Cyanogenesis in Eschscholzia Cham. I. Preliminary report on some polymorphic populations of annuals from Arizona and Southern California = Cyanogenese bei Eschscholzia Cham. I. Vorläufige Mitteilung über einige polymorphe Populationen einjähriger Taxa ...

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Cyanogenesis in *Eschscholzia* Cham.
I. Preliminary report on some polymorphic populations of annuals from Arizona and Southern California

Cyanogenese bei Eschscholzia Cham.
I. Vorläufige Mitteilung über einige polymorphe Populationen einjähriger Taxa in Arizona und Südkalifornien

by

Krystyna URBANSKA

Contents

1. Introduction

Taxa in which the cyanogenesis is a polymorphic character are of a particular interest to ecological genetics for selective factors involved in the maintenance of the polymorphism seem to remain in a certain balance. Hitherto obtained data suggests that respective frequencies of cyanogenic and acyanogenic individuals are likely to be related to some biotic and/or abiotic habitat components.

The production of cyanide is widespread among the plants, at least 750 species representing approximately 60 families and 250 genera being noted by HEGNAUER (1963). However, the number of polymorphic taxa known so far is very limited. Out of about a dozen examples reported in the Angiosperms, solely *Trifolium repens, Lotus corniculatus* and *L. alpinus* were studied in more detail on population level (e.g. DADAY 1954a, b, 1965, JONES 1970, 1972, 1973, FOULDS and GRIME 1972a, b, ARAUJO 1976, URBANSKA and WILDI 1975, URBANSKA et al. 1979, URBANSKA and SCHWANK 1980). All the species found to date polymorphic for the cyanogenesis are perennials.

Cyanogenesis in the *Eschscholzia* Cham. was reported for the first time by ROSENTHALER (1926); it was subsequently observed by HEGNAUER (1961) and some of his collaborators (TANTISEVIE et al. 1969, VAN VALEN 1978). The very few individuals investigated by these authors represented both perennial as well as annual types and were invariably cyanogenic. It seemed interesting to examine *Eschscholzia* for a possible polymorphism of cyanogenesis, especially in relation to iteroparous and semelparous strategies occurring in closely related taxa of the genus. Annuals being a prime object for such investigations, populations of *Eschscholzia* cf. *mexicana** from Arizona and Southern California were chosen. The present paper deals with the first results obtained in the field; some aspects of the cyanogenesis within the genus *Eschscholzia* that may prove relevant for further studies are briefly reviewed as well.

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* The nomenclature is provisionally retained; however, *E. mexicana* being rather variable, some characters considered as diagnostic should be revised. Plants exactly corresponding to *E. glyptosperma* Greena were not observed.

Acknowledgements

Prof. Dr. Stan Szarek from Dept of Botany and Microbiology, Arizona State University at Tempe sampled with us two populations of *Eschscholzia* in surroundings of Phoenix, AZ; his friendly help as well as interesting comments are greatly appreciated. Very cordial thanks are addressed to my son Christopher who was an excellent field assistant and did the long-distance driving. Prof. Dr. R. Hegnauer from Institute of Experimental Plant Systematics, University of Leiden, Netherlands, kindly provided a graded colour table for semi-quantitative evaluations of HCN content; we gratefully acknowledge his help. Thanks are also due to Dr. B. Krüsi, Geobotanical Institute SFIT Zürich who made the drawings as well as Prof. Dr. E. Landolt who translated the summary into German. Ms. A. Honegger carefully typed the manuscript.

2. Nature of cyanogenic compounds in *Eschscholzia*

In most of the cyanogenic species studied, glycosides are the main source of the HCN (see e.g. GIBBS 1963). This is also the case of the taxa belonging to the genus *Eschscholzia* that were studied to date. ROSENTHALER (1926) suggested the presence of a linamarin-type compound in *E. californica* and *E. aurantiaca*. On the other hand, RUIJGROK (1967) extracted from *E. lobbii* a cyanogenic constituent which was comparable in chromatographic behaviour to the compounds of some *Ranunculaceae* presently known to contain the tyrosine-derived triglochinin and dhurrin as principal glycosides (Fig. 1). TANTISEVIE et al. (1969) considered cyanogenic compounds occurring in *E. californica* and those in *E. minutiflora* s.l. as closely related to glycosides occurring in *Thalictrum aquilegifolium*, *Ranunculus arvensis* and *Isopyrum fumarioides*; however, except for a brief reference to the data of RUIJGROK (1967), he did not produce any further evidence in favour of this opinion. The only precise data, well supported by various experimental results,are those of VAN VALEN (1978) who found triglochinin as the sole cyanogenic glycoside in *Eschscholzia californica*. Curiously enough, TJON SIE FAT (1979) positively listed both triglochinin and dhurrin in *E. californica* referring not only to the data of VAN VALEN (1978) but also to the suggestions of TANTISEVIE et al. (1969). Other taxa of the taxonomically complex genus *Eschscholzia* remain to be investigated as far as the character of cyanogenic compounds is concerned.

The available data on the nature of cyanogenic constituents within the genus *Eschscholzia* are thus sometimes conflicting. It should be added that also other taxa within the family of *Papaveraceae* do not appear to be sufficiently known in this respect; for instance ABROL (1966) reported linmarin and lotaustralin in *Papaver nudicaule*, whereas VAN VALEN (1978) observed in this taxon exclusively dhurrin and triglochinin. It should be most instructive to know whether only tyrosine or some other amino acids as well (e.g. valine and isoleucine) might be considered as precursors of cyanogenic glycosides occurring within the family, and in particular, within the genus *Eschscholzia*.

It is interesting to note that plants capable to produce hydrocyanic acid can frequently be dried without appreciable losses of cyanogenic compounds and herbarium specimens can thus not only be used for the HCN-test but also

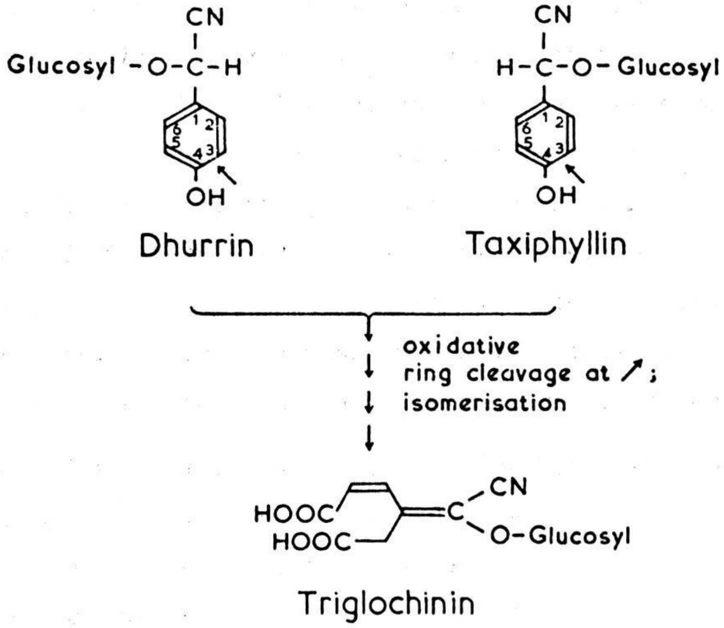


Fig. 1. Three tyrosine-derived cyanogenic glucosides: dhurrin, its diastereomer taxiphyllin and triglochinin.

Abb. 1. Drei cyanogene Glykoside, die aus Tyrosin enstanden sind: Dhurrin, dessen Diastereomer Taxiphyllin und Triglochinin.

the identification of cyanogenic glycosides (e.g. TJON SIE FAT 1977). As far as the genus *Eschscholzia* is concerned, specimens of *E. californica* s.l. and those of *E. minutiflora* s.l. invariably proved to be strongly cyanogenic when tested eight months after having been collected in their natural habitats (TANTISEVIE et al. 1969). On the other hand, no positive reaction was observed by the present author in a few specimens of *E. mexicana* representing the herbarium material gathered in the field about three months before the test; further investigations are planned. Our herbarium specimens not being tested prior to the pressing, a negative test does not necessarily correspond to a loss of cyanogenic compounds but might be related to acyanogenic individuals.

3. Methods used in studies on cyanogenesis within *Eschscholzia* and data on HCN content in some taxa of the genus

Quantitative procedures required for a precise evaluation of HCN content are very complicated and thus hardly satisfactory for scientists dealing with large numbers of plants but not particularly concerned with the absolute amount of the HCN. A simple qualitative method is largely preferable for field purposes and the standard picrate paper test (MIRANDE 1909, DAWSON 1941) represents a current treatment. In the course of the present study, the picrate paper test was carried out with a sulphur-free toluene as the organic dissolvent. Most frequently, leaves of *Eschscholzia mexicana* were examined but sometimes developing fruits were used as well.

The picrate paper test renders possible the distinction between two gross phenotypes respectively referred to as acyanogenic and cyanogenic. A negative test when the yellow colour of the picrate paper remains unchanged covers three possible situations viz. 1) glycoside but no enzyme present, 2) enzyme but no glycoside present and 3) both constituents absent. All these variants are collectively named acyanogenic. On the other hand, a positive test with the picrate paper turning orange to brownish-red obviously indicates cyanogenic plants carrying both glycoside and enzyme. According to HEGNAUER (1958), a positive picrate paper test should correspond to at least 10 mg of HCN per kg of fresh plant weight.

Data on HCN content in *Eschscholzia* are very fragmentary so far. Precise assessments were made first by ROSENTHALER (1926) in two plants; he found 50 mg of HCN/kg fresh weight in *Eschscholzia californica* and 60 mg of HCN/kg fresh weight in *E. aurantiaca*. HEGNAUER (1961) reported in four individuals of *E. californica* 17-20, 18, 19 and 38 mg/kg, respectively, whereas in *E. lobbii* 50 mg/kg were found It should be added that VAN VALEN (1978) recently obtained in *E. californica* 63 mg of triglochinin from only 40 g of fresh leaves and stems which should correspond to 1575 mg of the glycoside per kg.

For semi-quantitative evaluation of HCN content, HEGNAUER and his collaborators use a graded colour table prepared with various HCN concentrations (HEGNAUER, personal communication). This method proved to be useful for rough estimations of HCN content in the studied material of *Eschscholzia mexicana* (see p. 60-61). Our assessments have primarily a comparative value and should be further verified.

4. Field results

4.1. *Notes on site conditions and population structure*

Out of six populations of *Eschscholzia mexicana* studied in the course of the present work, four are situated in Arizona and two in Southern California. As far as the vegetation type is concerned, the Arizonian stations correspond to the Upper Sonoran level; the two Californian sites from Joshua Tree National Monument belong to the Mojave Desert range, *Yucca brevifolia* being the most outstanding element of the landscape.

The brief descriptions of the studied sites represented below are far from being complete and comprise only general characteristics; however, they were considered as useful references for a preliminary report.

Populations of *Eschscholzia* studied in spring 1981 obviously were not at their best as winter precipitations in the Southwest apparently have not reached a level sufficient for a more spectacular display of annuals.

Site A 1: Arizona, Pinal Co., Picacho Peak State Park: a SW-facing bajada. Coarse mineral soil. *Eschscholzia* observed most frequently in open surfaces between *Cercidium microphyllum, Cereus giganteus* and other high-growing species.

Population fairly large but scattered, small groups of individuals comprising four to twelve plants being only seldom noted. All plants at pre-dispersal stage with the developmental phases ranging from flower buds to overblown flowers with shed petals and well-advanced fruit development. Site visited on March 27, 1981.

Site A 2: Arizona, Pima Co., Organ Pipe Cactus National Monument: a NE-facing bajada within the Ajo Mountains range. Coarse mineral soil. *Eschscholzia* occurring in open sectors.

Population medium-sized, individuals very scattered. Plants with a very low growth yet the flower size mostly representative of the taxon. Pre-reproductive and reproductive stages, most frequently open flowers with anthers at dehiscence. Site visited on March 29, 1981.

Site A 3: Arizona, Maricopa Co., South Mountain State Park: a N-facing slope burnt in the previous year. Mineral soil with some large stones, size of the soil particles rather variable. *Eschscholzia* observed mostly in half-open or open surfaces.

Population medium-sized, plants tending sometimes to grow in patches. Pre-reproductive and reproductive stages, open flowers frequent. Site visited on April 1, 1981.

Site A 4: Arizona, Maricopa Co., an arroyo near the Saguaro Lake. The site apparently burned previously. Alluvial soil with bare sectors; *Acacia Greggii* rather frequent. Occurrence of *Eschscholzia* erratic.

Population exceedingly scattered: except for a few small groups comprising four to five individuals, only single plants were observed. In spite of careful search, only 68 plants altogether were found within a rather large surface. Nearly all individuals at the same reproductive phase with open flowers. Site visited on April 1, 1981.

Site C 1: California, San Bernardino Co., Joshua Tree National Monument: a gently sloping E-facing surface near the North Exit. Vegetation on sandy soil. *Eschscholzia* mixed with numerous other species (e.g. *Baeria chrysostoma, Lesquerella palmeri, Calycoseris parryi*); stands of flowering annuals locally quite dense between shrubs.

Population large, groups comprising numerous individuals frequent. Pre-reproductive and reproductive phases, very numerous plants with several young flower buds and open flowers. Site visited on April 8, 1981.

Site C 2: California, Riverside Co., Joshua Tree National Monument: a sandy basin south of the Cholla Garden. *Larrea tridentata, Franseria dumosa* and other shrubs alternating with dense stands of annuals at full blossom. *Eschscholzia* very abundant among them.

Population very large and locally quite dense. Pre-reproductive and reproductive stages, plants mostly with at least one open flower. Site visited on April 9, 1981.

4.2. Polymorphism of cyanogenesis in *Eschscholzia mexicana*

Save for one, the studied population samples of *E. mexicana* proved to consist of both cyanogenic as well as acyanogenic plants; thus, to the best of our knowledge, this is the first case of the polymorphism of cyanogenesis being found in an annual taxon and also the first one as far as the genus *Eschscholzia* is concerned.

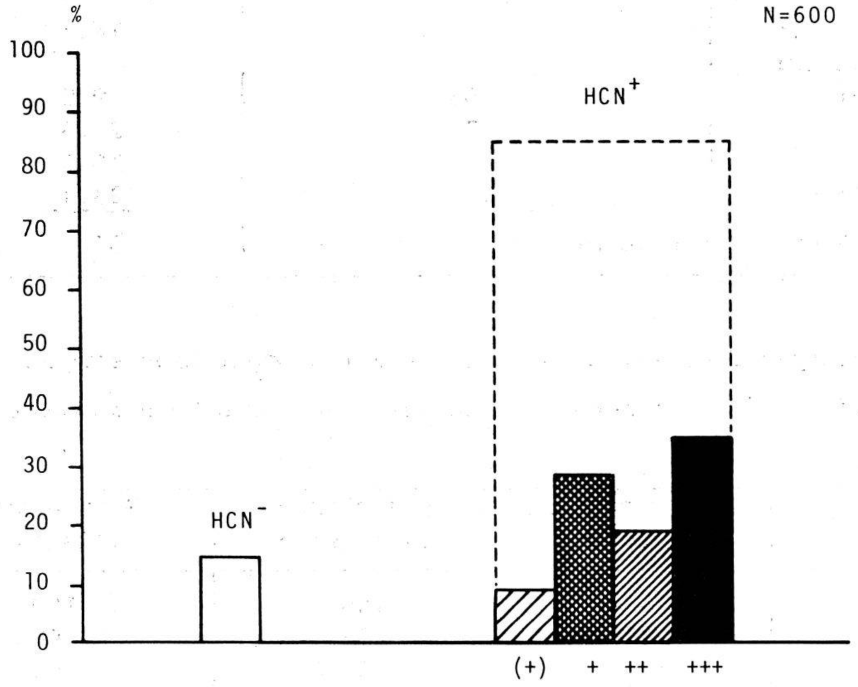


Fig. 2. Polymorphism of cyanogenesis in the studied material of *E. mexicana*: frequencies of cyanogenic and acyanogenic phenotypes globally evaluated. ▧ HCN(+) ▩ HCN+ ▨ HCN++ ■ HCN+++

Abb. 2. Cyanogenese-Polymorphismus bei E. mexicana: Häufigkeit der cyanogenen und acyanogenen Phänotypen (Gesamtauswertung der untersuchten Pflanzen).

A global evaluation of the HCN-tests carried out in 600 individuals reveals an exceedingly interesting situation: not only does the cyanogenic phenotype prevail largely over the acyanogenic one, but also there seems to occur a positive shift in frequencies towards strongly cyanogenic plants (Fig. 2, Table 1). However, acyanogenic individuals apparently are able to maintain their presence within populations.

Table 1. Phenotypic frequencies within the studied material of *E. mexicana*: a global evaluation based upon 600 HCN-tests.

Tab. 1. Häufigkeit der Phänotypen von E. mexicana (Gesamtauswertung aufgrund von 600 HCN-Tests.

Phenotype	Number of individuals	Frequency (%)
acyanogenic	88	14.7
cyanogenic:		
HCN (+)	54	9.0
HCN +	138	23.0
HCN ++	114	19.0
HCN +++	206	34.3
Total % of cyanogenic plants:		85.3

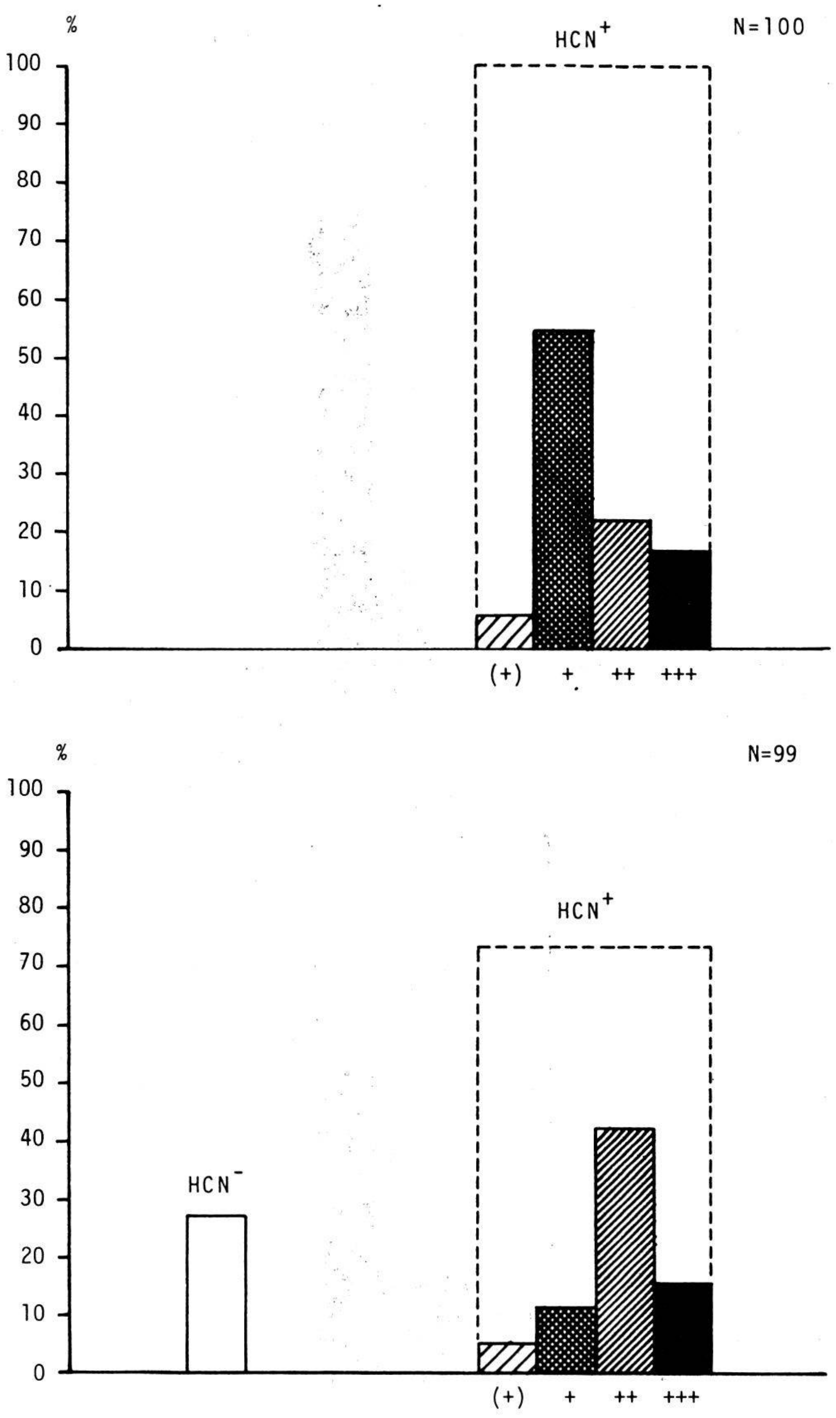
Table 2. Phenotypic frequencies within 6 studied population samples

Tab. 2. Häufigkeit der Phänotypen innerhalb von sechs Populationsproben

Sample code*	Frequencies (%) of phenotypes Acyanogenic	Cyanogenic	N of plants in sample
A 1	0	100.0	100
A 2	7.3	72.7	99
A 3	6.3	93.8	98
A 4	1.5	98.5	68
C 1	39.0	61.0	100
C 2	11.1	88.9	135

* see description of studied sites (p. 54)

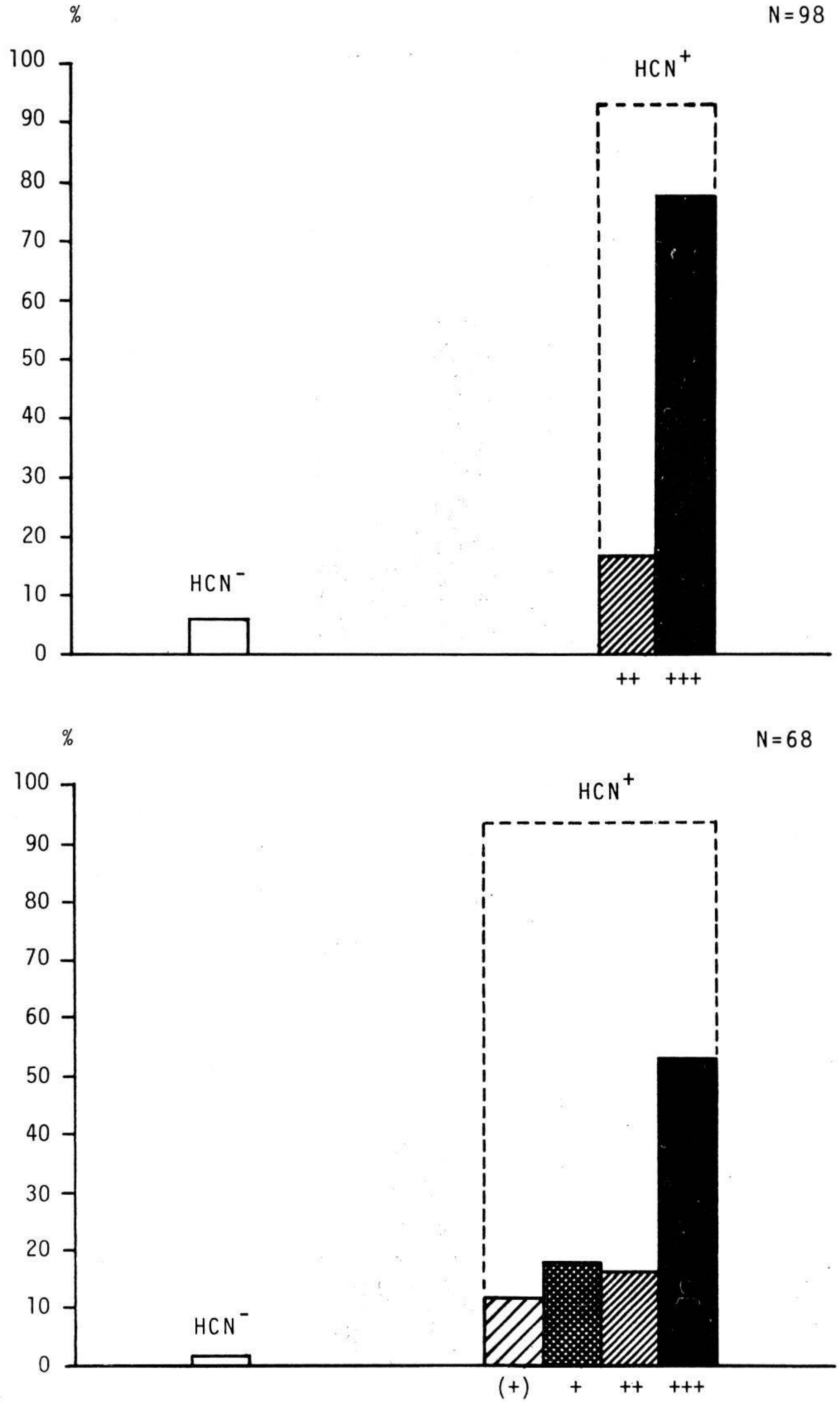
The second aspect of the polymorphism of cyanogenesis found in *E. mexicana* is an apparent variation in phenotypic frequencies occurring between populations (Table 2, Figs 3-8); this feature shall be given a particular attention



Figs 3-4. Phenotypic frequencies in populations from Arizona.
3. Site A 1. 4. Site A 2. Cyanogenic plants:

▧ HCN (+) ▦ HCN+ ▨ HCN++ ■ HCN+++

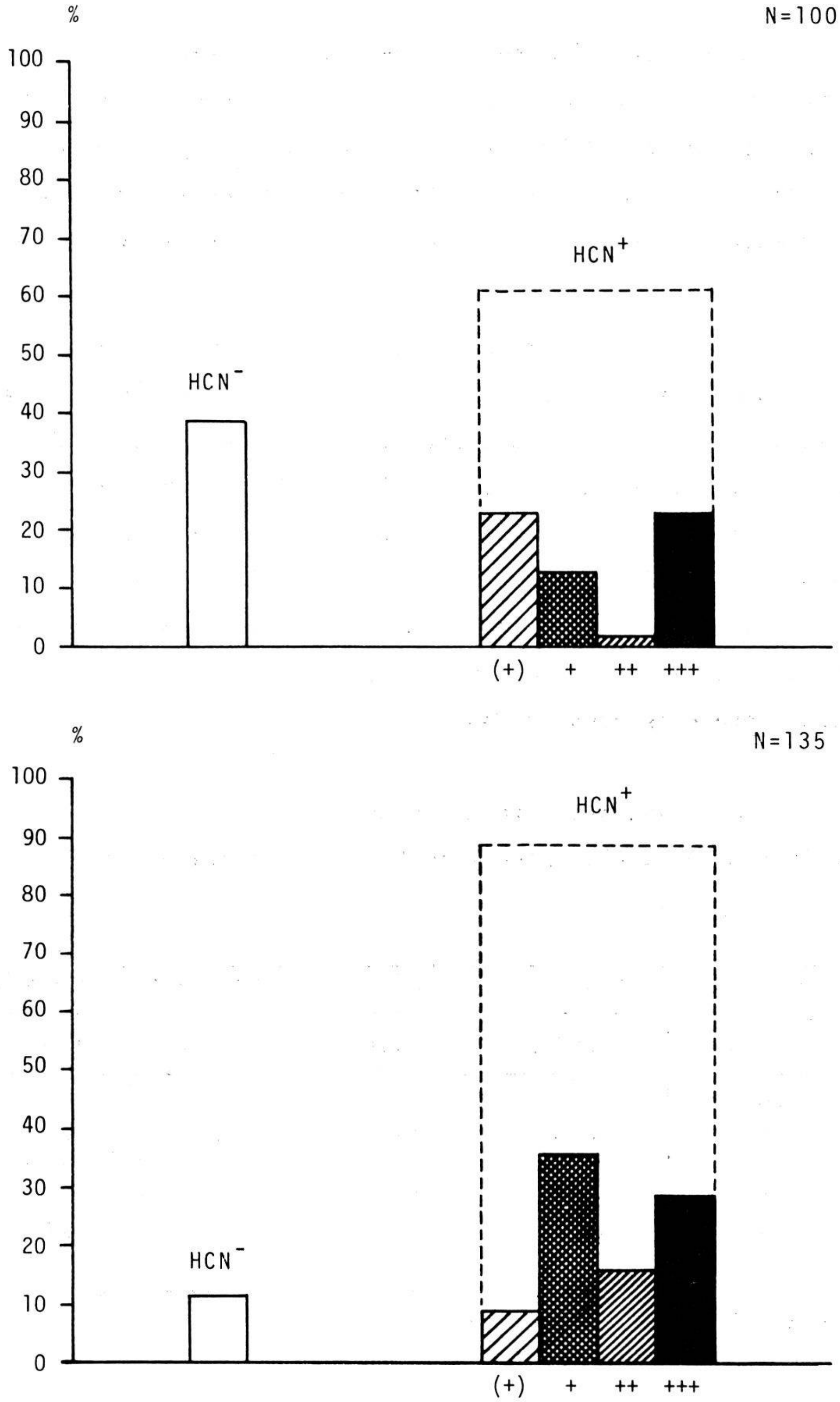
Abb. 3-4. Häufigkeit der Phänotypen in Populationen aus Arizona.
3. Fundort A 1. 4. Fundort A 2. Cyanogene Pflanzen:



Figs 5-6. Phenotypic frequencies in populations from Arizona.
5. Site A 3. 6. Site A 4. Cyanogenic plants:

▨ HCN (+) ▩ HCN+ ▨ HCN++ ■ HCN+++

Abb. 5-6. Häufigkeit der Phänotypen in Populationen aus Arizona.
5. Fundort A 3. 6. Fund A 4. Cyanogene Pflanzen:



Figs 7-8. Phenotypic frequencies in populations from California.
7. Site C 1. 8. Site C 2. Cyanogenic plants:

▨ (HCN)+ ▩ HCN+ ▨ HCN++ ■ HCN+++

*Abb. 7-8. Häufigkeit der Phänotypen in Populationen aus Kalifornien.
7. Fundort C 1. 8. Fundort C 2. Cyanogene Pflanzen:*

in future investigation. For the time being, the studied material is far too limited and any conclusions would be purely speculative. However, it should be pointed out that, given the annual habitat of *E. mexicana*, populations of this taxon might be liable to annual fluctuations in frequencies of cyanogenic/acyanogenic phenotypes influenced perhaps by current ecological conditions.

A further interesting detail is the variation in HCN content of cyanogenic plants apparently occurring within the examined population samples. Even allowing for some differences in the actual size of sample per individual that are inevitable in a field study and might sometimes influence the HCN-test, colour changes of the picrate paper were very distinct. Using this criterion, we assigned the studied material to four classes respectively codified as HCN(+), HCN+, HCN++ and HCN+++; the code HCN(+) corresponded to the weakest positive test, whereas HCN+++ indicated an exceedingly strong reaction. The resulting evaluations are presented in Table 3.

Table 3. Intra-populational variation in HCN content

Tab. 3. Variation des Blausäuregehaltes innerhalb von Populationen

Sample code*	Sample size (N)	N of cyanogenic plants	Frequencies (%) of particular cyanogenic types			
			HCN (+)	HCN+	HCN++	HCN+++
A 1	100	100	6.0	55.0	22.0	17.0
A 2	99	72	6.9	14.0	58.3	20.8
A 3	98	92	0	0	17.4	82.6
A 4	68	67	11.9	17.9	16.4	53.8
C 1	100	61	37.7	21.3	3.3	37.7
C 2	135	120	10.0	40.0	17.5	32.5

* see description of the studied sites (p. 54).

With help of a graded colour table kindly put at our disposal by Prof. Dr R. HEGNAUER (Leiden, Netherlands), an attempt was made to estimate HCN content within each of the four classes. The results suggest that *E. mexicana* may often contain rather important quantities of HCN, for HCN(+) should roughly correspond to about 8-40 mg of HCN/kg fresh weight, HCN+ - 60-80 mg/kg, HCN++

- 100-120 mg/kg and HCN+++ - 140-200 mg/kg. Our estimations are obviously subject to further verifications; be as it may, they do partly corroborate the detailed quantitative data of ROSENTHALER (1926) and those of HEGNAUER (1961) obtained in the genus *Eschscholzia* (see p. 53). It should be added that MIRANDE (1913) found in another member of the family *Papaveraceae* viz. hybrid *Papaver nudicaule x alpinum* the HCN content ranging from 10 to 180 mg/kg. It should be most interesting to know exactly the HCN content in *Eschscholzia mexicana*, maximal values being of a particular importance.

5. Discussion

No attempt is made in the present paper to do more than indicate a few aspects of the cyanogenesis and its importance for natural plant populations. It seemed advisable to place our preliminary data on *Eschscholzia mexicana* within a general frame of knowledge on the subject; for more extensive information, the reader is referred e.g. to the excellent reviews by ROBINSON (1930), JONES (1972, 1978) as well as CONN and BUTLER (1969).

A possible rôle in the nitrogen metabolism as well as defence against predators represent two main functions ascribed to cyanogenic glycosides. The third suggested function viz. waste products seems rather unlikely, especially in taxa that contain important concentrations of cyanide. It is hardly acceptable that e.g. 122 mg of HCN/kg fresh weight observable in *Melica uniflora* (HEGNAUER 1958), about 340 mg/kg occurring in *Trifolium repens* under pasture conditions (MELVILLE et al. 1940), let alone the exceedingly high content of 500-1030 mg/kg in *Taxus media* (HEGNAUER 1958), should be considered as mere waste products amassed and excreted by the plants.

As far as cyanogenic glycosides and the nitrogen metabolism is concerned, ABROL et al. (1966) positively showed an active turnover of cyanide in *Lotus* spp. and *Nandina domestica*. Results of BLUMENTAHL et al. (1968) indicate that the cyanogenic compound vicianin probably represents a step in the biosynthesis of β-cyanoalanine in *Vicia angustifolia*. According to recent contributions of SOLOMONSON and SPEHAR (1977) as well as ECK and HAGEMANN (1974), even a more fundamental rôle seems to be played by endogenous HCN in nitrate reductase regulation. BOYD et al. (1938) observed in *Sorghum vulgare* that a high level of available nitrogen and a low level of available phosphorus in the soil tended to increase the cyanide content, drought probably operating as an indirect factor by lessening the availability of phosphates. URBANSKA and SCHWANK (1980) found in natural populations of *Lotus alpinus* a racial differentiation apparently influenced by edaphic conditions: plants from dolomite soils where the water régime was unfavourable and bound nitrogen occurred mostly in form of the nitrate, were much more frequently cyanogenic than individuals from acidic silicate or serpentine, the respective global frequencies being 40.9 % vs. 16.9 % and 4.3 %. These data seem to suggest certain relationships between soil nitrogen, water deficiency and cyanogenesis in some taxa. As far as *Eschscholzia mexicana* is concerned, data on nitrogen and phosphorus content in the soil from the studied sites are unavailable so far; however, desert soils are generally considered as tending to be poor or deficient in these elements. It is not excluded that drought conditions might influence to some extent the pronounced cyanogenesis in *Eschscholzia*; however, only adult populations were studied to date and we do not know anything about germinating behaviour and seedling establishment in the taxon. It should be noted that data on germination and early life phases of desert annuals are sometimes conflicting. For instance, JUHREN, WENT and PHILLIPS (1956) as well as WENT (1973) reported only a negligible mortality of seedlings and apparently little selection acting at this life phase of annuals from Joshua Tree National Monument as well as Death Valley. Contrary to these data, BEATLEY (1967) supposed that the majority of desert annuals do not survive to maturity in most years on most sites in the northern Mojave Desert.

Another possible basic function of the cyanogenesis is a defence against herbivores of all kinds. CONN (1966) has suggested that plants have maintained the capacity to produce cyanogenic glycosides because of survival and protective value which they confer. EHRLICH and RAVEN (1965) consider cyanogenic glycosides together with other secondary compounds as a "biochemical shield" that assured the high degree of diversification in higher plants. JANZEN (1971) suggested that cyanogenesis might be a part of reproductive strategy of the plant species representing a kind of material investment in taxa subject to significant mortality from seed predators. It should be noted that FREELAND and JANZEN (1974) who reviewed the rôle of secondary compounds in strategies of herbivory pointed out to high metabolic expense involved in their production. It should be most interesting to obtain some more data in this respect, patterns of resource allocation in plant strategies being still largely unknown.

Both direct and circumstantial evidence of a protective function of the cyanogenesis is now available, studies in natural habitats as well as laboratory experiments being reported (e.g. JONES 1962, 1966, CRAWFORD-SIDEBOTHAM 1972, ANGSEESING and ANGSEESING 1972, ELLIS et al. 1977a, c, DEMENT and MOONEY 1974, SHERBROOKE 1976). On the other hand, numerous animals and plants are able to eat or parasitize cyanogenic plants so it seems that cyanogenesis represents a defence mechanism that is by no means absolute. However, as reasonably pointed out by JONES (1972), cyanogenesis may not be efficient but it may well be sufficient to defer many would-be grazers or parasites. This assumption seems to be particularly valid for plants that contain large quantities of cyanogenic compounds. As far as the studied populations of *Eschscholzia mexicana* are concerned, plants at reproductive stage did not manifest any particular herbivore damages either in vegetative parts or developing fruits; it could be supposed that the high HCN content may protect the adult but for a full evaluation studies on seeds and seedlings are indispensable. It also remains an open question whether much less frequent acyanogenic individuals might profit in this respect from the close neighbourhood of strongly cyanogenic plants.

The two explanations proposed for a possible rôle of cyanogenesis in plants obviously are not mutually exclusive but might both be pertinent. It is entirely conceivable that cyanogenic glycosides may have a double function and therefore be relevant both for nitrogen economy as well as defence purposes of a given plant. Such an interpretation was offered recently by DEMENT and MOONEY (1974) for a seasonal variation in production of cyanogenic glycosides in *Heteromeles arbutifolius*: glycosides are produced in the spring when nitrogen is available due to prevailing warm moist conditions favourable to rapid N-cycling; later on, as nitrogen becomes limiting and predation pressures decrease, nitrogen pool can be depleted i.e. glycosides metabolized and the nitrogen is utilized where it is needed by the plant.

Polymorphism of cyanogenesis revealed in *Eschscholzia mexicana* is of a particular interest for ecological genetics as the apparent balance of selective forces is not influenced by human interference. Fitness in a plant applies not only to survival but also to reproduction, the latter aspect being very important to annuals that depend solely on seeds for maintaining themselves in a given habitat. If the strategy is considered in terms of a budget where resources are allocated in a precise way, it should be remembered that not necessarily carbohydrates but other elements e.g. nitrogen, potassium or phosphorus may represent a limiting factor (HARPER 1977). The period of rapid growth in the annuals proceding their production is undoubtedly related to heavy demands made on environmental resources; it is not excluded that cyanogenic and acyanogenic individuals of *E. mexicana* might have different life strategies. For this reason, further studies in this taxon offer exciting perspectives.

Summary

Polymorphism of cyanogenesis was found in *Eschscholzia mexicana* (*Papaveraceae*) from Arizona and Southern California. In addition to inter-populational variation in frequencies of cyanogenic/acyanogenic individuals, an intrapopulational variation in HCN content of the cyanogenic plants was observed, a positive increase in frequencies towards strongly cyanogenic plants being noted. *E. mexicana* is the first annual taxon found polymorphic for cyanogenesis.

Possible functions and aspects of cyanogenesis that may prove relevant to further studies are discussed.

Zusammenfassung

Bei *Eschscholzia mexicana* (*Papaveraceae*) von Arizona und Südkalifornien konnte ein Polymorphismus in der Cyanogenese nachgewiesen werden. Neben einer Variation der Häufigkeitsverteilung von cyanogenen und acyanogenen Individuen zwischen den verschiedenen Populationen konnte auch innerhalb der Populationen eine Variation des HCN-Gehaltes der cyanogenen Pflanzen beobachtet werden: es zeigte sich eine Zunahme der Häufigkeit von den schwach

zu den stark cyanogenen Pflanzen. *E. mexicana* ist das erste bekannte einjährige Taxon, bei dem Polymorphismus der Cyanogenese nachgewiesen werden konnte.

Die mögliche Wirkungsweise der Cyanogenese und für weitere Untersuchungen bedeutsame Gesichtspunkte werden diskutiert.

References

ABROL Y.P. and CONN E.E., 1966: Studies on cyanide metabolism in *Lotus arabicus* L. and *L. tenuis* Waldst. et Kit. Phytochemistry *5*, 237-242.

-- and STOKER J.R., 1966: Studies on identification, biosynthesis and metabolism of a cyanogenic glucoside in *Nandina domestica* Thunb. Phytochemistry *5*, 1020-1027.

ANGSEESING J.P.A. and ANGESEESING W.J., 1973: Field observations on the cyanogenesis polymorphism in *Trifolium repens*. Heredity *31*, 276-284.

ARAUJO DE A.H., 1976: The relationship between altitude and cyanogenesis in white clover (*Trifolium repens* L.). Heredity *37*, 291-293.

BEATLEY J.C., 1967: Survival of winter annuals in the northern Mojave Desert. Ecology *48*, 745-750.

BLUMENTHAL S.G., HENDRICKSON H.R., ABROL Y.P. and CONN E.E., 1968: Cyanide metabolism in higher plants. III. The biosynthesis of β-cyanoalanine. J.Biol.Chem. *243*, 5302-5307.

BOYD F.T., AAMODT O.S., BOHSTEDT G. and TRUGG E., 1938: Sudan grass management for control of cyanide poisoning. J.Amer.Soc.Agron. *30*, 569-582.

CONN E.E. and BUTLER G.W., 1969: The biosynthesis of cyanogenic glycosides and other simple nitrogen compounds. In: HARBORNE J.B. and SWAIN T. (eds), Perspectives in phytochemistry. Acad.Press, 47-74.

CRAWFORD-SIDEBOTHAM T.J., 1972: The rôle of slugs and snails in the maintenance of the cyanogenesis polymorphism of *Lotus corniculatus* and *Trifolium repens*. Heredity *28*, 405-411.

DADAY H., 1954a: Gene frequencies in wild populations of *Trifolium repens*. I. Distribution by latitude. Heredity *8*, 61-78.

- 1954b: Gene frequencies in wild populations of *Trifolium repens*. II. Distribution by altitude. Heredity *8*, 377-384.

- 1965: Gene frequencies in wild populations of *Trifolium repens*. III. Mechanism of natural selection. Heredity *20*, 355-366.

DAWSON C.D.R., 1941: Tetrasomic inheritance in *Lotus corniculatus* L. J.Gen. *42*, 49-72.

DEMENT W.A. and MOONEY H.A., 1974: Seasonal variation in the production of tannins and cyanogenic glucosides in the chapparal shrub *Heteromeles arbutifolius*. Oecologia *15*, 65-76.

ECK H.V. and HAGEMAN R.H., 1974: Nitrate reductance activity in Sudangrass cultivars. Crop Sci. *14*, 283-287.

EHRLICH P.R. and RAVEN P.H., 1965: Butterflies and plants: a study in coevolution. Evolution *18*, 586-608.

ELLIS W.M., KEYMER R.J. and JONES D.A., 1977: The defensive function of cyanogenesis in natural populations. Experientia *23*, 309-311.

FOULDS W. and GRIME J.P., 1972a: The influence of soil moisture on frequency of cyanogenic plants in populations of *Trifolium repens* and *Lotus corniculatus*. Heredity *28*, 143-146.

\- 1972b: The response of cyanogenic and acyanogenic phenotypes of *Trifolium repens* to soil moisture supply. Heredity *28*, 181-187.

FREELAND W.J. and JANZEN D.H., 1974: Strategies in herbivory by mammals: the role of plant secondary compounds. Am.Nat. *108*, 269-289.

GIBBS R.D., 1963: History of chemical taxonomy. In: SWAIN T. (ed.), Chemical plant taxonomy. Acad.Press. 60-82.

GREENE E.L., 1905: Revision of *Escholzia*. Pittonia *5*, 205-308.

HARPER J.L., 1977: Population biology of plants. Acad.Press. 892 pp.

HEGNAUER R., 1958: Over de verspreiding van blauwzuur bij vaatplanten. Pharm. Weekblad *93*, 801-819.

\- 1961: Die Verbreitung der Blausäure bei Cormophyten. IV. Neue Untersuchungen über die Verbreitung der cyanogenese. Pharm.Weekblad *96*, 577-596.

\- 1963: Chemotaxonomie der Pflanzen. I-IV. Birkhäuser, Basel. 1800 pp.

JANZEN D.H., 1971: Seed predation by animals. Ann.Rev.Ecol.Syst. *2*, 465-493.

JONES D.A., 1962: Selective eating of the cyanogenic forms of the plant *Lotus corniculatis* L. by various animals. Nature, London, *193*, 1109-1110.

\- 1966: On the polymorphism of cyanogenesis in *Lotus corniculatus* L. I. Selection by animals. Can.J.Genet.Cytol. *8*, 556-567.

\- 1970: On the polymorphism of cyanogenesis in *Lotus corniculatus* L. III. Some aspects of selection. Heredidy *25*, 633-641.

\- 1972: Cyanogenic glycosides and their function. In: HARBORNE J.B. (ed.), Phytochemical Ecology. Acad.Press. 103-124.

\- 1973: Co-evolution and cyanogenesis. In: HEYWOOD V.H. (ed.), Taxonomy and ecology. Acad.Press. 213-242.

\- 1978: Cyanogenesis in plants and animal feeding. In: HARBORNE J.B. (ed.), Biochemical aspects of plant and animal co-evolution. Acad. Press. 21-34.

JUHREN M., WENT F.W. and PHILLIPS E., 1956: Ecology of desert plants. IV. Combined field and laboratory work in germination of annuals in the Joshua Tree National Monument. Ecology *37*, 318-330.

MELVILLE J., COOP I.E., DOAK B.W. and REIFER I., 1940: Cyanogenesis in white clover (*Trifolium repens* L.). IV. Methods of determination and general considerations. NZ.J.Sci and Techn. *22*, 144B-154B.

MIRANDE M., 1909: Influence exercée par certaines vapeurs sur la cyanogenèse végétale. Procédé rapide pour la recherche des plantes à acide cyanhydrique. Comp.Rend.Acad.Sci Paris *149*, 140-142.

\- 1913: Sur quelques plantes nouvelles à acide cyanhydrique. Comp.Rend. Soc.biol. *62*, 2, 434.

ROBINSON M.E., 1930: Cyanogenesis in plants. Biol.Rev. *5*, 125-141.

ROSENTHALER L., 1926: Beiträge zur Blausäurefrage. Pharm.Acta Helv. *1*, 167-168.

RUIJGROK H.W.L., 1967: Over de verspreiding van ranunculine en cyanogene verbindingen bij de *Ranunculaceae*. Diss.Univ.Leiden. 52 pp.

SHERBROOKE W.C., 1976: Differential acceptance of toxic jojoba seeds (*Simmondsia chinensis*) by four Sonoran desert heteromyid rodents. Ecol. *57*, 596-602.

SOLOMONSON L.P. and SPEHAR A.M., 1977: Model for regulation of nitrate assimilation. Nature *265*, 373-375.

TANTISEVIE B., RUIJGROK H.W. and HEGNAUER R., 1969: Die Verbreitung der Blausäure bei den Cormophyten. V. Ueber cyanogene Verbindungen bei Parietales und bei einigen weiteren Sippen. Pharm.Weekblad *104*, 1341-1355.

TJON SIE FAT L.A., 1979: Contribution to the knowledge of cyanogenesis in Angiosperms. Dirdrecht, Netherlands. 52 pp.

URBANSKA-WORYTKIEWICZ K. and WILDI O., 1975: Variation within *Lotus corniculatus* L.s.l. from Switzerland. I. Preliminary report on chromosome numbers and cyanogenesis. Ber.Geobot.Inst.ETH, Stiftung Rübel *43*, 54-82.

\- SCHWANK O. and FOSSATI A., 1979: Variation within *Lotus corniculatus* L.s.l. from Switzerland. II. Reproductive behaviour of *Lotus alpinus* (DC) Schleicher. Ber.Geobot.Inst.ETH, Stiftung Rübel *46*, 62-85.

\- and SCHWANK O., 1980: Variation within *Lotus corniculatus* L.s.l. from Switzerland. III. Microdifferentiation in *Lotus alpinus* (DC) Schleicher above the timberline. Ber.Geobot.Inst.ETH, Stiftung Rübel *47*, 29-45.

VAN VALEN F., 1978: Contribution to the knowledge of cyanogenesis in Angiosperms. IX. Cyanogenesis in Papaverales. Kon.Ned.Akad.Proc.Ser.C (Botany) *81*, 492-499.

WENT F.W., 1973: Competition among plants. Proc.Nat.Acad.Sci USA *70*, 585-590.

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