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ELECTROPHORETIC ENZYME STUDY OF THE VEGETATIVE AND FLORAL ORGANS OF THE NARCISSUS

Investigations of multiple molecular forms of enzymes-isoforms, with respect to tissue or organ specificity and in relation to germination and plant development have been approached with increased vigour over the last few years (Mills, Crowden, 1968; Bhatia, Nilson, 1969; Jaaska, Jaaska, 1969; Safonova et al., 1970; Splittstoesser, Stewart, 1970; Lázár, Farkas, 1970; Guzmán et al., 1971; Mallery, 1971, 1972; Zaden, Trippi, 1971; Spencer, Titus, 1972, etc.). However, little is known about the biochemical changes taking place in the floral organs during the aging of the flower. Therefore, in this paper we shall report upon polyacrylamide gel electrophoretic studies of eight different enzymes, three hydrolases, four dehydrogenases and peroxidase contained in different floral tissues with regard to flower age, and also upon the patterns of these enzymes from vegetative organs.

Materials and methods

The plant material used in this investigation was the narcissus *Narcissus pseudonarcissus* L. which had grown in the open. Extracts were made from the vegetative organs of the narcissus — bulbs, roots, leaves, stems — at the stage of flowering and from the floral organs — petals, anthers, stigma-styles and ovaries from unopened to four days opened flowers. Homogenates were made, centrifuged as previously described (Milius, 1974) and separated by vertical electrophoresis on polyacrylamide gel (Jaaska, Jaaska, 1969). Enzyme staining was carried out according to the procedure of Jaaska (1972).

Results and discussion

Acid phosphatase pattern from various organs of the narcissus, presented in Fig. 1, can be described as consisting of three groups of isoforms having nearly intermediate and faster electrophoretic mobilities. Seven bands were found to be common to all the vegetative organs studied. A band of low electrophoretic mobility was specific to the roots only, whereas it was absent in enzymograms of the other three vegetative organs. The pattern of leaves showed another slow-migrating distinct intensive phosphatase form which was characteristic of the leaf tissues only. Enzymograms from the floral organs revealed the presence of six common phosphatase forms which coincided with the fractions of

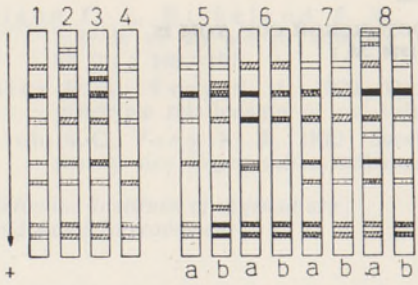

Fig. 1. Polyacrylamide gel electrophoretic patterns of acid phosphatase. Enzymograms: *1* — bulb, *2* — root, *3* — leaf, *4* — stem, *5* — petal, *6* — anther, *7* — stigma-style, *8* — ovary; *a* — unopened flower, *b* — four-days opened flower.

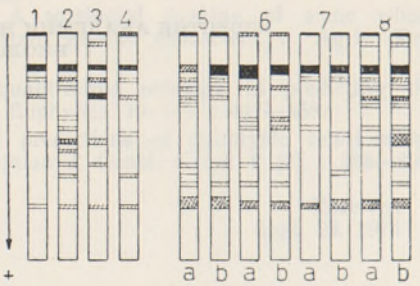

Fig. 2. Polyacrylamide gel electrophoretic patterns of esterase. Designations see under Fig. 1

the vegetative organs. Comparison of respective enzymograms of floral organs in Fig. 1 clearly demonstrates differences between the unopened and the four days opened flower parts, e. g. between the petals, anthers and ovaries. Two new phosphatase forms were detected in the four days opened petals, and, in addition to this, the intensity or activity of some fractions increased. Consequently, the results show an increase of phosphatase activity during the aging of petals. At the same time, the phosphatase pattern of the anthers changed both qualitatively and quantitatively with the flower's age. One phosphatase form, somewhat faster migrating from the middle of the gel, never observed in other floral and vegetative organs, disappeared, and the activity of the first doublet decreased from the unopened to the 4 days opened flower anthers. The phosphatase activity decreased quantitatively only in the stigma-style extracts. In the course of ovary development, two slow-moving fractions and one light band of intermediate electrophoretic mobility disappeared, and the staining intensity of some bands decreased. These results suggest an increase of acid phosphatase activity in the narcissus petals and an decrease of this activity in the ovary tissues with the flower's age.

Although extensive changes were noted in acid phosphatase patterns during the aging of the flower, nothing definite can be said about the physiological role of nonspecific phosphomonoesterases.

Esterases. Diagrammatic representation of the polyacrylamide gel tubes stained histochemically after electrophoresis for an esterase activity with 1-naphthyl acetate as substrate is presented in Fig. 2. The esterase enzymograms are more complex than those of acid phosphatase, showing the presence of numerous isoforms of different staining intensity and electrophoretic mobility, the exact number of which is impossible to determine in the enzymograms. All the enzymograms in the figure show a staining area near the origin at the site of sample application, and only two electrophoretically distinct esterase isoforms were found to be common to all the analyzed organs. The remaining numerous isoforms were located between the common fractions mentioned, except for the presence of one slow-migrating band in the leaf and ovary extracts. In all, up to 14 electrophoretically distinct esterase forms were demonstrated in the floral and vegetative organs of the narcissus, but not a single organ possessed all the enzyme fractions. It is interesting to note that the bulb tissue showed the lowest level of esterase activity and had only

five bands, one intensive and the remaining ones with a very light staining intensity.

Comparison of the respective enzymograms of the floral organs shows that each organ of the flower had its own specific isoform composition which also changed with the flower's age. The number of esterases decreased from 9 in the unopened petals to 7 in the oldest (4 days opened) petals; thus two bands disappeared and one slow-moving band increased in the staining intensity. Consequently, the esterase isoform composition decreased as the petals aged. At the same time, the patterns from anthers (unopened and pollinated anthers) were essentially similar, only a nearly centrally-located doublet increased in the staining intensity. The esterase patterns of the stigma-style tissues changed only slightly with the flower's age; a new light band appeared and electrophoretic mobility of a fraction near the middle of the gel varied. Esterase enzymograms changed both qualitatively and quantitatively in the course of the ovary's development. The change of pattern was clear, two new isoforms appeared, and the staining intensity of some fractions increased from the unopened flower buds to the fully expanded flower ovaries. Therefore, the esterase activity and isoform composition increased during the ovary's development.

More information is available on the electrophoretic properties of esterases than of other enzymes in plants (Macko et al., 1967; Barber, Steward, 1968; Mäkinen, 1968; Mäkinen, Macdonald ,1968; Upadhya, Yee, 1968; Яаска, Яаска, 1971; etc.). Plants contain a multiplicity of esterases which vary in different species, in different strains of the same species, in different organs of the same plant and even within the same organ at different stages of its development. Our data also confirm the observation that different organs or tissues have their own specific isoform patterns. Data pertaining to esterases during the aging of the flower are limited. It appears in this report that during the aging of the flower there is a qualitative and quantitative shift in the pattern and activity of the multiple molecular forms of esterase. The abundance and reactivity of these enzymes would indicate their important role in cellular metabolism. In spite of a great number of publications presenting data on esterases, the specific physiological function and the significance of enzymes remain almost entirely unknown.

Leucine aminopeptidase. Eight different organs of the narcissus showed the presence of an electrophoretically constant doublet of leucine aminopeptidase. Only a slight shift in the mobility of the fastest fraction was revealed in root tissues. In addition to these bands, a slightly slower migrating fraction was detected in the bulb and leaf tissues. Quantitatively the patterns differ considerably in the intensity of individual bands relative to one another.

Leucine aminopeptidase activity was distributed in the floral organs of the narcissus as follows: the ovary tissue showed the highest activity, the petals as well as the anthers had a somewhat lower activity, and the stigma-style — the lowest one. No pronounced differences were observed in the flower parts as they aged.

Aminopeptidase is widely distributed both in plants and animals (Scandalios, 1969). It is the hydrolytic enzyme that may play an important role in protein degradation during the growth and development, but its specific function in different tissues and organs is not understood as yet.

Peroxidases. Figs. 3 and 4 present enzymograms of anodically and cathodically moving narcissus peroxidases. The difference between the floral and the vegetative organs in anodic peroxidase enzymograms

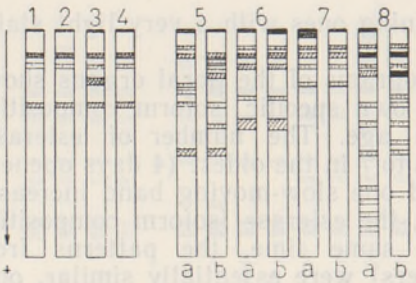

Fig. 3. Polyacrylamide gel electrophoretic patterns of anodic peroxidase. Designations see under Fig. 1.

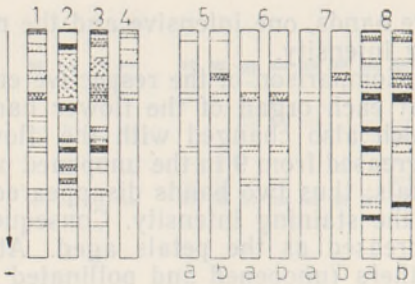

Fig. 4. Polyacrylamide gel electrophoretic patterns of cathodic peroxidase. Designations see under Fig. 1.

(Fig. 3) is striking. While the floral organs contained 5—10 isoforms, only three were present in the vegetative organs. No pronounced qualitative differences exist between the vegetative organs. There is only one band which is given by leaves, but not by other vegetative organs. The anodic peroxidase isoform composition changed in the petals and ovaries during the aging of the flower. The petals from the unopened flower had six bands. As they aged, they lost some bands and gained some others. In addition, the staining intensity of some bands increased. Thus, these data showed an increase of peroxidase activity during the aging of the petals. The nature of the changes occurring during the ovary's development resembled an alteration which took place in the petals, i. e. with the aging of the flower the ovary peroxidase enzymograms lost some bands and gained some others. Some quantitative differences were also noticed. Several isoforms which were absent from the petal, anther or stigma-style tissues, were present in the ovaries. Presumably these isoforms have different functions in ovary tissues.

No essential differences exist between the unopened and the 4 days opened flower anthers and the stigma-style tissues in anodic peroxidases. There is only one slow-migrating peroxidase form in the stigma-style tissues of the unopened flower, which disappeared during the aging of the flower.

Thus, the results revealed distinct qualitative differences between the unopened and the 4 days opened narcissus petals as well as the ovaries.

A contrary picture appeared in **cathodic peroxidases**. The enzymograms of the vegetative organs showed the presence of numerous isoforms of different staining intensity and electrophoretic mobility, and the cathodic peroxidase enzymograms from floral organs consisted of only 1—4 fractions, with the exception of the ovary tissue which had numerous cathodic as well as anodic peroxidase forms. Comparison of the respective enzymograms from the vegetative organs in Fig. 4 clearly demonstrates that different organs have their own specific isoform composition. Certain isoforms were common to all the four tissues, but showed different activities; others were specific of either one or two of these tissues. Thus, an isoform of intermediate electrophoretic mobility was found in the bulb only, and two peroxidase forms were specific of the roots. The cathodic peroxidase activity was strongest in the root tissue. The slow-moving broad peroxidase zone actually consisted of three or four closely spaced bands which fused together upon prolonged incubation aimed at detecting less active isoforms.

Different parts of the narcissus appear to have a specific cathodic peroxidase isoform pattern which can change with age. It is interesting

to note that a new slow-moving band of the same electrophoretic mobility appeared in the petal, stigma-style and ovary tissues as the flower aged. The appearance of this isoform may be explained by assuming a certain function in the aged floral organs.

We did not find any differences in the anther isoform patterns of the unpollinated to the four days opened flowers. The stigma-style tissue of the unopened flower showed a single band that corresponds to the slow-moving band of the anther, while the above-mentioned fraction appeared in the stigma-style tissues of the opened flowers.

The cathodic peroxidase enzymograms of the ovary tissues consisted of up to ten electrophoretically distinct fractions. During the ovary's development they lost one fraction and gained a new one. In some bands the staining intensity decreased, whereas in others it increased.

Thus, the cathodic peroxidase activity increased in the petal and stigma-style tissues with the flower's age, whereas the isoform composition of the ovary was more variable. It is not clear in what direction the total activity in the ovaries changed.

Our data pertaining to peroxidases in the petals during the aging of the flower agree with Trippi's and Tran Thanh Van's (1971) studies which showed an increase of the peroxidase activity during the aging of the corolla of *Phalaenopsis amabilis*. The exact physiological role of peroxidase in plants is obscure, and in the absence of genetic data it is difficult to say whether the appearance or disappearance of these bands is a result of differential activation or deactivation of genes or whether the product of the same genes is modified secondarily in each tissue to meet a special requirement necessary for either the development or senescence.

Glucose-6-phosphate dehydrogenase. From the rate of band development it was evident that the activity of the glucose-6-phosphate dehydrogenase was much higher than that of the other dehydrogenases investigated. The glucose-6-phosphate dehydrogenase pattern for the vegetative organs was characterized by the presence of one major zone. However, a comparison of the enzymograms in Fig. 5 clearly shows that the intensity of this fraction is highest in the bulb and lowest in the stem tissues. In addition to this fraction, one light band appeared near this broad zone in the bulb tissues. As to the leaves, a second light fraction of low electrophoretic mobility appeared.

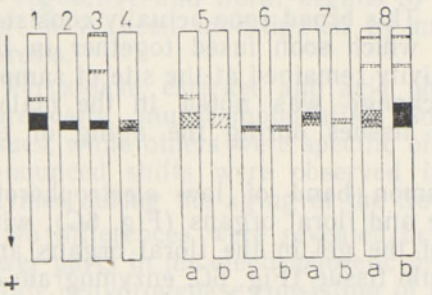

Fig. 5. Polyacrylamide gel electrophoretic patterns of glucose-6-phosphate dehydrogenase.
Designations see under Fig. 1.

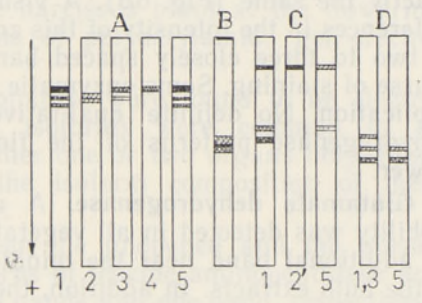

Fig. 6. Polyacrylamide gel electrophoretic patterns of (*A*) 6-phosphogluconate dehydrogenase, (*B*) malate dehydrogenase, (*C*) glutamate dehydrogenase, (*D*) leucine aminopeptidase
Enzymograms: *1* — bulb; *2* — root; *2'* — root, leaf, stem; *3* — leaf; *4* — stem; *5* — floral organs.

The enzymograms of the narcissus floral organs showed the same major fraction. The ovary tissue from the opened flowers contained the most intensive zone, and the lowest apparent activity was observed in the stigma-style which still diminished during the aging of the flower. The wide zone of the ovary tissues actually consists of three to four successive spaced bands close to each other; and the relatively lighter zone in the stigma-style of the unopened flowers actually consisted of two closely spaced bands. Upon a prolonged incubation of the gel in the substrate solution, one additional light band appeared in the petals, which corresponds to the minor fraction of the bulb tissues. The ovary tissues contained the same slow-moving light band that was found in the leaves.

During the aging of the flower the minor fraction disappeared in the petal tissues, and the intensity of the major zone diminished. Thus, the glucose-6-phosphate dehydrogenase activity decreased as the petals aged. Similarly, the patterns of the stigma-style tissues changed, namely the activity of this zone decreased with the flower's age. At the same time, the anther fraction of the unpollinated to the four days opened flowers appeared to have nearly equal levels of activity as judged by the band intensity. In contrast to the petal and stigma-style tissues which showed clear decreases in the glucose-6-phosphate dehydrogenase activity during the aging of the flower, that activity increased in the ovary tissues.

6-Phosphogluconate dehydrogenase patterns of all floral organs were qualitatively almost identical (Fig. 6*A*), showing the presence of three closely successive fractions of constant electrophoretic mobility. Quantitatively, the intensity of these fractions varied in different organs. In general, the petal and ovary tissue extracts exhibited the strongest 6-phosphogluconate dehydrogenase activity, whereas the stigma-style had a rather low activity that decreased with the aging of the flower. The activity was lowest in the anthers, scarcely detectable in the enzymograms. The enzymogram of the bulb tissues was exactly similar to that of the floral organs, showing the presence of the same three bands. The enzymograms of the leaf and stem revealed the presence of only one or two fractions of this triplet. There was only one diffuse zone in the roof tissues. Presumably this zone consisted of two closely spaced bands.

Malate dehydrogenase. The broad malate dehydrogenase band migrated in the intermediate gel region in each tissue, and the patterns were exactly the same (Fig. 6*B*). A visual observation also revealed only few differences in the intensity of this zone. This broad zone actually consisted of two to three closely spaced bands which soon fused together in the course of staining. Some enzymatic activity remained at the site of sample application. No definite qualitative change was noted in the malate dehydrogenase patterns of the floral tissues during the aging of the flower.

Glutamate dehydrogenase. A common band of low electrophoretic mobility was detected in all vegetative and floral organs (Fig. 6*C*), with an additional band near the middle of the gel in the floral organs and in the bulb extracts. In addition, the bulb tissue (Fig. 6*C*, enzymogram *1*) contained an intensive fraction in the intermediate gel region, which was specific of or characteristic of the bulb tissues only.

The glutamate dehydrogenase pattern changed only slightly with the flower's age. A slow-migrating band decreased in the staining intensity in the petals as they aged. In the case of anthers the activity of the fraction mentioned increased. The enzymograms of the stigma-style and ovary tissues did not change during the aging of the flower. Thus, the

activity of glutamate dehydrogenase diminished in the petals and increased in the anther tissues.

Our data pertaining to dehydrogenases show that several changes in the glucose-6-phosphate dehydrogenase isoform complex occur with the flower's age, whereas the changes in the 6-phosphogluconate dehydrogenase activity were less apparent. Both the glucose-6-phosphate and the 6-phosphogluconate dehydrogenases play a role in the metabolism of glucose via the pentose shunt. The glucose-6-phosphate and the 6-phosphogluconate dehydrogenases activity suggest that carbohydrate metabolism in the flower parts takes place via the pentose cycle; the Krebs cycle seems to be not so active if determined by the activity of glutamate dehydrogenase. Pollination seemed to induce a metabolic change by affecting the dehydrogenase activities according to the following order: glucose-6-phosphate, 6-phosphogluconate and glutamate dehydrogenases.

It is known that pollination induces accumulation of substances in the ovary and column as a result of translocation from the perianth (Hsiang Tsung Hsun, 1951a, b). This accumulation seems to modify the cytoplasm and the synthesis or activity of the enzymes in the corolla.

Regulation of the enzyme pattern after pollination might be caused by the presence of an active growth centre in the ovary which induces translocation of water and solutes from the petals.

It is also known that senescence induces a decrease of protein and nucleic acid content (Osborne, 1965; Shaw et al., 1965; Spencer, Titus, 1972). The low protein level seems to be the result not only of degradative processes and the size of the protein precursor amino acid pool (Tabares, Kende, 1970), but also of a diminution of the *de novo* synthesis mechanism as suggested by the final loss of all synthetic capacities.

Considering that changes in the enzyme pattern might be due to the activation and repression of genes, the aging of the flower seems to be related to a genic activation in the case of some enzymes and to a genic repression in the case of others.

Summary

Organ specificity and variability of eight different enzymes, three hydrolases, four dehydrogenases and peroxidase isoform composition in the vegetative and floral organs of the narcissus plant at the flowering stage have been investigated by means of polyacrylamide gel electrophoresis.

Peroxidase, esterase and acid phosphatase were found to be electrophoretically multicomponential. Some isoforms were common to all tissues, while others were specific of either one or two organs only. More pronounced shifts were observed in the isoform composition of these enzymes during the aging of the flower.

No differences were revealed between the unopened and the opened flower parts in the electrophoretic patterns of leucine aminopeptidase and malate dehydrogenase consisting of two bands and one band, respectively. Several changes in the electrophoretic pattern of the glucose-6-phosphate dehydrogenase occur, whereas the glutamate and 6-phosphogluconate dehydrogenase patterns varied only slightly with the flower's age.

The author expresses her sincere gratitude to senior research worker V. Jaaska for his valuable advice.

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NARTSISSI VEGETATIIVSETE JA ÕIEORGANITE ENSÜÜMIDE ELEKTROFOREETILINE UURIMINE

Resümee

Polüakrüülamiidgeelelektroforeetiliselt uuriti happelise fosfataasi, esteraasi, leutsiini aminopeptidaasi, peroksüdaasi ja dehüdrogenaaside isovormide organispetsiifilisust ja muutlikkust nartsissi organites seoses õie vananemisega.

Peroksüdaas, esteraas ja fosfataas jaotusid elektroforeesil paljudeks fraktsioonideks, millest mitmed olid ühised kõigile uuritud organeile, teised omased vaid mõnele või isegi ühele organile. Märgatavaid kvalitatiivseid ja kvantitatiivseid muutusi täheldati nimetatud ensüümide fraktsioonilises koostises õie vananemise vältel.

Kõige püsivamaks osutusid leutsiini aminopeptidaas ja malaadidehüdrogenaas, nende ensümogrammid olid kinnistel ning avatud õieorganitel kvalitatiivselt sarnased, esinedes vastavalt kahe ning ühe fraktsioonina. Mõningaid kvalitatiivseid erinevusi täheldati glükooso-6-fosfaadi dehüdrogenaasi fraktsioonilises koostises ja teatud kvantitatiivseid muutusi tuvastati glutamaadi ja 6-fosfoglükonaadi dehüdrogenaasi isovormses koostises õie vananemise vältel.

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Toimetusse saabunud
26. VI 1974

Ану МИЛИУС

ЭЛЕКТРОФОРЕТИЧЕСКОЕ ИЗУЧЕНИЕ ФЕРМЕНТОВ У ВЕГЕТАТИВНЫХ И ЦВЕТОЧНЫХ ОРГАНОВ НАРЦИССА

Резюме

Методом электрофореза в полиакриламидном геле изучался фракционный состав кислой фосфатазы, эстеразы, лейцинаминопептидазы, пероксидазы, дегидрогеназ у вегетативных и цветочных органов нарцисса и степень изменчивости этих ферментов при старении цветка.

Фосфатаза, эстераза и пероксидаза присутствуют в различных органах нарцисса в виде множественных молекулярных форм—изоформ, из которых многие фракции были общими для исследованных тканей, а некоторые свойственны только определенным органам. Более существенные сдвиги во фракционном составе наблюдались у этих ферментов при старении цветка.

Наиболее стабильными среди изученных ферментов оказались лейцинаминопептидаза и малатдегидрогеназа, по качественному составу они сравнительно устойчивы и в процессе развития цветка изменяются мало. Некоторые качественные сдвиги отмечались в составе глюкозо-6-фосфатдегидрогеназы и незначительные количественные изменения наблюдались в изоформах глутамат- и 6-фосфоглюконатдегидрогеназы в ходе старения цветка.

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