ROOTSTOCK-SCION RELATIONSHIPS IN HARDINESS OF DECIDUOUS FRUIT TREES.

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One of the key limiting factors in fruit production is bud or tree damage from fall or winter freezes. This is due to the selection of cultivars by criteria other than hardiness and to man's attempt to extend otherwise good cultivars beyond their hardiness range.

Damage from a freeze varies between root, trunk, twig and bud and is further complicated by the fact that at least 2 and sometimes 3 genetic systems are involved. Three-piece genetic systems have a root of one type on which is grafted a trunk or frame of a special type, which in turn is worked to the scion variety. These compound genetic systems, physiologically complex, are even more complex in hostile environments which result in cold injury to one or more organs or genetic systems.

Also several other factors influence the extent of cold injury. Such factors as nutrient deficiencies or excesses, diseases and pests, previous crop density, irrigation, tree vigor, pruning, preconditioning temperatures, short-term temperature variations, and the time at which the freeze occurs all affect the extent of injury.

Mechanisms inducing dormancy and rest in plants (discussed in detail in the previous papers) are important because actively growing tissues are damaged more than dormant ones at a given temperature. While these mechanisms are partly understood for simple plants, their interactions in compound genetic systems are poorly defined.

HARDINESS OF COMPOUND FRUIT TREES

Apple

One of the commonest types of winter injury comes in late fall such as occurred in November, 1955 in the Northwest states. Temperatures during the first 10 days of the month were generally mild. Leaves were still on the trees and many young trees were actively growing. On Nov. 11, temperatures dropped to or slightly below 0°F and remained for several days. Extensive damage occurred on most single-worked cultivars less than 12 years of age. The main site of injury was in the lower trunk and crotches. Under these conditions 'Yellow Transparent', 'Hibernal', 'Haralson', 'Canada Baldwin', 'Antonovka', 'Charlamoff', and 'Hyslop Crab' trunkstocks prevented this type of trunk damage. 'Virginia Crab' was partly incompatible and 'Spartan' trunks were not hardy. East Malling (EM) XVI and II roots were quite hardy, IX moderately so, but VII and IV were tender.

In Iowa (18) with a similar freeze of November, 1940, 'Duchess', 'Yellow Transparent', 'Wealthy', 'Haralson', and 'Hawkeye Greening' were uninjured.

In late December, 1968, temperatures in the apple areas of Washington and British Columbia dropped to as low as -47°F. In the coldest orchards scion varieties 'Delicious' and 'Golden Delicious' were killed to the hardy stock graft. According to Dr. Gene H. Oberly, injury in one orchard at Brewster (-22°F) was evident only on 'Hawkeye Greening' interstock. Those not showing apparent injury were 'Yellow Transparent', 'Astrachan', 'McIntosh', 'Beacon', 'Hibernal', 'Antonovka' and 'Ottawa-292'. Near Vernon, B.C. one orchard of 'Delicious' and 'Golden Delicious' scions were not seriously injured at a temperature of -36°F, apparently because of the heavy sod which reduced nitrogen levels in late summer, causing better tissue maturity.

In a research orchard at Vernon, B.C. (personal communication, D. V. Fisher) injury was assessed as follows after -38°F on December 29, 1968.

None - 'Heyer-20', 'Antonovka', 'Dr. Bill', 'Heyer-12'
Very Slight - 'Ottawa-271', 'J. Luke' sdlg., 'Hopa' crab, 'Anoka'
Slight - 'Red Astrachan', 'Minnesota-447'
Slight to Mod. - 'Haralson', 'McIntosh'

Injury, where present, was not severe and normal recovery occurred in 1969.

A recent review (16) separates the following apple rootstocks according to hardiness:

Very Tender or Tender	*Mod. Hardy to Hardy*	*Hardy*
EM I, II, IV, VII, IX, XXV	EM III, VIII, XI XVI	M.Robusta#5
MM[1]106, 109	MM104, 111	Maurer's Dab Selections
	Alnarp 2, N.Spy	
Commercial sdlg.	Antonovka sdlg.	Beautiful Arcade sdlg.
	Grahams sdlg.	Charlamoff sdlg.
		M.baccata sdlg.
		M.prunifolia sdlg.
		M.sargentii sdlg.
		M.virginiana sdlg.
		M.zumi sdlg.

Roots such as EM IX and VII that induce early maturity of the scion tend to protect trees more from fall freezes than mid-winter cold.

Intermediate frame stocks are characterized (16) as follows:

Moderately Hardy	*Hardy*	*Very Hardy*
Anoka	Antonovka	Anis
Canada Baldwin	Borovinka	Beautiful Arcade
McIntosh	Duchess	Charlamoff
Melba	Haralson	Heyer 12
Astrachan	*M. robusta* #5	Hibernal
Winter St. Lawrence	Robin	*M. prunifolia sikora-1*
	Yellow Transparent	

Stuart (27) tested EM layered stocks in March and found the following hardiness:

	Tender	*Intermediate*	*Hardy*
Stem tissue	XII, IX, I	IV, V, II	III, XIII, VII, XVI
Root tissue	I, XIII, II	V, XII, IX	III, VII, XVI, IV

Note that XIII stems were hardy but its roots were tender. Since this test was done in late winter, the results would likely differ if tests had been done in the fall. Fall tests might change the position of the early maturing clone IX relative to the late maturing XVI.

Another recent review (24) voiced the accepted view that any factor which increases tissue maturity increases hardiness. Factors which delay maturity, such as excess N, fall N application, late cultivation, early defoliation, heavy cropping, early pruning, all increase freeze injury.

Workers in Ohio (24) explored both environmental and stock-scion effects on hardiness of tender and hardy apples. On Nov. 21 varietal hardiness was: 'Franklin' > 'Delicious' > 'Rome Beauty' > 'Baldwin' > 'Staymared'. Differences in hardiness between these tender varieties and the hardy crabs ('Hibernal', 'Columbia', 'Virginia Crab', *M. robusta* #5) were greater during early dormancy than in February and March. 'Hibernal' was the most hardy all winter while other crabs lost hardiness in late winter. 'Hibernal' interstock increased hardiness of 'Staymared' and 'Baldwin' but not 'Delicious' scions.

Terminal twigs of EM stocks were checked for hardiness (24) with II and X were found to be less hardy in late November than VII, I, IV, and V. However, in March, II and X were hardier than the others. This study emphasizes that hardiness in early winter conforms to historical observations, but hardiness in late winter may be quite different.

Several studies (24, 9, 13, 12, 25, 27, 8) have shown that either the stock or scion can affect hardiness of another portion of the compound plant. Stuart (27) showed that while scion varieties were

[1]Malling Merton.

not influenced by rootstock hardiness, root hardiness was influenced by the scion, an effect not correlated with the hardiness of the scion. In North Dakota (25) 'Dolgo Crab' scions increased the hardiness of EM clonal roots. In Maine (13) 'Baldwin'/'Virginia Crab' was hardy but 'Baldwin'/'Hibernal' interstock was somewhat tender. A reciprocal influence of stock and scion on hardiness was apparent, but again the effects were not predictable. In Poland (12) root killing during a cold snowless winter was influenced by scion type. 'Cox's Orange Pippin'/EM IX *increased* root hardiness while the hardy 'Antonovka' scions decreased hardiness of EM IX roots. In Oregon (8) interstocks of 'Black Twig', 'Astrachan', 'Hibernal', 'Gold Medal', 'Minnesota-308' and 'Minnesota-447' increased the hardiness of the lower trunk.

Hardy interstocks do not harden properly under snow (6). 'Haralson' trunks covered with snow in November were uncovered later and exposed to -10°F, at which temperature they were killed.

Pear

The review by Lapins (16) indicates the following degrees of hardiness of pear rootstocks:

Tender to Mod. Tender	*Moderately Hardy*	*Hardy*
Quince:		
Pillnitz 1,2,3,5	Severnaya	Melitopolskaya
EM Quince A, C,		
Pfanderquitte		
Pyrus:		
Eierbirne sdlg.		*P. betulaefolia*
Einsiedeln sdlg.		Kirchensaller sdlg.
Intermediate stocks:		
Beurre Hardy	Grune Jagdbirne	Bertrams Stammbildner
	Neue Poiteau	Gute Graue
		Old Home
		Sacharnaya

In Oregon (8) interstocks of 'Comice', 'German Sugar', 'Orel 15', 'Vicar' and 'Flemish Beauty' prevented freeze injury to trunks and crotches. Much of the damage sustained at Hood River was winter sunscald which was partially prevented by painting the trunks white or by shading to prevent direct solar radiation.

Hardiness studies of *Pyrus* species in Minnesota (31) showed 3 groups:

Tender	*Intermediate*	*Hardy*
P. calleryana	*P. betulaefolia*	*P. communis* (several)
P. ussuriensis (1 type)	*P. bretschneideri*	*P. ovoidea*
	P. phaeocarpa	*P. ussuriensis* (several)
	P. ussuriensis (several)	

Field observations after a November freeze in Iowa (18) indicated that domestic pears were injured but not killed. Peaches and plums in the same area were killed. 'Anjou'/'Old Home'/French seedling in British Columbia came through the 1955 November freeze better than own-stem Anjou.

Long term tests in Oregon (8) showed that rootstocks of *P. serotina* and *P. ussuriensis* induced much greater winter injury to variety tops than did *P. communis* roots. This was true regardless of the intermediate stock used. The roots themselves were not injured. Similar responses from oriental stocks have been observed throughout the Northwest, but no good explanation for this has been advanced. Recently it was shown (29) that small potted 'Bartlett'/*P. calleryana* trees had a lower bud chilling requirement to break rest than did 'Bartlett'/*P. communis*. Field tests showed that larger trees had the same response (Fig. 1). With inadequate chilling (850 hr) 'Bartlett' on *P. calleryana* root flowered and forced normally while flowering and growth were retarded with 'Bartlett' on *P. communis* root. Futher studies showed that buds from 'Bartlett' shoots grown on *P. calleryana* and given 480 hours chilling grew much better than did 'Bartlett' buds with 480 hours chilling grown on *P. communis* root, both bud types of which were placed in a fully chilled host plant (Fig. 2).

While a change in chilling requirement of buds does not necessarily reduce hardiness of tissues it might do so under certain winter conditions. To further explore the rootstock influence in pear, studies were done to assess rest period inhibitors of buds as influenced by rootstock (26). Abscisic acid (ABA) was found to be the principal rest period inhibitor of *Pyrus*, but no consistent difference in ABA content was found as related to type of rootstock. Thus it was concluded that the lower chilling requirement of trees on *P.*

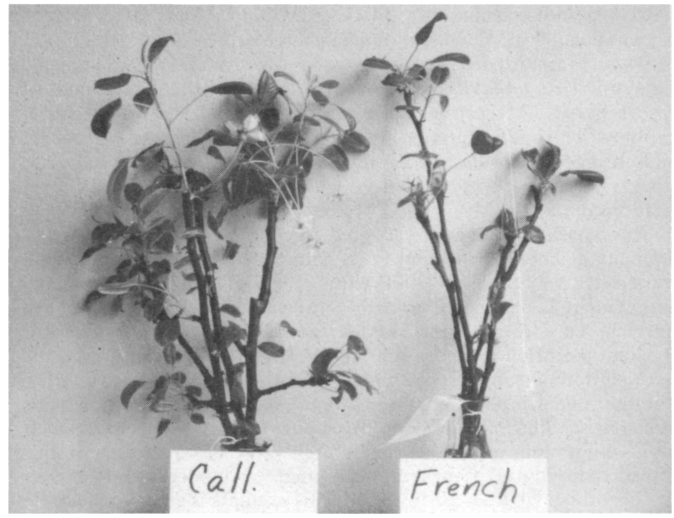

Fig. 1. Bartlett pear shoots forced at 70°F for 30 days following 850 hours chilling. Left, from tree on *P. calleryana* rootstock. Right, from tree on *P. communis* rootstock.

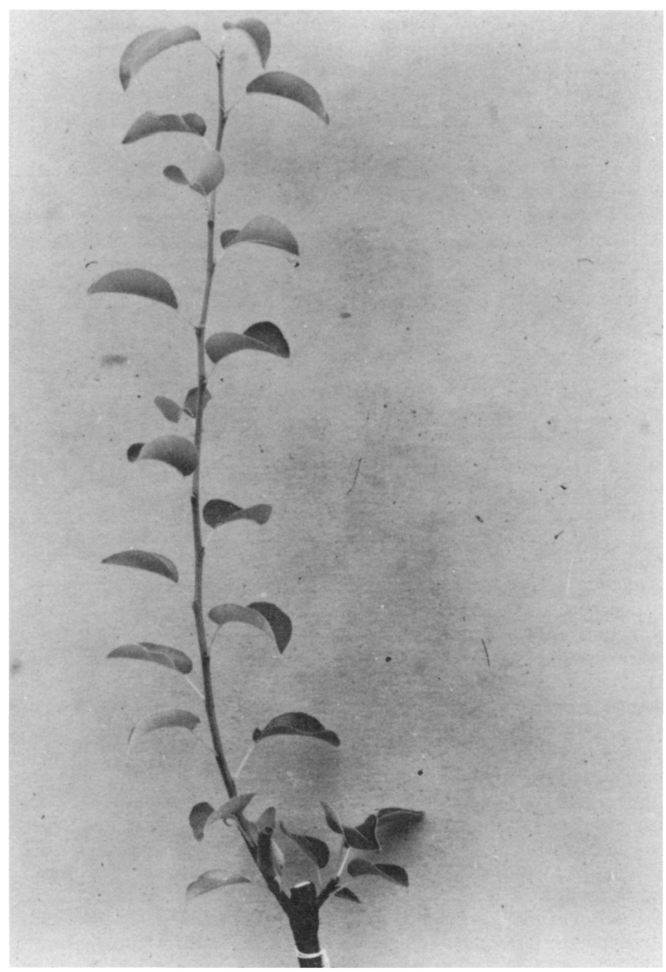

Fig. 2. Growth of Bartlett pear buds in response to 480 hours chilling at 40°F. One bud was taken from a tree on *P. calleryana* root (left) and one from another on *P. communis* root (right) and placed opposite each other on a fully chilled host plant. Photo was taken after 60 days from budding.

calleryana root was due to a shift in growth promoters rather than to a reduction of ABA. Observations in the Northwest indicate that *P. communis* varieties on *P. calleryana* stock are less hardy than the same varieties on *P. communis* root. Strausz (26) found that winter buds of *P. calleryana, P. serotina* and *P. ussuriensis* (all shown to reduce hardiness of varieties grafted to them) contained less ABA than did buds of *P. betulaefolia* and *P. communis,* both reported to be hardy stocks. More work is needed to clarify this complex stock-scion relationship.

P. ussuriensis is a species adapted to cold Siberian winters. It goes dormant in late summer and in its native habitat of constantly cold winters it easily survives -50°F without injury. Its moderate chilling requirement is completed in early spring as temperatures rise above freezing. This species is ill adapted to the mild winters at Corvallis, Oregon, and often suffers winter injury. Under Oregon conditions the trees go dormant in early fall and never suffer damage in early winter. But the mild winter temperatures between 30 and 50°F satisfy its moderate chilling requirement by about January 1, after which it begins to grow in response to even a few days above freezing. In this active state it has been severely injured by moderate late winter freezes no colder than 20 to 25°F. This example is given to illustrate the possible disparant results indicating different degrees of hardiness for a species when observed or tested under different conditions.

Stone fruits – cherry

Prunus mahaleb rootstocks were generally found to be hardier than *Pr. avium* (Mazzard) (16). Mahaleb P. I. 193702 and 194098 clones were hardier than mahaleb seedlings. Mazzard stocks, including F12/1 clone are considered tender. The Hüttner mazzard clones are somewhat less tender with Hüttner 170 rated relatively hardy. *Pr. fruiticosa* and *Pr. pensylvanica* were rated hardier than *Pr. mahaleb* (16). In Colorado (9) sour cherry/mahaleb was hardier and more resistant to chlorosis than sour/mazzard. Likewise in New York Montmorency/mahaleb was hardier than mazzard. Stocks infested with nematodes had reduced hardiness. In Pennsylvania, however, 'Schmidt'/mazzard was reported hardier than trees on mahaleb root (3). Enough variability exists between seed lots of these two species to explain this inconsistency. After the November, 1940 freeze in Iowa, Maney (18) reported that while most peaches and sour cherries were killed, 'Early Richmond' was hardier than 'Montmorency' and 'English Morello'.

Trunkstock hardiness for cherries has been little studied. Mahaleb, *Pr. pensylvanica* and *Pr. cerasus* ('Stockton Morello', 'Montmorency' and 'North Star') are known to be hardier than *Pr. avium* varieties. There is some evidence in Oregon that the graft unions of high-worked mahaleb are not as hardy as unworked mahaleb.

Plum and peach

Lapins (16) lists Ackermann, Brüssel and Damascena plums as tender; Brompton, Kroosjes, and Myrobalan as moderately tender; Marianna, Hüttner IV and St. Julien as moderately hardy; Pershore as hardy; and *Pr. americana* and *Pr. besseyi* as very hardy.

In the November, 1940 freeze, both American and Japanese plums along with peaches were killed, while some sour cherries and pears survived (18).

Root hardiness was reported (32) from hardy to tender:

Pr. besseyi, Pr. americana, Marianna, peach and myrobalan. Also in order from hardy to tender were *Pr. americana,* Marianna, *Pr. davidiana,* Myrobalan, southern natural (peach), Elberta seedling, and Florida peach. Stems were hardier than roots, but hardiness between the two organs was related (32).

North Caucasus peach showed better bud hardiness than 'Elberta' (1). A sharp drop from 60-70°F to 8°F in March killed 'Elberta' buds whereas more than 25% of the buds survived on 20 north Caucasus clones. More than 50% of the buds survived on 9 of the clones. Hardiness in the bud-swell and bloom stage would be of great value in domestic varieties. Blake (4) reported that 'Chili', 'Greensboro' and 'Cumberland' peach buds resisted low winter temperatures well, but high to low temperature fluctuations in winter resulted in less injury to 'Pallas' and 'Ambergem' buds than to those of other varieties. He showed that while the wood of *Pr. davidiana* was hardy, the flower buds were not.

Peaches grown in the relatively warm winters in Georgia (23) showed injury after sharp fluctuations in temperature following rest. Injury to crotch and trunk cambium occurred at 15-22°F when preceeded by a warm period. In this type of freeze no root damage occurred.

Blake (4, 5) reported that peach cambium near the ground line remains active into October some years. Such a condition probably is stimulated by the basipetal flow of auxin and predisposes the trunk and crotches to injury from fall and early winter freezes.

BREEDING AND GENETICS

There is a close relationship in apple hybrids between parental and progeny hardiness (22). Phenotype predicted the genetic potency for hardiness. Tender x tender progeny were mostly tender (15) but other crosses were variable. Antonovka produced hardy progeny (2). In Poland (19), 'Antonovka' x EM IX produced several hardy stocks of promise. Lantz and Pickett (14) stated that hardiness was predictable in apple progeny but comes from multiple factor inheritance. In the November, 1940 freeze, most progenies showed the full range from death to no injury. Hardy x tender types resulted in a high percentage of hardy seedlings, but with tender x tender crosses few offspring were hardier than the parents (14). Recent progress in breeding for hardiness has been made at the Ottawa Research Station (personal communication, L.P.S. Spangelo). This work was accelerated by the development of a portable freeze chamber suitable for field use. Both clonal and hybrid seedling apple stocks are being tested which are not only hardier than EM and MM stocks, but also show a range of size control comparable to that between EM 26 and EM II.

Peaches whose cambium at ground line remains active late in the fall are not hardy to early winter freezes (5). White fleshed seedlings with red at the stone and some red-leafed types were found to be hardy. These can be used as stocks and worked 18 inches above the ground to avoid ground-line injury.

Bud hardiness of peach was shown by Mowry (20) to be quantitatively inherited, with an undetermined number of genes involved. 'Redskin', 'Blake', 'Ranger', 'Redhaven' and 'Boone Country' as parents produced superior progeny for bud hardiness. Bud hardiness of crosses could be estimated by the average hardiness of the parents (20). Similar genetic control of blossom hardiness appears to exist with pear. The newly introduced Oregon pear 'Rogue Red' is quite resistant to frost during full bloom. Part of its parentage comes from 'Seckel' whose blossoms also are resistant to frost.

GENERAL DISCUSSION

The most severe low temperature injury to fruit trees usually occurs in late fall or early winter. Under such conditions tissue maturity is of prime importance. Any condition which prolongs active growth delays the physiological "hardening off" process. Some factors which delay or prevent tissue maturity and cold acclimation are high N nutrition, late cultivation and irrigation, early defoliation, heavy cropping and early pruning. Internal genetic factors may also delay plant maturity. Some cultivars or species do not cease growth in response to short days as do many temperate zone plants. Also, trees on vigorous rootstocks tend to cease growth later than desirable.

Hardiness can be affected indirectly in a number of ways. Insects or diseases can cause early defoliation which in turn prevents normal cold acclimation. Pests of roots may devitalize the tree or cause an upset in nutrient uptake. Soil conditions may cause nutrient deficiencies or imbalance which in turn affects hardiness. Dwarfing rootstocks may enhance early winter hardiness merely by causing shoot growth to cease earlier than would occur with a vigorous stock.

The different organs and/or genetic components of compound trees interact reciprocally with each other and are thus much more complex than ungrafted plants having a single genetic make-up. In some cases the influence of the scion upon the stock bears no relationship to the hardiness of the scion. In other cases the effects are predictable. Some of these apparently conflicting results result from the use of different methods of assessing hardiness (28, 15, 24) or from testing at different times during the season. But some of these anomolous stock/scion effects on hardiness probably are due to a number of *indirect* effects such as differences in balance of IAA, GA, ABA, ethylene and cytokinins, mineral element balance, pest and disease resistance, crop load, etc. One or more of these indirect effects may be superimposed upon the direct hardiness interactions (i.e. the direct interactions of hardiness promoters and inhibitors between root, interstock and scion).

Auxin balance in the tree plays an important role in hardiness development because it influences the amount of active growth of plant organs. Active growth is negatively correlated with hardiness. Auxin is synthesized mainly in subapical regions of active shoots and in developing seeds within the fruits. Dormant twigs of pear were recently shown (30) to contain 3 times as much IAA in trees which had born seeded fruits rather than seedless ones. The carryover effect of a seeded crop aided in setting seedless fruit for at least 3 years. Indirect evidence indicates that the fruit setting factor produced by seeds moves downward to the roots and becomes completely systemic the following spring, possibly by upward xylar transport. The depletion of the setting factor is different with pear than with quince rootstock. Because auxin varies in the same way as seedless fruit set, the setting factor is assumed to be auxin. The basipetal movement of auxin through the trunk in the fall could stimulate cambial activity and reduce hardiness of that portion. The genetic make-up of the rootstock would determine (by leakage to the soil solution, enzymatic inactivation, etc.) how much carryover auxin remained in the system, perhaps to influence hardiness in following years.

Gibberellins (GA) also are produced in seeds of apple and pear. Such GA could decrease fall hardening. GA is known to delay cold acclimation. Thus the observed reduction in hardiness following a large crop could be due to the increase of GA and auxin rather than to a "depletion of reserves" as is so often assumed.

Field observations indicate that trees carrying a crop retain green foliage later in the fall than do trees with no crop. In November, 1955 in Washington many trees of late varieties had not been picked at the time of the sudden freeze. The leaves of these trees were killed and failed to abscise. Freeze damage to such trees was much greater than to trees of the same cultivar which had been picked only a few days before. Detailed observations in 1956 showed that with cultivars maturing after September 1, leaf senescence and fall coloration occurred only after the crop was harvested. Fruit removal quickly and radically altered the physiology of the trees. Fruit on the tree is both a source and a sink. It is a source of auxin and GA and a strong sink for carbohydrates and ABA. Thus after harvest, there must be a concommitant reduction of auxin and GA in the tree and a sharp rise in photosynthate and ABA in the other tissues. These changes seem to favor cold acclimation, because in 1955 trees harvested only one week before the freeze sustained much less injury than unharvested trees. The role of ABA in senescence and initial hardening is unclear but it probably aids hardening at least by its action as a GA antagonist.

Aside from the possible movement of hardiness promoters and/or inhibitors to and from the organs of a compound tree, the balance of auxin, GA, ethylene and cytokinins in a 3-piece tree must be very complex. The cybernation of kinins moving up from the root with the downward movement of auxin and other hormones from the top probably affect early hardiness at least indirectly if not directly. For example, consider the auxin levels in these two compound trees:

1) *Pyrus ussuriensis/P. communis/P. calleryana*
2) *P. calleryana/P. communis/P. ussuriensis*

The first has leaves and shoots of a sub-arctic species, the trunk of a temperate species, and the root of a sub-tropical species. Growth of this tree in late summer is dominated by the *P. ussuriensis* top. In response to shortening days it ceases growth in August and is often half defoliated by October 1. Under these conditions cambial activity of the *P. communis* trunk ceases early in the fall and the system is hardy. The second tree system listed above is dominated by the sub-tropical *P. calleryana.* It does not cease growth in response to short days and under favorable environment will continue active shoot growth into December. At Corvallis, active cambium permits the budding of *P. calleryana* nursery stock in November. With this species as a top, auxin is produced late in the fall, stimulating late cambial activity of the *P. communis* trunk, thus predisposing it to injury by an early freeze.

Pruning immediately prior to a freeze greatly increases injury to the tree (8, 24). The fresh cut apparently stimulates cellular activity and/or creates a strong sink for growth hormones, both of which deharden the tissue.

While much empirical data are available, we know very little about the physiological mechanisms by which one component of a compound plant affects the hardiness of another component. Yet the proper use of grafted plants might elucidate the fundamental nature of cold hardiness. For example, all *Pyrus* species are graft compatible and the genus represents the entire range of hardiness from sub-arctic species (*P. ussuriensis* is hardy at -50°F) to tropical species (*P. koehnei,* an evergreen which is killed at 10 to 12°F). These extreme types, when grafted together would facilitate the testing of any general theory of the origin, movement and fate of hardiness promoters or inhibitors.

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