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Influence of various rootstocks for cherries on p-coumaric acid, genistein and prunin content and their involvement in the incompatibility process

Einfluß verschiedener Kirschenunterlagen auf die P-Cumarsäure-, Genistein- und Prunin-Gehalte und ihre Rolle im Inkompatibilitätsprozess

Valentina Usenik and F. Štampar
(University of Ljubljana, Biotechnical Faculty, Agronomy Department, Institute for Fruit Growing, Viticulture and Vegetable Growing, Ljubljana, Slovenia)

Summary

The influence of rootstocks for cherries of different genetic origin on the polyphenol content in the phloem above and below the graft union was investigated. Three-year-old trees of cv. 'Lapins', which were grafted on rootstocks F 12/1, Gisela 4, Gisela 5, Gisela 195/20, Maxma 14, Pi-Ku 4/20, Edabriz, W 13, W 72 and W 158, were analysed. Statistically significant differences were found in p-coumaric acid and prunin contents in the phloem of cv. 'Lapins' with regard to various rootstocks below the graft union and a statistically significant different genistein content above the graft union. Differences in the phenol content between heterospecific graftings of different genetic origin and homospecific ones were ascertained. It has been assumed that rootstocks for cherries which are hybrids or clones of various species from the genus *Prunus* can cause faster decay of cherry trees than does F 12/1 (*Prunus avium* L.) rootstock.

Zusammenfassung

Der Einfluß von Kirschenunterlagen unterschiedlichen genetischen Ursprunges auf den Polyphenolgehalt im Phloem über und unter der Veredlungsstelle wurde untersucht. Es wurden dreijährige Bäume cv. 'Lapins' auf Unterlagen 'F 12/1', 'Gisela 4', 'Gisela 5', 'Gisela 195/20', 'Maxma 14', 'Pi-Ku 4/20', 'Edabriz', 'W 13', 'W 72' and 'W 158' in den Versuch einbezogen. Statistisch gesicherte Unterschiede wurden in den p-Cumarsäure- und Prunin-Gehalten im Phloem bei cv. 'Lapins' bei verschiedenen Unterlagen unter der Veredlungsstelle und im Genistein-Gehalt über der Veredlungsstelle festgestellt. Es zeigten sich Unterschiede im Phenolgehalt zwischen heterospezifischen Veredlungen verschiedenen genetischen Ursprungs und homospezifischen Veredlungen. Bei verschiedenen Hybriden bzw. Klonen verschiedener Arten aus der Gattung *Prunus* als Kirschenunterlagen wurden größere Ausfälle der Bäume als bei der Unterlage 'F12/1' (*Prunus avium* L.) ermittelt.

Introduction

Trees of small size are pivotal to the success of high density planting systems (WEBSTER 1998). A lack of dwarfing rootstocks has for years been an obstacle to orchard development in the production of cherries. For many years the standards have been *Prunus avium* L. or *Prunus mahaleb* L. seedlings or clones of high vigour. Some *Prunus* species, in particular *P. canescens* and *P. cerasus*, and *Prunus* hybrids (the Gisela series, M x M series, Pi-Ku, etc.) have proved successful as dwarfing rootstocks (CALLESEN 1998). Unfortunately, most of these promising rootstock clones of the *Prunus* species have exhibited inconsistent performance in orchard trials. Some of these inconsistencies in performance can be attributed to the soils on which they were planted and associated abiotic and/or biotic stress factors. The causes of these site and/or scion interactions with rootstock demand further study (WEBSTER 1998). The term 'incompatibility' with respect to grafted fruit trees is defined as a phenomenon of premature senescence caused by physiological and biochemical processes (FEUCHT 1988). One of the types of incompatibility responses is a compatibility of callus layers but no or incomplete differentiation of vascular tissue and incompatibility due to cell necrosis at the graft interface (MOORE 1981).

The limitation of transport of xylem sap constituents from the rootstocks to the scion has been cited as a possible role in dwarfing (FAUST 1989). A reduction of the sieve plates in graftings with poor compatibility was paralleled by a loss of differentiation, especially below the union (SCHMID and FEUCHT 1981). Differentiation of the sieve tubes and vessels is induced by two hormonal signals, auxin (IAA) and cytokinin (ALONI 1995). Indolacetic acid (IAA) is thought to play a role in the dwarfing of an apple. The bark of the more dwarfing apple rootstocks causes a higher rate of auxin destruction (GUR et al. 1968). LOCKARD and SCHNEIDER (1981) proposed that the level of auxin reaching the root in active form influences root growth and metabolism, including the synthesis of cytokinins, which in turn should promote growth on top. A limiting auxin transport capacity could explain the reduced cambial activity and subsequent xylem formation and thus make an important contribution to the dwarfing effect (SOUMELIDOU et al. 1994). The activity of IAA oxidase can be altered by naturally occuring substances such as minerals, phenols, coumarins and organic acids (ALONI 1995). Phenolic acid, which inhibits growth, also enhances oxidative decarboxylation of IAA. IAA antagonists or auxin-oxidase cofactors are ferulic acid, *p*-hydroxybenzoic acid and *p*-coumaric acid (LOCKARD and SCHNEIDER 1981). Naringenin and genistein decrease the polarity of IAA transport (STENLID 1976).

GEBHARDT and FEUCHT (1982) found that low compatibility resulted in a pronounced accumulation of polyphenols above the graft union (cv. 'Hedelfinger'/W 8 and W 13 and 'Charmes'/W 8 and W 13). The same was established for genistein and prunin when cv. 'Van' on own roots and *P. avium/P. cerasus* were analysed (TREUTTER and FEUCHT 1991). DIRR et al. (1994) suggested that the accumulation of prunin indicates an incompatibility of heterospecific (*P. avium/P. cerasus*) graftings only in the early stage. TREUTTER et al. (1986) ascertained that a rise of prunin was evident also in healthy but potentially incompatible graftings of different cultivars of *Prunus avium* L. grafted on rootstocks F 12/1, W 10, W 11 and W 13. One of the accumulating compounds in graft incompatibility between *Prunus avium* L. cultivars and *Prunus cerasus* L. rootstocks (W 10, W 11 and W 13) in comparison with rootstock F 12/1 is p-coumaroyl-glucose ester (TREUTTER 1989). FEUCHT and TREUTTER (1991) found step gradients between scion (cv. 'Van') and rootstock (W 13) in heterografts in genistin and prunin; higher amounts in the scion. Prunin and genistein were increased in senescent heterospecific graftings compared to healthy ones (cv. 'Sam' grafted on F12/1 and 'Sam'/*P. cerasus*) (TREUTTER et al. 1987).

The purpose of the research is to establish what influence new promising rootstocks for cherries have on the contents of p-coumaric acid, genistein and prunin in the phloem of the cultivar and rootstock in comparison to the rootstock F 12/1 (*Prunus avium* L.). Included rootstocks are selections of *Prunus cerasus* L. and hybrids of various *Prunus* spp., which have not yet been analysed (except F 12/1 and W 13). The possibility of involvement of these substances in incompatibility in cherry will be investigated.

Material and methods

Three-year-old trees of cv. 'Lapins', which were grafted on rootstocks F 12/1 (homospecific grafts), Gisela 4, Gisela 5, Gisela 195/20, Maxma 14, Pi-Ku 4/20, Edabriz, W 13, W 72 and W 158 (heterospecific grafts) were determined. All plants were grown in the same orchard in Sadjarski center Bilje near Nova Gorica.

The experimental design included 5 blocks. From each stock/scion combination 5 trees were analysed. Samples were collected at the end of November. Small sections of bark (1 cm above and below the graft union, 1.5 cm in length) were removed with a knife and immediately frozen in liquid nitrogen. Phloem with cambium was used for analyses.

For polyphenol analyses samples were extracted with acetone-water (80:20, v/v) containing Triton X-100 (0.4 %) for 10 days at 4 °C according to TREUTTER (1988). In a mortar, 100 mg of plant material was homogenized with 20 ml of extraction solution. The mixture was stored in a refrigerator at 4 °C in closed plastic containers (made of PEP – polyethylenpropylen). The mixture was left during the entire extraction tightly closed in the refrigerator. After extraction, the samples were decanted into small glasses. The solvent was evaporated at 40 °C. The residue was dissolved in methanol (2 ml). The samples were clarified by centrifugation at 6000 g for 15 min (Centronic 322 - A). Before injection onto the column the samples were filtered through membranes (Sartorious RC 25, 0.45 µm pore size). The samples were stored at –20 °C until HPLC analysis.

Table 1: Tested rootstocks and their genetic origin.
In den Versuch einbezogene Unterlagen und ihr genetischer Ursprung.

Rootstock	Genetic origin
F 12/1	*Prunus avium* L.
Gisela 4	*Prunus avium* L. x *Prunus fruticosa* Pall.
Gisela 5	*Prunus cerasus* L. x *Prunus canescens* Bois.
Gisela 195/20	*Prunus canescens* Bois. x *Prunus cerasus* L.
Maxma 14	*Prunus mahaleb* L. x *Prunus avium* L.
Pi-Ku 4/20	*Prunus avium* L. x (*Prunus canescens* Bois. x *Prunus tomentosa* Thunb.)
Edabriz	*Prunus cerasus* L.
W 13	*Prunus cerasus* L.
W 72	*Prunus cerasus* L.
W 158	*Prunus cerasus* L.

Polyphenols were determined with reversed phase HPLC of Thermo Separation Products (TSP). The HPLC equipment consisted of X-ACT™ deggaser, P2000 TSP pump, Chromsep SS (250 x 4.6 mm) Hypersil 5 ODS, reversed phase column, guard column Chromsep Guard SS (10 x 3 mm) reversed phase, autosampler AS 1000, detector WellChrom K-2500 for detection at 280 nm (UV), and OS/2 Warp IBM Operating System (1994). Solvent A was acetic acid-water (1:99, v/v) and solvent B: methanol-butanol (5:1, v/v) with a gradient range according to MARTELOCK et al. (1994). The gradient range was: 0 – 10 min, 8 % B isocratic; 10 – 20 min, 8 – 10 % B in A; 20 – 30 min, 10 – 14 % B in A; 30 – 40 min, 14 – 17 % B in A; 40 – 50 min, 17 – 20 % B in A; 50 – 60 min, 20 – 27 % B in A; 60 – 70 min, 27 – 33 % B in A; 70 – 80 min, 33 – 49 % B in A; 80 – 90 min, 49 – 62 % B in A; 90 – 100 min, 62 – 80 % B in A; 100 – 110 min 80 % B isocratic. Flow rate was 0.5 ml/min. Injection volume was 5 µl.

The individual phenolic compounds were identified by comparison of their UV absorbance spectra with authentic samples (Fluka Chemical). With the aid of the peak area of the internal standard (6-methoxy-flavon), for prunin for which there was no standard, only the relative amount in individual tissue was measured (peak area/peak area of internal standard) (MARTELOCK et al. 1994).

Statistical analysis was done with the program Statgraphics Plus 2.1. Differences between the two treatments were tested with a t-test, while differences among a higher number of treatments ($n > 3$) were tested with a Duncan test. A risk of 0.05 % was taken into consideration.

Results

Mean values of p-coumaric acid, genistein and prunin are shown in Table 2. There is more p-coumaric acid than genistein in the phloem, and with prunin relative amounts are given. It is evident from the Table 2 that we established statistically significant differences in the contents of p-coumaric acid and prunin among different rootstocks below the graft union and of genistein above the graft union.

The rootstocks influenced different concentrations of p-coumaric acid both below and above the graft union. Trees of cv. 'Lapins' grafted on rootstock F 12/1 were

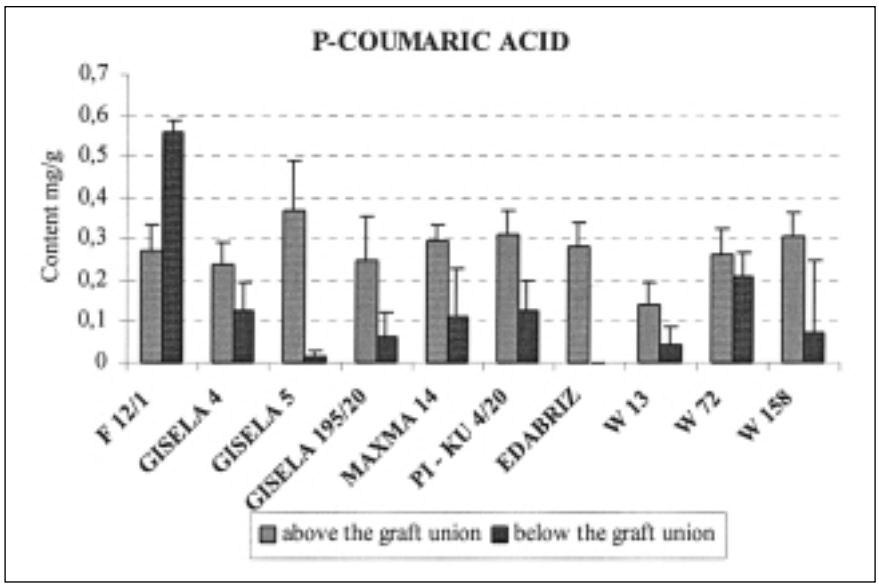


Fig. 1. Mean p-coumaric acid content in the phloem above and below the graft union with regard to different rootstocks. Each bar represents the mean of 5 trees. The vertical line represents the standard error.
Durchschnittlicher p-Cumarsäure -Gehalt im Phloem über und unter der Veredlungsstelle in Abhängigkeit von verschiedenen Unterlagen. Jede Säule stellt den Mittelwert von 5 Bäumen dar. Die senkrechte Linie stellt den Standardfehler dar.

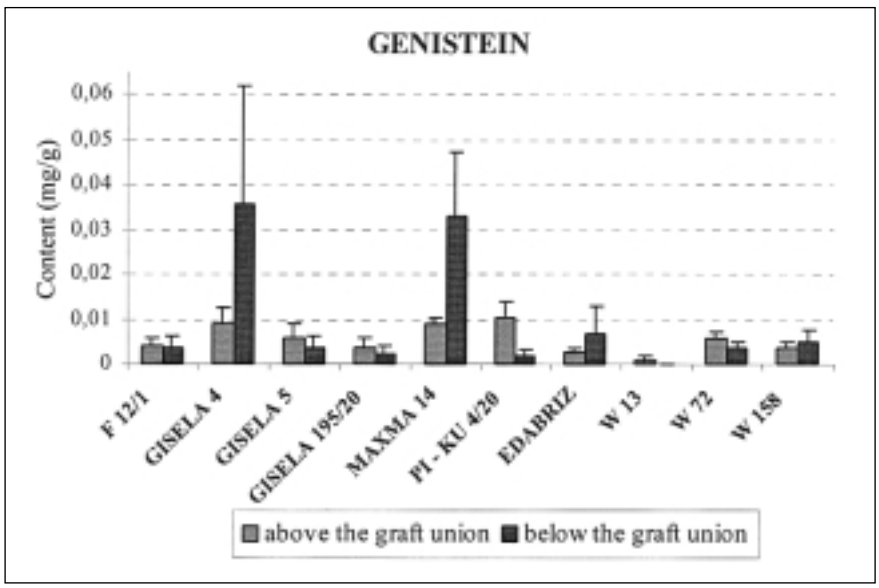


Fig. 2. Mean genistein content in the phloem above and below the graft union with regard to different rootstocks. Each bar represents the mean of 5 trees. The vertical line represents the standard error.
Durchschnittlicher Genistein-Gehalt im Phloem über und unter der Veredlungsstelle in Abhängigkeit von verschiedenen Unterlagen. Jede Säule stellt den Mittelwert von 5 Bäumen dar. Die senkrechte Linie stellt den Standardfehler dar.

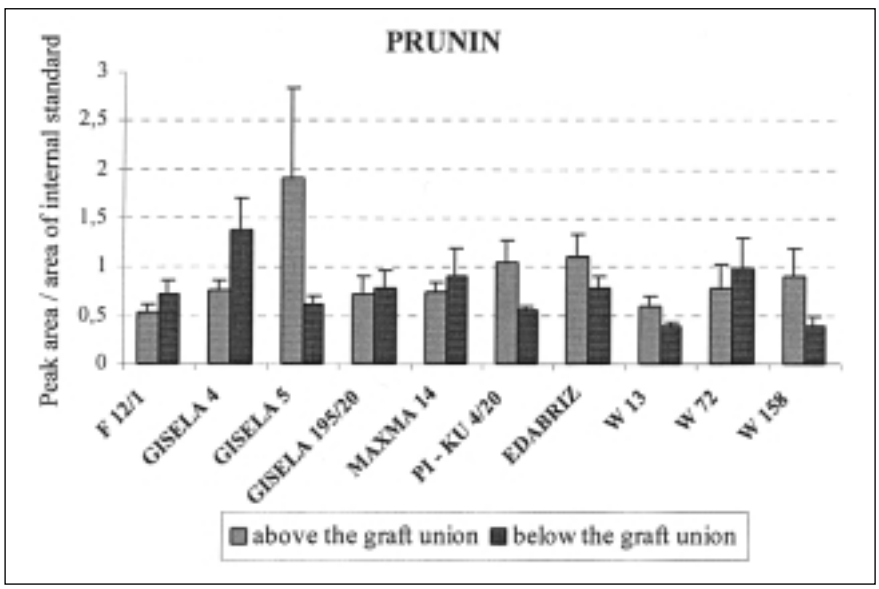


Fig. 3. Mean prunin content in the phloem above and below the graft union with regard to different rootstocks. Each bar represents the mean of 5 trees. The vertical line represents the standard error.
Durchschnittlicher Prunin-Gehalt im Phloem über und unter der Veredlungsstelle in Abhängigkeit von verschiedenen Unterlagen. Jede Säule stellt den Mittelwert von 5 Bäumen dar. Die senkrechte Linie stellt den Standardfehler dar.

significantly different from other cultivar/rootstock combinations (Table 2). The difference is obvious in higher concentrations of p-coumaric acid below the graft union with regard to other rootstocks. Trees cv. 'Lapins' grafted on other rootstocks had more p-coumaric acid above the graft union. The differences in the contents of p-coumaric acid below and above the graft union were statistically significant in cv. 'Lapins'/F 12/1, cv. 'Lapins'/Gisela 5, cv. 'Lapins'/Edabriz and cv. 'Lapins'/W 158 (Table 2).

Trees of individual cultivar/rootstock combinations differed statistically significantly in the contents of genistein above the graft union. There were no statistically significant differences among the rootstocks in the contents of genistein below the graft union although differences were considerable (Table 2).

The highest amounts of genistein were determined in cv. 'Lapins'/Gisela 4 and cv. 'Lapins'/Maxma 14 above and below the graft union. Higher amounts of genistein in one tree of each cultivar/rootstock combination influenced a higher mean concentration of genistein in the trees cv. 'Lapins'/Gisela 4 and cv. 'Lapins'/Maxma 14 (0.0355 mg/g and 0.0329 mg/g). The tree cv. 'Lapins' grafted on Gisela 4 had a 0.561 mg/g concentration of genistein below the graft union. When taking the samples we noticed colouring of the phloem and the tree deteriorated in 6-7 months after sampling. In the trees cv. 'Lapins'/F 12/1, the concentrations of genistein above and below the graft union were similar, while in other cultivar/rootstock combinations, differences in amounts above and below the graft union were noticed.

Figure 3 shows the differences in the relative contents of prunin in cv. 'Lapins' with regard to different rootstocks. Only in some cultivar/rootstock combinations can statistically significant differences in the mean relative amounts of prunin below the graft union be seen (Table 2).

The lowest amount of prunin above the graft union was determined in cv. 'Lapins'/F 12/1. On average, the lowest amounts of prunin were in cv. 'Lapins'/F 12/1 and cv. 'Lapins'/W 13 which are the most vigorous of

Table 2. Mean values (n=5) of p-coumaric acid, genistein (mg/g) and relative amount of prunin in the phloem above and below the graft union by cv. 'Lapins', grafted on different rootstocks.
Durchschnittliche (n=5) p-Cumarsäure- und Genistein-Gehalte (mg/g) und relative Prunin-Menge im Phloem über und unter der Veredlungsstelle bei cv. 'Lapins' auf verschiedenen Unterlagen.

	P-coumaric acid (mg/g)	Genistein (mg/g)	Prunin (relative amount)
F 12/1			
above the graft union	0.27 ± 0.063*	0.0038 ± 0.0019^{abc}	0.530 ± 0.093
below the graft union	0.56 ± 0.027*^{c}	0.0034 ± 0.0027	0.722 ± 0.15^{ab}
GISELA 4			
above the graft union	0.24 ± 0.052	0.0088 ± 0.0036^{bc}	0.757 ± 0.1
below the graft union	0.12 ± 0.069^{ab}	0.0355 ± 0.0264	1.375 ± 0.33^{b}
GISELA 5			
above the graft union	0.37 ± 0.123*	0.0057 ± 0.0031^{abc}	1.910 ± 0.923
below the graft union	0.02 ± 0.015*^{ab}	0.0036 ± 0.0025	0.610 ± 0.094^{ab}
GISELA 195/20			
above the graft union	0.25 ± 0.103	0.0036 ± 0.0020^{abc}	0.719 ± 0.188
below the graft union	0.06 ± 0.061^{ab}	0.0021 ± 0.0021	0.787 ± 0.176^{ab}
MAXMA 14			
above the graft union	0.30 ± 0.038	0.0088 ± 0.0013^{bc}	0.748 ± 0.087
below the graft union	0.11 ± 0.119^{ab}	0.0329 ± 0.0141	0.913 ± 0.27^{ab}
PI - KU 4/20			
above the graft union	0.31± 0.061	0.0102 ± 0.0036^{c}	1.039 ± 0.242
below the graft union	0.13 ± 0.069^{ab}	0.0016 ± 0.0015	0.563 ± 0.038^{ab}
EDABRIZ			
above the graft union	0.28 ± 0.061*	0.0025 ± 0.0011	1.117 ± 0.228
below the graft union	0 *^{a}	0.0066 ± 0.0065	0.788 ± 0.118^{ab}
W 13			
above the graft union	0.14 ± 0.052	0.0008 ± 0.0009^{a}	0.598 ± 0.097
below the graft union	0.04 ± 0.043^{ab}	0	0.392 ± 0.045^{a}
W 72			
above the graft union	0.26 ± 0.061	0.0059 ± 0.0014^{abc}	0.784 ± 0.249
below the graft union	0.21 ± 0.054^{b}	0.0034 ± 0.0017	0.989 ± 0.305^{ab}
W 158			
above the graft union	0.30 ± 0.063*	0.0036 ± 0.0014^{abc}	0.914 ± 0.278
below the graft union	0.07 ± 0.175*^{ab}	0.0049 ± 0.0027	0.397 ± 0.097^{a}

* means above and below graft union are significantly different (t-test; $p \leq 0.05$).

a means with the same letter are not significantly different (Duncan, $p \leq 0.05$). Mean contents of poliphenolic compounds in different rootstocks below the graft union, and especially above it, were compared.

the investigated rootstocks. In cv. 'Lapins'/Gisela 5, the mean amounts of prunin above the graft union were higher than below it, influenced by a higher relative amount of prunin in one tree (5.58), while relative amounts in other trees of the same combination were considerably lower (0.78 – 1.26).

Discussion

Different contents of p-coumaric acid, genistein and prunin in the rootstocks for cherries (amounts below the graft union) of different genetic origin were established. Different contents of the investigated substances are influenced by different rootstock genotypes and the adjustment of metabolisms of grafting union partners. A comparison with the results of other authors is not possible as the investigated rootstocks, except F 12/1 and W 13 rootstocks, have not yet been studied, nor has the combination cv. 'Lapins' on different rootstocks been studied in such research works. TREUTTER et al. (1990) discovered slight quantitative differences of p-coumaric acid due to the genotypes of *Prunus avium* L. and *Prunus cerasus* L. in the phloem of shoots.

We established that different rootstocks influenced the contents of p-coumaric acid, genistein and prunin in the phloem of cv. 'Lapins' above the graft union. TREUTTER et al. (1985) also found an increase in flavonoids of the phloem, especially in prunin and genistein, this being the reaction of the cultivar to the influence of the rootstock.

A comparison of individual contents of phenolic substances in the phloem above and below the graft union in each tree shows that there are great differences among the trees of individual cultivar/rootstock combinations. A typical example is cv. 'Lapins'/Gisela 5 which had considerably higher amounts of all investigated substances, especially of prunin above the graft union, than other trees of the same combination. TREUTTER et al. (1986), FEUCHT and TREUTTER (1991), TREUTTER et al. (1987) and COHEN et al. (1994) found an increase in prunin above the graft union in incompatible combinations. According to findings so far, we can assume that a tree is showing incompatibility although the visible signs of incompatibility cannot yet be observed.

A significantly higher concentration of genistein below the graft union in the trees of cv. 'Lapins'/Maxma 14 combination was ascertained in the experiment. This may be due to the presence of viruses in trees grafted on the rootstock Maxma 14. In a one-year testing of rootstocks for CLRV (cherry leaf roll virus) and CRLV (cherry rasp leaf virus) susceptibility, BUSER (1999) discovered a high infection of the rootstock Maxma 14 (all trees were infected by CLRV, five from six trees were infected by CRLV).

A higher mean concentration of genistein below the graft union in trees of cv. 'Lapins'/Gisela 4 was influenced by a high concentration in one tree of the combination. The tree of cv. 'Lapins'/Gisela 4 with a markedly higher concentration of genistein below the graft union deteriorated in 6 to 7 months after sampling. We can conclude that the accumulation of genistein below the graft union is an indicator of incompatibility between the cultivar and rootstock, although FEUCHT and TREUTTER (1991) found higher concentrations of genistein above the graft union in an analysis of one-year-old grafts with symptoms of leaf yellowing. On the basis of the results, we can conclude that the proportion in the concentrations of phenolic substances above and below the graft union is very important. This agrees with the findings of GEBHARDT and FEUCHT (1982).

We determined different concentrations of the investigated substances in trees of cv. 'Lapins', grafted on the rootstock F 12/1 (*Prunus avium* L.) than in trees grafted on rootstocks which are different clones or hybrids of *Prunus* spp. The differences in contents of p-coumaric acid above the grafted union between homospecific and heterospecific combinations were small, but TREUTTER (1989) discovered higher concentrations of p-coumaroylglucose above the graft union in heterospecific combinations than in homospecific combinations.

In the experiment, the trees of heterospecific combinations had higher concentrations of p-coumaric acid above the graft union. LOCKARD and SCHNEIDER (1981) discovered that p-coumaric acid is an auxin-oxidase cofactor. With regard to the reaction sequences typical of graft incompatibility (TREUTTER 1989) prunin and genistein can be synthetized under stress conditions from p-coumaric acid. This hypothetical formula can be proved by the results of our experiment. We determined higher concentrations of genistein and a considerably lower amount of prunin than in other trees of the combination in the tree of cv. 'Lapins'/Gisela 4 which deteriorated.

An accumulation of prunin and genistein inhibits the synthesis of ATP (TREUTTER et al. 1985) and has an influence on a decrease in the polarity of the IAA transport (STENLID 1976). Phenolic acid inhibits growth as well as enhances oxidative decarboxylation of IAA (LOCKARD and SCHNEIDER 1981), which is true for prunin, too (TREUTTER and FEUCHT 1988). The reduction of the sieve plates in the graftings with poor compatibility was paralleled by a loss of differentiation, especially below the union (SCHMID and FEUCHT 1981), influenced by a decreased concentration of IAA. All the metabolic changes cause the outside signs of incompatibility and the trees deteriorate rapidly.

With regard to the contents of polyphenolic substances in individual cultivar/rootstock combinations, especially in prunin above the graft union, it can be assumed that in heterospecific cultivar/rootstock combinations there is always low level stress present due to the adjustment of the metabolism of two different genotypes. YURI et al. (1990), COHEN et al. (1994) established higher concentrations of prunin during stress conditions. A certain level of stress causes weaker growth of trees, a shorter life span and greater fruitfulness (IEZZONI et al. 1990). IEZZONI et al. (1990), WEBSTER and SCHMIDT (1996) and SANSAVINI et al. (1986) point to the fact that when stress is augmented by the presence of viruses and various environmental factors, this can lead to severe incompatibility.

According to previous information and the results of the experiment, it can be concluded that incompatibility is a complex physiological state of a plant defined by: adjustment of the metabolisms of the grafting union partners (cultivar/rootstock combinations), growth

conditions, presence of viruses and other factors (nutrition, stress …). To decrease possibilities of stress which can cause deterioration of trees due to incompatibility, intensive care and optimal growth conditions must be provided for cherry trees which have been grafted onto selections and hybrids of various *Prunus* spp.

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Valentina Usenik and Franci Štampar, University of Ljubljana, Biotechnical Faculty, Agronomy Department, Institute for Fruit Growing, Viticulture and Vegetable Growing, Jamnikarjeva 101, 1000 Ljubljana, Slovenia