Life Table Statistics of the Rice Weevil, *Sitophilus oryzae*(L.) (Coleoptera: Curculionidae) on the Degree-Day Scale

溫日度를 시간단위로 한 쌀바구미 生命表 統計量

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ABSTRACT Life table statistics of the rice weevil, *Sitophilus oryzae* were estimated under constant and room temperature conditions on polished rice. On the degree-day time scale, the statistics under the constant temperatures were not significantly different from those under room temperatures. The variations of the statistics under different temperatures seemed largely due to the variations between the cohorts rather than due to the temperature effects. The weevil started oviposition from $368.0\pm41.2DD$ and ceased around $1391.0\pm33.7DD$. The intrinsic rate of increase, population doubling time and mean generation time were calculated to be 0.0052 ± 0.0006, $134.7\pm15.0DD$ and $715.2\pm53.6DD$, respectively.

KEY WORDS rice weevil, life table, degree-day

抄　　錄　쌀바구미 생명표 통계량을 정온 조건과 실온 조건에서 산출하였다. 溫日度를 단위로 하였을 때 20°~30°C 범위내 정온 조건에서의 통계량은 실온 조건에서의 통계량과 有意한 차이를 보이지 않았으며 온도간의 변이는 실온에서의 群間 변이와 유사하였다. 이 결과는 온일도를 시간단위로 할 때 쌀바구미의 생활사가 표준화 될 수 있음을 시사하는 것이었다. 쌀바구미는 368.0±41.2DD에서 산란을 시작하여 1391.0±38.7DD에서 멈추는 것으로 추정되었다. 內的 自然增加率, 密度 倍加 기간과 평균 세대 기간은 각각 0.0052±0.0006/DD, 134.7±15.0DD 그리고 715.2±53.6DD인 것으로 산출되었다.

檢 索 語　쌀바구미, 生命表, 溫日度

If an insect population model was based on calendar time, the effect of temperature has to be considered. But it would be much simpler and consistant if a model was studied on the base of insect's own physiological time scale (degree-days=*DD*) (Gilbert et al. 1976). By using physiological time scale, the simple effect of temperature is removed and any other effects are thereby exposed. Many authors, therefore, presented their population model or phenomenological models based on the physiological time scale.

Summers et al. (1984) constructed life table of *Acyrthosiphon kondoi* on the base of physiological time and reported that the

time unit was found to be much more realistic in describing population dynamics of the insect. Their consideration, however, did not based on the firm ground. Barlow et al.(1986) criticized that the value of intrinsic rate of natural increase was unlikely to yield fruitful biological insight.

Life table of the rice weevil, *Sitophilus oryzae*, has been constructed in relation to the temperature and moisture content of the grain or medium(Birch 1948, 1953, Evans 1982, Sharma et al. 1979, Ryoo and Cho 1986, Cho et al. 1988). Longstaff and Evans(1983) constructed the weevil's life table based on physiological time scale(duration of the immature stages) and reported that the shape of the fecundity curves was

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largely unaffected by environmental conditions, and the peak rate of productivity always occurred at a particular time. However, their consideration was based only on the life history studied under the constant temperatures.

The life history under fluctuating temperature condition could be different from those under constant temperature conditions (Gordon 1984) and, thus, the life table should also be examined under fluctuating temperature conditions. Present study was to compare the weevil's life tables under the constant and room temperature conditions, and to consider the possibility of standardization of the life table statistics based on physiological time scale, the degree day.

MATERIALS AND METHODS

Experimental procedure

Adults of the rice weevil were collected from the stock culture, which have been maintained for 5 years. They were bred for one genration on polished rice of the Chucheong variety under different temperature conditions: 20°, 25°, 28°, 30°C (all 4 with±0.5°C as a standard error) and room temperatures under 4 different seasons. One pair of adult weevil (0—1days after the emergence) was introduced into a vial (2cm diameter and 4cm high) containing 5 grams of the polished rice, and topped with gauze. Here, those pairs of the adults bred from the constant temperature were placed back to constant temperature of the same temperature (from 20°C back to 20°C, 25°C to 25°C, 28°C to 28°C, but 30°C to 30°C and 32°C), while those from room temperatures were placed under the room temperatures. Thereby, life history of the weevil was studied with 9 cohorts; 5 under constant temperatures and 4 under room temperatu-

res. Each cohorts was composed of 19—38 pairs of adult weevil. Room temperature was recorded throughout the experimental period by a hygrothermometer, and ranged from 10° to 34°C. Moisture content of the grain was maintained about 14% with saturated salt (NaCl) solutions followed by Wyniger(1974). Longevity and fecundity of the weevil were assessed based on the weekly observations. Every week, the living pairs were transferred to new vials containing 5 grams of the polished rice for further observations under the same conditions. To avoid possible effect of the males on the behaviour of the females, the males were replaced by other individuals of the same age whenever the male only was found to be dead. Number of eggs laid per female per week and the mortality of immature stages were estimated through the number of adults emerging and of remainder in grains by dissection.

Estimation of physiological time unit (degree-day)

The weevil is reported to develop within the range of 15°—34°C with the optimum about 30°C (Birch 1945, Ryoo & Cho 1988). The degree-day estimation was, therefore, based on 15°C with the assumption of the linear relationship between the weevil's developmental rate and temperature. A method of the estimation was presented by Hochberg et al.(1986) as follows:

$DD_i=0,$ if $H_i \leqslant T_h,$

$DD_i=\overline{X}_i-T_h,$ if $L_i>T_h,$

$DD_i=(\overline{X}_i+((T_h-L_i)/2))F_i,$ if $L_i<T_h<H_i,$

where H_i is daily maximum temperature, L_i daily minimum temperature, T_h low thres hold temperature, $\overline{X}_i$ mean daily temperature caculated as $(H_i+L_i)/2$ and F_i is the fraction of the time for which temperatures
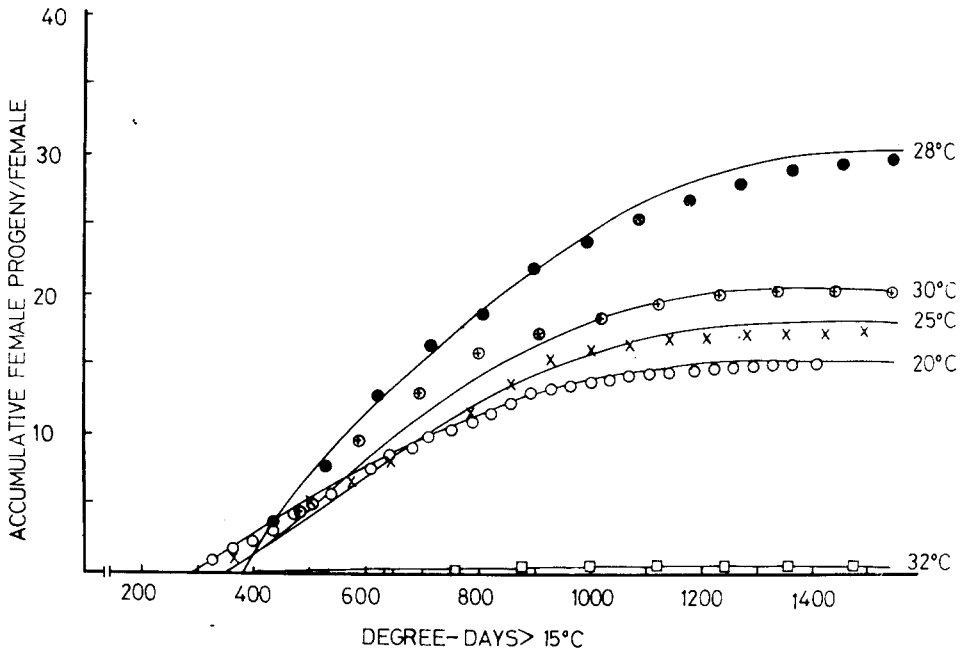
Fig. 1. Cumulative female progeny $(\sum l_x m_x)$/female under the constant temperatures.
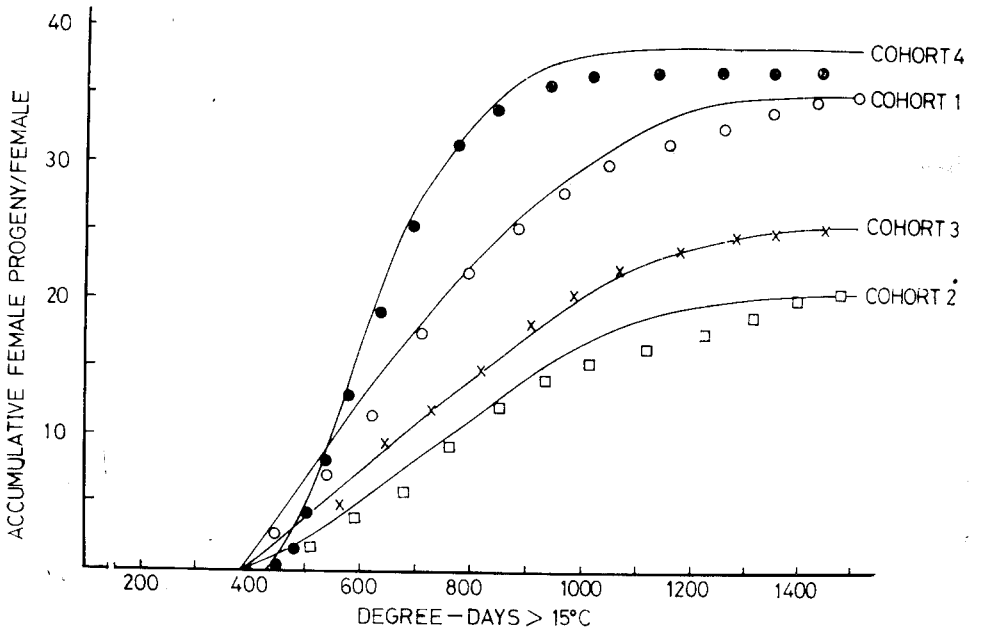

Fig. 2. Cumulative female progeny $(\sum l_x m_x)$/female under room temperatures.

Table 1. Parameters of curves of the cumulative number of female progeny per female rice weevil under the influence of the temperature fitted to the equation of Stinner et al.[a]

Temp(°C)	N	DD_{start}	DD_{end}	θ	k	R^2
20	35	289	1324	0.85	1.11	0.996
25	35	350	1402	0.96	1.23	0.993
28	33	383	1400	0.82	0.84	0.996
30	25	345	1422	0.91	1.22	0.984
Mean		341.8	1387			
±S.D.		±39.0	±43.2			
32	30	404	1420	1.30	2.11	0.999
Room 1	24	386	1384	0.84	0.99	0.998
Room 2	20	380	1430	1.18	1.23	0.996
Room 3	19	380	1400	0.62	0.62	0.996
Room 4	38	431	1366	0.91	3.45	0.999
Mean		34.93	1395.0			
±S.D.		±24.7	±27.2			

[a] For the equation, see text.

N=Number of females examined; DD_{start}=Starting point of oviposition; DD_{end}=End point of oviposition; θ and k=constants.

Table 2. Life table statistics for the rice weevil under the constant and room temperatures[a]

Temp(°C)	r_m	λ	T	t	R_0
20	0.0053	1.0053	632.2	133.3	15.41
25	0.0048	1.0048	712.1	144.4	18.45
28	0.0057	1.0057	744.0	131.6	30.68
30	0.0047	1.0047	720.1	147.4	20.71
Mean	0.0051	1.0051	705.5	136.7	21.31
±S.D.	±0.0004	±0.0004	±48.0	±11.7	±6.61
32	−0.0006	0.9994	746.41	—	0.63
Room 1	0.0058	1.0058	729.7	119.5	35.31
Room 2	0.0050	1.0050	755.94	138.6	25.60
Room 3	0.0044	1.0044	786.15	157.5	20.71
Room 4	0.0060	1.0060	641.59	115.5	37.42
Mean	0.0053	1.0053	721.5	132.8	29.75
±S.D.	±0.0007	±0.0007	±54.8	±19.3	±7.94

[a] The temperature range during the experiment varied from 10° to 34°C.

r_m=intrinsic rate of increase; λ=finite rate of increase; T=mean generation time; t=population doubling time; and R_0=net reproduction rate.

are estimated to be above T_h expressed as $(H_i-T_h)/(H_i-L_i)$.

Estimation of the life table statistics

The cumulative curves of the number of female progency($\sum l_x m_x$) were fitted to the equation presented by Stinner et al.(1974):

$$P(Y)=(1-Z)^{\theta \cdot Z^k}$$

where $P(Y)$ is the proportion of net reproduction rate(R) at the time, $Z=(DD_{end}-DD_{current})/(DD_{end}-DD_{start})$, θ and k are empirical constants. By an iteration procedure using personal computer, the intrinsic rate of increase (r), the finite rate of increase (λ), the net reproduction rate (R_0) and the mean generation time (T) were estimated from the cumulative curves.

RESULTS

The cumulative number of female progeny

Fig. 1 and 2 illustrate the curves at constant and room temperature conditions. The equation of Stinner et al.(1974) provided a good description of the curves and the coeficients of determination were higher than 0.99 in all cases. The parameters of the equation were shown in Table 1. Starting point of the oviposition under constant temperatures was appeared to be dependedent on the temperature, so that the point was estimated to start earlier under lower temperature than higher temperature. It is still not clear whether the feature suggests that the weevil under lower temperaturs matures faster. Results under the room temperature shows that the start points of oviposition were similar from all 4 room temperature conditions, which could be an evidence that the physiological maturation of the weevil was more or less consistent in terms of degree-day(DD). The difference in the start and end point of oviposition between constant and room temperatures were not statistically different, and the average of the start and end points were esitmated as 381.8 ± 49.9, and $1391.0\pm33.7DD$, respectively. Hardman(1978) reported that the rice weevil require the average of $422.7DD$ to pass from egg to the maturity, which is somewhat higher than the value of the present study. However, his estimation was made with DD above 12.6°C instead of 15°C in this paper.

Life table statistics

The life table statistics of the rice weevil were estimated using Lotka's equations (Pielou, 1967) and shown in Table 2. At 32°C under which the weevil's development was retarded (Ryoo & Cho 1988), its life table was abnormal and the value of the intrinsic rate of increase (r) was estimated to be negative. The feature indicates that the temperature above 32°C is deleterious to the weevil population. The generation time of the weevil under the constant temperatures was estimated to be ranged from 632.2 to $744.0DD$, and those under the room temperatures was from 641.6 to $786.2DD$. The C.V. value of the generation time estimated from the cohorts under constant temperatures was similar to that under room temperatures with 6.9% and 8.5% under constant and room temperatures, respectively. This indicates that the variations under constant temperatures occurred largely due to the variations between cohorts than due to the physiologically different response of the weevil to the temperature. There was no significant difference in the generation time between the cohorts under constant and room temperatures and the pooled mean was 715.2 ± 53.6 DD. Intrinsic rate of natural increase (r) of the weevil under constant temperatures except 32°C, and under room temperatures ranged from 0.0047 to 0.0057 and from 0.0044 to 0.0060, respectively. C.V. under constant and room temperatures were 8.9% and 13.2%, respectively. No significant difference was found between r values from constant and room temperatures, and, so, the pooled r value was 0.0052 ± 0.0006/female/DD. Population doubling time ($\ln(r/2)$) was then 134.7 ± 15.0 DD.

The net reproduction rate (R_0) under 20°C was 15.4/female and apparently lower than that under 28°C. Summers et al.(1984) reported similar phenomenon from *Acyrthosiphon kondoi*: the net reproduction rate of aphid became significantly lower at the

condition of 7.2°C than those at the tempe-
rature range from 10.0°C to 21.1°C. The
mean value of the net reproduction rate
under room temperatures was somewhat
higher than that under constant temperat-
ures. The difference, however, was not
significant.

DISCUSSION

The life table statistics estimated by Lo-
tka's equations are an abstraction from the
nature, since it measures the rate of incre-
ase of a population with stable age distribu-
tion growing in an environment of unlim-
ited resources (Andrewartha & Birch 1984),
which occurred rarely in nature. However,
the statistics could be used as indices of
the inherent capacity of the population
increase. The present study showed that
the life table statistics of the rice weevil
could be reasonably unified on the basis of
degree-day scale at least in the range of 20°
to 30°C. The statistics estimated under con-
stant temperatures were not significantly
different from those under changing temp-
eratures, so as the C.V values from both
conditions. The results indicated that the
response of the weevil to the temperature
could be integrated to the concept of degree-
day. Although the net reproduction rate
seemed to be influenced by temperature,
especially under low temperature range, the
effect would not excert influencing on the
life table statistics such as intrinsic rate of
natural increase, population doubling time
or mean generation time. The low net rep-
roduction rate seemed to be compensated for
by earlier start of the weevil's oviposition
on the degree-day time scale. The problem
of adopting degree-day as a time unit for
the life table of the insect is that the unit

is inappropriate in the temperature range
of the boundary layers, especially over the
optimum conditions where the insect's de-
velopment is retarded or stopped. This phe-
nomenon was also shown in the present
study where the intrinsic rate of increase
at 32°C was estimated to be—0.0006. But the
situation rarely happens in nature: the tem-
perature requirement of different species
and populations are adjusted to suit the
local temperature regimes (Gilbert et al. 19
76) and if it occurs in nature, the population
respond to it by specific physiological and
morphological adaptations such as diapause.
Therefore, the constraint in adopting degree-
day could not obscure the perception of re-
ality of the populations concerned.

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