



The Net Reproductive Rate (R_0) and Stable Age Distribution of the Leaf Roller (*Hedylepta indicata* F.) on Soybean (*Glycine max* L.)

Manas Titayavan¹ and Panisara Thepkusol^{2*}

¹Division of Agriculture, School of Agriculture and Natural Resources, University of Phayao, Phayao, 56000, Thailand

²Department of Agricultural Science, Faculty of Agriculture, Natural Resources and Environment, Naresuan University, Phitsanulok, 65000, Thailand

* Corresponding author. E-mail address: panisarat@nu.ac.th

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Abstract

The present study aimed to determine the net reproductive rate (R_0) and stable age distribution of the soybean leaf roller (*Hedylepta indicata* F.) on soybean (*Glycine max* L.). All experiments were conducted at the entomology laboratory of the School of Agriculture and Natural Resources, University of Phayao. At 24-h intervals, twelve pair of adult moths less than 24 hours, were transferred to a new set of host plants until all insects died. Consequently, the old host plants served as a source of the freshly laid eggs. The number of live daughters produced per day per female (m_x) in her life time (l_x) was determined and a net reproductive rate (R_0) calculated. The results show a value of R_0 6.808, indicating that a population of *H. indicata* had the capacity of multiply 6.808 times in each generation under the given conditions. The stable age distribution was constructed with 1-day-old eggs of *H. indicata*. A Petri dishes containing 20 eggs each on soybean leaves were incubated in a rearing room held at 25 ± 2 °C and 70 ± 2 % RH with 12 hours photo-phase. Ten replicates were run for a total of 200 eggs tested. After hatching, the early instar larvae were transferred singly into a 6x6x3.5 cm plastic cage. A tender leaf was placed into the cage to provide food for larva. At 24-h intervals, larva in each cage was transferred to a new leaf and the duration of each stage of development was observed until adult emergence. Newly emerged adult moths were examined daily until all of them had died. The investigation reveals that when the population reached the stable age distribution, 89.1% consisted of immature stages, and 10.9% of the total number of individuals were adults. The innate capacity for increase (r) attained in the given environment and the finite rate of increase (λ) was 0.0744 and 1.0772 respectively. When the birth rate (b) 0.6634 exceeded the death rate (d) 0.5890 then the population of *H. indicata* increased over each succeeding time period.

Keywords: net reproductive rate, stable age distribution, soybean leaf roller, *Hedylepta indicata*, innate capacity for increase

Introduction

Thirty nine species of insect pests were found to infest soybean crop at their different growth stage in northern region of Thailand (FCRC, 2018). Among the recorded pest species, 6 species namely hairy caterpillar, *Spilarctia oblique* (Walker); common cutworm, *Spodoptera litura* F.; pod borer, *Helicoverpa armigera* (Hubner); stem fly, *Ophiomyia phaseoli* (Tryon); whitefly, *Bemisia tabaci* Genn. and leaf roller, *Hedylepta indicata* F. were considered as major pests while the remainder were of minor importance on the basis of population densities per plant, nature and extent of damage and yield reduction (Biswas & Das, 2011; Biswas, Hossain, & Majumder, 2001; Pimchan, 2004; Sachan & Gangwar, 1980). Most of the major and minor pests appeared in the crop during the vegetative to flowering stages (Biswas, 2013). The soybean leaf roller or bean leaf weber, *H. indicata* has been reported as a potential key pest of soybean in northern Thailand (FCRC, 2018) and other parts of the world (Bapatla, Patil, & Yeddula, 2018; Fehr, 1989). This defoliating species habitually feeds as a larva in the upper one-half to one-third of the soybean leaf canopy (Biswas & Islam, 2012). Adult moth oviposit on the lower surface of leaves where a female lays an average of 330 eggs. The eggs hatch in 4 days; the green



larvae feed on the parenchyma of leaves which they weave together and hold in place by silken threads (Zeng et al., 2018). Therefore, they are protected from exposure to insecticides. Serious damage results where the leaves are held against the blossom buds with silk that prevent setting of pods (Raju, Khandwe, & Sharma, 2013). Meena and Sharma (2006) reported 9 species serving as host plants of *Hedylepta* spp. as follows: soybean, *Glycine max* L.; mung bean, *Phaseolus aureus* Roxb; cowpea, *Vigna unguiculata* (L.) Walp; *V. radiata* (L.) Wilczek; *V. mungo* (L.) Hepper; pigeon pea, *Cajanus cajan* (L.) Millsp; mulberry, *Morus alba* L. and chrysanthemum plants. The innate capacity for increase (r) defined by Krebs (1972) as the intrinsic growth rate of a population under environmental conditions without the restraining effects of competition. r is measured by a combination of 4 classical parameters; the fertility, the longevity, the birth rate and the death rate (Caswell, 1982). Andrewartha and Birch (1970) derived a function which they called the net reproductive rate (R_0) as the multiplication rate per generation obtained by multiplying together the age-specific survival rate (l_x) and age-specific birth rate (m_x) and summing over all age groups, $R_0 = \sum l_x m_x$. Lotka (1922) has shown that a population which subject to a constant schedule of age rates will gradually approach a fixed or stable age distribution. Understanding the pest's biology combined with the stable age distribution and net reproduction rate studies should yield the necessary information on which to base the further action.

Methods and Materials

Stock culture of soybean leaf roller

The major source of *H. indicata* came from field collections. These were made at frequent intervals from early the growing season throughout the late season in soybean growing areas of Chiang Mai. The parasite free larvae were reared on the soybean variety Chiang Mai 60 leaves in a rearing room maintained at $25 \pm 2^\circ \text{C}$ and $70 \pm 2\%$ RH, with a light-dark photoperiod of 12:12.

An 11x11 cm with 6.5 cm high plastic cages were used to confine the larvae. Ten larvae of mixed instar were transferred with a soft camel's hair brush onto a piece of disposable paper which were placed in the box, water was then added to moisten the paper. Five tender leaves were placed daily in the box on moist paper. The box containing larvae were kept in the rearing room under the conditions as mentioned above. There were 20 cages at started for a total of 200 larvae. The larvae were reared until they had entered pupal stage. Pupae in each cage were isolated into a 6x6 cm with 3.5 cm high plastic box until adult emergences.

The net reproductive rate (R_0) of *H. indicata*

Twelve pair of adults *H. indicata* were used for the net reproductive rate tests. They were less than 24 hours old. A cylindrical wire cage, 20 cm diameter and 28 cm high streaked with undiluted honey to provide food for adult insects was used to confine the insects. The cage was positioned on a 30 day-old soybean plant above the plant canopy level. The cage was fastened tightly to the soil surface to keep insects from escaping. A hole for the introduction of adult moths was cut in the center of the cage. Moths were introduced into the cage and left for 24 hours. These insects had not been exposed to a host plant for oviposition prior to the experiments. After the insects were introduced, the hole in the cage was plugged with cotton. Moths were allowed to deposit their eggs on host plants for 24 hours. At 24 hour intervals, all insects were transferred to a new set of host plants until all insects had died. Consequently, the old host plants served as a source of the freshly laid eggs. The soybean plants containing eggs of leaf roller were examined daily by using a hand lens. The influence of insect



age on egg production was determined by providing adult females with a new set of host plants each day for the life of adult females *H. indicata*. Data on the number of eggs produced daily per female in her lifetime was obtained. The mean number of live daughters produced per day per a single female (m_x) as by the probability of her living to be that old (l_x) during a single generation (R_0) was determined by adding all the numbers $l_x m_x$, $R_0 = \sum l_x m_x$ (Andrewartha & Birch, 1970).

A cohort life table was constructed with the heading proposed by Begon and Mortimer (1981) and Varley, Gradwell, and Hassell (1973). The initial l_x was based on the total number of 132 eggs. The daily development of each instar was observed by using a hand lens until all larvae had matured or died. The number of individuals either alive or dead during each age interval was recorded. The subsequent mortality of each stage was calculated as k -value, expressed logarithmically and obtained by subtracting the logarithm of the population after mortality occurred from the logarithm of the preceding population. The summation of k -values yielded the generation mortality (K).

The stable age distribution of *H. indicata*

The stable age distribution life table was constructed with the headings proposed by Andrewartha and Birch (1970) and Poole (1974). One-day-old eggs were used for this experiment. Twenty eggs on the soybean leaves were transferred onto a piece of 10 cm filter paper which was placed in a 10x1.5 cm Petri dish. Water was added to moisten the paper. The Petri dishes containing eggs of *H. indicata* were incubated in a rearing room held at $25 \pm 2^\circ \text{C}$ and $70 \pm 2\% \text{RH}$ with 12 hours photo-phase and left undisturbed until first instar larvae began to emerge. Ten replicates were run for a total of 200 eggs tested. After hatching, the early instar larvae were transferred singly into a 6x6x3.5 cm plastic cage. A piece of disposable paper was placed in the cage, water was added to moisten the paper. A tender leaf was placed into the cage to provide food for larva. At 24 hour intervals larvae in each cage were transferred to a new leaf with a moist camel's hair brush. The duration of each stage of development was determined by careful daily observations until adult emergence. Newly emerged adult moths were examined daily until all of them had died. In this experiment it was assumed that the time interval (t) equals the generation time (T) and R_0 equal the finite (geometric) rate of increase (λ). The mean generation time or the mean period elapsing between the birth of parents and the birth of offspring was estimated by dividing the log to the base e of R_0 by the intrinsic rate of increase (r), $T = \log_e R_0 / r$, where $T = \sum l_x m_x \cdot x / \sum l_x m_x$ (Krebs, 1972). Given T , the estimation of r is $r = \log_e R_0 / T$. For computing the finite birth rate (β) during one interval of time the equation $1/\beta = \sum L_x \cdot e^{-r(x+1)}$ was used (Andrewartha & Birch, 1970). The L_x , is proportion of individuals alive between age x to $x+1$, $L_x = \int_x^{x+1} d_x l_x$. Proportion of individuals in the age group x to $x+1$ in the stable age distribution (p_x) was given by $p_x = \beta \cdot L_x \cdot e^{-r(x+1)}$ (Birch, 1948).

Results and Discussion

The net reproductive rate (R_0) of *H. indicata*

Sequential examination of the development of individuals revealed that the mortality of *H. indicata* occurred sequentially in the successive developmental stages. Stages at which death occurred were recorded. The k -value for eggs of this species was 0.024, and 0.553, 0.147, 0.054 and 0.112 for larval mortality of first to fifth instar respectively. The mortality rate was fairly low in the egg stage when compared to the larval mortality but



no mortality occurred in third instar larvae and pupal stages. Males became distinguishable from females during the late pupal stage. The summation of k -value (K) yielded the generation mortality 0.890 (Table 1).

Beginning soon after emergence, twelve pair of adults were used to begin this experiment. Moths were introduced into the cage and left for 24 hours. At 24 hour intervals, all insects were transferred to a new set of host plants until all moths had died. The number of eggs laid daily in a life time is summarized in Table 2.

Table 1 A cohort life-table for *Hedylepta indicata* F. reared under laboratory conditions at $25 \pm 2^\circ$ C and $70 \pm 2\%$ RH with a 12 hours photo-phase

| Stage at beginning of interval (x) | Standardized number surviving at the start of age interval x (I_x) ¹ | Standardized number dying between x and x+1 (d_x) | Mortality rate (q_x) | Killing power (k_x) |
|------------------------------------|---|---|--------------------------|-------------------------|
| Egg | 1,000 | 53 | 0.053 | 0.024 |
| Larva | | | | |
| First instar | 947 | 682 | 0.720 | 0.553 |
| Second instar | 265 | 76 | 0.297 | 0.147 |
| Third instar | 189 | 0 | - | - |
| Fourth instar | 189 | 22 | 0.116 | 0.054 |
| Fifth instar | 167 | 38 | 0.228 | 0.112 |
| Pupa | 129 | 0 | - | - |
| Adult | 129 | - | - | - |
| | | | | $K=0.890$ |

¹ 132 eggs at start and 17 adults at completion

Table 2 The net reproductive rate (R_0) of *Hedylepta indicata* F. reared under laboratory conditions at $25 \pm 2^\circ$ C and $70 \pm 2\%$ RH with a 12 hour photo-phase

| Age at beginning of interval (x) | Age specific survivorship (l_x) | Expected daughters (m_x) | Reproductive expectation ($l_x m_x$) | Reproductive expectation at age of interval x ($l_x m_x \cdot x$) |
|----------------------------------|-------------------------------------|------------------------------|--|---|
| 1 | 0.129 | 0 | 0 | 0 |
| 2 | 0.126 | 2.112 | 0.266 | 0.532 |
| 3 | 0.118 | 6.426 | 0.758 | 2.275 |
| 4 | 0.098 | 10.815 | 1.060 | 4.240 |
| 5 | 0.098 | 7.105 | 0.696 | 3.481 |
| 6 | 0.098 | 8.386 | 0.822 | 4.932 |
| 7 | 0.088 | 10.479 | 0.922 | 6.454 |
| 8 | 0.082 | 9.331 | 0.765 | 6.120 |
| 9 | 0.082 | 9.016 | 0.739 | 6.651 |
| 10 | 0.077 | 5.334 | 0.411 | 4.110 |
| 11 | 0.067 | 3.836 | 0.257 | 2.827 |
| 12 | 0.051 | 1.778 | 0.091 | 1.092 |
| 13 | 0.036 | 0.525 | 0.019 | 0.247 |
| 14 | 0.007 | 0.294 | 0.002 | 0.028 |
| 15 | 0 | - | - | - |
| Gross reproductive rate | | 75.437 | $R_0=6.808$ | $\sum l_x m_x \cdot x=42.990$ |



Small numbers of eggs were laid during the second day of experiment. The number of eggs increased markedly from 2.112 eggs on the second day to 10.815 eggs on the fourth day but declined thereafter from 10.479 eggs on the seventh day to 0.294 eggs on the fourteenth day. The data indicate that the total number of daughters produced per female during a life time was 75.437. Peak production was on the fourth day. The data also indicated that total number of eggs (150.874) per a single female laid was significantly different from that of reported by Lewatanakarn, Sutayavirut, and Sepswadi (1974). They found that *H. indicata* laid up to 299.40 eggs per female. Thus the conditions used for this experiment might be considered unsuitable for the laboratory propagation of *H. indicata*. The m_x value for *H. indicata* in Table 2 gives the mean number of live daughters born per day per female of ages shown in the x column. The $L_x m_x$ products for each age group were summed, the total being the value of $R_0=6.808$. It is the multiplication per generation or net reproductive rate under the given conditions. In other words, a population of *H. indicata* has the capacity of multiplying 6.808 times in each generation.

The stable age distribution of *H. indicata*

In this experiment, less than 50% of *H. indicata* became adult insects. Knowing the multiplication rate per generation (R_0) and the mean generation time (T), the intrinsic rate of increase (r) was found to be 0.0744. Thus the finite rate of increase (λ) was 1.0772 per individual per day. Table 3 shows the calculation of the stable age distribution of *H. indicata* which was heavily loaded with the immature stages (89.093%).

Table 3 The stable age distribution of soybean leaf roller, *Hedylepta indicata* F. reared under laboratory conditions at $25 \pm 2^\circ \text{C}$ and $70 \pm 2\%$ RH with a 12 hours photo-phase

| Age at beginning of interval in days | Percent distribution | | | |
|--------------------------------------|----------------------|-------------------|--|------------|
| (x) | L_x | $L_x e^{-r(x+1)}$ | $100 \beta \cdot L_x e^{-r(x+1)}$ | |
| 0.5 | | | } 89.093 percent total immature stage | |
| 1.5 | | | | |
| 2.5 | 0.9470..... | | | |
| --- | | | | |
| --- | | | | |
| --- | | | } 10.907 percent total adults | |
| 37.5 | 0.4450 | 0.02537271 | | 1.74745797 |
| 38.5 | 0.4260 | 0.02254784 | | 1.55290478 |
| 39.5 | 0.3770 | 0.01852359 | | 1.27574843 |
| 40.5 | 0.3420 | 0.01559906 | | 1.07433150 |
| 41.5 | 0.3420 | 0.01448061 | | 0.99730211 |
| 42.5 | 0.3245 | 0.01275452 | | 0.87842361 |
| 43.5 | 0.2965 | 0.01081839 | | 0.74507933 |
| 44.5 | 0.2860 | 0.00968707 | | 0.66716356 |
| 45.5 | 0.2755 | 0.00872525 | | 0.60092153 |
| 46.5 | 0.2515 | 0.00734076 | | 0.50556955 |
| 47.5 | 0.2060 | 0.00558160 | | 0.38441347 |
| 48.5 | 0.1520 | 0.00411846 | | 0.28364474 |
| 49.5 | 0.0750 | 0.00175118 | | 0.12060649 |
| 50.5 | 0.0490 | 0.00106207 | | 0.07314641 |
| $1/\beta=1.45197827$ | | | 100.000 | |



Only 10.907% of the total number of individuals in the stable age distribution were adults. From the experiment $1/\beta = 1.452$, and thus instantaneous birth rate (b), $b = r\beta / (e^r - 1) = 0.6634$. Since the rate of population growth = r , and $r = b - d$ (Krebs, 1972), the difference between r and b was determined as the instantaneous death rate (d), $d = 0.5890$. Consequently, the population of *H. indicata* has potentially increased under the given conditions. The observations of the present study were similar to the findings of several authors. They observed that the age composition of the population was fixed and unchanging during a period of constant population size (Caswell, 1982; Chi & Liu, 1985). Under other circumstances, the age distribution population shifted over time which was assumed to satisfy the usual conditions in nature (Lotka, 1913, 1922; Taylor, 1979).

Conclusion

The present study shows that the soybean leaf folder, *H. indicata* life cycle went through 4 basic stages; egg, larva, pupa and adult. Table 1 showed a consistent rise in the rate of mortality, leading to an increasingly rapid decline in survivorship. From the raw data collected by mapping the positions of 132 eggs, the I_x values were calculated by converting the numbers observed at the start of each time interval to the equivalent number of the starting density of the cohort 1,000. The total k_x 's or killing-power which is referred to as the intensity or rate of mortality was 0.890. Each generation lasted for 50.5 days. The number of offspring produced per unit of time per female *H. indicata* aged x or m_x function was 75.437. The age specific patterns of fecundity and mortality indicated an initial sharp rise in fecundity reaching the peak during the 4-7 days followed by a gradual decline until the end after the 14-day period. The multiplication rate per generation (R_0) was 6.808. The population structure consisted of 89.093% immature stages and 10.907% adults. The innate capacity for increase (r) attained in the given environment and the finite rate of increase (λ) were 0.0744 and 1.0772 respectively. The birth rate (b) 0.6634 exceeded the death rate (d) 0.5890, thus *H. indicata* population increased over each succeeding time period.

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References

- Andrewartha, H. G., & Birch, L. C. (1970). *The distribution and abundance of animals*. Chicago: University of Chicago Press.
- Bapatla, K. G., Patil, R. H., & Yeddula, S. (2018). Impact of leaf damage by defoliators on yield of soybean as a sole crop and as a main crop in intercropping systems. *International Journal of Pest Management*, 64(1), 51-58. doi:10.1080/09670874.2017.1297508
- Begon, M., & Mortimer, M. (1981). *Population ecology; a unified study of animals and plants*. Oxford, Boston, Melbourne: Blackwell Scientific Publications.



- Birch, L. C. (1948). The Intrinsic Rate of Natural Increase of an Insect Population. *Journal of Animal Ecology*, 17(1), 15–26. doi:10.2307/1605
- Biswas, G. C. (2013). Insect pests of soybean (*Glycine Max* L.), their nature of damage and succession with the crop stages. *Journal of the Asiatic Society of Bangladesh, Science*, 39(1), 1–8. doi:10.3329/jasbs.v39i1.16027
- Biswas, G. C., & Das, P. G. (2011). Insect and mite pests diversity in the oilseed crops ecosystems in Bangladesh. *Bangladesh Journal of Zoology*, 39(2), 235–244. doi:10.3329/bjz.v39i2.10594
- Biswas, G. C., Hossain, M. M., & Majumder, U. K. (2001). Screening of some soybean entries against leaf roller (*Lamprosema indicata* F.). *Bangladesh Journal of Agricultural Research*, 26(2), 295–300.
- Biswas, G. C., & Islam, R. (2012). Infestation and management of leaf roller (*Lamprosema indica* Fab.) in soybean (*Glycine max* L.). *Bangladesh Journal of Agricultural Research*, 37(1), 19–25.
- Caswell, H. (1982). Stable Population Structure and Reproductive Value for Populations with Complex Life Cycles. *Ecology*, 63(5), 1223–1231. doi:10.2307/1938847
- Chi, H., & Liu, H. (1985). Two new methods for study of insect population ecology. *Bulletin of the Institute of Zoology, Academia Sinica*, 24, 225–240
- FCRC. (2018). Insecticide performance in key insect pests control: Crop Research Institute and Renewable Energy Crops. Retrieved from <http://www.fcrc.org.au/member-news/fcrc-2018-conference-highlights>.
- Fehr, W. R. (1989). Soybean, importance and distribution. In G. Robbelen, R. Keith Downey & A. Ashri (Eds.), *Oilcrops of the World* (pp. 283–300). London, United Kingdom: McGraw–Hill Education – Europe.
- Krebs, C. J. (1972). *Ecology: The experimental analysis of distribution and abundance*. New York: Harper & Row.
- Lewatanakarn, S., Sutayavirut, T., & Sepswadi, P. (1974). *Study on biology of soybean leaf roller [Lamprosema diamenalis Guen. (leaf roller), Lamprosema indicata F. (leaf folder), Cacoecia micaceana Wkr. (leaf rolling caterpillar) in Thailand*. Retrieved from <https://www.semanticscholar.org/topic/Cacoecia-desmotana/12303365>
- Lotka, A. J. (1913). A natural population norm. I. *Journal of the Washington Academy of Sciences*, 3(9), 241–248.
- Lotka, A. J. (1922). The Stability of the Normal Age Distribution. *Proceedings of the National Academy of Sciences of the United States of America*, 8(11), 339–345.
- Meena, N. L., & Sharma, U. S. (2006). Effect of sowing date and row spacing on incidence of major insect-pests of soybean, *Glycine max* (L.) Merrill. *Soybean Research*, 4(1/6), 73–76.
- Pimchan, C. (2004). *Farmers' knowledge and practice on insect control of soybean pests of farmers in Sanpatong district, Chiang Mai province*. Chiang Mai University, Chiang Mai.
- Poole, R. W. (1974). *An introduction to quantitative ecology*. New York: McGraw–Hill Education
- Raju, G. S., Khandwe, N., & Sharma, S. (2013). Efficacy of insecticides against defoliators and stem borers of soybean. *Annals of Plant Protection Sciences*, 21(2), 250–253.
- Sachan, J. N., & Gangwar, S. K. (1980). Insect pests of soybean in Khasi Hills of Meghalaya and their control. *Bulletin of Entomology (India)*, 21(1–2), 105–112.



- Taylor, F. (1979). Convergence to the stable age distribution in populations of insects. *The American Naturalist*, *113*(4), 511–530.
- Varley, G. C., Gradwell, G. R., & Hassell, M. P. (1973). *Insect population ecology: An analytical approach*. Berkeley and Los Angeles: University of California Press
- Zeng, W., Sun, Z., Lai, Z., Cai, Z., Chen, H., Yang, S., & Tang, X. (2018). Correlation analysis on transcriptomic and proteome of soybean resistance to bean pyralid (*Lamprosema indicata*). *Scientia Agricultura Sinica*, *51*(7), 1244–1260. doi:10.3864/j.issn.0578-1752.2018.07.003

