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GRAFT INCOMPATIBILITY IN WOODY PLANTS

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Grafting is an old method of plant propagation and since ancient times propagators have been aware of the problem of scions failing to make satisfactory growth when budded or grafted to an understock. Compatibility is defined as the ability of two different plants, when grafted together, to produce a successful union and develop satisfactorily into one composite plant (5). The opposite, failure to develop satisfactorily, is called incompatibility. Several excellent reviews on stock-scion incompatibility have been published by Argles (1), Hartmann and Kester (5), Mosse (10), and Nelson (11). The publication by Nelson (11) in our Proceedings is particularly important for plant propagators because of the extensive number of ornamental graft combinations surveyed and reported on in tabular form. However, just what constitutes graft-incompatibility has presented difficulties because many of the symptoms are nonspecific and similar to those which can be caused by unfavorable environmental conditions, viral infection, desiccation of the tissues, or poor techniques. Also, incompatibility can take numerous forms from slight symptoms of ill-health to complete graft failure when no union is formed.

SYMPTOMS OF INCOMPATIBILITY

Garner (3) proposed that incompatibility should be reserved for distinct failure to unite in a mechanically-strong union, failure to grow in a healthy manner, or premature death, when such failure can be attributed with a reasonable degree of certainty to differences between stock and scion. Moore and Walker (8, 9), however, define incompatibility in a more restricted sense as mutual physiological influences (or lack of them) between tissues of the stock and scion that ultimately result in an unsuccessful graft. Such a restricted definition more realistically describes true incompatibility, I feel.

Mosse (10) divided graft-incompatibility into translocated and localized types and proposed that the two types corresponded to some fundamental difference in underlying causes. The following summarizes the main distinguishing features of the two types:

1. Translocated
   a. Accumulation of starch above and its almost complete absence below the union.
   b. Phloem degeneration.
   c. Different behavior of reciprocal grafts.
   d. Normal vascular continuity at the union.
   b. Early effects on growth.
2. Localized
   a. Characteristic breaks in cambial and vascular continuity.
   b. Similar behavior of reciprocal combinations.
   c. Gradual starvation of the root system, with slow development of external symptoms proportional in severity to the degree of vascular discontinuity at the union.

CAUSES OF STOCK-SCION INCOMPATIBILITY

Although graft incompatibility is related to mutual physiological influences, whether positive or negative, between cells of the rootstock and scion, the underlying cause(s) leading a particular combination to succeed or fail is unknown. Therefore, successful graft combinations through history have been determined by trial and error.

At an anatomical level, Moore and Walker in a recent series of publications (8, 9) investigated the compatibility reaction in a system known to be obviously incompatible, *Sedum telephioides* and *Solanum pennellii*. Several major structural events were shown to occur during the ontogeny of the compatible graft (*Sedum* autographs). Initially, ruptured cells at the graft interface collapse and form a necrotic layer that separates the graft partners. By 6 hours, a pronounced accumulation of dictyosomes was noted along the cell walls adjacent to the cut surface and adhesion of stock and scion was detectable soon after. Adhesion of the stock and scion appeared to result from the activity of the dictyosomes that secreted materials into the cell wall space at the graft interface. Cell divisions ruptured the necrotic layer by 2 to 3 days. Procambial differentiation occurred across the graft union by 10 to 14 days. A similar pattern was noted earlier in coleus autographs by Stoddard and McCully (12).

Major structural events occurring during the ontogeny of the incompatible heterograft (between *Sedum* and *Solanum*) were similar to the *Sedum* autographs during the initial 24 hour period. However, *Sedum* cells adjacent to the graft union subsequently deposited an insulating layer of suberin along the cell walls and ultimately underwent a lethal cellular senescence. Moore and Walker concluded that cellular senescence in the heterograft resembled the hypersentitive response induced by plant pathogens and may be an example of a cellular defense mechanism or toxicity response.

At the biochemical level, the only incompatible graft that has been characterized is the pear/quince system. Gur *et al.* (4) showed that the anatomical disturbance at the union resulted from the seasonal inactivation of the cambium, due to cyanide liberated from the hydrolysis of prunasin near the graft union.

At Penn State University I have been conducting biochemical studies on vegetative compatibility in *Prunus* species. The *Prunus* stock-scion incompatibility systems were selected because their compatibility relationships have been well documented (1, 5, 10). In addition, they contain prunasin, already known to be responsible for graft failure in the pear/quince graft, and this compound could be utilized to test the hypothesis that vegetative incompatibility is a toxicity response. A problem in conducting studies on graft incompatibility is that potentially toxic compounds cannot be administered under controlled conditions. Callus cultures provide a unique system for investigating factors regulating plant growth and development and were adapted to study graft incompatibility. Complications resulting from microbial contamination and nutritional and environmental variations are eliminated. In addition, callus cultures allow for the incorporation of compounds under controlled conditions.

I have found that prunasin can inhibit the growth of a number of *Prunus* species. For example, in the almond/'Marianna 2624' graft combination, the almond cultivar, *P. amygdalus* 'Nonpareil', forms an incompatible union (7). When prunasin is added to callus cultures from both plants, the growth of 'Marianna 2624' is differentially inhibited (Table 1).

Table 1. Fresh weight (mg/callus) of 'Marianna 2624' plum and 'Nonpareil' almond callus.

	Prunasin concentration (mM)	
Plant	0	1
'Marianna 2624' plum	928.7	20.3
'Nonpareil' almond	2,676.4	2,476.6

Cyanogenic gylcosides, such as prunasin, do not directly cause the incompatibility reaction but must be decomposed to release a toxic product (4). The enzymatic hydrölysis of prunasin proceeds in a two-step process: prunasin is hydrolyzed to mandelonitrile and glucose; and mandelonitrile is hydrolyzed to hydrocyanic acid and benzaldehyde. The decomposition product hydrocyanic acid has been shown to cause the anatomical disturbance at the union of the incomptabile pear/quince combination (4). I have demonstrated that Nanking cherry (*P. tomentosa*) and sand cherry (*P. besseyi*) callus cultures have a greater sensitivity to cyanide than do peach (*P. persica*) callus. Callus growth of both cherry species was very severely inhibited by concentrations in the order of 1 mM cyanide. Growth inhibition in peach was mainly a reduction in fresh weight, with little reduction in dry matter (Figs. 1 and 2). Both cherry species are dwarfing understocks for peach and are known to have stock-scion incompatibility problems with peach.

In conclusion, prunasin and its toxic breakdown product, hydrocyanic acid, are capable of inhibiting the growth of callus from understocks known to exhibit vegetative incompatibility, and this suggests that cyanogenesis may be a causal factor in *Prunus* stock-scion graft failures.

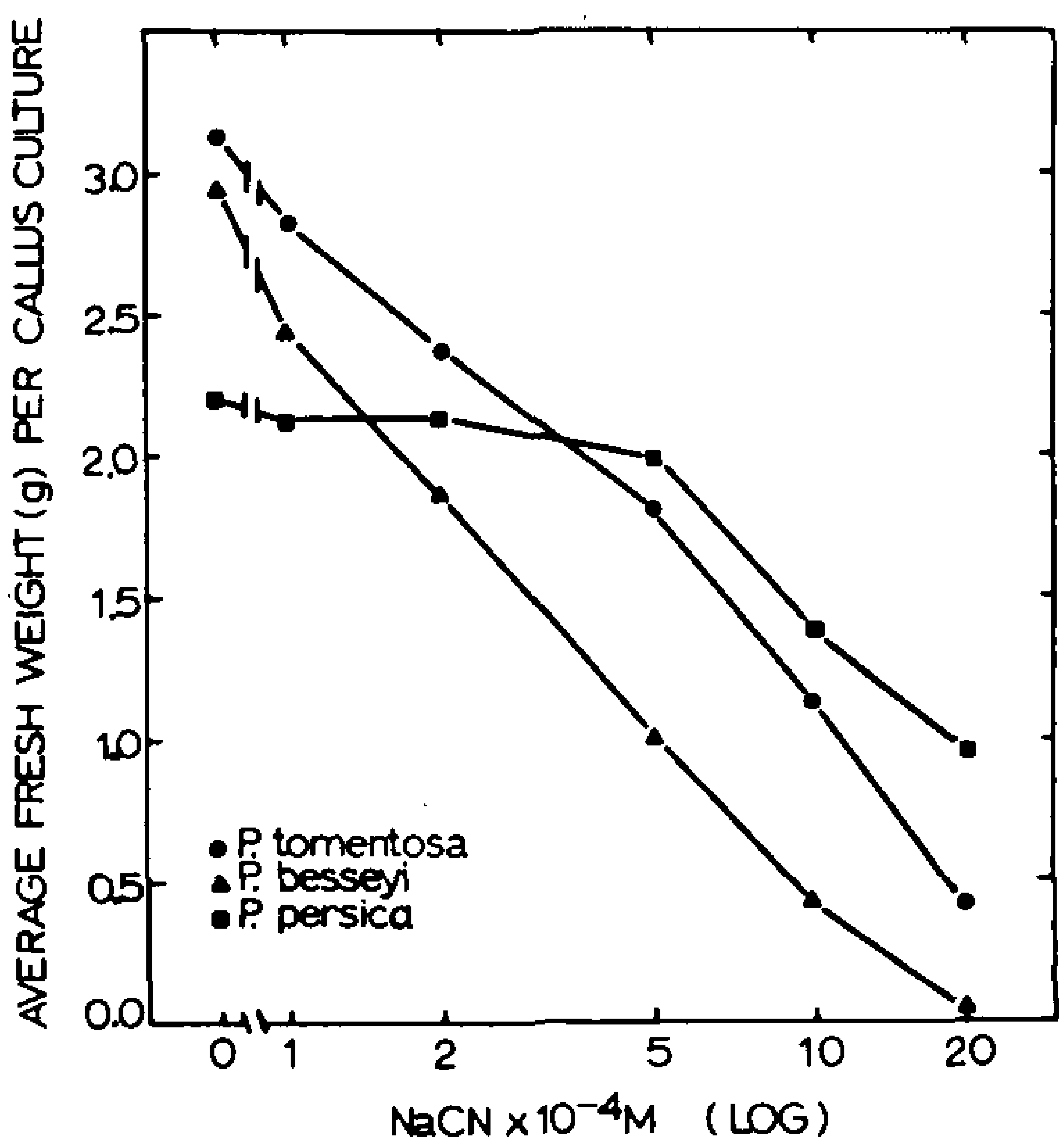

Figure 1. Influence of sodium cyanide concentration on fresh weights of *Prunus persica*, *P. tomentosa*, and *P. besseyi* callus cultures.

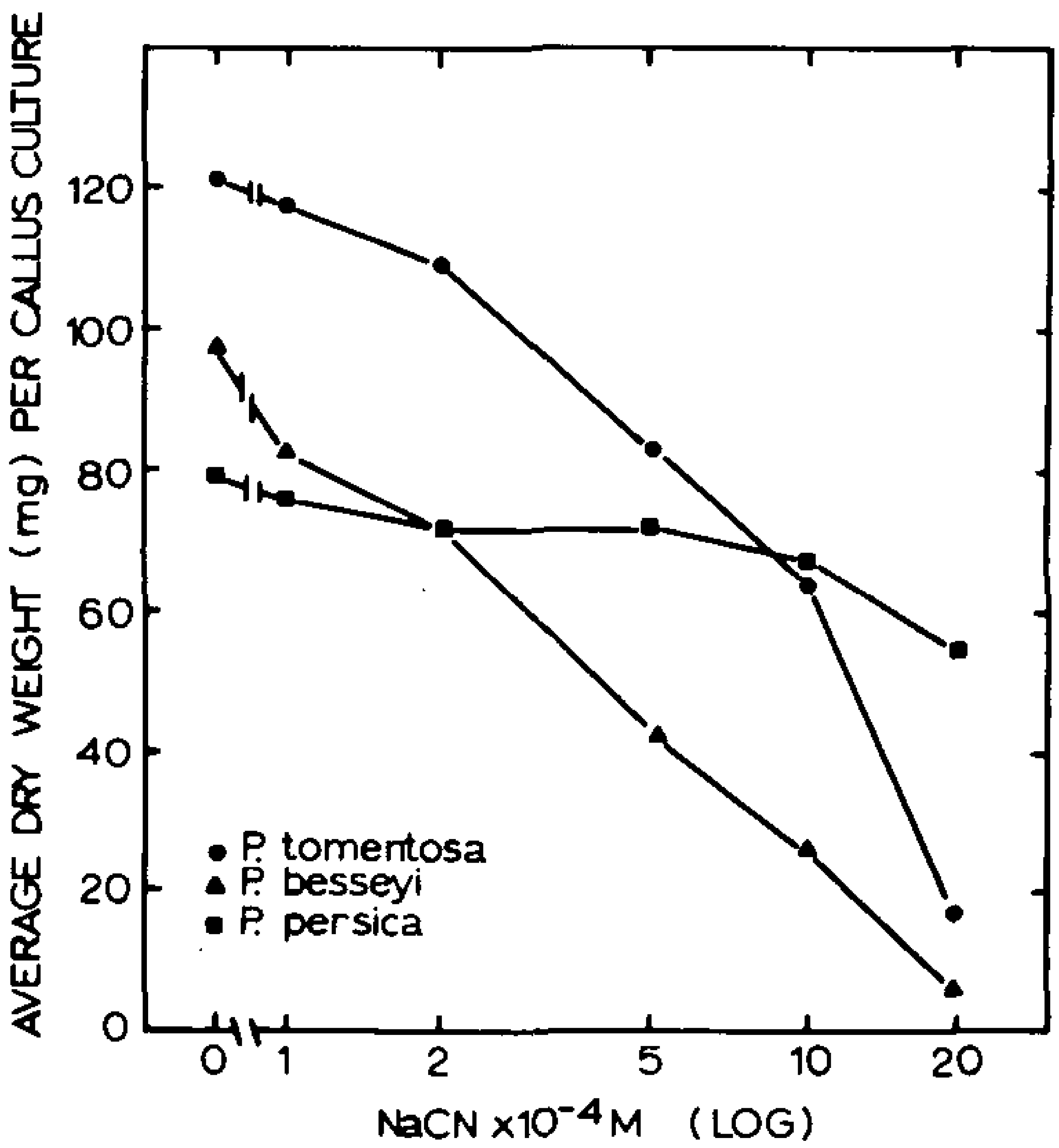

Figure 2. Influence of sodium cyanide concentration on dry weights of *Prunus persica*, *P. tomentosa*, and *P. besseyi* callus cultures.

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THE USE OF PRE-EMERGENCE HERBICIDES TO CONTROL CHICKWEED IN NEWLY-BUDDED CRABAPPLES

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The dormant buds on newly-budded crabapple trees are susceptible to injury or even death if they are smothered by common chickweed *(Stellaria media)* during the winter and in the early spring. The chickweed can grow over the bud, shutting out light and reducing air movement around the bud. There are many preemergence herbicides that will control