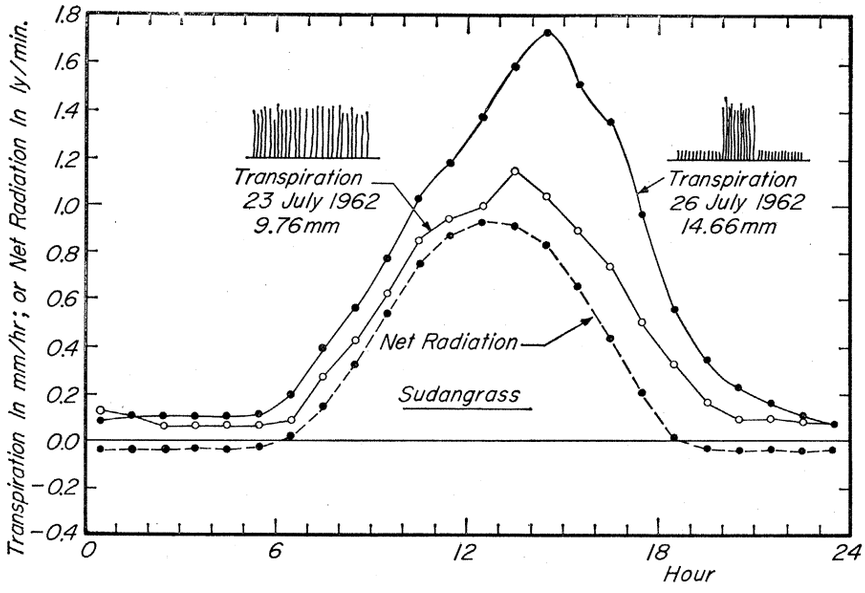

Fig. 1. Transpiration in millimeters per hour from a closed stand of sudangrass on 23 July 1962 at Tempe, Arizona, and from an isolated 1-m² plot of the same sudangrass 3 days later. Also, net radiation in langleys per minute, given as the average for the 2 days, the two values differing by only 5 percent.

that transpiration from a stand of sudangrass under conditions of high soil-moisture content, is fully regulated by external factors, that is, meteorological and morphological, and not by any physiological ones.

The observations were made during the summer of 1962 in the Salt River Valley of Arizona. Sudangrass, planted in May, had developed into a dense stand about 100 cm high by the middle of June. Measurements with miniature net radiometers (*1*) showed that under such conditions net radiation at the soil surface was negligible, implying that practically all water loss from the crop was transpiration. Flow of heat into or out of the soil was also negligible. Water loss was measured continuously with a weighing lysimeter installation (*2*), precise to the nearest 0.01 mm of water.

Table 1. Weather data at Tempe, Arizona, on 23 and 26 July 1962.

Data	23 July	26 July
Total solar radiation	683 ly	668 ly
Total net radiation*	377 ly	399 ly
Maximum temp.	42°C	41°C
Minimum temp.	28°C	28°C
Av. vapor pressure	16 mbar	16 mbar
Rel. humidity at noon	0.25	0.32
Av. windspeed	3.2 m/sec	3.6 m/sec

* Measured at site over sudangrass; all other values, U.S. Weather Bureau—Phoenix airport data (aerial distance to site, 5.0 km).

On 23 July, a clear day, an hourly record of transpiration was obtained, as shown in Fig. 1. Also shown is the energy gain of the surface as net radiation. Evaporation follows and is of the same order of magnitude as the net radiant energy input. However, energy was also derived as sensible heat from the air, particularly in the afternoon, implying that the leaves were cooler than the air. The potential input of sensible heat energy is not readily assessed, and it would be possible to argue that on 23 July physiological factors were involved in determining the transpiration rate.

In order to test such a supposition, the energy input into the crop growing on the lysimeter was greatly increased —both as radiative and, in particular, as sensible heat—by cutting the sudangrass around it. Figure 1 shows the data so obtained on 26 July under virtually identical weather conditions (see Table 1). Transpiration increased greatly as a result of cutting and, again, seemed to follow the energy input as it varied throughout the day. The rate of transpiration, whether on an hourly or daily basis, greatly exceeded values that are ever to be expected for a closed stand. In an unpublished report, W. O. Pruitt, of the University of California, gives as the highest observed value for evapotranspiration from perennial ryegrass at Davis, California, a value of 11.6 mm/day and 1.1 mm/hr.

The drastic response to increase in energy input is taken as proof that in a closed stand as on 23 July, physiological factors played no role in determining transpiration rates. Additional proof results from the observation that, when fully exposed to radiant heat and wind movement on 26 July, the sudangrass showed no visible signs of water stress such as leaf edge rolling or change in color during any time of the day. Furthermore, depression of transpiration at midday was conspicuously absent, even under extreme evaporative demand, as Fig. 1 demonstrates.

We conclude that a full stand of sudangrass under conditions of high temperatures, high light intensity, very low humidity of the air, and sufficient soil moisture—in short, in a highly evaporative environment—can transpire upon atmospheric demand. This should not be construed to mean that a sudangrass stand is physically identical to an open water surface nor that the conclusion would apply to another crop. Both the radiation balance and the convective sensible heat exchange of a crop differ materially from those of an open water surface.

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References

1. L. J. Fritschen, *J. Appl. Meteorol.* **2**, 165 (1963).
2. C. H. M. van Bavel and L. E. Myers, *Agr. Eng.* **43**, 580, 586 (1962).

29 April 1963

Pontine Reticular Formation: Relation to Lateral Geniculate Nucleus during Deep Sleep

Abstract. *Irregular groups of monophasic waves (seven waves per second) appear synchronously in the pontine reticular formation and in the lateral geniculate nucleus during the deep (low-voltage, fast) phase of sleep. The geniculate potentials can be triggered by low-rate stimulation of the pontine reticular formation, but the reverse effect has never been obtained.*

Several recent studies have described the appearance of discrete intervals in the course of normal feline sleep during which the cortical electroencephalogram develops a low-voltage, fast pattern, erratic eye movements ap-

pear, and posterior cervical muscle tone completely disappears (*1, 2*). These brief episodes of what may be termed deep sleep (*3*) appear between much longer periods of time during which the well-known synchronized pattern may be recorded from the cortex of the sleeping animal. Lesion experiments have suggested that certain regions of the brain stem are critical for the development of deep sleep (*2*), and therefore the objective of the present report has been to study brain-stem electrical activity during deep sleep. A movable electrode system, somewhat similar to one previously used with microelectrodes, but modified for use with concentric bipolar macroelectrodes (*4*), has permitted recording, always in complete darkness, from over 350 brain-stem points under these conditions in a series of 19 experiments performed on unrestrained cats.

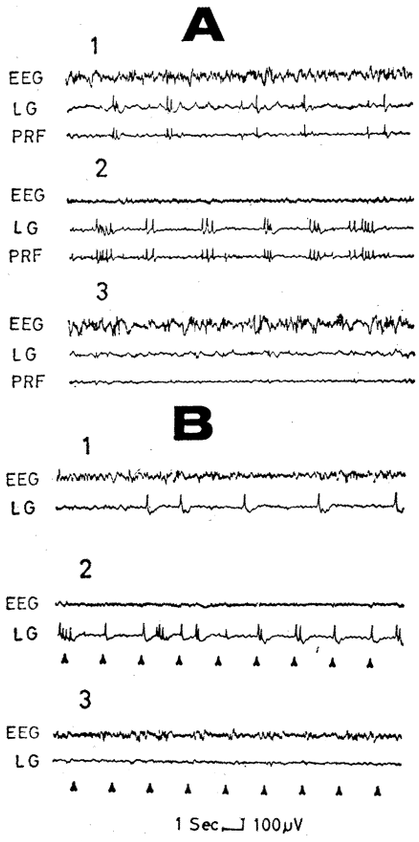

Fig. 1. *A* and *B* are from two separate "deep sleep episodes." In each case, records 1 were obtained just before the beginning of the cortical manifestations of deep sleep, records 2 from the mid-portion of deep sleep, and records 3 just after the end of deep sleep. In *B* the markers indicate the timing of the 3-msec, 3-volt square wave stimuli delivered to an electrode in that part of the pons from which monophasic waves had previously been recorded. Electroencephalographic recording is from the fronto-parietal cortex. *LG,* lateral geniculate nucleus; *PRF,* pontine reticular formation.

During deep sleep, a distinctive electrical pattern has been recorded from three "brain-stem structures"; the pontine reticular formation, the oculomotor nucleus, and the lateral geniculate nucleus (*2, 5*). This pattern consists of waves which have a rather uniform amplitude of 100 to 200 μv, a predominantly monophasic shape, and a tendency to appear at a frequency of seven per second in irregular groups separated by flat intervals. The appearance of this pattern invariably precedes the other manifestations of deep sleep by several seconds; during deep sleep there is a close temporal correlation between groups of waves and periods of eye movement.

Simultaneous recordings from the pons and the lateral geniculate nucleus reveal that the trains of waves appear synchronously in both structures (Fig. 1*A*). Oscilloscope tracings demonstrate that the interval between the onset of a given wave in the pons and the onset of the related wave in the lateral geniculate nucleus never exceeds 5 msec, but within this limit it has not been possible to determine if the individual waves in one of these structures consistently precede those in the other. The same results have been obtained in cats with acute ablations of both visual cortices. Waves were never observed in the optic chiasma in the same conditions of dark adaptation and deep sleep.

Stimulation studies have been carried out to explore this phenomenon further. If electrodes are so placed as to record monophasic waves from both the pontine reticular formation and the lateral geniculate nucleus, and the pontine electrode is then used for electrical stimulation, the following results may be obtained (Fig. 1*B*):

1) A 3-msec square wave stimulus delivered to the pons at low frequencies evokes a lateral geniculate response consisting of monophasic waves identical to the spontaneous ones.

2) This response can be obtained only during deep sleep, that is, when some waves are already present spontaneously in the lateral geniculate body. During the pontine stimulation they become time-locked to the electrical pulses. Even a fourfold increase in stimulus amplitude fails to evoke any detectable response in the lateral geniculate nucleus during arousal or synchronized sleep.

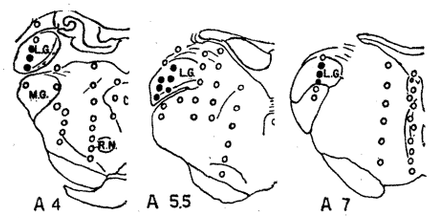

Fig. 2. Site of recording in the lateral geniculate nucleus. Filled circles, monophasic waves; open circles, nonspecific changes; *LG,* lateral geniculate nucleus; *MG,* medial geniculate nucleus; *RN,* red nucleus. Notation under each cross section refers to the level of the plane in conventional stereotaxic coordinates.

3) The latency of the triggered potentials is 25 to 35 msec.

4) If a series of stimuli are delivered to the pons during deep sleep, the majority of them will evoke "single wave responses" in the lateral geniculate nucleus. A few will evoke a train of waves, and a few will fail to evoke any detectable response. The amplitude of the triggered potentials is "all-or-none" in character. Figure 2 shows the site of recordings in the lateral geniculate nucleus.

Each stimulation trial, of the sort described above, was paired with one in which the lateral geniculate electrode was used for stimulation, and recordings were obtained from the pontine reticular formation electrode. During deep sleep, synchronized sleep, and arousal it proved impossible to trigger in this fashion the pontine waves, even when the intensity of the stimulus to the lateral geniculate nucleus was increased fourfold.

These experiments show (i) that a close relationship exists, during the deep phase of sleep, between pons and lateral geniculate body, and (ii) that only during this phase may the geniculate waves be triggered by pontine shocks.

Connections between reticular neurons and lateral geniculate body have been shown by Golgi studies (*6*), but we are unable to explain the long latencies of the triggered geniculate potential. Our experiments have shown physiological evidence for these ascending connections, but only for the state of deep sleep (*7*).

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References and Notes

1. W. Dement, *Electroencephalog. Clin. Neurophysiol.* **10**, 291 (1958).
2. M. Jouvet, *Arch. Ital. Biol.* **100**, 125 (1962).
3. D. H. Hubel, *ibid.* **98**, 171 (1960).
4. ———, *J. Physiol. London.* **147**, 226 (1959); E. V. Evarts, *Federation Proc.* **19**, 828 (1960); D. C. Brooks, in preparation.
5. D. C. Brooks and E. Bizzi, *Anat. Record*, in press; T. M. Mikiten, P. H. Niebyl, C. D. Hendley, *Federation Proc.* **20**, 327 (1961).
6. M. E. Scheibel and A. B. Scheibel, in *Reticular Formation of the Brain*, H. H. Jasper *et al.*, Eds. (Little, Brown, Boston, 1958), p. 766.

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Stomatal Penetration of Wheat Seedlings by Stem and Leaf Rust: Effect of Light and Carbon Dioxide

Abstract. *Removal of atmospheric carbon dioxide enhanced penetration of seedling wheat by stem rust* Puccinia graminis *in light and dark but did not materially affect penetration by leaf rust* P. recondita. *A concentration of 5 percent CO_2 nearly suppressed penetration by* P. graminis *but not by* P. recondita. *Thus light may promote penetration by* P. graminis *through photosynthetic reduction of CO_2 within the leaf and* P. recondita *may penetrate independently of light because it is relatively insensitive to the effects of CO_2.*

Stem rust, *Puccinia graminis* Pers. f. sp. *tritici,* seldom penetrates stomata of seedling leaves of wheat (*Triticum* spp.) in the dark, while leaf rust, *P. recondita* Rob. ex Desm. f. sp. *tritici,* penetrates well in either light or darkness. Hart (*1*) concluded that *P. graminis* penetrates largely through open stomata, attributing the near failure of infection after inoculation in the dark to exclusion of the fungus by closed stomata. Germination of urediospores and appressorial formation by *P. graminis* occur in the dark, but light is required for appreciable development of substomatal vesicles (*2, 3*). Since there is a stimulatory effect of light on substomatal vesicle formation on artificial substrates (*4*), Sharp *et al.* (*2*) concluded that light-induced penetration by *P. graminis* resulted in part from direct stimulation of the fungus. The leaf-rust fungus penetrates wheat stomata equally well in light or dark and stomata, if originally open, close before penetration (*5*).

This study was made to elucidate further the mechanism of action of light on penetration by *P. graminis* and the very different responses to light by the two species of wheat-rust fungi. Seedlings of Axminster and Michigan Amber wheats were inoculated with urediospores of *P. graminis,* races 48A and 15B, and with *P. recondita,* races 2 and 104C. After an incubation period of 10 hours for stemrust and 4 hours for leaf rust in a dark moist-chamber, the seedlings were transferred to 2-quart Mason jars fitted with transparent plastic lids, and treated with combinations of light and dark, at different concentrations of CO_2. Aluminum foil wrapped around the jars provided the necessary darkness. Carbon dioxide was added by circulating a moistened mixture of 5 parts CO_2 and 95 parts air. It was removed for the "CO_2-free" experiments by absorption in a solution of KOH or $Ba(OH)_2$ or by circulating moistened air from which CO_2 had been absorbed. After exposure to experimental conditions for 9 to 10 hours, abaxial epidermal strips were taken from the first leaf of five plants in each group and the strips were microscopically examined for penetration. Each leaf was treated as one replication in the statistical analysis. Penetration is expressed as the percentage of appressoria from which substomatal vesicles had been produced. Stomatal opening was determined by observing living leaves and epidermal strips fixed in absolute alcohol. Germination and apressorial formation were normal and little penetration of either rust had occurred before the experiments were begun.

In the dark, little penetration by *P. graminis* occurred in normal air, while in CO_2-free air the average penetration increased to about ½ of that occurring in normal air in light (Table 1). In the light, penetration was somewhat greater in CO_2-free air than in normal air. Each of these differences between CO_2-free and normal air was significant ($p \leq .05$) for each trial and for the grand mean of trials with race 15B. The differences were also significant with race 48A in each of four trials in darkness, and in three of four trials in light. Similar and significant differences were obtained with the Michigan Amber wheat seedlings.

The capacity of stem rust to penetrate in light or in CO_2-free air in darkness might be interpreted as resulting from stomatal opening that occurs under these conditions. However, stomata, which were closed when occupied by appressoria of *P. graminis* in darkness, failed to open when exposed to light. Maximum opening was to narrow slits, and occurred in only 2 percent of the occupied stomata. Nearly all adjacent, unoccupied stomata opened widely. Thus the fungus can penetrate closed stomata.

Penetration of *P. graminis* in the light in 5 percent CO_2 was limited and comparable with that in darkness in normal air (Table 1). Results were similar with the Michigan Amber wheat.

The results with *P. recondita* (Table 1) contrast markedly with those for *P. graminis* and confirm the results obtained by Caldwell and Stone (*5*) in showing that abundant penetration occurs in darkness and through closed stomata. The addition of CO_2 did not significantly reduce penetration as it did with *P. graminis.* The removal of CO_2 had no significant effect on penetration of race 104C. A proportionately small, but statistically significant reduction resulted with race 2.

The results on the penetration of the Axminster wheat were corroborated for

Table 1. Percentage of penetration of *Puccinia graminis* f. sp. *tritici* and *Puccinia recondita* f. sp. *tritici* on Axminster wheat seedlings under different light and CO_2 treatments. The percentage penetrations are the grand means of four replicated trials with race 48A, and two trials with race 15B of *P. graminis* and three trials each with races 2 and 104C of *P. recondita.* The numbers in parentheses indicate the average number of pustules per predetermined 6-cm linear segments of the primary leaf in ten trials, replicated three times for *P. graminis;* and in one trial, replicated three times for *P. recondita.*

Race	Light			Dark		
	Normal air	CO_2-free	5 percent CO_2	Normal air	CO_2-free	5 percent CO_2
			P. graminis f. sp. *tritici*			
48A	59.8	70.4	2.4*	2.0	24.6*	
15B	49.8 (38.5)	73.8*	2.8* (4.4)	4.9 (3.1)	28.4* (3.2)	
			P. recondita f. sp. *tritici*			
2	(59.1)		(52.9)	64.3 (55.2)	42.3* (49.0)	50.8
104C				61.3	55.7	59.2

* A significant deviation ($p \leq .05$) of the grand mean from the grand mean in normal air, under the same light condition, as calculated by arc sine transformation.