ACTA
BOTANICA FENNICA

85

Liisa Kaarina Simola: Comparative studies
on the sugar pools of three
Lathyrus species

ACTA BOTANICA FENNICA

1—19 vide Acta Botanica Fennica 20—50.

20—49 vide Acta Botanica Fennica 50—82.

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COMPARATIVE STUDIES
ON THE SUGAR POOLS OF THREE
LATHYRUS SPECIES

BY

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Contents

Abstract

The free sugar pools of different plant organs of *L. maritimus*, *L. sylvestris* and *L. niger* have been analysed at four developmental stages (seedlings, and budding, flowering and fruiting plants). Glucose, fructose and sucrose were the most abundant sugars. An unidentified ketosugar was found in all three species but it was very common, especially in *L. niger*. Arabinose was found in low concentrations in most parts of *L. maritimus*. Sucrose accumulated in old leaves of *L. sylvestris*. Glucose and fructose were found in the stems of all three species studied, but each species also had a third, characteristic sugar.

I. Introduction

The free sugar content of plants is usually rather low except in exceptional organs like nectaries, and in some plant species or plant groups (e.g. sugar-beet, sugar-cane and many liliaceous species) which store mono- and disaccharides. Despite the fact that free monosaccharides are important as energy sources and photosynthetic products, they no longer arouse any great interest, because the free sugar pools are of no great economic importance and because the monosaccharides mostly occur as polymers or constituents of other chemical derivatives. Owing to the fact that there is relatively little qualitative variation between the carbohydrates of higher plants, very few physiological or chemotaxonomic comparisons have been made. Information about the free sugar pools is therefore sporadic and is mostly related to economically important plants, and the physiological role of the free mono- and disaccharides is in general poorly understood.

The first comprehensive study in this field dealt with the free sugar pool of the sugar-cane. The sugar composition in this plant proved to be relatively invariable and the non-growing parts of this plant store sucrose, while the growing parts contain fructose and glucose (WENT 1898). The variation in

the sugar pool of mangold leaves (CAMPBELL 1912) was also followed in several stages of development. The amount of hexoses showed diurnal variation but that of sucrose was relatively stable. During the early stages of growth sucrose was the main sugar in the leaves; later, hexoses predominated (DAVIS 1916 and DAVIS et al. 1916).

The study of NURMIA (1935) showed that plants within the same family can have different free sugars, e.g. *Vicia faba* contains mainly fructose, *Trifolium pratense* sucrose. Some later studies have shown that clover also contains glucose and fructose in free state (LAIDLAW & REID 1952 and MACKENZIE & WYLAM 1957).

The physiology of fruit-ripening was effectively studied before the Second World War. The carbohydrate metabolism of many crop plants was clarified, such as apple (EVANS 1928; KOKIN 1930 and ARCHBOLD 1932), watermelon (IWANOW et al. 1929) and peaches (KOKIN 1930). For example, in the sugar content of the watermelon three periods can be detected. At first glucose dominates in the pool, then fructose and finally sucrose (IWANOW et al. 1929). MEUNIER (1936a) detected stachyose and some other heterosides in the seeds of several *Lathyrus* species. He found that the sugar pool of seeds did not give good results for characterization of groups within the genus *Lathyrus*. He succeeded in establishing the presence of maltose in underground parts of some *Lathyrus* species *(L. tuberosus, L. sylvestris)* (MEUNIER 1933, 1936b).

The free sugar pool of pea seeds has been thoroughly investigated by TURNER et al. (1957) and also compared with that of the leaves, stems and hulls. Sucrose was found to be the main sugar in the seeds and leaves. The sucrose, fructose and glucose concentrations increased in the early stages of development but decreased when rapid starch formation began. The stems contained only glucose, the hulls both glucose and fructose.

One of the few comparative studies has been made on the water-soluble carbohydrates in the grain of several grass genera (MACLEOD & MCCORQUODALE 1958). All the 22 species studied contain glucose, fructose and sucrose. Raffinose and stachyose are relatively common. Mannan is confined to the genus *Nardus* and galactan to *Molinia*.

Sedoheptulose does not commonly occur in the free sugar pool of plants, but it is the actual storage product in the families Saxifragaceae and Crassulaceae, as well as in some Basidiomycetes. In some other families it occurs sporadically (KULL 1965 and 1968). That sedoheptulose and many other early products of photosynthesis do not accumulate in plant cells may be due to the rapid saturation of their pools, as it has been established in the leaves of *Avocado* (BEAN et al. 1963).

Another exceptional family in respect of its carbohydrate metabolism is the Compositae. The main constituents of the sugar pool in stems, roots and

tubers are oligosaccharides with a fructofuranoside residue (BACON & EDEL-
MAN 1951). This may be the result of the occurrence of inulin as a storage
carbohydrate.

In the present study the free sugar pools of three *Lathyrus* species were
investigated from the same samples from which amino acids were studied
(SIMOLA 1968). There is a relatively close connection between sugar and amino
acid metabolism, owing to the fact that the carbon skeletons of amino acids
are derived from monosaccharides and these two groups of substances are
among the early products of photosynthesis.

The aim of the present study is to

1. Compare the sugar pool of three *Lathyrus* species having dissimilar
amino acid pools.

2. Compare the free sugar pool of different plant organs at known devel-
opmental stages and

3. Compare the free sugar pool of each plant organ during development.

II. Material and methods

The free sugar pools of different organs of three *Lathyrus* species (*L. niger* (L.) Bernh.
L. sylvestris L. and *L. maritimus* (L.) Bigel.) have been studied at four stages of develop-
ment (seedlings, and budding, flowering and fruiting plants). The same material has been
used for these analyses as for the comparative study on the free amino acid pools of these
species (cf. SIMOLA 1968). The material was extracted with 70 per cent ethanol and passed
through a cationic ion-exchanger. The ethanolic eluate was evaporated on a warm plate
at 50°C. The residue was dissolved in an aliquot of water corresponding to half the fresh
weight of the sample. The samples were stored in small bottles under toluol.

The sugars were usually analysed by one-way paper chromatography on Whatman
No. 1 sheets, 61 × 61 cm in size. 50 μl of the analysis solution was pipetted on each spot
and known amounts (from 2.5 to 40 μl) of standard sugar solutions (10 mg/ml) on each
sheet. Sugars were chromatographed with the upper phase of the mixture butanol-acetic
acid-water (4:1:5). The descending runs were performed at room temperature for three
days. After this the chromatograms were left to dry in a fume cupboard from one to
24 hours. The rests of the solvent were evaporated in a ventilated oven at 80°C for 30
minutes. Phenolic water (4:1, pH 4.2) and ethylacetate-acetic acid-water (60:17:17.5; cf.
STOY 1965) were used as a second solvent system for identification of sugars in two-dimen-
sional chromatography.

Each sugar chromatogram was in duplicate. The positions of phenolic compounds
visible on chromatograms were marked with pencil before staining. One of the chromato-
grams was sprayed with aniline-phthalate solution (see PATRIDGE 1949) and heated at
105°C for 10 minutes. The sugar phosphates which give the same reaction do not dissolve
well in the extractant (70 % ethanol) used (LINSKENS 1959). Aminosugars were detected
with ninhydrin solution after dying with aniline-phthalate (STAHL 1962). The other
chromatogram was sprayed with orcin (0.5 %) in water-saturated butanol containing
12.5 % trichloroacetic acid (cf. BEVENUE & WILLIAMS 1951). The chromatogram was
heated at 110°C for 20 minutes. Some chromatograms were stained using aniline-diphenyl-

amine-phosphoric acid reagent described by Smith (1958). This reagent gives many colours from yellow to blue for different sugars, and a wide range of sugars (including ketoses) can be detected by it. All chemicals used were produced by Merck.

Semiquantitative determinations: The area and intensity of each spot were compared with chromatograms containing reversal standard sugars in different concentrations (25, 50, 100, 150, 200, 250, 300, 400 μg). The following sugars were used as controls:

Arabinose (Merck)	Melibiose dihydrate (puriss., Fluka)
Fructose (Merck)	Rhamnose
Galactosamine (Sigma)	monohydrate (puriss., Fluka)
Galactose (Merck)	Ribose (Hoffman - La Roche)
Galacturonic acid (Fluka)	Ribulose (Koch-Light Lab.)
Glucose (Merck)	Sedoheptulose anhydride
Glucose-6-phosphate (Sigma)	monohydrate (Sigma)
Glucuronic acid (Fluka)	Sorbose (Merck)
Glyceraldehyde (Sigma)	Stachyose (Mann)
Maltose (Merck)	Sucrose (Merck)
Mannoheptulose (N.B.C.)	Trehalose (Merck)
Mannose (Merck	Xylose (Merck)

Presentation of results: The results are presented in the form of diagrams (Figs. 1—3) in mg/g fresh weight. The sugar components have been grouped in aldoses and ketoses and arranged within these groups, usually according to their Rf-values in butanol-acetic acid-water.

III. Results

The diagrams (Figs. 1—3) of the free sugar pools of *Lathyrus* species studied show that their quality and quantity are highly dependent on the species and plant organ and the latter's stage of development. There are few common features, although the commonest chemical constituents of the sugar pool, glucose, fructose and sucrose, are the same. An unidentified ketosugar was found in all three species studied, and was abundant in *L. niger*. This compound has about the same Rf-value as sedoheptulose in butanol-acetic acid-water; however, it does not stain blue but greenish yellow with the trichloroacetic acid-orcin reagent. Arabinose is a common constituent of the sugar pool in *L. maritimus*. Melibiose, maltose and xylose were found only sporadically. Owing to the semiquantitative nature of the method, no conclusions can be drawn from small differences in sugar concentrations.

1. Lathyrus (Orobastrum) maritimus Bigel.

In the rootstocks of seedlings there are relatively large quantities of glucose and fructose (up to 2 mg/g fresh weight, cf. Fig. 1). The same sugars dominate in the young stems. The carbohydrate reserves stored in the underground parts are apparently used in the growth of the shoot, and sugars are transported in the form of monosaccharides. The amount of fructose in the
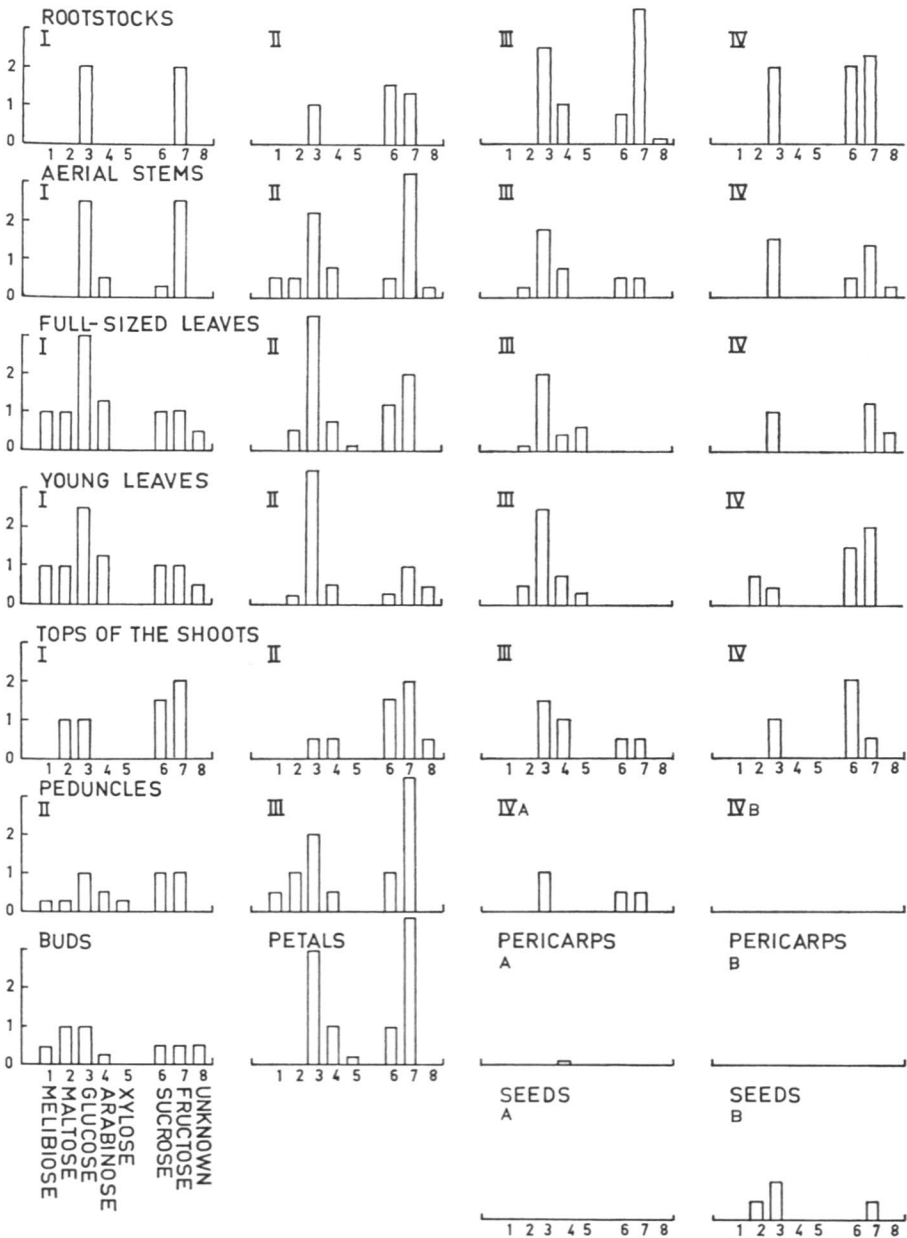
FIG. 1. The free sugar pools (mg/g fresh weight) of different vegetative and reproductive organs of *Lathyrus maritimus* at different stages of development (I = seedlings, II = budding, III = flowering, IV = fruiting plants).

leaves is relatively low, which may be due to the fact that this compound is effectively used in metabolism. Arabinose occurs in exceptionally large quantities. It plays an important role at this stage in the formation of hemicellulose. Melibiose and maltose were also found in rather high concentration.

In the budding plant the quantity of sucrose increases but that of glucose and fructose decreases in almost corresponding amounts. In addition, there are many compounds possibly belonging to the group of oligosaccharides or amino sugars present in small quantities in the leaves. Full-grown leaves contain much glucose and more fructose than growing ones.

In a flowering plant rootstocks have a high content of free sugars, especially fructose. The content of free sugars in other plant organs at this stage is surprisingly low, especially the amount of ketosugars. The amount of pentoses is relatively large compared with the fruiting stage. From the fact that the peduncles, like the petals, contain much fructose, it is apparent that in this stage of development ketoses are translocated to the flowers. In some earlier stages these parts of the plant contain several other sugars in small quantities.

In the rootstocks of the fruiting plant there is an increase in free sugars, especially sucrose. It is evident that carbohydrates are translocated from the assimilating organs of the plant in the form of glucose and fructose. The leaves contain only small quantities of free sugars, which may be due to the transport of glucose to the fruits for the synthesis of starch reserves. What remains, consists mainly of ketoses, which like glucose, however, are also translocated in the fruits. Free sugars do not accumulate in pericarps but are translocated to the seeds, where they are found in large amounts only in the later stages of development. During these stages, the synthesis of starch dominates (cf. McKEE et al. 1955).

2. L. (Eulathyrus) sylvestris L.

A rather low concentration of free sugars is typical of the rootstocks and stems of the seedlings of L. *sylvestris*. Ketoses form a considerable proportion of the sugars. In the rootstocks of the budding plant fructose dominates, but glucose is also present in moderate quantities. The sugar pool of the different parts of the stems is very variable. There are many compounds in relatively small quantities in the lower part of the stem (maltose and arabinose). The amount of sucrose is greater and that of glucose smaller than average. The lower part of the stem (II) contains large amounts of both glucose and fructose. In the leaves (I and II) of the upper part of the shoot glucose is plentiful, in those of the lower parts (I) sucrose and fructose as well. In
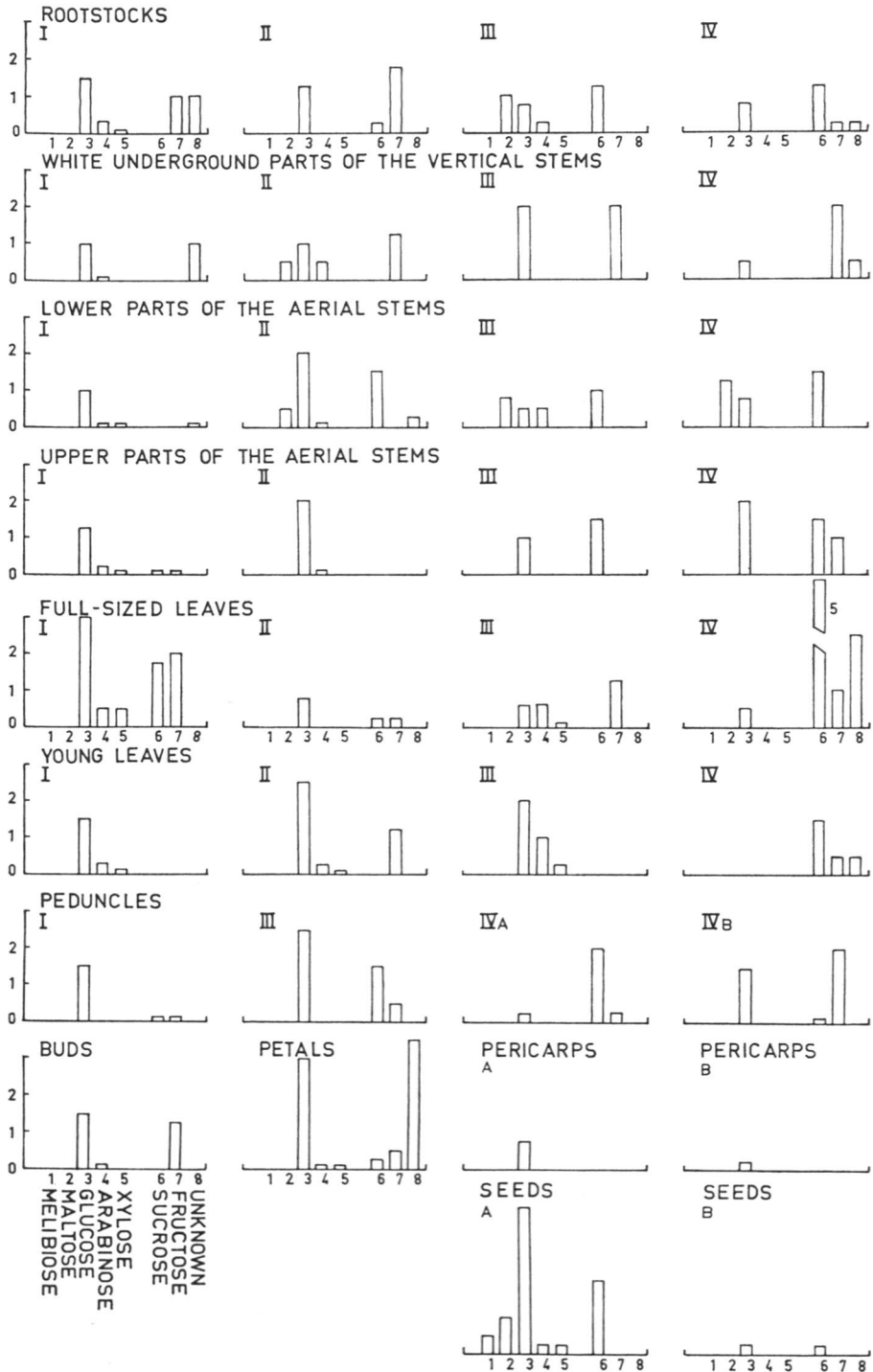
FIG. 2. The free sugar pools of different vegetative and reproductive organs of *L. sylvestris* at different stages of development (cf. Fig. 1).

budding plants the transportable sugars in the peduncles are glucose, sucrose and fructose. In the buds there are relatively small quantities of sugars, which may be due to a high metabolic activity in relation to transport in this part of the plant, which, in respect to its carbohydrate metabolism, is rather heterotrophic.

At the flowering stage sucrose is the main contituent of the free sugar pool in aerial stems. At the fruiting stage this sugar is concentrated in the older parts of the plant, which are also nearer to the storage organs. Glucose is the predominant sugar in the pedundes and petals of the flowering plant. In the fruiting plant the main monosaccharides in the upper part of the stem are glucose and fructose. In the lower part of the stem these compounds are more condensed to sucrose, which is the commonest transportable sugar in plants. The sugar pool of the upper and lower leaves are rather similar and very distinctly dominated by sucrose; there is also a small amount of the unidentified ketosugar in the leaves. In the peduncles of older fruits fructose predominates. Sugars do not accumulate in the pericarps, and the seeds only contain relatively large amounts of glucose and sucrose (cf. Fig. 2, seeds A) in the middle stage of the development.

3. Lathyrus (Orobus) niger (L.) Bernh.

A characteristic feature of the seedling stage of L. niger is the rather large quantity of glucose found in all parts of the plant. In the rootstocks there are many different sugars, including maltose, melibiose and an unidentified ketosugar. Glucose is the main free sugar in the stem and is possibly also transportable. Glucose is likewise the most abundant sugar in the leaves but they also contain small quantities of maltose, sucrose and the unidentified ketosugar.

In the budding plant the main sugar of the stem is glucose. The different parts of the stem have very similar sugar pools, the only constituents of which are glucose and fructose. In the young leaves sucrose is present as well as glucose. The fully expanded leaves contain only glucose (cf. Fig. 3). These compounds are also found in the peduncles. In the buds the main sugars are glucose, fructose and sucrose. The sugar pool of the young racemes has similarities with both leaves and stems.

At the flowering stage the main sugar in the rootstocks, as well as in the lower parts of the stem, is fructose. The upper parts of the stem also contain unidentified ketosugar, but the amount of glucose is low. Glucose, fructose, sucrose and the unidentified ketosugar are characteristic of the peduncles. Fructose dominates in the flowers. This species does not contain arabinose
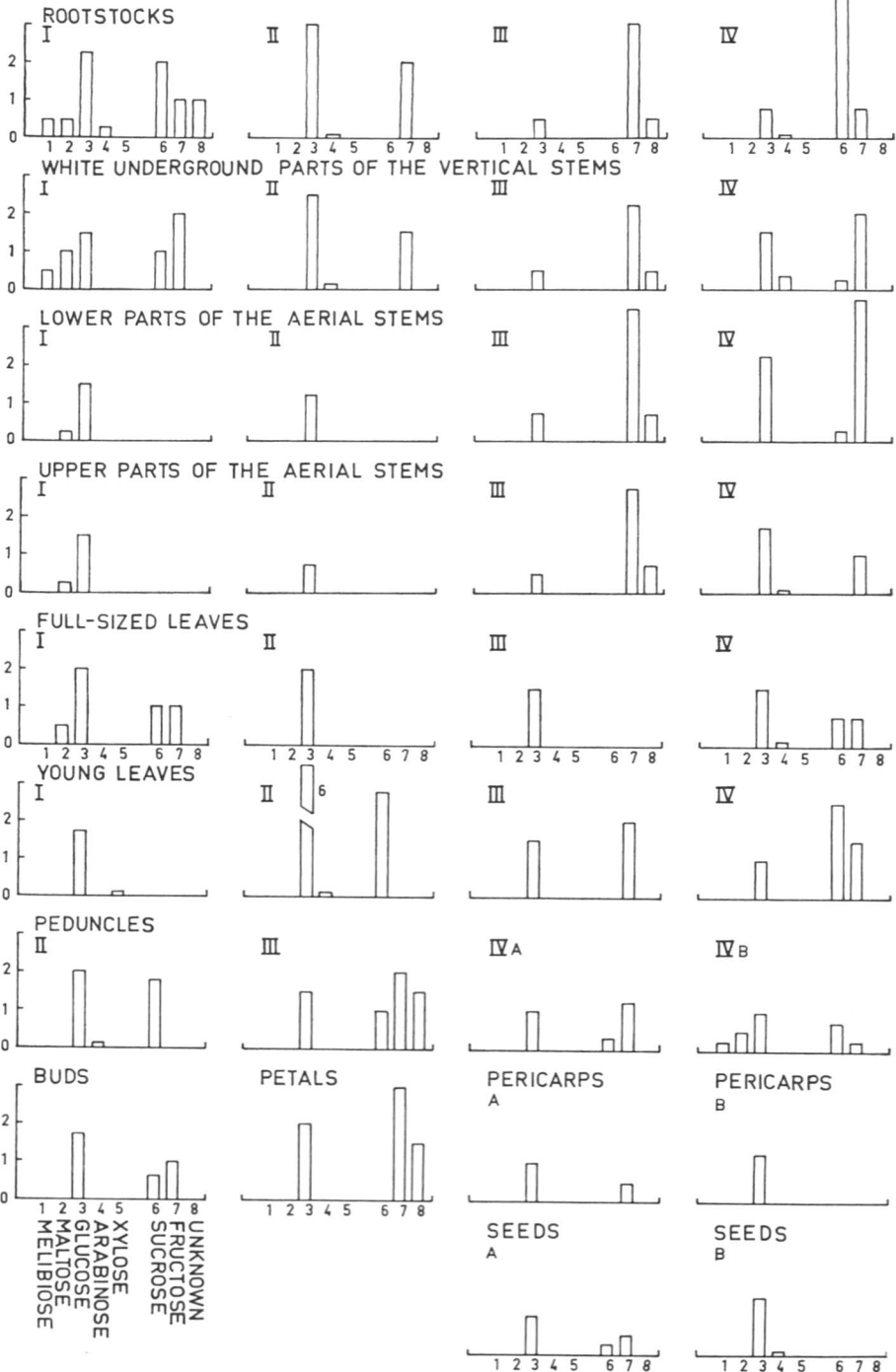
FIG. 3. The free sugar pools of different vegetative and reproductive organs of L. *niger* at different stages of development (cf. Fig. 1).

at this stage of development, being in this respect dissimilar to the other two species studied.

In the fruiting plant the dominant sugars are glucose and fructose. In this stage even young leaves contain the unidentified sugar. In an early stage the peduncles contain large quantities of sucrose. Later, the sugar content decreases in them and the translocated compounds are fructose and glucose, as in older seeds. Arabinose is found only sporadically but the unidentified ketosugar is abundant.

IV. Discussion

Glucose, fructose and sucrose are the most abundant constituents of the free sugar pool of *L. niger, L. maritimus* and *L. sylvestris.* The quantity of free sugars varies from 0 to 9 mg/g fresh weight, depending on the plant organ and its stage of development.

The sugar pool of *L. niger* contains the least variety of constituent, like its amino acid pool (SIMOLA 1968). The most distinct difference from the other two species is the relatively high content of the unidentified ketosugar. However, this compound is also found in fruiting *L. sylvestris* as well as in all stages of development of *L. maritimus* except in the flowering stage. The presence of rare ketosugars, heptuloses and octuloses, has been established, especially in *Saxifraga, Sedum* and *Avocado* (NORDAL & OISETH 1952, NORDAL & BENSON 1954 and KULL 1968). Arabinose was found most constantly in *L. maritimus,* although in low concentrations, but was lacking at the fruiting stage. Arabinose occurred only sporadically in *L. niger* but was somewhat more common in *L. sylvestris.* This sugar and likewise most other pentoses and some hexoses are toxic to several plant species and cannot be used by them as carbon sources (cf. GAUTHERT 1959).

The sugar pool of these species of *Lathyrus* contains several components at all stages. Accumulation of sucrose could be found in older leaves of *L. sylvestris,* as in the grapevine and sugar cane (WENT 1898 and KLIEWER 1966). In *L. maritimus* and *L. niger* there are not striking changes in the pools of each organ at different ages. Young seeds of *L. maritimus* and *L. niger* usually contain only traces of mono- and disaccharides, apparently owing to the rapid transformation to starch, unlike the young seeds of *Pisum,* which contain on the contrary a wide range of free sugars (TURNER et al. 1957).

Nor does sucrose accumulate in the pericarps of the species studied, although it is known to be the best carbon source for the embryos of most species, including representatives of the genus *Lathyrus* (PECKET & SELIM 1965 and RAGHAVAN 1966). This sugar also effects the differentiation and

development of some plants (YATES & CURTIS 1949; DEMAGGIO & WETMORE 1961 and JEFFS & NORTHCOTE 1966). It can therefore be supposed that the endogenous free sugar pool also can regulate plant growth and differentiation.

Glucose and fructose were found in the stems of all three species studied, but every species also has a third, characteristic sugar in the stem. *L. sylvestris* contains sucrose, which is the most abundant transportable sugar in most trees and herbaceous plants (MASON & MASKELL 1938; WANNER 1953; BIDDULPH & CORN 1957; ZIMMERMAN 1957; EDELMAN et al. 1959; KURSANOV 1963 and HARTT et al. 1963), *L. maritimus* arabinose and *L. niger* the unidentified ketosugar. The form in which carbohydrate is translocated varies considerable. In *Phaseolus* glucose and galactose are present besides sucrose but the phloem of *Clivia* contains hexoses only (MEYER-MEVIUS 1959). The bulk of the assimilates of *Cucurbita* are transported in the form of oligosaccharides of the stachyose group (cf. KURSANOV 1963). In stems of the peach and the plum the main sugars are sucrose, glucose and fructose, and in these plants the concentration of raffinose is also increased and stachyose is formed during the resting period (KATZFUSS 1965).

The peduncles of each *Lathyrus* species studied have relatively dissimilar sugar pools, which change during the course of development. The sugar pool of the peduncles apparently indicates the form in which carbohydrate is transported, owing to the high dry weight of this tissue (cf. SIMOLA 1968). The sugar pools are mainly the same in stems and peduncles but the sucrose concentration is usually greater in the peduncles of *L. maritimus* and *L. niger* than in the stems. In *L. niger* the peduncles mainly contain glucose and sucrose. Fructose and the unidentified ketosugar are present at the flowering stage.

In budding and flowering *L. maritimus* the peduncles contain a variety of sugars (fructose, glucose, sucrose, arabinose, melibiose and maltose) but there is a decrease both qualitatively and quantitatively during development. In *L. sylvestris* the transported sugars are mainly glucose and sucrose in the flowering stage but fructose and glucose in the fruiting plants (cf. Fig. 2, peduncles IV B). There are also very striking quantitative changes in the amino acid pools of the peduncles in all three species (SIMOLA 1968).

When inferences are drawn from the changes in the sugar pool, it must be noticed that changes in the amounts of glucose, fructose and sucrose may be results of changes in the activity of the sucrose synthetase or saccharase. Sugar transport needs an active mechanism and it may be that there are great differences between tissues in the transport of sugars and therefore the sugar must be converted into a more easily transportable form.

The changes in the sugar pool may be due to some external factors regulating the rate of photosynthesis and/or to endogenous factors in the cell

which regulate carbohydrate metabolism. First, a known compound may be synthesized in a tissue which has the conditions requisite for the formation of the enzymes needed for its biosynthesis. The compound in question may also be transported to other tissues, which do not synthesize it. In addition, some compounds are so labile as metabolic intermediates that they are not found in the free state in the sugar pool; for example, sedoheptulose, an intermediate in photosynthesis is very rarely detected free in cells. Thus seeds, to which sugars are effectively translocated, contain only small amounts of free sugars, because polymerization to polysaccharides is effective. Similarly, in growing tissues sugars are used for biosynthesis and as a source of energy.

The free sugar pools considered in my study account for only a small proportion of the total energy-yielding reserves of the plant, but they are the compounds involved in the active metabolism and physiology of carbohydrates from which biosynthetic pathways lead via ketoacids both to amino acid and lipid synthesis. The free sugar pool of the cell forms not only a distinct osmotic milieu but also raw material for the synthesis of other compounds, but owing, presumably, to dissimilarities in enzyme activities it is not easy to link the changes in the sugar pool with those in the amino acid pool.

Summary

The free sugar pools of three *Lathyrus* species (*L. maritimus*, *L. sylvestris* and *L. niger*) having dissimilar amino acid pools have been studied. The sugar pools of a number of plant organs (rootstocks, stems, leaves, buds, flowers, peduncles, pericarps, seeds etc.) were analysed at four developmental staged (seedlings, budding, flowering and fruiting). Each species had characteristic features, although the sugar pools of all three species were almost the same. Glucose, fructose and sucrose were found to be predominant. Arabinose was most abundant in *L. maritimus*. An unidentified ketosugar was found in all the three species studied, but was most abundant in *L. niger*. The stems always contained glucose and fructose but each species also had a third, characteristic sugar. The sugar pool was rather stable in *L. niger* and *L. maritimus*, but in *L. sylvestris* sucrose accumulated in the older leaves.

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