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Colour-polymorphism and dynamics of larch bud moth populations (*Zeiraphera diniana* Gn., Lep. Tortricidae)*

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When subjected to low temperatures (10 °C) larch bud moth larvae of the larch form are more readily modified towards dark and exhibit higher larval mortality as larvae of either the light cembran pine form or the intermediate colourform. Since the dark larch form is also selected against when reared on foliage of larch trees which have been defoliated in previous years, we interpret the cyclic population fluctuation in the subalpine larch-cembran pine forest as the result of an alternate directional selection for two fitness types.

Zeiraphera diniana GUENÉE is a model object for the study of population dynamics as it exhibits the three most important fluctuation types within the relatively small area of Switzerland:

- (1) the cyclic fluctuation with outbreaks at regular intervals of 8-10 years occurs at an altitude of 1800 m in the subalpine larch-cembran pine forest;
- (2) the temporary fluctuation with outbreaks occurring irregularly only in the lower zone of the Norway spruce forest around 1400 m; and
- (3) the latent fluctuation with no signs of defoliation, observed in the artificially grown larch stands in the beech-oak forest of the Swiss plateau at 500-700 m.

The three fluctuation types have been quantified by large scale population sampling. The cyclic population fluctuates at a maximum amplitude of 30 000 in 5 generations, whereas the latent population fluctuates at an amplitude of 12 at a relatively high mean density when expressed on a logarithmic scale (BALTENSWEILER, 1970; AUER, 1975). A thorough analysis of the bud moth life cycle along the altitudinal profile revealed why population growth is continuously favored at the 1800 m level. At this altitude the realisation of the egg potential is best timed with the seasonal temperature cycle. At lower elevations moth longevity is generally short and egg survival is low due to high summer temperatures whereas at higher altitudes moth activity in September is often hindered by evening temperatures below 7 °C. Thus climate and weather determines the optimum zone of development (BALTENSWEILER, 1966; BALTENSWEILER *et al.*, 1969). Maximum larval numbers at defoliation density have been found to vary only within narrow limits, i. e. 259.94 ± 20.93 larvae per kg larch foliage ($n = 8$). This is an indication of maximum carrying capacity. Overpopulation phenomena such as competition for food and space cause heavy larval mortality, lower the fecundity and favour emigration of the moths. In addition, defoliation in June and July changes the physiology of the

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larch tree, which in turn affects the quantity and quality of food for subsequent bud moth generations. After heavy defoliation the larch tree generally refooliates in August, but annual shoot growth is fully or partly inhibited. Even more important is the fact that needle length in the following year may be reduced to less than 50% of the normal length. These shorter needles have a tougher texture and contain a higher proportion of raw fibre and less nitrogen (BENZ, 1974).

Increased larval mortality and reduced fecundity are the most spectacular effects of this induced negative feed back mechanism, which initiates the regression phase of the cycle. Thus the larch bud moth cycle could be understood as the fluctuation of an insect which transgresses the carrying capacity of the host plant periodically due to continuously favourable weather conditions. However, there are additional phenomena which indicate that qualitative changes within the bud moth population are relevant to the cycle.

COLOURMORPHS, DEFINITION AND METHODS

In 1959 we recognized in several field populations a considerable variation in the colouration of 5th instar larvae. The head capsule and the analplate, which are usually black, appeared redbrown or even orange light coloured. The knowledge of dark and light colourforms of the bud moth, confined to either larch or cembran pine (BOVEY & MAKSYMOW, 1959) urged us to investigate the biological implications and possible causes of this phenomenon more closely. The colours of the head capsule (KK), thoracic shield, analplate (AS) and body were assigned to 7, 4, 4, 7 classes respectively ranging from black (class 1) to light orange (class 4) or yellow (class 7). Thus the individuals of the extreme colour phases were characterized by the symbol 1111 and 7447 respectively. For ease of discussion, 5th instar individuals of either a larch form population or a cembran pine form population are grouped according to the following 4 morphotype classes (fig. 1 and fig. 2):

| Larchform (LF) | Cembran pine form (AF) |
|---|--------------------------------------|
| KK, AS completely dark | KK, AS completely and/or partly dark |
| KK dark, AS partly or fully light | KK partly black AS fully light |
| KK partly light AS black | KK light AS partly dark |
| KK, AS range from partly black to completely light | KK, AS completely light |

By expressing the morphotype frequencies in a population as proportions of these 4 classes, the slope of the regression line is a simple measure or index of morphotypic population structure. Thus a negative slope of the regression line means a predominantly dark population, whereas a slope near zero represents a colourtypically heterogenous population containing all phenotypes in \pm equal proportions and a positive slope indicates a light coloured population.

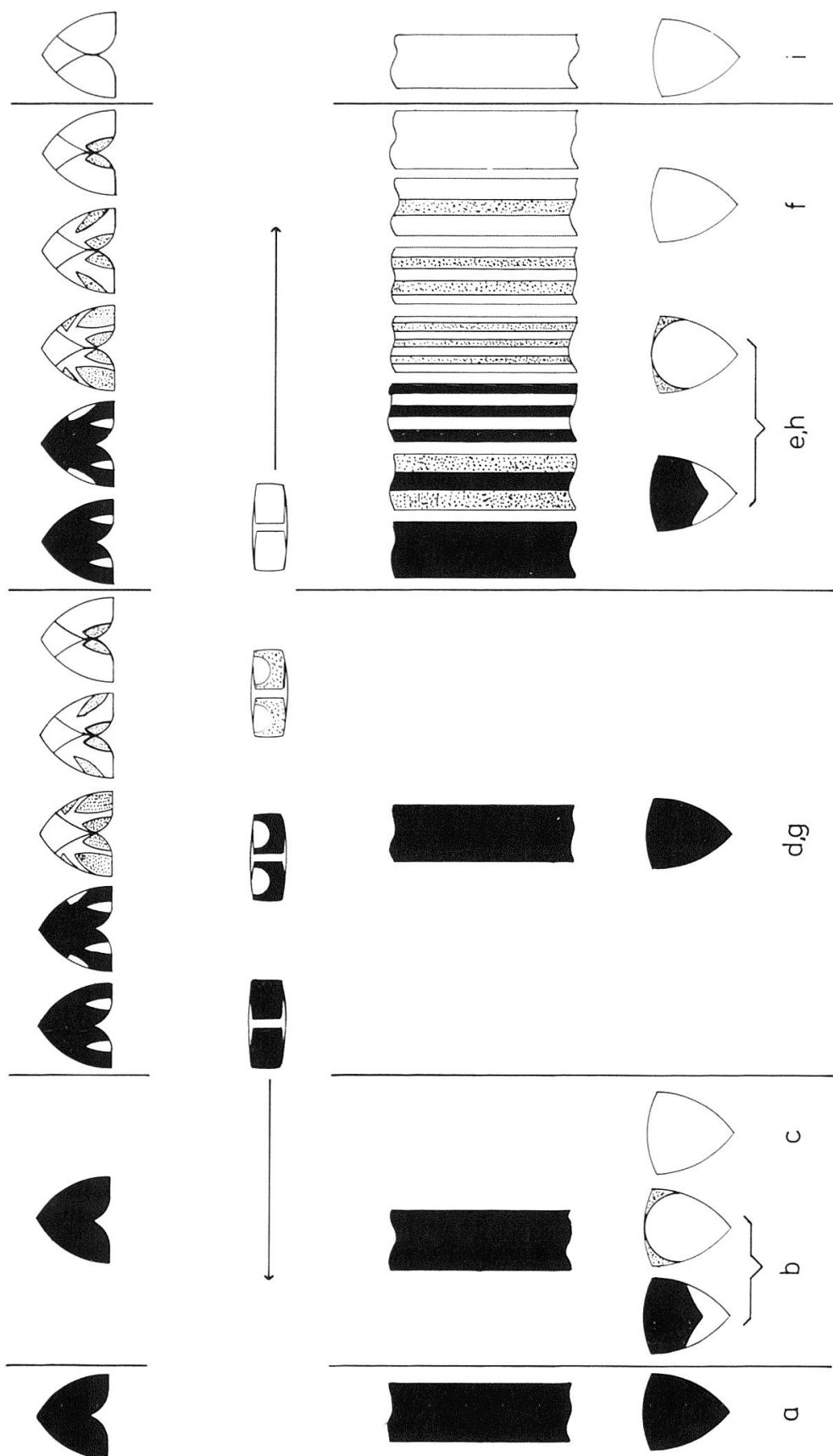


Fig. 1: Scheme of colour-trait-combinations of 5th instar larvae of *Zeiraphera diniana* and definition of colourtype classes

| Treatments | L ₁ -L ₃ | L ₄ -L ₅ |
|------------|--------------------------------|--------------------------------|
| WW | 18 ⁰ C | 18 ⁰ C |
| WC | 18 ⁰ C | 10 ⁰ C |
| CW | 10 ⁰ C | 18 ⁰ C |
| CC | 10 ⁰ C | 10 ⁰ C |

Table 1: X²-test for colour-type frequencies of *Zeiraphera diniana* when reared at various temperature conditions during the larval stage.

| | LF WW | LF WC | LF CW | LF CC | AF WW | AF CC |
|---------------|--------------|--------------|-------------|--------------|----------|----------|
| WW - 3.7 § | -- | | | | | |
| WC -14,7 § | 16.16 *** | -- | | | | |
| CW + 3.8 § | 6.0 | 36.0 *** | -- | | | |
| CC -17.3 § | 27.9 *** | 2.2 | 51.4 *** | -- | | |
| WW 18.3 § | 79.6 *** | 102.3 *** | 58.7 *** | 109.5 *** | -- | |
| CC 10.5 § | 57.1 *** | 73.2 *** | 44.8 *** | 78.8 *** | 7.8 * | -- |

LF: Larchform
AF: Cembran pine form
§ : Structure index
(see text)

*, **, ***, :
P < 0.1, 0.01, 0.001,
resp., df = 3

HEREDITY OF COLOUR TRAITS

Crosses between the dark LF and the light AF forms result in the full range from extreme and intermediate morphotypes, with a morphotypic structure index of 3.3. Crosses of intermediate phenotypes with one of the extreme types result in a preponderance of morphotypes related to the extreme type. By assortative pairing for various colourtraits a complete segregation may be obtained in the second or third generation within a single family. These characteristics suggest that colour morphotypes are determined by an additive expression of multiple genes.

THE INFLUENCE OF NUTRITION ON COLOURTRAITS AND SURVIVAL

Raising of LF and AF on their alternate hosts does not affect the colourtraits of the 5th instar larvae at all; however, the rate of survival is quite distinct. The LF does hardly survive on cembran pine, whereas the AF thrives on larch equally well as on pine (BOVEY & MAKSYMOW, 1959). Similar results were found by DAY & BALTENSWEILER (1972) when rearing dark and intermediate colourmorphs on either optimum (larch) or suboptimum (a semi-synthetic medium; ALTWEGG, 1971) food conditions. Although relative survival for offsprings of dark parents is slightly higher than for those of intermediate parents, the F₁-generation shows on both media higher proportions of intermediate colourtypes.

On the assumption that the experimental results represent a true picture of what would happen in the field, populations under nutritional stress should change faster from one generation to the next to a population of intermediate colourtypes as compared to a population reared on optimal food conditions (DAY & BALTENSWEILER, 1972).

THE INFLUENCE OF TEMPERATURE ON COLOURTYPE FREQUENCY AND SURVIVAL

Bud moth larvae of either the LF or the AF were single reared ex ovo to the fifth instar in equal proportions at 10 °C on larch foliage. In addition, equal proportions of LF were transferred after the completion of their 3rd larval instar from either 10 °C or 18 °C to the alternative temperature.

LF-experiments (tab. 1): The colourtype frequencies of the 4 experimental populations differed in 4 out of 6 comparisons significantly ($P < 0,1$) from each other.

Larvae raised continuously or at least during their latter larval stage at 10 °C were darker than larvae reared at 18 °C. Larval mortality before the 5th instar was significantly higher in the continuous cold treatment, as compared to the other treatments; the high mortality of 38% was due to additional mortality during the 3rd-4th instars (fig. 2).

AF-experiments (tab. 1): In accordance with the LF-experiment the larvae reared at 10 °C are also darker than the 18 °C-population. The Chi-square falls just short of the 5% significance level. The mortalities differ not between the two treatments, but with 14 and 17% they are clearly lower than for the LF-populations (fig. 2).

Discussion: The effect of darkening by the cool temperature on the 5th instar larvae of *Z. diniana* confirms the wide spread phenomenon of Gloger's rule. However, we cannot decide without further analysis whether the significant deviation towards the darker population structure in *Z. diniana* is solely a matter of modification or whether it is due to a selective survival of dark morphotypes prior to the final larval instar. The coincidence of a relatively high proportion of untyped larvae and the greatest deviation in morphotype structures for the 10 °C-LF-population lend support to this argument. However, a first attempt to compare the morphotype structures of the surviving and the dead typed 5th instar populations turned out to be inconclusive. From the four possible comparisons only the warm-cool treatment exhibited a significant difference, and the surviving larvae were more intermediate in colour than the dead ones.

In the following trial, the frequencies of the colour traits AS and KK were evaluated separately as if they were independently inherited. AS-frequencies (tab. 2a) differed three times significantly, whereby the surviving populations were in two cases darker than the dead population. The comparison of the KK-trait (tab. 2b) resulted in two significant differences; but in contrast to the AS-criterion, the surviving population was somewhat lighter than the dead population. This was due to the fact that within each population a few individuals with very light KK (6,7) survived. This result again is in accordance with the general observation that AF-populations suffer significantly less mortality than the LF, irrespective of temperature or nutritional stress.

a to i : morphotypes grouped in 4 classes
 tt : temperature treatment
 m : larval mortality in %
 b : colourtype-structure index (slope of regression line)
 r_2 : correlation coefficient
 χ^2 : Chi-square for morphotype-structure, see legend table 1

| | | tt | m | b | r | χ^2 |
|-------|----|------|------|-------|------|----------|
| ----- | LF | 10°C | 38.2 | -17.3 | 0.94 | *** |
| ———— | LF | 18°C | 24.0 | -3.7 | 0.99 | |
| ----- | AF | 10°C | 16.7 | 18.3 | 0.53 | * |
| ———— | AF | 18°C | 14.2 | 10.5 | 0.71 | |

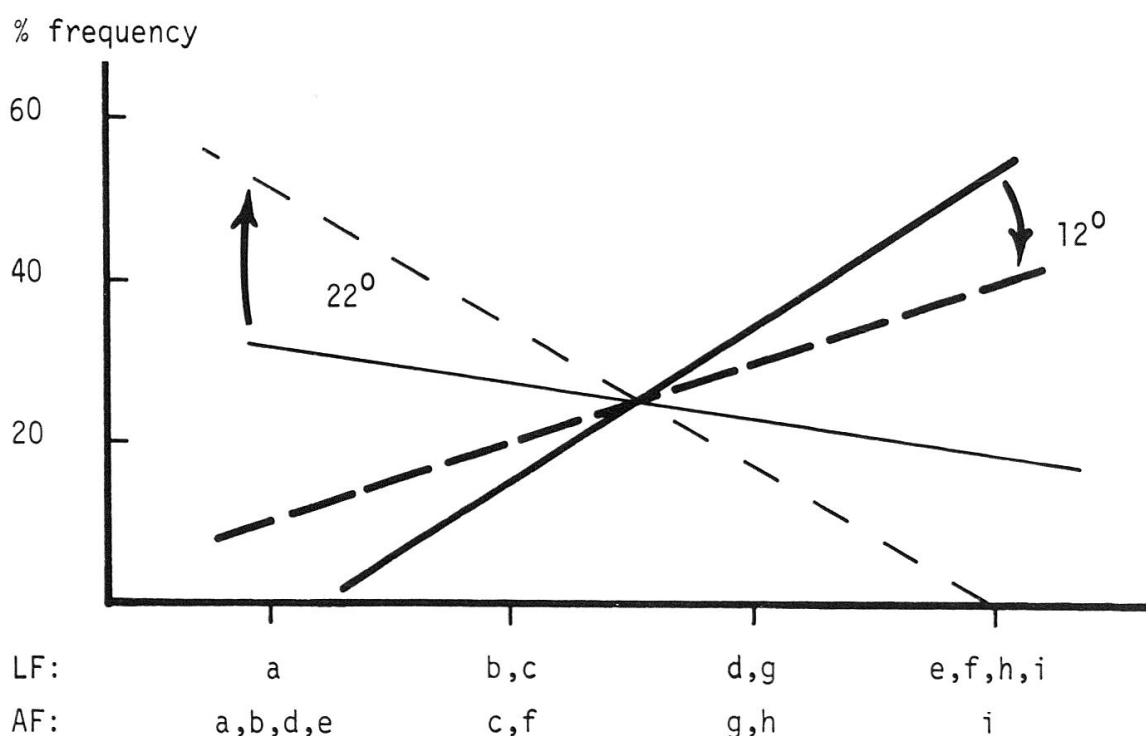


Fig. 2: Influence of rearing temperatures, either 10 °C or 18 °C, on colouration of 5th instar larvae expressed by the frequencies of colour-types. LF: larchform; AF: cembran pine form

From these findings it is concluded that temperature influences the colourtype structure also through selection. In summary, any evaluation of colourtype structure of *Z. diniana* populations should consider the effect of temperature through modification or selection. Since rearing conditions which confer minimum mortality reflect the intrinsic colourtype structure in the best possible way, a colourtype structure derived from individuals reared at constant 18 °C could serve as a standard structure index against which the field structure index may be compared.

VARIATION OF MORPHOTYPE STRUCTURE IN TIME AND SPACE

In connection with annual routine sampling of the eggstage and the late larval instars we determined the standard and the field morpho-structures for

| s | d | WW -9.1 § | WC -18.5 § | CW -6.5 § | CC -8.5 § |
|----|---------|--------------|---------------|--------------|--------------|
| WW | -10.3 § | 4.9 | | | |
| WC | -11.3 § | | 8.8 * | | |
| CW | -8.5 § | | | 6.4 * | |
| CC | -16.8 § | | | | 9.7 * |

Table 2: χ^2 -test for colourclass-frequencies of the analplate (table a) and head capsule (table b) of surviving and dead individuals when reared in various temperature conditions (see legend table 1)

a

| s | d | WW -7.5 § | WC -10.3 § | CW -8.1 § | CC -10.3 § |
|----|---------|--------------|---------------|--------------|---------------|
| WW | -8.1 § | 4.1 | | | |
| WC | -9.3 § | | 5.8 | | |
| CW | -7.2 § | | | 11.0 * | |
| CC | -10.1 § | | | | 8.7 * |

b

s, surviving 5th instar larvae

d, dead 5th instar larvae

§, structure index

*, Chi-square: $P < 0.1$, $df = 3, 4, 5$

several years. The variation of the morphotype indices and of the larval density/kg larch foliage are presented for 3 populations:

The Sils and the Val Aurina population are characteristic for the cyclic fluctuation type, the Lenzburg population is representative for the latent fluctuation area (SCHWERDTFEGER, 1968; AUER, 1975) (fig. 3).

The morphotype indices of the Sils population exhibit a remarkable synchrony with the density curve. At maximum densities in 1972 and 1973, the field colour index reflects by its large negative values a dark population, whereas at low density colourstructure is intermediate. The variation of the standard index is very similar, but it remains largely in the range of positive or zero-index values which indicates an intrinsically much more heterogenous colour type structure.

The increase of the Val Aurina population was stopped in 1972 well below defoliation density. Although the reasons for this phenomenon are not yet fully understood, we interpret the immediate return of the field structure index to zero values to signify a powerful selection process.

The latent Lenzburg population is characterized at first by positive structure indices, both for field and standard populations, but in 1972 they begin to fluctuate in antagonistic manner. BALTENSWEILER & VON SALIS (1975) and GRAF (1974) detected in fall 1971 large distance immigration from subalpine outbreak areas. Their offsprings shift the field index in 1972 considerably towards dark and with a time-lag of one year, their impact is reflected in the standard index. Moth immigration continued until 1974 but the local density

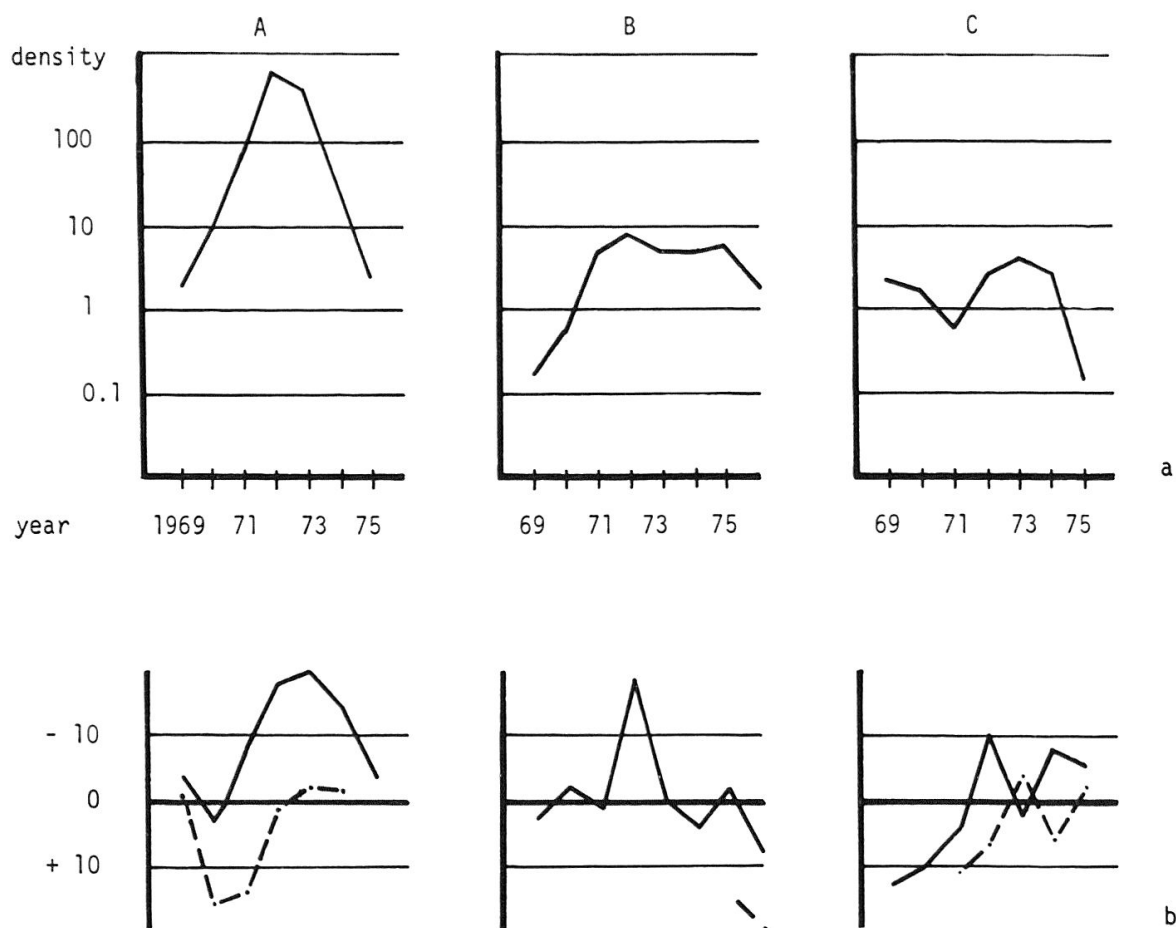


Fig. 3: Variation in field- and standard morphotype-structure index for three larch bud moth populations. a: Fluctuation of population density, larvae per 1 kg larch branches. b: Variation of the colourtype-structure index b: - field colourtype-structure index: --- standard colourtype-structure index. A: Sils, Engadine, 1800 m; B: Val Aurina, Southern Tyrol, 1800 m; C: Lenzburg, Aargau, 500 m.

failed to increase beyond 3 larvae/kg foliage. Temperature and/or nutrition are considered to exert a strong selection pressure on this latent population, but analogous to the Val Aurina case, the specific processes await further analysis.

CONCLUSIONS

The experimental evidence that a temperature difference of constant 8 °C at otherwise identical rearing conditions increases the colour index of the LF by 22 degree, but lower the AF-index by only 12 degree suggests that the LF is either more responsive to cool temperatures and/or more easily subjected to selection by temperature. At the more restricted scale within the LF-population we recognized that the extreme LF-colourtype is much more vulnerable to nutritional selection than the intermediate LF. The dark bud moth type represents therefore a highly specified phenotype, which increases relatively and absolutely under optimum environmental conditions only, whereas after defoliation the intermediate phenotype is selected for.

The bud moth cycle in the subalpine larch-cembra pine forest is conceived as the result of directional selection for two phenotypes, whereby

the selfinduced periodic deterioration of the nutritional environment, the rate of recovery of the host tree as well as the time-lag involved in the recombination of genes are considered as the driving forces.

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ZUSAMMENFASSUNG

Farbpolymorphismus und Dynamik von Lärchenwicklerpopulationen (Zeiraphera diniana Gn., Lep. Tortricidae) – Aufzuchtversuche mit Larven der Lärchenform und der Arvenform zeigen, dass sich die Lärchenform durch kühle Temperaturen stärker gegen schwarz modifizieren lässt und auch eine höhere Mortalität erleidet als die Arvenform oder die intermediären Formen. Weil die durch Kahlfrass verursachte Verschlechterung der Nadelqualität ebenfalls die intermediäre Form begünstigt, wird die zyklische Populationsbewegung im subalpinen Lärchen-Arvenwald als das Ergebnis einer alternierend gerichteten Selektion für zwei Phaenotypen unterschiedlicher Fitness interpretiert.

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