and thermalized (antenna temperature independent of J), while the latter, if hot and optically thin, has an antenna temperature $\propto J^2$. More detailed calculations including the effects of radiative transfer (*21*) show that this gas is in a hot region and has an excitation temperature > 180 K, considerably higher than previous lower limits. Since the values derived from the density of the gas indicate that the transitions up through $J = 6$ are essentially thermalized, the excitation temperature should be close to the gas kinetic temperature. The more detailed analysis (*21*) indicates that the fractional abundance of CO appears to be reduced by a factor of 5 in this region compared to that typical of interstellar clouds.

These initial observations demonstrate that high-resolution ground-based submillimeter astronomy can add significantly to our understanding of active regions in interstellar molecular clouds. The angular resolution achievable at submillimeter wavelengths with modest-sized telescopes is comparable to the highest obtained with any single radio antenna (~ 30 arc seconds). A next step would be to accurately map the spatial distribution and homogeneity of CO in the central regions of interstellar clouds. In addition, with modest improvements in sensitivity, a wide variety of molecular lines should be accessible for study by astronomers.

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Virus in a Parasitoid Wasp: Suppression of the Cellular Immune Response in the Parasitoid's Host

Abstract. *A virus that replicates in the ovary of a parasitoid wasp is injected into the parasitoid's host during oviposition. Successful development of the parasitoid egg within the host depends on the presence of the virus, which acts to suppress the host's immune response (encapsulation) toward the egg. This is an example of obligatory mutualism between a virus and a eukaryotic organism.*

An indigenous virus (*1, 2*) exists in the ovaries of all females of several species of parasitoid wasps belonging to the family Ichneumonidae (*1-6*). These viruses replicate in the nuclei of calyx cells, an epithelial tissue located between the ovarioles and oviducts of the parisitoid (*3, 7*). The virus buds from the calyx cells into the lumen of the oviduct. As part of a calyx fluid, it is injected together with an egg into the hemocoel of host caterpillars. Subsequently, viral nucleocapsids enter host cells (*1, 6, 8*), apparently by a membrane-fusion event, and are uncoated within the nucleoplasm.

Crude calyx fluid (*9*) from the parasitoid wasp, *Campoletis sonorensis* (Hymenoptera: Ichneumonidae), interferes with host cellular immune defense mechanisms by suppression of parasitoid egg encapsulation (*10*), and inhibits host growth (*11, 12*). However, prior to our

Table 1. Host caterpillars, *Heliothis virescens*, were dissected 5 days after treatment to recover eggs or larvae of the parasitoid wasp, *Campoletis sonorensis*.

Host treatment	Eggs + larvae recovered (No.)	Encapsulated eggs (%)	Larvae (%)
a) Parasitized (control)	20	0	100
b) Egg + saline	36	100	0
c) Egg + calyx fluid	30	20	80
d) Egg + calyx fluid supernatant	20	100	0
e) Egg + ultraviolet-irradiated calyx fluid	35	100	0
f) Egg + purified virus	30	27	73
g) Egg + ultraviolet-irradiated purified virus	21	100	0
h) Virus-fed host; egg + saline	20	100	0

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study, it was unknown whether the virus or some other component of the calyx fluid was responsible for this activity. We present evidence here that it is the virus, purified from the calyx fluid of the parasitoid wasp, *C. sonorensis*, that suppresses encapsulation of parasitoid eggs in the host.

Parasitoid wasps were reared on larvae of the tobacco budworm, *Heliothis virescens* (Lepidoptera: Noctuidae) (*12, 13*). For each experiment, the contents of the calyxes and lateral oviducts of 25 female parasitoids were extirpated and placed in 150 μl (*9*) of Pringle's saline (*14*), and a suction micropipette was used to collect 150 μl of calyx fluid solution free of parasitoid eggs and ovarial tissue fragments. In one series of tests the crude calyx fluid solution was centrifuged at 12,000*g* for 30 minutes at 4°C. Rinsed, viable eggs were injected together with 1.0 μl of the supernatant into hosts as described below. In other tests, the calyx fluid solution was layered onto a 20 to 50 percent (by weight) continuous sucrose gradient and centrifuged at 20,000*g* for 60 minutes at 4°C (SW-50 rotor). The virus band was removed by side puncture of the tube with a syringe. The sucrose was removed by dialysis for 24 hours against Pringle's saline (*14*) at 4°C. The virus was concentrated to 150 μl by placing the closed dialysis bag in Sephadex G-100–120 for approximately 45 minutes. Homogeneity of virus preparations was assessed by electron microscopy of negatively stained preparations.

The biological activity of the virus was assayed by injecting 1.0-μl portions (0.16 μg of protein) together with rinsed, viable eggs (*12, 15*) into host caterpillars. Virus, in 50-μl droplets, was exposed to ultraviolet irradiation for 20 minutes (*12, 16*) and assayed as above. To determine whether the virus was capable of affecting the host by oral ingestion, we fed caterpillars 10 μl of virus and injected them 24 hours later with a parasitoid egg in 1 μl of saline.

Hosts were dissected 5 days after treatment to determine whether the injected eggs were encapsulated or developing in a manner comparable to controls (parasitized). Table 1 shows that eggs injected into hosts together with saline were encapsulated. However, eggs injected together with calyx fluid were rarely encapsulated (Table 1, treatment c), but rather such eggs hatched and continued development. To ascertain whether the virus or other components of the calyx fluid were responsible for suppressing the host's ability to encapsulate the parasitoid's eggs, the virus was removed by centrifugation. The supernatant was ineffective in suppressing encapsulation (Table 1, treatment d). The virus, separated from other calyx fluid components by gradient centrifugation, effectively suppressed encapsulation (Table 1, treatment f). To confirm that the virus was responsible for the suppression of encapsulation, we exposed calyx fluid and the virus, separated by gradient centrifugation, to ultraviolet irradiation. In both cases the host retained the ability to encapsulate parasitoid eggs (Table 1, treatments e and g). Although ultraviolet irradiation may have inactivated other components of the calyx fluid responsible for the suppression of encapsulation, such an explanation is unlikely since the calyx fluid supernatant was inactive. The virus was effective only when injected into hosts in that eggs injected into virus-fed hosts were also encapsulated.

Table 2. Host caterpillars, *Heliothis virescens*, held at 27°C for 25 days after treatment. Adult parasitoids, *Campoletis sonorensis*, emerged from hosts 14 to 21 days after treatment.

Host treatment	Treated (No.)	*C. sonorensis* adults emerged (%)
a) Parasitized (control)	20	100
b) Egg + saline	28	0
c) Egg + calyx fluid	30	70
d) Egg + purified virus	36	44

Groups of hosts were held at 27°C for 25 days after treatment so that the number of adult parasitoid wasps that emerged could be determined (Table 2), this being the ultimate criterion for successful parasitism. The development of parasitoid eggs into larvae and subsequently into adults occurred only when virus was introduced into the host at oviposition or during experimental injection of virus into the hemocoel (Table 2, treatments a, c, and d). The absence of encapsulation (Table 1, treatments a, c, and f) and emergence of adults (Table 2, treatments a, c, and d) are directly comparable. The reduction in emergence of parasitoids when purified virus (rather than calyx fluid) was injected may be due, in part, to the increased manipulation of the eggs and reduced viability of virus that occurs during purification.

The results of our experiments indicate that, at least in the parasitoid-host relationship examined, only the viral component of calyx fluid is capable of inhibiting encapsulation of parasitoid eggs in host insects. Since hemocytic encapsulation represents a major natural barrier to successful parasitism (*10*), its abrogation by virus from the calyx fluid must be considered as beneficial to the parasitoid. Thus, since viral replication occurs only in parasitoid ovaries (*1*), the relation between parasitoid and virus can be described as mutualistic. The parasitoid-virus system described above appears to be the first example of obligate mutualism between a virus and a eukaryotic organism.

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16. The virus sample was exposed to ultraviolet irradiation at 69 erg mm^{-2} sec^{-1} at the sample surface (*12*).
17. Approved for publication as TA 15922 by the director, Texas Agriculture Experiment Station, in cooperation with the U.S. Department of Agriculture.

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