listed in Table 1 (as well as some that are relevant but, due to space constraints, are not explicitly discussed).

LIGHT RECEPTION IN FUNGI

Without light reception, there is no photoperiodic response. Light regulates fungal reproduction (e.g., promotion of development or inhibition of germination; see Brook, 1969; Calpouzos and Chang, 1971; Degli-Innocenti and Russo, 1984; Durand, 1982; Ingold and Nawaz, 1967a), carotenoid or other pigment formation, and phototropism (Delbruck et al., 1976; Linden et al., 1999). Action spectra and/or fluence response curves have been determined for photoinhibition of spore maturation (Leach, 1968), carotenoid induction (see list in Berjarano et al., 1990; De Fabo et al., 1976), and phase-shifting circadian rhythms (Crosthwaite et al., 1995; Dharmananda, 1980; Sargent et al., 1956). Most of these photoresponses derive from the short end of the spectrum (sometimes including the UV region, e.g., reported for circadian phase shifting; see West, 1976). There are, however, also reports of red or far-red light responses in the fungi, among them asexual spore (conidia) formation in *Aspergillus*, which is regulated by both red and blue light (Mooney and Yager, 1990).

Are all fungi responsive to light? Notably absent from the catalog of photoresponsive fungi is *Saccharomyces cerevisiae*. Although decreased growth rate has been observed with increasing illumination in this yeast, the phenotype is generally weak and apparently occurs only at low temperatures (Edmunds et al., 1979b; Edmunds et al., 1978). In addition, cell division

Table 1. Taxonomy of fungi and protocista.

Kingdom	Phylum	Genus
Protocista	Labyrinthulomycota	
	Acrasiomycota	<i>Dictyostelium</i>
	Myxomycota	
	Plasmodiophoromycota	
	Hypochytridiomycota	
	Chytridiomycota	
Fungi	Oomycota	<i>Phytophthora</i>
	Zygomycota	<i>Phycomyces</i>
		<i>Pilobolus</i>
		<i>Daldinia</i>
		<i>Emericella</i>
		(<i>Aspergillus</i>)
		<i>Erysiphe</i>
		<i>Hypoxylon</i>
		<i>Mycosphaerella</i>
		<i>Neurospora</i>
		<i>Saccharomyces</i>
		<i>Schizosaccharomyces</i>
		<i>Sordaria</i>
		<i>Venturia</i>
		<i>Armillaria</i>
		<i>Coprinus</i>
		<i>Pellicularia</i>
		<i>Sphaerobolus</i>
		<i>Ustilago</i>
		<i>Alternaria</i>
		<i>Cercospora</i>
		<i>Cladosporium</i>
		<i>Colletotrichum</i>
		<i>Exserohilum</i>
		<i>Fusarium</i>
		<i>Helminthosporium</i>
		<i>Metarhizium</i>
		<i>Pyricularia</i>
		<i>Stemphylium</i>
	Basidiomycota	
	Deuteromycota—not a "real" but a form phylum; the Deuteromycota (also called mitosporic fungi or fungi imperfecti) contain species belonging either to the Ascomycota or to the Basidiomycota, which never appear to form sexual spores	
		<i>Mycohyphocorypha</i>
		Lichens—
		fungi living in symbiosis with cyanobacteria or algae

NOTE: The taxonomy of fungi is extremely complicated and differs depending on source and year. The systematic distribution of fungi in this table is based on Margulis and Schwartz (1988) and places several of the lower fungi in the kingdom of the Protocista. For reasons of simplification, classes, orders, and families have been omitted. Genera that are mentioned in the text or the references are listed in the right column.

and amino acid transport in *S. cerevisiae* are synchronized to light:dark (LD) cycles in the circadian range (Edmunds et al., 1979a). Synchronization with LD cycles has also been reported for the fission yeast, *Schizosaccharomyces pombe* (Kippert et al., 1991b). Considering that wild-type *S. cerevisiae* are heterogeneous in their appearance relative to standard lab strains, it could be that robust photoresponsiveness was selected out, as occurred with *Aspergillus* (Mooney and Yager, 1990).

Although numerous light-regulated or light-dependent physiologies have been described for the

fungi, in no case has the photoreceptor been characterized beyond action spectra, which generally indicate flavin-mediated blue light reception. On one hand, pharmacological experiments or experiments with mutants have suggested cytochrome b (Kippert et al., 1991a, 1991b) and molybdenum cofactors (Ninmann, 1991) participating in light reception of fission yeast and *Neurospora*, respectively. On the other hand, mutagenesis experiments identified two loci in *Neurospora*, *white-collar-1* and *white-collar-2* (*wc-1* and *wc-2*), which control most photoresponses (Degli-Innocenti and Russo, 1984; Russo, 1988). The *white-collar* gene products are transcription factors, as judged by sequence analysis (Linden et al., 1999), and thus, if they prove to be part of the photoreceptive machinery, may participate in a manner similar to what has been indicated for PHYTOCHROME in plants (Martinez-Garcia et al., 2000). In addition, WC-1 has homology to the PAS/LOV domains of the plant NPH1 protein sequence, which is a blue-light photoreceptor in plants (Huala et al., 1997).

CIRCADIAN AND DAILY RHYTHMS IN FUNGI

A second requirement for photoperiodism—the assessment of the light or the dark period—entails a timer, which in plants and animals is generally linked to the circadian system. Perhaps the first indication of endogenous rhythms in the fungi derives from the dung-loving fungus *Pilobolus*, which shoots spores as far as 2 m. Klein submitted *Pilobolus* to various symmetrical non-24-h LD cycles and found that the spore-shooting rhythm was absent in LD 4:4, 8:8, and 24:24 but had a large amplitude in LD 16:16, even larger than in any 24-h cycles with varying photoperiods (Klein, 1948). This series of experiments probably represents the first systematic investigation of the influence of photoperiod on the sporulation rhythm: Both short (LD 4:20) and long (LD 20:4) photoperiods appear to suppress rhythmicity, while it persists with a low amplitude in LD 9:15 and 15:9, and with a higher amplitude in LD 12:12.

The first article to prove the endogenous nature of this rhythmicity included experiments both in constant light (LL) and darkness (DD) (Schmidle, 1951). When *Pilobolus* is kept in an LD cycle of 12:12 and released to constant light, the rhythm rapidly dampens, whereas it continues when released to DD. Rhythmicity in DD also persists after release from several days in LL. Although spore shooting is arrhythmic

Figure 1. Phase angle of the sporulation maximum of *Pilobolus sphaerosporus* in different photoperiods (drawn after Uebelmesser, 1954).

mic in LL, the amount of spores shot is 20-fold compared with DD. At the same time that Schmidle published his findings, Esther-Ruth Uebelmesser (1954) dedicated her thesis work to the same subject. Her thesis is remarkable in many ways. Many of her experiments anticipated circadian protocols, frequently used in later years (different T-cycles and photoperiods, reciprocity, night interruption experiments, entrainment by temperature cycles, etc.). Although she did not fully exploit the richness of her experimental approaches in her interpretations, she must be considered a pioneer of the field and has certainly inspired Colin Pittendrigh to use *Pilobolus* as a circadian model system (Bruce et al., 1960). Probably, Pittendrigh abandoned this model system because of the unbearable smell penetrating the laboratory when the bovine dung media was prepared (Michael Menaker and Gene Block, personal communication, December 2000).

Uebelmesser reported species-specific phase angles in LD cycles (*P. sphaerosporus* peaks at ZT 03, *P. crystallinus* at ZT 08). Unlike Klein's (1948) earlier report, the rhythm was observed in all photoperiods (except for LL) with a systematically different phase angle (Fig. 1). Uebelmesser also showed that the *Pilobolus* circadian system is capable of multiplication: When the zeitgeber was near a multiple of the endogenous period (e.g., LD 1:47), sporulation peaked twice every cycle.

She also investigated the ranges of entrainment and found that synchronization persisted in 29-h cycles (both LD 2:27 and 17:12). She submitted *Pilobolus* sys-

tematically to symmetrical LD cycles, ranging from 18:18 down to 2:2. While in *Neurospora* accumulation of conidia (conidial bands) appears to be driven in these protocols with a constant phase angle in reference to lights-off (Fig. 2A; Merrow et al., 1999), the phase angle of the spore-shooting rhythm in *Pilobolus* was systematically different with changing cycle lengths (Fig. 2B), possibly reflecting circadian entrainment. Closer investigation, however, revealed that the *Pilobolus* sporulation rhythm is also driven by the LD cycle, but unlike in *Neurospora*, by lights-on. Sporulation in *Pilobolus* is triggered by light, and the spores mature for approximately 28 h before they are shot (see arrows in Fig. 2B and C). The maturation time represents a kind of memory capacity for prior events. This is seen in experiments in which the fungi were released to DD (e.g., from LD 4:4 shown in Fig. 2C). The rhythm, synchronized to a given light cycle, persists for another 28 h until the endogenous circadian control takes over. Thus, depending on conditions, the production of asexual spores in *Pilobolus* is controlled both by the clock (phase angle) and by light (a driven spore release once per LD cycle).

Fungal circadian clocks can be exquisitely light sensitive, concerning both fluence and duration. The *Pilobolus* clock requires no more than half a millisecond of light to be completely reset (Bruce et al., 1960), and in *Neurospora* conidial banding is driven by light fluences down to moonlight levels (Merrow et al., 1999). In *Neurospora crassa*, conidial banding occurs about once per 22 h in DD. In LL, the banding pattern stops (following a transient suppression of conidiation by light), a phenomenon that has been observed in many fungi. Light appears to stop the circadian system completely, an observation supported by nonrhythmic, elevated clock gene expression in LL (Crosthwaite et al., 1995), in addition to a set phase relationship of the free-running circadian rhythm on release to DD.

Sordaria fimicola and *Daldinia concentrica* (both also *Ascomycetes*, like *Neurospora*) show circadian rhythms in sexual spore shooting in DD, which are entrainable in LD (Austin, 1968; Ingold and Cox, 1955). In *Daldinia*, circadian rhythmicity persists in LL, though it damps after several days—in *Sordaria*, LL appears to suppress rhythmic release (Austin, 1968). Interestingly, *S. fimicola* shares a functional frequency (*frq*) ortholog, relative to *N. crassa* (Merrow and Dunlap, 1994), suggesting mechanistic similarities in the photobiology and in the circadian programs of these species. Like *Daldinia*, spore release of the *Basidiomycete Pellicularia*

Figure 2. Entrainment of rhythmicity in symmetrical LD cycles. (A) In *Neurospora*, the phase angle of the conidiation rhythm relative to the light → dark transition is specific for the different *frq* strains (circles: *frq* + period = 22 h; squares: *frq1* – period = 16 h; triangles *frq7* – period = 29 h) and is independent of T (except in longer T-cycles). Conidiation starts after approximately one third of the circadian period, as determined in DD (redrawn after Merrow et al., 1999). (B, C) Phase angles of the *Pilobolus* spore-shooting rhythm in symmetrical LD cycles. The rhythm is driven by the onset of light 28 h earlier. This span represents the time that spores take to mature when triggered by light. When released to DD, the rhythm synchronized by the light cycle persists for another 28 h, when the cultures initiate a self-sustained rhythm under circadian control (e.g., release from LD 4:4 in panel B). Data from Uebelmesser (1954).

filamentosa is circadian in either LL or DD and entrainable by LD cycles (Carpenter, 1949). There are also species that show rhythmicity in LD but neither in LL nor DD (e.g., *Pyricularia*; see Barksdale and Asai, 1961), indicating that sporulation is not always controlled by a circadian clock. Among the fungal organisms in the Protocistic kingdom, reports for rhythmic spore discharge have only been published for the *Oomycota* (e.g., *Phytophthora*; see Hirst, 1953). Considering that fungi are in many cases plant or animal pathogens, the observations that their reproductive success depends on the light regime is of high practical importance (e.g., the oat pathogen *Erysiphe graminis* produces many fewer spore-forming structures in constant light, relative to DD or LD; see Carver et al., 1994).

SEASONALITY AND PHOTOPERIODISM IN FUNGI

There can be no doubt that the reproduction of fungi is just as seasonal as in other organisms, especially if they live far enough away from the equator. Like in other poikilotherms, fungal seasonality will be controlled both by photoperiod and by temperature. The interplay between these factors has been extensively studied in insects (Pittendrigh et al., 1991). Any collector or gourmet of mushrooms knows that the appearance of fungal fruiting bodies is restricted to certain times of the year. The concentration of spores (most frequently assessed by air filtration) also changes drastically over the course of a year (see examples in Fig. 3). These annual rhythms are thought to be correlated directly to environmental conditions such as available nutrients, humidity, wind speed, or temperature (Ingold, 1971). Some fungi can consolidate rhythmicity in reproduction with nondaily and nonannual periodicities (cf. Ingold, 1971). The discharge of glebal mass from a fruiting culture of *Sphaerobolus stellatus* in constant conditions oscillates in a 10- to 12-day rhythm when grown in LL at 20 °C. This infradian reproduction rhythm is, like so many other rhythmic processes, based on negative feedback (Ingold and Nawaz, 1967b). The interval between peaks correlates with the time span "from the first visible initiation of sporophores to maturity, and suggests that existing fruit-bodies inhibit the development of new ones" (Ingold, 1971, p 215).

As with many photoperiodic plants, some diurnal sporulators require light induction followed by a dark period to initiate their seasonal reproduction (Durand, 1982; Leach, 1967). As with short-day plants, their maturation process is exquisitely light sensitive and is inhibited when a short light pulse (in the range of seconds) interrupts the required dark period (Durand, 1982), with the timing of the light pulse and the length of the dark period crucial for the inhibitory effect.

While there is no question about seasonality in fungi, investigations into photoperiodic mechanisms and/or photoperiodic memory are very sparse. For reasons of economic incentive, many of the investigations into the influence of photoperiod on fungal development and reproduction concern host-infecting pathogens. When the entomopathogenic (insect-infecting) fungus *Metarhizium anisopliae* is grown in different temperatures (25, 28, and 30 °C) and photoperiods (24, 16, 12, and 8 h), its colony size

Figure 3. Annual distributions of (sexual) ascospores in the air. Examples shown for *Cladosporium* collected in Wales with maximum concentrations in June (top, redrawn from Harvey, 1967) and for *Hypoxylon rubiginosum* with a maximum in October (bottom, redrawn from Hodgkiss and Harvey, 1969).

and the number of spores produced are maximal at 28 °C and a day length of 16 h (Alves et al., 1984). Linear mycelial growth in *Colletotrichum manihotis* (a plant pathogen from the Congo) is greater in DD than in LL (Makambila, 1984). The inhibitory effect of light depends on photoperiod, as it is less in LD 12:12 compared with longer and shorter photoperiods. The amplitude of this photoperiodic response increases with light fluence and temperature and is absent at lower temperatures (20 °C). The formation of chlamydospores (thick-walled, asexual resting spores) of the corn pathogen *Exserohilum turcicum* is also affected by photoperiod and temperature (Levy, 1995). In addition to photoperiodic effects on growth and asexual spore formation, day or night length can also modify the development of sexual spores. The formation of perithecia in *Mycosphaerella pinodes*, for example, favors temperatures around 20 °C and a 16 h photoperiod when grown under controlled laboratory conditions (Roger and Tivoli, 1996).

This incomplete list of the effects of photoperiod on fungal propagation and reproduction mainly concerns species that are either difficult to study in the laboratory or that have not been characterized genetically and are not readily transformable. Proof for the involvement of the circadian system or the existence of a photoperiodic memory will involve a wide range of experiments, ranging from a good characterization of the organism's circadian system and its photobiology, as well as photoperiodic response curves, night-interruption, and Nanda-Hamner type experiments (systematic light cycles with long nights, up to cycle lengths of several days; Nanda and Hamner, 1958), with an organism that has good genetics and transformation possibilities.

NEUROSPORA—A POTENTIAL MODEL SYSTEM FOR PHOTOPERIODIC RESEARCH

A good candidate for such an approach is *Neurospora crassa*. It is amenable to biochemical, molecular, genetic, and physiological experiments, and it can easily be grown in large quantities. The sequence of its haploid genome is complete (<http://www-genome.wi.mit.edu/annotation/fungi/neurospora/>, <http://www.mips.biochem.mpg.de/proj/neurospora/>) and microarrays are in production. Many mutants have been characterized and are available. In addition, it constitutes one of the pioneer model systems, both for the circadian clock and photobiology.

Geoclimatic Environment

When the three chronobiologists had finished their mushrooms and ordered another Weißbier and some camembert and blue cheese for dessert, they returned to the question of fungal photoperiodism and the prospect that this phenomenon could be best investigated in *Neurospora*. Yet, doubts were raised whether this fungus, although an excellent model system in many ways, could be useful for photoperiodic studies. "It doesn't live far enough from the equator," was one of the arguments, and "Doesn't it just sit there as a dormant sexual spore, waiting for the next fire?" was another. A subsequent review of the literature weakened these skepticisms. Granted, not a whole lot is known about the life cycle of wild *Neurospora* throughout the course of the year, but there are indications that sexual and asexual reproduction, dormancy, and

growth are segregated over time (Pandit and Maheshwari, 1994). In addition, *Neurospora crassa* strains have been found over a large range of southern and northern latitudes (Fig. 4). *Neurospora intermedia* and other *Neurospora* species have been found as far north as the Canadian border and as far south as New Zealand (Turner et al., 2001). So, the genus *Neurospora* is found at latitudes corresponding to regions where winter nights and summer days are as long as 16 h and the winter days and summer nights as short as 8 h. *Neurospora*, therefore, amends itself to investigations of wild-type strains according to native latitudinal cline similar to the ones performed by Pittendrigh on *Drosophila* (Pittendrigh, 1993; Pittendrigh et al., 1991).

The large number of *N. crassa* samples collected in Louisiana and Florida tells us something about their preferred habitat, concerning both nutrition and climate. *Neurospora* is a pioneer organism after fires have destroyed most of the vegetation, living on the remaining carbon sources (e.g., quinic acid). The strain used by practically all laboratories that study *Neurospora* was first isolated by Shear and Dodge (1927) from sugar cane bagasse in Louisiana. Although in this region the humidity remains relatively constant over the year (however, with large daily changes), the photoperiod changes even in this southern location (30°N) by 4 h over the course of the year, with temperatures ranging from 8 to 34 °C (Grünwald, 1982). These changes would certainly make it advantageous for *Neurospora* to anticipate seasons with the help of photoperiodic and/or thermoperiodic mechanisms, especially as they correlate with large differences in rainfall. Latitudes around 30° actually produce the largest amplitudes in the annual human reproduction rhythm (Roenneberg and Aschoff, 1990).

Chrono- and Photobiology in *Neurospora*

Figure 5 shows the components of the *Neurospora* circadian transcription/translation feedback loop. The products of the two *white-collar* genes (*wc-1* and *wc-2*) form a protein complex (WCC) that interacts with the FRQ protein (Denault et al., 2001; Mellow et al., 2001). *frq* transcription depends on the WHITE-COLLAR proteins, and FRQ feeds back negatively on its own expression (Aronson et al., 1994b; Crosthwaite et al., 1997) and positively onto WC-1 levels (Lee et al., 2000; Mellow et al., 2001). An additional "box" in the *Neurospora* circadian system (Fig. 5, the FLO; McWatters et al., 1999) is indicated by physiological evidence showing entrainment of FRQ-less strains by

Figure 4. Latitudinal and geographical distribution of the wild-type strains of *Neurospora crassa* deposited in the Fungal Genetic Stock Center, Kansas (source: <http://www.fgsc.net>, as well as Metzenberg and Turner et al., 2001). The respective photoperiodic differences between longest and shortest day of the year are drawn as a line (upper horizontal axis).

temperature cycles in the circadian range (Merrow et al., 1999) and also by experiments indicating residual self-sustained oscillations in the absence of FRQ (Aronson et al., 1994a; Lakin-Thomas and Brody, 2000; Loros et al., 1986). These boxes—the transcription/translation feedback loop and the FLO—may correspond functionally to A and B oscillators in *Drosophila*, which were modeled to explain different phase-shifting patterns to distinct zeitgeber (Pittendrigh, 1960).

frq was uncovered in circadian mutant hunts, whereas screens for defects in light perception resulted in the isolation of “blind” mutants at two loci,

wc-1 and *wc-2* (Degli-Innocenti and Russo, 1984; Harding and Turner, 1981). They were only identified as integral for clock function some years later (Crosthwaite et al., 1997) and are good candidates for photoreceptor molecules in *Neurospora*. Interestingly, it has been noted that perithecial development, even in darkness, is poor in *wc* mutants (i.e., in the absence of light responsiveness; Degli-Innocenti and Russo, 1984). This suggests a role for light and/or the clock in the reproductive success of *N. crassa*, something that has been alluded to in the past (Lakin-Thomas et al., 1990).

Figure 5. The components of the *Neurospora* circadian transcription-translation feedback loop. See text for details. Rhythmic or constitutive expressions are indicated by a wiggle or a straight line, respectively, and light inducibility by the sun symbol (redrawn after Merrow and Roenneberg, 2001).

Effects of Photoperiod on *Neurospora crassa*

The work of Uebelmesser on *Pilobolus* included two types of experiments in LD cycles—those in which the length of the LD cycle was changed (with light and darkness each filling half of the cycle) and those in which only the photoperiod was altered in the context of a 24-h-cycle (compare Figs. 1 and 2B). It is quite striking that in the latter type of experiments (Fig. 2 B,C), the phase angle was driven, with a maximum in spore shooting appearing always 28 h after an onset of light, whereas the phase angle in the former type of experiments was locked neither to dawn nor dusk. We have observed similar differences in *Neurospora*. In symmetrical T-cycles (Fig. 2A), bands always begin to form approximately 7 h after onset of the dark period (one third of circadian period in DD), while experiments in 24-h cycles with differing photoperiods show that the phase distribution of conidiation is not strictly locked to dusk or dawn (Ying Tan, Martha Merrow, and Till Roenneberg, unpublished results; Chang and Nakashima, 1997).

Is there something special about the equinox (regardless of whether it is in the context of 24 h, as in nature, or in experimentally shorter and longer days) or are there other explanations for the different behaviors in the two sets of experiments? The answer probably lies in the interplay of many required factors that apparently control development: maturation time,

refractoriness to light, length and timing of the light and dark periods, and circadian control. In the case of *Pilobolus* (Uebelmesser, 1954), maturation of the asexual spores takes 23.8 h when controlled by the circadian clock, 25.5 h when triggered by a 1- or 2-h light period, 29 h after 16 or 18 h of light, and as long as 34 h when the lights are kept on (thus, the length of the triggering light episode is important). Because no further sporulation maxima appear in LL, an additional dark → light transition is obviously required, which again must be timed appropriately. When it comes less than 4 h into maturation, it appears to reset the ongoing maturation so that it can never proceed (hence, arrhythmicity in LD 2:2). When it is placed 4 h or more into maturation, it triggers a new maturation process that can proceed in parallel to the ongoing one (hence, rhythmicity in LD 4:4 and all longer T-cycles, see Fig. 2 B and C). On the other hand, when the dark → light transition is placed too far into maturation (approximately 7 h before the sporulation peak), it again begins to obstruct normal development, without simply triggering a new maturation process. The complicated interplay of the listed factors can be used to explain the differences between the phase angles of the two sets of experiments in *Pilobolus*.

Control mechanisms of conidiation in *Neurospora* are different from *Pilobolus*. For example, we have never seen the “developmental memory” shown in Figure 2C. Yet, similar factors must also play a role in

Neurospora development. For example, the WHITE-COLLAR-dependent, light-receptive system becomes refractory to additional light for several hours after an initial light signal (Arpaia et al., 1999; Lauter and Yanofsky, 1993; Schmidhauser et al., 1990), and complete resetting of the circadian clock requires light pulses longer than 2 h (Tan, Merrow, and Roenneberg, unpublished data; Chang and Nakashima, 1997; Dharmananda, 1980). In addition, light signals of different lengths appear to be transduced via different mechanisms. While short light pulses (and the resulting phase shifts) correlate well with the amount of *frq* RNA produced (Crosthwaite et al., 1995), longer light periods can synchronize conidiation without light-induced *frq*-transcription, as long as FRQ protein is present (expressed off an inducible light-independent promoter; see Merrow et al., 2001). Also, the *rib-1* (riboflavin) and *lis* (light insensitive) strains allow rhythmic conidiation in constant light, though phase shifting and carotenoid production are intact, albeit sometimes with modest deficits (Paietta and Sargent, 1981, 1983). The regulation of conidiation by light thus has at least two functional components, one that mediates phase shifting and one that contributes to the apparent arrhythmicity in constant light, and these are intertwined with components of the circadian system.

Most photoperiodic response mechanisms measure night rather than day length (Saunders, 1982). For this, some timer must measure the length of darkness (scotoperiod). A likely candidate for measuring scotoperiod in *Neurospora* is the *frq*/FRQ system. The *Neurospora* clock appears to be a pure night clock in the sense that light, down to moonlight levels (Merrow et al., 1999), drives conidiation rhythmicity, possibly by not allowing the decay of *frq* (Crosthwaite et al., 1995). The decay kinetics of FRQ in darkness depend on the *frq* allele (Liu et al., 2000). Thus, the sequence of the FRQ protein appears to determine its kinetics leading to (a) strain-specific periods in DD and (b) staggered phase angles in symmetrical LD cycles (Aronson et al., 1994a; Chang and Nakashima, 1997; Liu et al., 2000; Merrow et al., 1999). The prediction would be that possible photoperiodic mechanisms are also strain specific (i.e., requiring different photoperiods or the same proportional photoperiods in different cycle lengths for the same response in the different *frq* mutant strains) and will be absent in FRQ-less strains, similar to what has been shown in period mutants in plants (reviewed in Roenneberg and Merrow, 2000).

Effects of Thermoperiod on *Neurospora crassa*

Unlike in mammalian photoperiodism, temperature will play an important role in fungal photoperiodism. The *Neurospora* circadian system (Merrow et al., 1999), its responsiveness to light (Gooch et al., 1994; Nakashima and Feldman, 1980), and the levels of *frq* RNA and FRQ protein (Liu et al., 1998) are strongly affected by temperature (although the circadian period is temperature compensated in the intact system; Feldman and Hoyle, 1973). We have shown that *Neurospora* can be entrained in the circadian range to temperature cycles even without the expression of FRQ protein (Merrow et al., 1999), indicating that circadian qualities exist in *Neurospora* outside of the *frq*/FRQ feedback loop (Fig. 5: by the FLO or B oscillator). In addition, the circadian system is light-blind in FRQ-less strains (Chang and Nakashima, 1997; Lakin-Thomas and Brody, 2000; Merrow et al., 1999), while other light responses remain intact (Merrow et al., 2001). It will be interesting to see what role FRQ plays as a constitutively expressed versus a regulated protein in measuring night length and how it transduces this information to reproductive development. The use of temperature will be an important tool for these studies.

At the End of the Day . . .

The distinction between light reception (the first requirement for photoperiodism) and the circadian system (the second requirement) is becoming less clear in all molecular genetic model systems for circadian rhythms research. In plants, photoreceptor mutants have altered free-running periods and the strength of light-induction of RNA is modulated by the circadian system (Anderson et al., 1997; Somers et al., 1998). In *Neurospora*, the *white-collar* genes are integral to the circadian clock (Crosthwaite et al., 1997), and *frq*, previously considered only essential for the circadian system, is an absolute requirement for light-regulated conidiation (see Fig. 5; Chang and Nakashima, 1997; Lakin-Thomas and Brody, 2000; Merrow et al., 1999). As in plants, numerous light-induced responses in *Neurospora* are modulated by the circadian system (Heintzen et al., 2001; Merrow et al., 2001). Straightforward fluence titration experiments indicate that the light input pathway is branched: regulated conidiation requires less light than does carotenoid induction (Merrow et al., 2001). Based on

these collective data, it is not clear how separable light input pathways are from circadian transcription/translation loop. But *N. crassa* is clearly a powerful molecular genetic system with which to probe these questions.

Recently, scientists have begun to investigate the molecular mechanisms of photoperiodism in mammals (see review in Daan et al., 2001; Hastings, 2001). Earlier work has shown that "clock genes" may or may not be involved in insect photoperiodism: the *Drosophila per* gene has systematic sequence differences according to latitude, corresponding functionally to temperature compensation of the circadian system (Sawyer et al., 1997), yet photoperiodic response curves and Nanda-Hamner type experiments determined that photoperiodic responses remain intact in *per*⁰ flies (Saunders, 1990) (but see Tauber and Kyriacou, 2001 [this issue]). Many of these classical circadian experiments remain to be performed with *Neurospora*, and these will strengthen it as an experimental system for photoperiodism.

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