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# Prediction of assimilation efficiency of lepidopterans

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**Abstract.** From 206 values reported for over 60 lepidopteran species, it was found that nitrogen content of food shows a significant ($P<0{\cdot}001$) and a positive correlation ($r=0{\cdot}704$) to assimilation efficiency with standard error of 10·33. Unlike in aquatic animals, water content of food influences assimilation efficiency in these terrestrial lepidopterans; however, the relation between leaf water and assimilation efficiency is also correlated, but the correlation is lower than that ($r=0{\cdot}529$; SE$=11{\cdot}8$) obtained for leaf nitrogen. Considering the individual effect of water on assimilation efficiency as well as its covarying relation with nitrogen, leaf water was included as a co-predictor. The inclusion of leaf water as a co-predictor of leaf nitrogen content improves the precision of prediction ($r=0{\cdot}868$; SE$=9{\cdot}7$). The role of digestive reducing substances (e.g. Tannins) on assimilation efficiency was considered as a second co-predictor. Realising the difficulties of considering the digestive reducing substances as a second co-predictor, and observing the closeness of the observed and predicted values in the present study, nitrogen and water contents of leaf are considered as adequate explanatory variables for the prediction of assimilation efficiency.

**Keywords.** Assimilation efficiency; lepidopteran species; leaf water; digestive reducing substances.

## 1. Introduction

The ease and accuracy, with which faeces egested by the lepidopterous larvae can be estimated, have prompted several workers to choose either a component of faeces (e.g. Uric acid: Bhattacharya and Waldbauer 1969, 1970) or the whole of faeces (Mukerji and Guppy 1973; Mathavan and Pandian 1974) as an index of food consumption. Such an indirect procedure of estimation of food consumption is based on an assumption that assimilation efficiency (Ase) remains constant around 45%. Scriber and Slansky (1981) showed that nitrogen and water contents of food may significantly influence Ase of lepidopterans fed on juice, forb, root or wood. Pandian and Marian (1985a) observed that the constancy of Ase at 45% is limited for forb-feeding lepidopterans alone. Hence, there is a need to identify a marker for indirect estimation of Ase of lepidopterans feeding on juice, root or wood. More recently, Pandian and Marian (1985b, c, d, e) have found that nitrogen content of food is positively and significantly correlated to absorption efficiency of fishes, reptiles, aquatic insects and polychaetes and can be used as an index of absorption/assimilation efficiency in these animal groups; they have further shown that the scope for the applicability of their method is greater, and their method is more reliable than any other indirect procedure described thus (Pandian and Marian 1985b). Therefore, an attempt is made to explore the possibility of using nitrogen content of food as an index of Ase of lepidopterans.

### 1.1 *Prerequisite for prediction*

Basic information reported for Ase of over 66 species is summarized in table 1. An

**Table 1.** Ase of lepidopterous larvae fed on plants containing different nitrogen and water levels under different experimental conditions.

| Species, stage and sex | T (°C) | Rh (%) | R (%) | Plant species | W (%) | N (% dry wt) | Ase (%) | Remarks | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *Danaus chrysippus* | | 80 | *ad lib* | *Calotropis gigantea* | 84 | 3·0 | | | Mathavan and Pandian (1975) |
| ♂ | 19 | | | | | | 57 | T affects Ase | |
| ♀ | 19 | | | | | | 58 | | |
| ♂ | 27 | | | | | | 58 | | |
| ♀ | 27 | | | | | | 48 | | |
| ♂ | 32 | | | | | | 49 | | |
| ♀ | 32 | | | | | | 43 | | |
| ♂ | 37 | | | | | | 48 | | |
| ♀ | 37 | | | | | | 46 | | |
| *D. chrysippus* | 30 | 80 | | *C. gigantea* | 84 | 3·0 | | | Mathavan and Muthukrishnan (1976) |
| | 30 | | 100 | | | | 47 | Food restriction affects Ase | |
| | | | 50 | | | | 46 | | |
| | | | 25 | | | | 41 | | |
| | | | Fed for 3, 6, 9, 12 and 24 h/d | | | | 43 | | |
| *D. chrysippus* | | 75 | | *C. gigantea* | 85 | 3·0 | | | Pandian *et al* (1978) |
| | 20 | | *ad lib* | | | | 30 | T and R affect Ase | |
| | 25 | | *ad lib* | | | | 23 | | |
| | 30 | | *ad lib* | | | | 28 | | |
| | 35 | | *ad lib* | | | | 51 | | |
| | 30 | | 56 | | | | 36 | | |
| | 30 | | 37 | | | | 40 | | |
| | 30 | | 32 | | | | 43 | | |
| | 30 | | 30 | | | | 41 | | |
| | 30 | | 15 | | | | 49 | | |
| | 30 | | 7 | | | | 51 | | |
| *D. chrysippus* (I–V instar) | 29 | 80 | *ad lib* | *C. gigantea* | | | | | Marian and Pandian (1980) |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Young leaf | 84 | 3·0 | 60 | Old leaf reduces Ase | |
| | | | | Old leaf | 88 | 0·8 | 36 | | |
| *D. plexippus* | 27 | | *ad lib* | *Ascelpias syriaca* | | | | | |
| | | 85 | | | 77 | 4·0 | 60 | | Schroeder (1976a) |
| | | 85 | | | 77 | 3·6 | 47 | | |
| | | 82 | | | 76 | 3·2 | 46 | | |
| *Lymantria dispar* | 22 | 35 | *ad lib* | | | | | | |
| | | | | *Quercus rubra* | 2·3* | 22 | | | Barbosa (1978) |
| | | | | *Q. alba* | 3·8* | 47 | | | |
| | | | | *Fagus grandifolia* | 2·2* | 23 | | | |
| | | | | *Acer rubrum* | 2·3* | 22 | | | |
| | | | | *Betula populifilia* | 3·8 | 30 | | | |
| *L. dispar* | 24 | 90 | *ad lib* | | | | | | |
| | | | | *B. populifolia* | 3·3* | 30 | | | Barbosa and Greenblatt (1979) |
| | | | | *F. grandifolia* | 2·2* | 19 | | | |
| | | | | *A. rubrum* | 2·3* | 22 | | | |
| | | | | *Q. alba* | 3·8* | 47 | | | |
| | | | | *Q. rubra* | 1·9* | 23 | | | |
| *L. monacha* | 30 | | *ad lib* | Beech | 60 | 2·0* | 21 | | Sattler (1939) |
| *Catopsilia crocale* | | 81 | | *Cassia alata* | 84 | 3·6 | | | Christopher (1983) |
| | 17 | | 25 | | | | 47 | T and R affect Ase | |
| | | | 50 | | | | 52 | | |
| | | | 75 | | | | 54 | | |
| | | | 100 | | | | 61 | | |
| | 22 | | 25 | | | | 50 | | |
| | | | 50 | | | | 52 | | |
| | | | 75 | | | | 54 | | |
| | | | 100 | | | | 60 | | |
| | 27 | | 25 | | | | 50 | | |
| | | | 50 | | | | 50 | | |
| | | | 75 | | | | 51 | | |
| | | | 100 | | | | 54 | | |
| | 32 | | 25 | | | | 50 | | |
| | | | 50 | | | | 49 | | |
| | | | 75 | | | | 49 | | |
| | | | 100 | | | | 52 | | |

**Table 1.** (*Contd.*)

| Species, stage and sex | T (°C) | Rh (%) | R (%) | Plant species | W (%) | N (% dry wt) | Ase (%) | Remarks | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *C. crocale* (I–V instar) | 30 | 85 | *ad lib* | *C. alata* | 84 | 3·8 | 50 | | Mathavan and Nambirajan (1976) |
| *Polydorus aristolochiae* | 30 | 85 | *ad lib* | *Aristolochia bractiata* | 86 | 3·6 | 67 | | Haniffa *et al* (1982) |
| *Bombyx mori* | 22 | 75 | *ad lib* | mulbery | 74 | 4·2* | 42 | | Hiratsuka (1920) |
| *B. mori* | | | *ad lib* | mulbery | 74 | 4·2* | | | Horie and Watanabe (1983a) |
| ♂ | | | | | | | 42 | | |
| ♀ | | | | | | | 42 | | |
| *Tinea pellionella* | 20 | | | | | | | | Chauvin and Gueguen (1978) |
| | | 95 | *ad lib* | | | | 52 | Humidity affects Ase | |
| | | 5 | *ad lib* | | | | 39 | | |
| *Ostrinia nubilabis* | 26 | 75 | *ad lib* | Wheat germ | | 2·5* | | | Hubner and Chiang (1982) |
| Healthy | | | | | | | 36±8 | Parasitism does not affect Ase | |
| Parasitised | | | | | | | 46±15 | | |
| *Diatraea saccharalis* | 26 | 75 | *ad lib* | Wheat germ | | 2·5* | | | Hubner and Chiang (1982) |
| Healthy | | | | | | | 40±13 | | |
| Parasitised | | | | | | | 50±17 | | |
| *Pericallia ricini* (I to V instar) | 28 | 85 | *ad lib* | | | | | | Krishnan (1984) |
| | | | | *Gossypium hirsutum* | 89 | 2·8 | 48 | | |
| | | | | *Raphanus sativus* | 90 | 2·7 | 50 | | |
| | | | | *Solanum melongena* | 85 | 2·2 | 47 | | |
| | | | | *Hibiscus rosasinensis* | 81 | 1·4 | 46 | | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | *Hibiscus esculentus* | 76 | 1·1 | 44 | |
| | | | | | *Gossypium hirsutum* | 89 | 2·8 | 50 | |
| *Spodoptera eridania* | | 22 | 35 | *ad lib* | | | | | Scriber (1981) |
| | P | | | | Dill | 88 | 4·4 | 50 | |
| | P | | | | Bean | 87 | 4·9 | 77 | |
| | F | | | | Dill | 88 | 4·4 | 73 | |
| | F | | | | Cabbage | 93 | 4·6 | 78 | |
| *S. eridania* | | 22 | | *ad lib* | | | | | Scriber (1978b) |
| | P | | | | *Phaseolus vulgaris* | 88 | 5·6 | 75 | |
| | F | | | | | | | 73 | |
| | P | | | | *Lotus corniculatus* 4 wks old, CN+ | 88 | 4·3 | 68 | |
| | F | | | | | | | 45 | |
| | P | | | | 4 wks old, CN− | 87 | 4·2 | 59 | |
| | F | | | | | | | 48 | |
| | P | | | | 20 wks old, CN+ | 79 | 4·1 | 53 | |
| | F | | | | 20 wks old, CN+ | | | 40 | |
| | P | | | | 20 wks old, CN− | 80 | 4·3 | 52 | |
| | F | | | | 20 wks old, CN− | | | 34 | |
| *S. eridania* | | 22 | 75 | *ad lib* | Corn | | | | Manuwoto and Scriber (1982) |
| | P | | | | B49 | 81 | 7·0 | 81 | |
| | P | | | | San Juan | 87 | 5·8 | 79 | |
| | P | | | | DIMBOA-less | 91 | 7·0 | 75 | |
| | F | | | | B49 | 90 | 6·3 | 58 | |
| | F | | | | San Juan | 87 | 5·8 | 61 | |
| | F | | | | DIMBOA-less | 90 | 6·4 | 64 | |

**Table 1.** (*Contd.*)

| Species, stage and sex | T (°C) | Rh (%) | R (%) | Plant species | W (%) | N (% dry wt) | Ase (%) | Remarks | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *S. eridania* | 21 | | *ad lib* | Vernal alfalfa | 83 | | | | Kingsley *et al* (1983) |
| | | | | control | | 4·7 | 70 ± 3 | No significant effect of parasitism | |
| | | | | *Verticillium* infected | 83 | 4·8 | 66 ± 2 | | |
| *S. eridania* | | | *ad lib* | | | | | | Scriber (1982) |
| | | | | *Sorbus americana* | 65 | 3·5 | 46 | | |
| | | | | *Betula papyrifera* | 71 | 3·2 | 49 | | |
| | | | | *Prunus serotina* | 73 | 4·4 | 62 | | |
| *S. eridania* | 22 | | *ad lib* | Maize | | | | | Scriber *et al* (1975) |
| | | | | Low DIMBOA | 92 | 4·7 | 71 | | |
| | | | | | 92 | 4·9 | 68 | | |
| | | | | | 91 | 7·0 | 68 | | |
| | | | | High DIMBOA | 89 | 2·0 | 52 | | |
| | | | | | 92 | 3·7 | 59 | | |
| | | | | | 92 | 4·1 | 73 | | |
| | | | | | 91 | 7·0 | 81 | | |
| *Spodoptera littoralis* | 27–33 | 56–62 | *ad lib* | | | | | | Duodu and Biney (1981) |
| | | | | *Urena* | | 3·3* | 35 | | |
| | | | | Cotton | | 3·6* | 41 | | |
| | | | | Cabbage | 93 | 4·6* | 73 | | |
| *S. litura* | | | *ad lib* | *Zinnia elegans* | 82 | 3·1* | | T does not affect Ase | Chockalingam and Somasundaram (1983) |
| | 25 | | | | | | 40 | | |
| | 30 | | | | | | 40 | | |
| | 35 | | | | | | 50 | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Pseudoplusia includens* | | 27 | 60 | *ad lib* | Soyabean | 86 | 4·6 | | Life stage affects Ase | Kogan and Cope (1974) |
| | I | | | | | | | 71 | | |
| | II | | | | | | | 75 | | |
| | III | | | | | | | 62 | | |
| | IV | | | | | | | 43 | | |
| | V | | | | | | | 53 | | |
| | VI | | | | | | | 44 | | |
| | | | | | | | | 58 ± 14 | | |
| *Pieris brassicae* (II–V instar) | | | | | *Raphanus sativus* | | 3·1 | 78 | | Yadava *et al* (1979) |
| *P. brassicae* | | | | *ad lib* | *Raphanus sativus* | | 3·6* | 65 | | Vats *et al* (1977) |
| *P. rapae* | | 18–24 | 60–80 | *ad lib* | | | | | | Slansky and Feeny (1977) |
| | | | | | *Cleoma spinosa* | 86 | 3·8 | 33 | | |
| | | | | | *Hesperis matronalis* | 81 | 3·2 | 31 | | |
| | | | | | *Barbarea vulgaris* | 82 | 2·8 | 35 | | |
| | | | | | *Lunaria annua* | 88 | 3·7 | 26 | | |
| | | | | | *Dentaria diphylla* | 88 | 4·4 | 38 | | |
| | | | | | *Thlaspi arvense* | 87 | 4·6 | 43 | | |
| | | | | | *Lepidium virginicum* | 83 | 3·7 | 29 | | |
| | | | | | *Brassica oleracea* | 87 | 3·0 | 31 | | |
| | | | | | *B. oleracea* | 85 | 2·1 | 26 | | |
| | | | | | *B. oleracea* | 86 | 2·4 | 28 | | |
| | | | | | *B. oleracea* | 87 | 2·5 | 34 | | |
| | | | | | *B. oleracea* | 84 | 2·4 | 29 | | |
| | | | | | *B. oleracea* | 84 | 1·9 | 28 | | |

**Table 1.** (*Contd.*)

| Species, stage and sex | T (°C) | Rh (%) | R (%) | Plant species | W (%) | N (% dry wt) | Ase (%) | Remarks | Reference |
|---|---|---|---|---|---|---|---|---|---|
| | | | | *B. juncea* | 88 | 3·8 | 33 | | |
| | | | | *B. nigra* | 87 | 4·8 | 41 | | |
| | | | | *B. perkinensio* | 90 | 2·9 | 36 | | |
| | | | | *Tropaeolum majus* | 86 | 3·0 | 42 | | |
| *P. rapae* | 21 | 60–84 | *ad lib* | *Brassica oleracea* | 85 | 1·7 | | | Slansky (1978) |
| Normal | | | | | | | 41 | No parasitic effect | |
| Parasitized | | | | | | | 39 | | |
| *Pachysphinx modesta* | 27 | 60–80 | *ad lib* | *Populus deltoides* | 53 | 1·6* | 41 | | Schroeder (1973) |
| *Euchaetias egle* | 27 | 87 | *ad lib* | *Asclepias syriacea* | 76 | 3·2 | 46 | | Schroeder (1977) |
| *Papilio glaucus* (III and IV instar) | 20–24 | | *ad lib* | | | | | | Scriber (1979a) |
| | | | | *Prunus serotina* | 61 | 2·1 | 29 | | |
| | | | | *Fraxinus americana* | 51 | 2·0 | 29 | | |
| | | | | *Sassafras albidum* | 68 | 3·0 | 36 | | |
| | | | | *Lindera benzoin* | 70 | 2·0 | 35 | | |
| | | | | *Sassafras albidum* | 68 | 3·0 | 24 | | |
| *P. glaucus* | | | *ad lib* | *Prunus serotina* | 66 | 3·2 | | | Scriber and Lederhouse (1983) |
| P | 15 | | | | | | 34 | | |
| P | 22 | | | | | | 44 | | |
| F | 22 | | | | | | 32 | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | P | 26 | | | | | | 37 | | |
| | F | 26 | | | | | | 32 | | |
| | P | 30 | | | | | | 41 | | |
| | F | 30 | | | | | | 55 | | |
| | P | 37 | | | | | | 37 | | |
| | F | 37 | | | | | | 47 | | |
| *Hyalophora cecropia* | | 27 | 70 | *ad lib* | *Acer negundo* | | 2·7 | 37 | | Schroeder (1971) |
| *H. cecropia* | | 20–20 | 60–90 | | *Prunus serotina* | 88 | 3·7 | | Food restriction does not affect Ase | Grabstein and Scriber (1982a) |
| | | | | Fed for 24h/d | | | | 33 | | |
| | | | | 16h/d | | | | 34 | | |
| | | | | 16h/ after 4 days | | | | 33 | | |
| | | | | 16h/ after 5 days | | | | 28 | | |
| *H. cecropia* | | | | *ad lib* | Black cherry | 67 | 3·1 | 36 | | Grabstein and Scriber (1982b) |
| | | | | | Paper birch-Black cherry | 68 | 3·1 | 37 | | |
| | | | | | | 62 | 2·3 | 27 | | |
| | | | | | | 63 | 2·3 | 26 | | |
| *H. cecropia* | | 22 | 75 | *ad lib* | | | | | | Scriber (1977) |
| | | | | | *Prunus serotina* | 70 | 2·8 | 32 | Water does not affect Ase | |
| | | | | | | 59 | 2·8 | 31 | | |
| | | | | | | 55 | 2·6 | 34 | | |
| | | | | | *Quercus alba* | 49 | 2·7 | 37 | | |
| *Calocalpe undulata* | | 27 | 80 | | *Prunus serotina* | 62 | 3·3 | | | Schroeder (1976b) |
| | | | | Fed for 24 h/d | | | | 33 | Food restriction increase Ase | |
| | | | | 20 h/d | | | | 34 | | |
| | | | | 16 h/d | | | | 36 | | |

**Table 1.** (*Contd.*)

| Species, stage and sex | T (°C) | Rh (%) | R (%) | Plant species | W (%) | N (% dry wt) | Ase (%) | Remarks | Reference |
|---|---|---|---|---|---|---|---|---|---|
| *Operophthera brumata* | 15 | | *ad lib* | | | | | | Axelsson *et al* (1975) |
| (II–V instar) | | | | Hazal leaf | | 3·0* | 41 | | |
| (II–V instar) | | | | Oat leaf | | 3·1* | 42 | | |
| *Mamestra configurata* | 25 | 70 | *ad lib* | | | | | | Bailey (1976) |
| | | | | Potato | | 3·7* | 52 | | |
| | | | | Lambsquarters | | 3·7* | 51 | | |
| | | | | Rape (Zephyr) | | 3·6* | 51 | | |
| | | | | Rape (Span) | | 3·7* | 50 | | |
| *M. configurata* | 25 | 70 | *ad lib* | *Brassica napus* | | 3·0* | 40 | | Bailey and Singh (1977) |
| *Achaea janata* (II–V instar) | | 80 | *ad lib* | *Ricinus communis* | 84 | 3·8 | | | Muthukrishnan and Pandian (1983) |
| | 22 | | | | | | 63 | T and life stage affect Ase | |
| | 27 | | | | | | 60 | | |
| | 32 | | | | | | 60 | | |
| | 35 | | | | | | 64 | | |
| *A. janata* | | 80 | | *R. communis* | 84 | 3·8 | | | Muthukrishnan and Pandian (1984) |
| | 22 | | 30 | | | | 67 | | |
| | | | 46 | | | | 62 | T and R affect Ase | |
| | | | 56 | | | | 61 | | |
| | | | 73 | | | | 59 | | |
| | | | 78 | | | | 61 | | |
| | | | 100 | | | | 58 | | |
| | 27 | | 24 | | | | 61 | | |
| | | | 35 | | | | 58 | | |
| | | | 48 | | | | 57 | | |
| | | | 53 | | | | 58 | | |
| | | | 74 | | | | 59 | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | 100 | | | | 58 | |
| | 32 | | 37 | | | | 57 | |
| | | | 54 | | | | 61 | |
| | | | 64 | | | | 60 | |
| | | | 74 | | | | 63 | |
| | | | 77 | | | | 63 | |
| | | | 100 | | | | 63 | |
| | 37 | | 38 | | | | 58 | |
| | | | 49 | | | | 60 | |
| | | | 52 | | | | 61 | |
| | | | 65 | | | | 62 | |
| | | | 86 | | | | 64 | |
| | | | 100 | | | | 63 | |
| *Protoparce sexta* | | | *ad lib* | Tobacco | | 3·5* | 43 | Waldbauer (1964) |
| *Diacrisia virginica* | 27 | 78 | *ad lib* | *Prunus serotina* | 55 | 3·2 | 34 | Schroeder and Malmer (1980) |
| *Hyphantria cunea* | | | | | 46 | 3·2 | 38 | |
| *Bapta vestiliata* | | | | | 56 | 3·2 | 39 | |
| *Scopula* sp. | | | | | 65 | 4·2 | 50 | |
| *Hydria prunivorata* | | | | | 60 | 3·4 | 36 | |
| *Malacasoma americana* | | | | | 68 | 4·3 | 53 | |
| *Phobetron pithecum* | | | | | 55 | 3·0 | 31 | |
| *Hemerocampa leucostigmata* | | | | | 59 | 3·5 | 41 | |

T, Temperature; Rh, relative humidity; R, ration (% of *ad libitum*); W, water content of food; N, nitrogen content of food; P, penultimate instar; F, final instar.
*Values obtained from Sreeramulu (1982); Varma *et al* (1982); Winton and Winton (1939).

incisive analysis of the table reveals the following: (i) The publications by Kogan and Cope (1974), Axellson *et al* (1975), Yadava *et al* (1979), Marian and Pandian (1980) and Krishnan (1984) are the only 5 reports available on the effect of life stage on Ase; all these authors have uniformly reported that the life stage significantly affects Ase; for instance, the efficiency of *Danaus chrysippus* decreases from 90% in the first instar to 58% in the final instar (Marian and Pandian 1980). (ii) The publications by Mathavan and Pandian (1975), Pandian *et al* (1978), Muthukrishnan and Pandian (1983, 1984), and Chockalingam and Somasundaram (1983) are the only 5 reports available on the effect of temperature on Ase; the first 4 reported that temperature significantly affects Ase, while the fifth contradicted the observation. (iii) The publications by Pandian *et al* (1978), Mathavan and Muthukrishnan (1976), Schroeder (1976b), Grabstein and Scriber (1982a) and Muthukrishnan and Pandian (1984) are the only 5 reports available on the effects of ration on Ase; a recalculation of their data revealed that of these, the first 4 indicated that ration significantly affects Ase, whereas the fifth one contradicts this observation. (iv) A couple of other publications indicated that humidity prevailing in the terrarium and water content of food may or may not affect Ase. Apparently, life stage definitely affects Ase, whereas the effect of the remaining factors on Ase is questionable. Since some or all these factors may or may not significantly alter the expected linear relation between food N and Ase, it is a necessary prerequisite to identify the factors, which may significantly alter the expected relation. Such an approach is necessary to improve the prediction of Ase of lepidopteran. To evaluate the magnitude of each one of these factors on the Ase, we have chosen to study basic information reported by Krishnan (1984).

Krishnan (1984) carried out a series of experiments on the moth *Pericallia ricinii*: the larva of the moth passes through 5 instars before pupation; all feeding experiments were undertaken from hatching to prepupation, exposing adequate number of individuals to a range of temperature (26–35°C), ration (25–100% of *ad*

**Table 2.** ANOVA to test the effect of different variables on Ase of lepidopterans. For combinations 1, 2 and 3, basic data were obtained from Krishnan (1984). For combination 4, data were selected from table 1.

| Variable | *F* | *P* |
|---|---|---|
| Combination | | |
| 1. *Nitrogen × life stage × ration* | | |
| Nitrogen | $F(1)4, 240 = 45$ | $<0{\cdot}005$ |
| Life stage | $F(1)2, 240 = 205$ | $<0{\cdot}0005$ |
| Ration | $F(1)3, 240 = 5$ | $<0{\cdot}01$ |
| 2. *Temperature × life stage* | | |
| Temperature | $F(1)3, 80 = 37$ | $<0{\cdot}001$ |
| Life stage | $F(1)4, 80 = 244$ | $<0{\cdot}0005$ |
| 3. *Temperature × Nitrogen* | | |
| Temperature | $F(1)2, 71 = 16$ | $<0{\cdot}05$ |
| Nitrogen | $F(1)2, 71 = 151$ | $<0{\cdot}0005$ |
| 4. *Water content × nitrogen* | | |
| Water | $F(1)2, 4 = 4$ | $<0{\cdot}001$ |
| Nitrogen | $F(1)2, 4 = 12$ | $<0{\cdot}05$ |

*libitum*), food quality with reference to different levels of nitrogen (1·1–2·8%). Thus Krishnan reported adequate information for suitable statistical analysis (ANOVA) to identify magnitude of the effects of the chosen parameters on Ase. The results obtained from two and three-way ANOVA tests conducted in different combinations of the variables nitrogen vs life stage vs ration: temperature vs life stage: temperature vs nitrogen: water content vs nitrogen on the Ase are summarized in table 2. It is understood from the table that all the variables are significantly ($P<0{\cdot}05$) influencing the Ase; however, the magnitude of influence varies from one variable to other, which is inferred from the $F$ values. Among these variables, the magnitude of influence of life stage on Ase is the greatest ($F \geqslant 205$), i.e. it is 5, 7 and 41 times more than that of nitrogen, temperature and ration, respectively. Food nitrogen has the next greatest magnitude of influence on Ase; its level of effect on Ase is 9, 9 and 3 times greater than that of temperature, ration and water content of food, respectively. On the whole, the level of influence on Ase by the tested factors is in the following order: life stage > food nitrogen > food water > temperature > ration.

Hence, it is chosen to include only the Ase values reported for the final instar in all the ensuing analyses for prediction of Ase. In a few cases, it was also possible to consider the total amount of ingestion and egestion from hatching to prepupation; in such cases, the mean Ase values were included (e.g. *Danaus chrysippus*, Marian and Pandian 1980). Such a prerequisite is justified for following reasons: (i) of information available for 66 species (table 1), Ase values are reported only for final instar of 61 species (table 1); (ii) most lepidopterans consume over 75% of the larval food during the final instar (Pandian and Delvi 1973; Pandian 1973) and (iii) the chances of errors introduced in estimating Ase in the first few instars are more, as the amount of ingestion or egestion is so little; for instance, the first instar *D. chrysippus* consumes 2·3 mg and egests 0·47 mg on the first day (Marian and Pandian 1980).

## 2. Materials and methods

Pertinent publications, which appeared during the period from 1920–1984, served as the basic material for the present study. From a survey over 240 publications were considered. Of these about 178 publications were not selected for the following reasons: (i) Lack of information on N content of food (e.g. Schowalter *et al* 1977); (ii) vague information on N content (e.g. Mukerji and Guppy 1970); (iii) reporting information on Ase, following the method of Mathavan and Pandian (1974), which assumes Ase to remain constant around 45% (e.g. Mathavan *et al* 1984); (iv) reporting desired information for insects reared under abnormal stress conditions such as exposure to pesticides (e.g. Chockalingam and Krishnan 1984) and other chemicals (e.g. caffeine and theophylline: Muthukrishnan *et al* 1979).

We have chosen about 60 publications reporting reliable information on total assimilation efficiency (in terms of dry weight or energy) of final instar fed on natural food under normal, healthy and experimental conditions. In some cases, it has been possible for us to secure nitrogen content of food, for which desired information is reported elsewhere (e.g. Sreeramulu 1982). Efforts were made to give due representation to forb and tree-leaf feeding lepidopterans so that the entire range of food nitrogen spectrum would be represented. Information thus obtained was analysed under the following heading (table 1): (i) species, stage and sex, (ii) temperature, relative humidity and ration, (iii) water and nitrogen contents of food and (iv) Ase:

$$\text{Ase}(\%) = \frac{\begin{array}{c}\text{Food ingested—faeces} \\ \text{(mg dry wt or energy)} \quad \text{(mg dry wt or energy)}\end{array}}{\begin{array}{c}\text{Food ingested} \\ \text{(mg dry wt or energy)}\end{array}} \times 100$$

Statistical analyses were done following Zar (1974), and computations were done using IBM 1130 computer.

## 3. Results

Available information on Ase of lepidopterans is presented in table 1; it reveals that (i) of over 60 species, more than 36 are moths and the remaining are butterflies; (ii) life stage of some tested species ranged from hatchling (e.g. *Pseudoplusia includens*: Kogan and Cope 1974) to final (upto VI) instar; (iii) nitrogen content of the tested food ranged from 0·8% (e.g. senescent *Calotropis gigantea* leaf; Marian and Pandian 1980) to 7% (e.g. maize B49 varieties; Manuwoto and Scriber 1982); (iv) water content of the food ranged from 49% (e.g. *Quercus alba*; Scriber 1977) to 93% (e.g. cabbage; Duodu and Biney 1981); (v) some species were given different rations; 7% (e.g. *D. chrysippus*; Pandian *et al* 1978) to 100% (e.g. *Pieris brassica*: Yadava *et al*

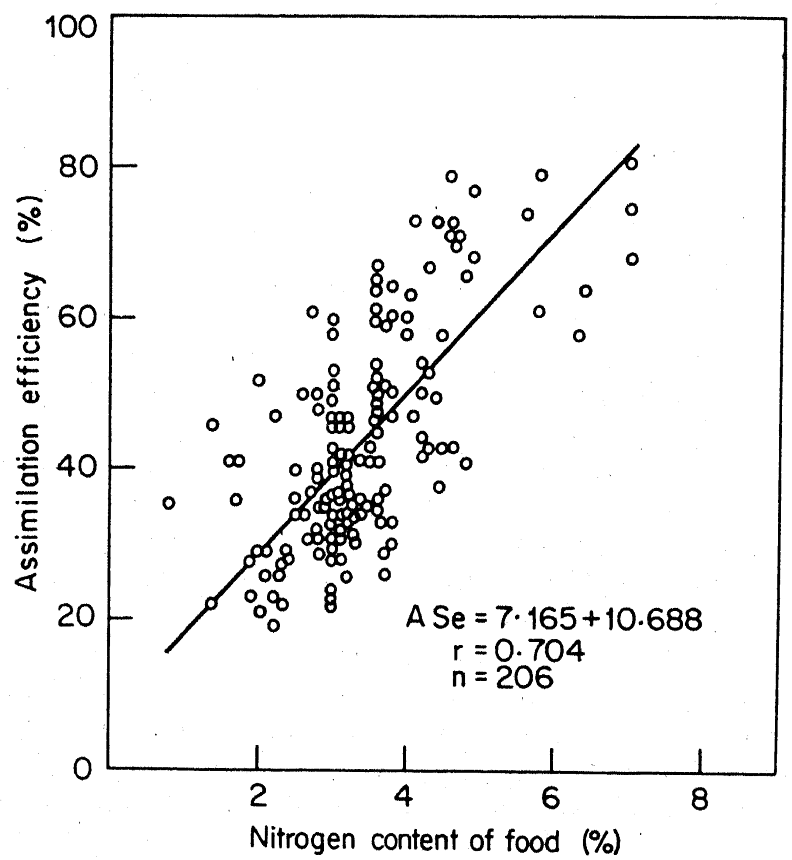


**Figure 1.** Assimilation efficiency of lepidopterans as a function of nitrogen content of food.

1979) of *ad libitum*; (vi) few temperate species were experimented at a temperature of 15°C (e.g. *Operohthera brumata*; Axelsson *et al* 1975) and (vii) the lowest Rh recorded during the experiment was 5% and the maximum 95% (e.g. Chauvin and Gueguen 1978). Thus it has been possible to summarize data on assimilation efficiency of a number of lepidopterans tested under a range of feeding regimes and experimental conditions.

Figure 1 illustrates the relationship between nitrogen content of food and Ase of the final instar of the selected lepidopterans. The Ase was the lowest (19%) for *Lymantria dispar* fed *ad libitum* on *Fagus grandiflora* containing 2·2% N at 24°C (Barbosa and Greenblatt 1979). With increasing food-N, the efficiency increased linearly to 81% in the armyworm *Spodoptera eridania*, which was fed on the corn B49 containing 7% N (Manuwoto and Scriber 1982). It is obvious that the nitrogen content of food is related to the Ase in lepidopteran larvae.

The relationship between the two variables was tested by computing the available data ($N=206$) using simple regression model. The regression (Ase$=7{\cdot}165+10{\cdot}688$ N) obtained with 0·704 correlation coefficient was statistically highly significant ($F=200{\cdot}3$; $P<0{\cdot}0005$) but the standard error (SE) of the estimate was high (10·33) (table 2). Hence, there is vast differences between the observed and predicted values, when food-N alone is used as predictor of Ase (table 8).

In general terrestrial animals acquire water mainly from food, and gain or lose water through body surface (Tracy 1976). Restriction of ration or exposure to higher temperature may result in dehydration, and force lepidopterous larvae to replenish water from food by accelerating the feeding and alimentation processes; such an acceleration may lower the Ase. Hence it is very likely such factors like water content of food, ration, temperature and Rh may modify the simple linear relationship observed between food-N and Ase, and may be responsible for the wide scatter of Ase values around the regression line fitted for the relation between food-N and Ase. Clearly, these 4 independent variables besides food-N may play a significant or negligible role in the determination of Ase. To understand the magnitude, to which the said 5 independent variables affect the dependent variable, Ase, hundred values were randomly selected from table 1. These values were used for correlation matrix analysis and the computed values are presented in table 4. The correlation values obtained for Ase for ration, temperature and Rh are very low, indicating that their effect on Ase is negligible. Moreover, the obtained matrix is singular; hence further computation of these 3 variables is neither possible nor required. The values obtained for nitrogen and water contents of food are equally high that it is difficult to identify from this analysis which has greater influence on Ase. To identify this, 164 values representing the relationship between water content of food and Ase were selected from table 1. The relation between these two variables is positive and linear but the Ase values are widely scattered at any chosen water level. In other words the situation recalls that observed for food-N-Ase relation, confirming the observation of Mattson (1980). He observed that water and nitrogen contents of food usually covary positively and make it difficult to comprehend the individual and combined effects of these variables on Ase.

An attempt was made to understand the magnitude of independent-effect of nitrogen and water contents of food on Ase. For this a partial correlation matrix was computed considering 145 observed values from table 1. The partial correlation values obtained for Ase clearly show the overriding importance of nitrogen over

**Table 3.** Summary of the simple regressions and related statistics computed for the relationships between the two independent variables (nitrogen, water) and the dependent (Ase) variable.

| Simple regression equation | Correlation coefficient ($r$) | Standard error of estimate | $F$ value of ANOVA | Level of significance ($P$) |
|---|---|---|---|---|
| Ase (%) = 7·165 + 10·688 N | 0·704 | 10·328 | $F(1)$ 1,204 = 200·4 | < 0·0005 |
| Ase (%) = − 0·311 + 0·598 W | 0·529 | 11·8 | $F(1)$ 1,162 = 62·8 | < 0·0005 |

**Table 4.** The correlation matrix obtained for the relationships between the independent variable, i.e. Nitrogen (N), Water (W) content of food, Ration (R), Temperature (T), or Relative humidity (Rh) and dependent variable, i.e. Assimilation efficiency (Ase) of lepidopterans. The original values were obtained from those presented in table 1.

| | N | W | R | T | Rh | Ase |
|---|---|---|---|---|---|---|
| N | 1·00000 | | | | | |
| W | 0·08678 | 1·00000 | | | | |
| R | 0·04216 | 0·32398 | 1·00000 | | | |
| T | 0·05860 | 0·12107 | 0·07234 | 1·00000 | | |
| Rh | 0·06534 | 0·19381 | 0·07662 | 0·07007 | 1·00000 | |
| Ase | 0·51596 | 0·51031 | 0·10398 | 0·00428 | 0·00504 | 1·00000 |

**Table 5.** Matrix of partial correlation coefficients computed for the relation between the independent variable, i.e. Nitrogen or water content of food and dependent variable. Ase of selected Lepidopterans (for original values, refer table 1).

| Variable | Nitrogen | Water | Ase |
|---|---|---|---|
| Nitrogen | 1·00000 | | |
| Water | 0·33223 | 1·00000 | |
| Assimilation efficiency | 0·69281 | 0·50928 | 1·00000 |

water in determining the efficiency (table 5). Still it is also apparent that water also exert a recognizable influence in determining the Ase, as the value obtained for water is not too low (0·51) in comparison to that (0·69) obtained for nitrogen. Therefore one has to include water as a co-predictor to improve the accuracy of prediction.

For this, a multiple regression was computed (Ase $= a + b_1 N + b_2 W$) considering a model, in which water is included as a co-predictor of food-N (table 6). When relevant data were fitted into this model, the correlation coefficient value was considerably improved ($r = 0{\cdot}868$) with 9·7 SE. In other words, the multiple regression thus obtained is Ase = − 11·610 + 8·246 N + 0·509 W. Since the overall SE of the regression model is 9·7, it is necessary to give some examples to show the reliability of the model (table 7). For this, examples were randomly selected from table 1 representing the entire range of nitrogen (0·8–7·0%) as well as water (49–92%) contents of the food. The observed and predicted values, in which water served as a co-predictor of food-N, are closer to each other (table 8) than those predicted considering food-N as a sole predictor.

**Table 6.** Regression statistics computed for the model: $Ase = a + b_1N + b_2W$ fit to the data presented in table 1.

| Variable | Mean | Standard deviation | Correlation $x$ vs $y$ | Regression coefficient | Std. error of reg. coef. | Computed '$t$' value |
|---|---|---|---|---|---|---|
| *Independent* | | | | | | |
| Nitrogen | 3·53515 | 1·04585 | 0·69281 | 8·24567 | 0·81966 | 10·05978 |
| Water | 76·80000 | 12·70910 | 0·50928 | 0·50891 | 0·06745 | 5·36218 |
| *Dependent* | | | | | | |
| Ase | 45·31724 | 14·65176 | | | | |
| Intercept | | −11·61021 | | | | |
| Multiple correlation ($R^2$) | | 0·75336 | | | | |
| Std error of estimate | | 9·70268 | | | | |

**Table 7.** Analysis of variance for the regression computed for the model $Ase = a + b_1N + b_2W$

| Source of variation | Sum of squares | Degrees of freedom | Mean squares | $F$ value |
|---|---|---|---|---|
| Attributable to regression | 2 | 17545 | 8772 | 93 |
| Deviation from regression | 142 | 13368 | 94 | |
| Total | 144 | 30913 | | |

## 4. Discussion

The term Ase is equivalent to 'Approximate Digestibility' (AD) of (Waldbauer 1968) or the 'coefficient of digestibility' of House (1965). It refers to the percentage of ingested food transferred through the gut into the lumen of insect body. It is generally calculated from the estimates of ingestion (I), egestion (E), i.e. faeces and excretary products (FU). Unlike in aquatic animals, the recovery and quantification of FU of lepidopterans are easier and complete, but the quantitative estimates of I is laborious and time-consuming, requiring the following gravimetric estimates: (i) weights of the offered food and the unfed remains, (ii) weight of transpiratory loss from the offered leaves and (iii) water content of the aliquot for each leaf offered, as each leaf of the same plant species varies considerably (Pate 1975). Considering the transpiratory water loss and photosynthetic production in the offered food leaves, Axelsson and Agren (1979) and Wightman (1981), respectively suggested several measures to improve the accuracy of the method, which however, involve additional estimates. To avoid the difficulties involved in the quantitative estimates of I, indirect methods were devised. However, the applicability of indirect marker methods like the chromic oxide ($Cr_2O_3$) (e.g. Horie and Watanabe 1983b) in phytophagous lepidopterans is limited and questionable; pointing out the differential passage of $Cr_2O_3$ in the digestive tract from that of feed. Bowen (1979) questioned the validity of $Cr_2O_3$ as a marker in the study of food assimilation. Park and Kogan (1981) have also pointed out that $Cr_2O_3$ interfere with food consumption. Thus, there is a need to identify an easily measurable component of food, which could serve as a reliable index of Ase of lepidopterans.

**Table 8.** Observed and predicted values of assimilation efficiency of selected Lepidopterans.

| Species | Food | Water content of food (%) | Nitrogen content of food (%) | Assimilation efficiency (%) Predicted from N | N&W | Observed | Reference |
|---|---|---|---|---|---|---|---|
| *Danaus chrysippus* | *Calotropis gigantea* | 80 | 3·0 | 39 | 54 | 51 | Mathavan and Pandian (1975) |
| *D. chrysippus* | *C. gigantea* (young) | 84 | 3·0 | 39 | 56 | 60 | Marian and Pandian (1980) |
| *D. chrysippus* | *C. gigantea* (senescent) | 88 | 0·8 | 16 | 40 | 36 | Marian and Pandian (1980) |
| *Spodoptera eridania* | DIMBO A. less mutant maize | 92 | 4·7 | 57 | 74 | 71 | Scriber *et al* (1975) |
| *Polydorus aristolochiae* | *Aristolochia bractiata* | 86 | 3·6 | 45 | 62 | 67 | Haniffa *et al* (1982) |
| *Achaea janata* | *Ricinus communis* | 84 | 3·8 | 48 | 63 | 63 | Muthukrishnan and Pandian (1983) |
| *S. eridania* | Corn variety 1 | 81 | 7·0 | 82 | 87 | 81 | Manuwoto and Scriber (1982) |
| *S. eridania* | Corn variety 2 | 87 | 5·8 | 69 | 81 | 79 | Manuwoto and Scriber (1982) |
| *Hyalophora cecropia* | *Quercus alba* | 49 | 2·7 | 36 | 36 | 37 | Scriber (1977) |
| *Hyphantria cunea* | *Prunus serotina* | 46 | 3·2 | 41 | 39 | 38 | Schroeder and Malmer (1980) |

Nitrogen content of animals is usually higher than that of plants; animals consist mainly (>50%) of protein (Hafez and Dyer 1969; DeFolliart 1975) or nitrogen (7·14%); plants consist mainly of carbohydrates and their nitrogen content ranges from 0·03–7% (Mattson 1980), averaging to 2% nitrogen (Russell 1947). Nitrogen requirements of animals is far higher than that of plants, as the former use proteins as structural building-blocks, whereas the latter use carbohydrates. Besides, animals also use nitrogen less efficiently than plants, as a significant fraction of daily wastes consists of various nitrogen compounds, whereas plants excrete little nitrogen (Mattson 1980). Consequently herbivores such as lepidopterans must consume, sequester and assimilate as much nitrogen from food stuffs as possible; if the process of assimilation is 50% efficient, then most lepidopterans must eat 4–5 units of food stuff to obtain adequate nitrogen to make one unit of their body tissue. Hence food plants containing low nitrogen are likely to be assimilated less efficiently so that more food is consumed to procure adequate nitrogen; the reverse would be true for the plants with high nitrogen. Thus it is appropriate that nitrogen, a non-inert moiety of the food is considered as an index of Ase of lepidopterans. Pandian and Marian (1985d) found that nitrogen content of food nitrogen was significantly ($P<0{\cdot}001$) and positively correlated ($r=0{\cdot}97$) to Ase of aquatic insects as well as in several other animals groups and it has been possible for them to predict Ase from food nitrogen of several animal groups with less than 10% error (Pandian and Marian 1985b, c, d, e). Hence our attempt to predict Ase of lepidopterans using food nitrogen is likely to hold good.

However, it must be noted that whereas the correlation coefficients ($r$) obtained for food-N and Ase relationship were higher than 0·9 for other animal groups, that obtained for lepidopterans is far less ($r=0{\cdot}7$) and involves a higher SE too. The low $r$ and high SE obtained for lepidopterans reflect the wide scattering of Ase data against food-N (figure 1). Such wide scattering of Ase data indicates the influence of other factors like water and digestibility reducing substances of the food plants. The relationship between N content of leaf and Ase, and the effect of water as a co-explanatory variable in the determination of Ase of lepidopterans have also been documented by Rausher (1981) in the pipevine swallowtail butterfly *Battus philenor* fed with two host plants, *Aristolochia reticulata* and *A. serpentaria*. The $F$ value of Rausher's multiple regression was less ($F$ 1, 26 = 14·6) than that reported in the present study ($F$ 1, 145 = 93). Despite the variation in the $F$ values, the common concept inferred is that both N and water contents of a food plant interact to determine the digestibility or Ase of lepidopterans; among the two, N displayed an overriding importance over water content of leaves in the determination of Ase. Incidentally, McNeill and Southwood (1978) and Morrow and Fox (1980) have also observed a positive and significant correlation between food-N and Ase in non-lepidopteran insects, i.e. *Leptopterus dolabrata* (Homoptera) and *Parapsis atomaria* (Coleoptera). Feeding 22 lepidopteran species belonging to Papilionidae and Bombycoidae on the leaves of different food plants (trees and forbs), Scriber (1978a) found that larvae fed on low water content tree leaves exhibited low Ase, whereas those fed on forbs exhibited relatively higher Ase. A glance over figure 2, in general confirms the observation of Scriber that leaf water content of trees is in general lower than the forbs. However, leaf water content of some trees (e.g. *Cassia alata*; Christopher 1983) is as high as that of some forbs and *Catopsilia crocale* feeding on *C. alata* leaf displays as high Ase as those feeding on forbs containing 85% water

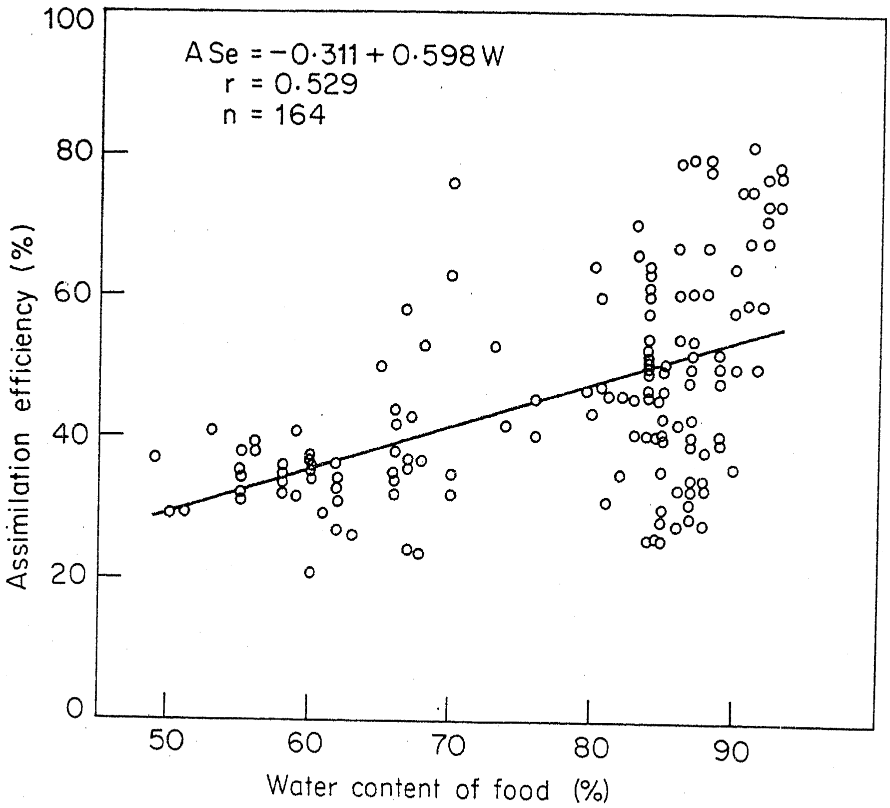


**Figure 2.** Assimilation efficiency of lepidopterans as a function of water content of food.

content. It is therefore suggested that there is a need for the collection of more information on this aspect before the observation of Scriber could be confirmed or contradicted.

The ability to digest and assimilate the plant parts by phytophagous insects may considerably be altered by the presence of digestibility reducing secondary chemicals such as tannin (e.g. Feeny 1969). Feeny (1970) observed that the Ase of tested lepidopterous larvae decreased with increasing tannin content; however, the data reported by him do not lend themselves to estimate the order of importance of leaf N, water and tannin in determining Ase. Incidentally, Coleopterans are known to display a high tolerance to tannin compared with lepidopterous larvae (Bernays 1978; Fox and Macauley 1977). Information on the importance of other digestive reducing substances (DRS) in determining the Ase of lepidopterans is vague. For instance Rausher (1981) fed *Battus philenor* larvae with young and old leaf of *Aristolochia reticulata* and *A. serpentaria* containing different levels of N and DRS. When values for equal N consumption from young and old leaves were considered, he could find no differences in the growth rate of *B. philenor*, which implies that Ase has remained equal. Rausher (1981) came to the tentative conclusion that N is more important. While due consideration for DRS as a second co-predictor to increase the precision of prediction of Ase (to increase the *r* over 0·9 as well as to decrease the SE to 7·7, as has been reported for fishes, reptiles, aquatic insects, amphibians, polychaetes; Pandian and Marian 1985b, c, d, e) is considered necessary, but it is too early to consider it in the present work. What seems to be more important is that it is not the N content of plant food, but the ultimate availability of N that determines Ase. To determine N availability of the plant, one needs to know the profile of DRS in host plants. While much information is still required about DRS, it may be noted that our predictive model can easily accommodate the components of DRS indicated below:

$$\text{Ase} = a + b\text{N} + b_2\text{W} + b_3\text{DRS}.$$

In an attempt to study the effect of different protein qualities on the Ase of *Bombyx mori*, Horie and Watanabe (1983b) fed the silkworm on a variety of synthetic diets containing different N levels. The recalculated values of Ase reported by them are presented against food N in figure 3, from which the following became apparent: (i) Irrespective of changes in protein quality, Ase shows a highly significant correlation ($r = 0.9$) with food-N, and this finding confirms our concept of using food-N as a predictor of Ase. (ii) The levels of the slope describing the Ase-food-N relationship appear to be fixed by the protein quality. Thus, the trend obtained for milk casein is far higher than that of gluten. Briefly, N content of food determines the trend, but the protein quality determines the level of the trend. (iii) The cumulative trend obtained for Ase-food-N relationship of all the synthetic diets stands far lower than that reported for the lepidopterans fed on natural plants. It is not clear whether

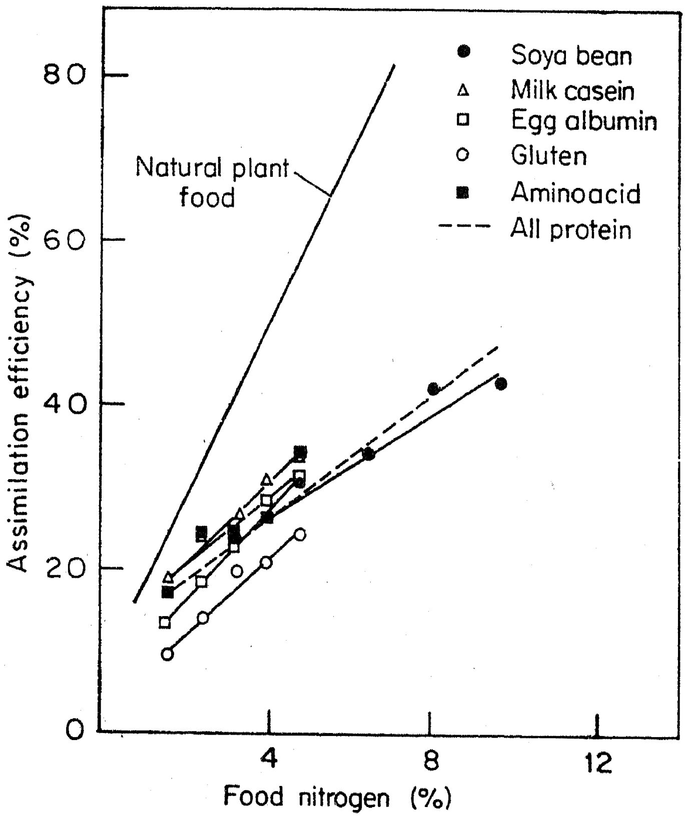


**Figure 3.** Assimilation efficiency of final instar larvae of *Bombyx mori* fed on synthetic diets containing different proteins as a function of food nitrogen. The Ase values reported by HORIE & WATANABE (1983b) were regressed and presented for comparison; the trend obtained for the relation between food nitrogen and Ase of lepidopterans fed on host plants (reported in figure 1 of this paper) is also given.

the low water content of the synthetic diet is responsible for lowering the slope obtained for the synthetic diet. In this context a report by Schramm (1972) is interesting; he observed that synthetic diet for insects generally must contain a minimum of 24% or more of protein but natural feeds containing protein level as low as 14% were adequate for supporting a moth and a beetle. Hence natural and synthetic diets appear to differ in their ability to get assimilated and to support insect growth. Hence, much is to be known to understand the significant differences in the Ase values obtained for natural and synthetic feeds; however it is important for the present to note that food N holds a significant positive relation with Ase.

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