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Frost Susceptibility of Palms: Experimental Data and Their Interpretation

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The frost susceptibility of palms has been thoroughly documented on the basis of injuries observed following frost conditions. A wealth of data on this subject is to be found in Smith (1958, 1964), Barry (1961), Saakov (1963), Kellett (1969), and Campbell et al. (1977). Experimental investigations, on the other hand, have been made only on a few species (Larcher 1954, 1980, Biebl 1964). In his review on systematics and ecology of palms P. B. Tomlinson very justifiably states that "the physiological basis for the ecological preferences of palms is not understood. The needed research might well study physiological tolerances of individual palm species first in artificially controlled environments and then in field circumstances" (Tomlinson 1979, p. 97). The data presented here were obtained by experimental measurements. In their interpretation the ecological, geobotanical, and evolutionary aspects will be given priority.

Plants and Methods

Samples for the experiments were selected from the Arboretum Arco (Lake Garda Region, Northern Italy) and the Acclimatation Garden "La Orotava" at Puerto de la Cruz (Tenerife, Canary Islands). Arco (45°55′N, 112 m a.s.l.) has a southern alpine climate with strong Mediterranean influence. The annual mean temperature is 14°C, the mean temperature of the coldest month (January) +4.1°C, and the average of annual minimum temperatures −4°C; the lowest temperatures observed are −10°C (Larcher 1979). In Arco entire five year old juvenile plants of *Trachycarpus fortunei* (W. J. Hook) H. Wendl., and leaves of adult *Chamaerops humilis* L., *Washingtonia filifera* (Linden) H. Wendl., and *Jubaea chilensis* (Molina) Boillon were sampled several times during three years.

Puerto de la Cruz (La Orotava: 28°24′N, 110 m a.s.l.) has a maritime-subtropical climate with an annual mean temperature of 19.5°C, a mean temperature of the coldest month of +16.2°C, and average annual minimum temperatures of +10.8°C. The lowest minimum temperatures are +8°C (Abreu 1977). The experiments at Puerto de la Cruz were performed in February, the coldest month of the year. Mature leaves of (a) tall adult specimens, of (j) juvenile plants before shoot extension of ca. 1 m height and of (s) seedlings with typical seedling leaves (cf. Tomlinson 1961) were taken from the following species:

CORYPHOIDEAE: (a) *Livistona australis* Mart., (a) *Livistona chinensis* (Jacq.) R. Br. ex Mart., (a) *Rhapis excelsa* (Thunberg) Henry, (a) *Sabal minor* (Jacq.) Pers., (a) *Trithrinax acanthocoma* Drude.

PHOENICOIDEAE: (a) *Phoenix*

Table 1. Freezing susceptibility of the leaves of subtropical fan palms. At the mean freezing temperature a large part of the leaves is killed

Species	First injury below °C	Mean freezing temperature (°C)
Washingtonia filifera (s)	−4	−6
Washingtonia filifera (a)	−8	−10
Livistona australis (a)	−8	−9
Livistona chinensis (a)	−9	−10.5
Rhapis excelsa (a)	−8	−10.5
Trithrinax acanthocoma (a)	−9	−10.5
Chamaerops humilis (a)	−9	−11.5
Serenoa repens (s)	−10	−12.5
Sabal minor (a)	−10.5	−13.5
Trachycarpus fortunei (s)	−9	−12
Trachycarpus fortunei (a)	−11	−14

(s) = seedling.
(a) = adult plant.

canariensis Hort. ex Chabaud, (a) *Phoenix dactylifera* L., (a) *Phoenix reclinata* Jacq., (a) *Phoenix roebelenii* O'Brien.

CARYOTOIDEAE: (a) *Caryota urens* L.

CHAMAEDOROIDEAE: (a) *Chamaedorea costaricana* Oersted.

ARECOIDEAE: (j) *Chrysalidocarpus lutescens* H. Wendl., (s) *Euterpe edulis* Mart., (a) *Howea forsterana* (C. Moore et F. Müller) Beccari.

COCOSOIDEAE: (a) *Aiphanes acanthophylla* (Mart.) Burret., (j) *Cocos nucifera* L., (j) *Elaeis guineensis* Jacq., (s) *Jubaea chilensis* (Molina) Baillon.

PHYTELEPHANTOIDEAE: (a) *Phytelephas macrocarpa* Ruiz et Pavon.

Seedlings of *Trachycarpus fortunei* (Hook) Wendl., *Serenoa repens* (Bartr.) Small, *Washingtonia filifera* (Linden) H. Wendl., *Sabal minor* (Jacq.) Pers. and *Phoenix canariensis* Hort. ex Chabaud were raised from seeds and kept outdoors in the Botanical Gardens of Innsbruck during summer and in a cool greenhouse in winter. Two weeks before starting the measurements seedlings of various ages (up to five years old) were conditioned at temperatures of +5 to +10°C.

The frost susceptibility was determined by 12 hrs exposure of plant parts or entire seedlings to a series of constant test temperatures between 0°C and −20°C in research refrigerators, and by evaluation of the freezing exotherms of water saturated leaves. Tissue temperatures were monitored by copper-constantan thermocouples connected with a recorder. All data presented are average values of at least five replicates (in the case of seeds 15–20 replicates). Injury was assayed by visual change in color, by conductometric detection of electrolyte leakage from tissues, and by loss of enzymatic triphenyl tetrazolium chloride reduction. Details of the employed methods are given by Larcher (1977a, b, 1980).

Specific Freezing Limits for the Leaves of Various Species

The temperatures below which the first injuries appear and which cause severe freezing of palm leaves are listed in Tables 1 and 2. It appears that, among subtropical fan palms, *Trachy-*

Table 2. Freezing susceptibility of the leaves of feather palms

Species	First injury below °C	Mean freezing temperature (°C)
Aiphanes acanthophylla (a)	−3	−3.5
Elaeis guineensis (s)	−3	−3.5
Cocos nucifera (j)	−3	−3.8
Chrysalidocarpus lutescens (j)	−3	−4
Caryota urens (a)	−4	−5.5
Chamaedorea costaricana (a)	−4.5	−6
Euterpe edulis (s)	−5	−6.5
Howea forsterana (a)	−5.5	−6
Phytelephas macrocarpa (a)	−6	−6.5
Jubaea chilensis (s)	−7	−7.5
Jubaea chilensis (a)	−7	−9
Phoenix roebelenii (a)	−7	−8
Phoenix reclinata (a)	−7	−10.5
Phoenix dactylifera (a)	−8	−9.5
Phoenix canariensis (s)	−6	−7.5
Phoenix canariensis (a)	−9	−10.5

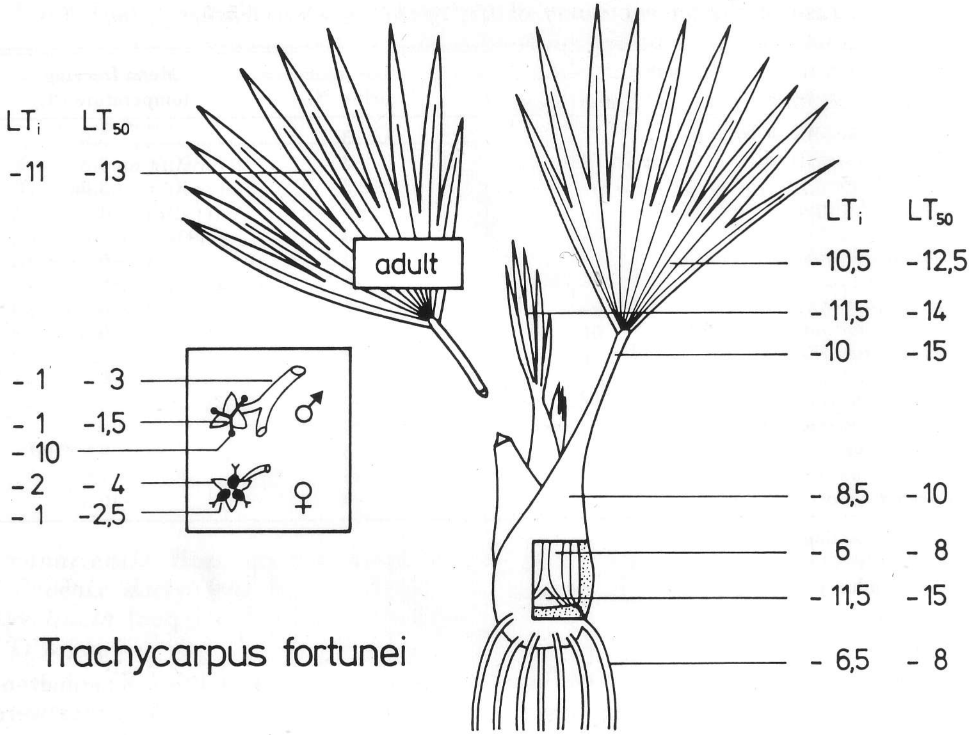
(s) = seedling.
(j) = juvenile.
(a) = adult plant.

carpus fortunei and *Sabal minor* are the most resistant whereas the representatives of the *Livistona* alliance are much more sensitive to frost temperatures. Species of *Phoenix* and *Jubaea chilensis* sustain considerably lower temperatures than the other feather palms investigated. Unfortunately it was not possible to determine the survival limits of leaves of *Ceroxylon*.

The experimental data correspond well with experience from occasional observations of frost damage to cultivated palms in gardens and parks (cf. Gola 1929, Odishariya 1952, Smith 1958, 1964, Barry 1961, Larcher 1963, Saakov 1963, Manley 1967, Kellett 1969, Campbell et al. 1977). There is some additional information on frost survival of particularly resistant species: *Trachycarpus fortunei* is successfully cultivated outdoors in several places in the British Isles (e.g. in the Botanical Gardens of Kew and of Edinburgh, where the lowest temperatures are −12.8°C and −9.4°C, respectively; Lamb 1972). In Seattle, Washington, the leaves of adult *Trachycarpus* were severely damaged at −14°C, but the plant recovered (R. B. Walker, pers. comm.). *Trachycarpus* in the Huntington Botanical Gardens at San Marino, California, suffered leaf damage at −11°C and was defoliated at −19°C (M. Kimnach, pers. comm.). Tall specimens of *Washingtonia filifera*, *Phoenix canariensis* and *Jubaea chilensis* sustained temperatures of −10 to −12°C in the Lake Garda Region, at various locations of the Northern Mediterranean Regions, and at Sukhumi on the Black Sea Coast.

Frost Susceptibility of Various Vegetative Organs

Leaf damage and even complete defoliation can be, but is not necessarily, lethal for palms. Recovery of *Trachycarpus fortunei* after severe frost damage of the foliage has been repeatedly observed. In all these cases the shoot apex was still living due to better pro-



1. Frost susceptibility of various parts of juvenile and adult plants of *Trachycarpus fortunei*. LT_i = Temperature (°C) limit for initial frost damage; LT_{50} = Lethal temperature at 50% killing rate.

tection and probably also higher frost resistance. A thorough susceptibility analysis of a species can therefore not be restricted to the leaves but should include each plant organ and tissue determining survival.

Variations in the frost susceptibility of different organs and tissues of *Trachycarpus fortunei* are shown in Figure 1, of seedlings of *Washingtonia filifera* in Figure 2, and of *Phoenix canariensis* in Figure 3. From Figure 1 it becomes evident that the shoot apex may indeed attain higher frost resistance than the leaves, provided preceding cold weather has forced the plant to arrest its growth processes. If the plant is in the active state the shoot apex is killed together with the leaves or still earlier (Fig. 2). The most sensitive parts of juvenile plants are fast growing tissues such as the intercalary elongation zone of young leaves and the succulent bases of the leaf sheaths.

The roots are very susceptible to freezing, especially the root tips. The roots are also the most vulnerable organs of palms. Parts of them are already damaged at temperatures of −1 to −2°C. Even the crown roots above the soil surface, where during a radiative frost the lowest temperatures normally occur, are more sensitive than most of the shoot tissues. As a consequence, palms are severely affected by ground frost. If only the roots have been frozen the leaves remain turgid and green for several days and there is a still longer delay before wilting occurs. Because of the susceptibility of roots, if frost events are to be expected, temperature measurements should not only be made in air but also near to the ground and in the rooted soil layers. This facilitates the interpretation of subsequently appearing injuries.

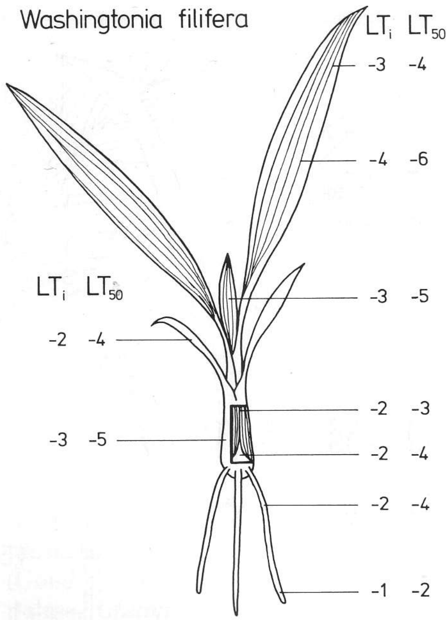
Frost Susceptibility of Propagative Organs and Young Seedlings

As a rule, flowers are the least resistant parts and germinating seeds and young seedlings the weakest developmental stages of a plant (Larcher 1973, Larcher and Bauer 1981). Frost therefore affects propagation at temperatures which would still be harmless to the vegetative organs of adult plants.

Flowers of *Trachycarpus fortunei* are damaged at −1 to −3°C; at −4.5°C they are entirely killed (see Fig. 1). In the male flowers the perianth and the filaments are the most sensitive parts; anthers and pollen remain visually unharmed until −10°C. In female flowers the ovaries are considerably more sensitive than the perianth.

Seeds are very resistant to frost. If air-dry seeds of *Trachycarpus fortunei* and of *Washingtonia filifera* were cooled to −70°C for 12 hrs, most maintained their ability to germinate. Hydrated seeds are considerably less resistant: 50% of water soaked seeds of *Trachycarpus* were killed after cooling to −20°C, of *Washingtonia* to −10°C. After cooling to −16°C, 20% of hydrated seeds of *Washingtonia* remained still alive. As soon as germination occurs and the primary root becomes visible, the embryo of *Washingtonia* is killed below −2°C, that of *Trachycarpus* below −10°C.

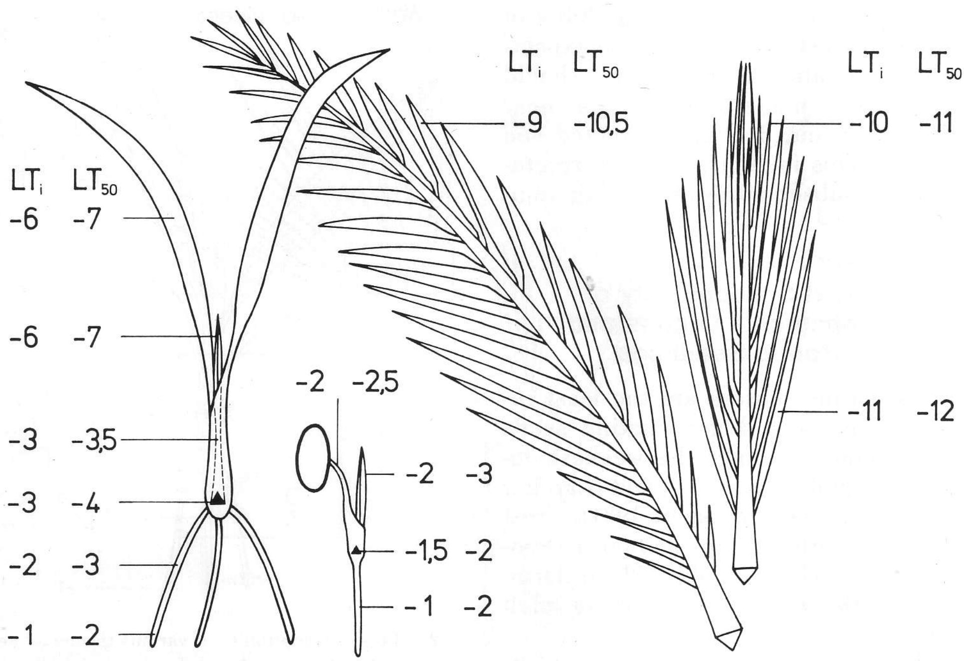
Young seedlings in the coleoptile stage and during the extension of the primary leaf are the most sensitive steps in the life cycle (see Figs. 3 and 4). Again the roots and the elongating leaf bases are the first to be damaged by frost. With aging the susceptibility decreases rapidly in *Trachycarpus fortunei* and *Sabal minor*, more slowly in *Washingtonia filifera* and *Phoenix canariensis*. Juvenile plants of *Trachycarpus* attain nearly the same frost resistance as adult palms.



2. Frost susceptibility of various tissues of actively growing one year old seedlings of *Washingtonia filifera*. LT_i = °C causing initial injuries; LT_{50} = °C causing 50% injury.

Seasonal and Adaptive Variations of Frost Susceptibility

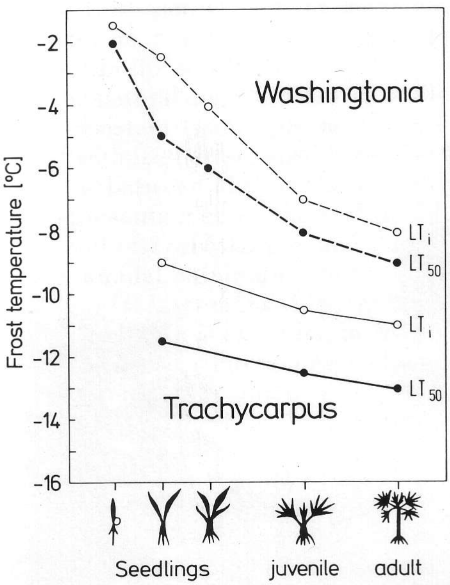
The clearly positive correlation between growth activity and frost susceptibility leads us to expect seasonal variations of the sensitivity level. Such seasonal differences can in fact be demonstrated, but only in those tis-



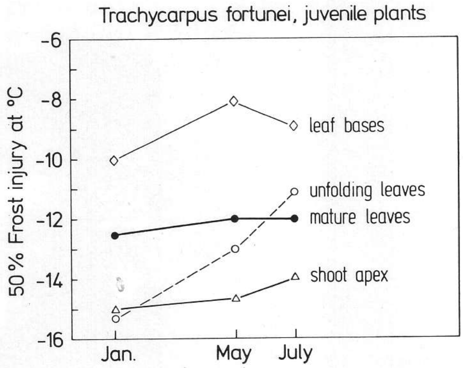
3. Frost susceptibility of germinating and one year old seedlings, and of still folded and mature leaves of adult plants of *Phoenix canariensis*. LT_i = °C causing initial injuries; LT_{50} = °C causing 50% injury.

sues capable of extension growth, i.e. the shoot apex and, above all, the intercalary growth zones of the leaves and leaf sheaths (Fig. 5). Fully differentiated leaves, on the other hand, show no appreciable variations throughout the year. This remarkable property is peculiar to palms. In contrast to other plant species the mature tissues exhibit approximately the same temperature limit for frost injuries in summer and winter. In palms the state of activity of individual organs and tissues apparently does not affect the rest of the vegetative plant body. This kind of autonomy of the individual parts of the organism typifies certain tropical trees, in which development is not synchronized with climatic seasonality. The analogous behavior of *subtropical* palms leads to the conclusion that, in contrast to woody plants that penetrate to higher latitudes, palms have not been able to evolve a complete timing of their annual pattern of growth with the increasing seasonality of climate (Larcher 1981). Nevertheless, certain processes in development are very well synchronized, as for example the process of flowering in *Trachycarpus fortunei* with photoperiod.

If mature organs exhibit only slight seasonal variability of their frost susceptibility, little effect on hardening can be expected from lowering temperatures or from other environmental stressors such as drought. Leaves of juvenile plants of *Trachycarpus fortunei* were 1–2°C less frost resistant after 10 days' exposure to 20°C as compared with cold-conditioned plants. A drought period of 10 days, during which the plants wilted to a water sat-



4. Effect of aging on the frost susceptibility of leaves of *Washingtonia filifera* and *Trachycarpus fortunei*. LT_i = °C causing initial injuries; LT_{50} = °C causing 50% injury.



5. Seasonal changes in frost susceptibility of mature leaves and growing parts of juvenile plants of *Trachycarpus fortunei*.

uration deficit of 66%, also induced an increase in frost resistance of 1–2°C. Combined drought and cold treatment resulted in a shift of the injurious temperature level to −12.5°C for initial injuries, and to −14°C for 50% leaf damage. Thus, the greatest adaptation amplitude of juvenile *Trachycarpus* does not exceed 3°C. The seasonal and adaptive range of mature leaves of *Washingtonia filifera* and *Chamaerops humilis* was only 1°C or less.

Frost Susceptibility and Distribution Range of Palms

The palm family has evolved a wealth of adaptations, which accounts for their presence in widely differing environments (Read 1974). However, they have never succeeded in establishing themselves in regions with cold winter and severe frost. The Arecaceae therefore represent the classical textbook example of a plant group almost entirely confined to the tropics (Good 1974). Among the coryphoid palms, *Chamaerops humilis* advances as far as 40°N in Spain and Sardinia thus delimiting the extreme northward deviation of the distribution area of palms. Species of *Sabal* and *Washingtonia* in North America and of *Trachycarpus* in East Asia proceed up to 35°N (Moore 1973). Among the feather palms, *Phoenix canariensis* is native to the Canary Islands and Madeira (30°N), naturalized *Phoenix dactylifera* is found in Crete (35°N), and *Phoenix sylvestris* at 35°N in the Pandjab (Meusel 1965). In the Southern hemisphere, *Jubaea chilensis* delimits at 33°S the distribution area of palms in South America, *Phoenix reclinata* at 32°S in South Africa, and arecoid palms at 40°S in New Zealand. Altitudinal limits are 2,400 m a.s.l. for *Trachycarpus* species in the Himalayas (Beccari 1933) and 3,000–4,000 m a.s.l. for *Ceroxylon* species (McCurrach 1960, K. Mägdefrau pers. comm.) in the tropical Andes.

An absolute limit of distribution for both native and cultivated palms is undoubtedly the ground frost limit. Palms are unable to survive in regions

6. *Trachycarpus fortunei* in the Arboretum Arco, Garda Lake Region, Northern Italy.

where frost periods are of sufficient duration for negative temperatures to develop in the soil itself.

If the natural distribution area of the most resistant palm species is compared with isotherms, good agreement appears between the northern limits for representatives of the *Sabal* alliance and of *Trachycarpus* and the average annual minimum isotherm of −10°C. It is remarkable that the −10°C isotherm is exceeded in Arkansas. It would be interesting to investigate whether the *Sabal minor* that pushes so far north is more resistant than experimental data suggest, or whether these dwarf palms have simply occupied favorable habitats where the temperatures are higher than those recorded in the meteorological stations. Since for naturally propagating plants the frost susceptibility of juvenile plants is decisive, the temperature limit for seedling establishment of *Sabal* and *Trachycarpus* should be at about −12°C.

In North America the distribution limits of species of the *Livistona* alliance (including *Washingtonia*) and in Southern Europe of *Chamaerops humilis* seem to correspond with the isotherm for absolute minimum temperatures of −5°C and average annual minimum temperatures of 0°C. Again a connection with survival limits of seedlings (and probably also roots) rather than adult palms appears.

Frost limitation of the natural distribution of feather palms seems to be very unlikely. *Phoenix canariensis*, which survives −10°C as an adult and −5°C as a juvenile plant, can be cultivated but does not naturally distribute at elevations much higher than 600 m a.s.l. at the Canary Islands (Santos, pers. comm.). At this altitudinal level the lowest temperatures are in the average +6°C and never lower than 0°C (Ceballos and Ortuño 1976, Abreu 1977). If the distribution areas (as presented by Moore 1973) of the other feather palms investigated are compared with isotherms below 0°C (e.g. Hoffmann 1960) no clear correlation can be recognized.

This indicates that survival limitation by low temperatures is not necessarily due to freezing. Many tropical plants suffer from chilling at temperatures between +10 and 0°C and can also be irreversibly damaged without freezing (Lyons 1973, Levitt 1980, Larcher and Bauer 1981). There is still no evidence as to whether palms are chilling sensitive. None of the species investigated showed visible damage due to acute chilling stress of 24 hrs at 0°C. However, unpublished measurements of CO_2-gas exchange and of chlorophyll fluorescence transients (as an expression of photosynthetic function) revealed pathologic reactions near 0°C in seedlings of *Washingtonia* but not of *Trachycarpus* and *Serenoa*. The decrease in CO_2-uptake at suboptimal temperatures is much steeper in *Washingtonia* than in *Serenoa* (Moraes 1980). Thus, chronic impairment of metabolic processes during long-lasting low temperatures near 0°C may result in weakening the plant and eventually lead to decay.

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Dedicated with appreciation to Volkmar Vareschi on the occasion of his 75th birthday.