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Plant responses of quinoa (*Chenopodium quinoa* Willd.) to frost at various phenological stages

S.-E. Jacobsen[a,*], C. Monteros[a,1], J.L. Christiansen[b], L.A. Bravo[c], L.J. Corcuera[c], A. Mujica[d]

[a] *International Potato Center (CIP), Apartado 1558, Lima 12, Peru*
[b] *Department of Agricultural Sciences, Royal Veterinary and Agricultural University, Thorvaldsensvej 40, DK-1871 Frederiksberg C, Denmark*
[c] *Departamento de Botánica, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile*
[d] *Proyecto Quinua CIP-DANIDA, Universidad Nacional del Altiplano, Puno, Peru*

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Abstract

Frost is one of the principal limiting factors for agricultural production in the high Andean region. One of the most important grain crops in that region, quinoa (*Chenopodium quinoa* Willd.), is generally less affected by frost than most other crop species, but little is known about its specific mechanisms for frost resistance. This study was undertaken to help understand quinoa's response to various intensities and durations of frost under different levels of relative humidity (RH). The effect of frost on seed yield and plant death rate was studied, and content of soluble sugars, proteins, and free proline, was analyzed, in order to develop criteria for the selection of cultivars with improved resistance to frost. On the basis of greenhouse and phytotron experiments, it was concluded that at the two-leaf stage, cultivars from the altiplano of Peru, 3800 m above sea level, tolerated −8 °C for 4 h, whereas a cultivar from the Andean valleys tolerated the same temperature for only 2 h. At −4 °C, plant death rate increased from 25% at high relative humidity to 56% at low RH After a frost treatment of −4 °C applied at the two-leaf stage, final seed yield was reduced by 9% compared to control plants not exposed to frost. For the same treatment applied at the 12-leaf and flowering stages, yield reductions were 51 and 66%, respectively, indicating that frost for 2 h or more during anthesis caused significant damage to the plants. In general, an increased level of soluble sugars implied a greater tolerance to frost, resulting in higher yields.
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Keywords: Quinoa; Soluble sugar; Proline; Freezing tolerance; Frost duration; Frost intensity; Phytotron

* Corresponding author. Present address: Department of Agricultural Sciences, Royal Veterinary and Agricultural University, Højbakkegaard Alle 9, DK-2630 Taastrup, Denmark. Tel.: +45-35283388; fax: +45-35283384.
E-mail address: seja@kvl.dk (S.-E. Jacobsen).
[1] Present address: Instituto Nacional de Investigaciones Agropecuarias (INIAP), Apartado Postal 17-17-1362, Quito, Ecuador.

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1. Introduction

Agriculture in the Andean highlands is characterized by a high degree of risk due to a range of adverse climatic factors such as drought, frost, wind, hail, and soil salinity (Mujica and Jacobsen, 1999; Jensen et al., 2000; Jacobsen et al., 2003; Garcia et al., 2003). A certain degree and duration of frost is lethal to most organisms, due to dehydration of the intracellular environment and physical damage by ice crystals. This adverse factor is of great importance in the Andes with significant diurnal temperature variations, and frost at night up to 200 days a year. Temperatures below 0 °C normally occur in the Andean region for a period of time between 12 p.m. and 6 a.m. (Grace, 1985; Capelo, 1993). The two most common types of frost are radiative and convective, also known as white and black frost, respectively. White frost, which causes relatively little damage in nature, occurs under high relative humidity (RH) and a relatively high dew point temperature (Ruiz, 1995). With this type of frost, water vapor condenses and freezes on the leaf surface, causing the release of heat and a gradual cooling of the environment. Black frost occurs when the air is dry, with temperatures not reaching the dew point temperature. In this case, the water in the leaf tissue freezes rather than the water vapor. Because there is no atmospheric vapor to alleviate this phenomenon, the air temperature drops rapidly. At sunrise the following morning, the ice evaporates quickly, leaving necrotic spots in the foliage (Ruiz, 1995).

In the Andean highland adverse factors such as frost and drought affect the length of the growth season and the crops and varieties to grow. The process of acclimation, for instance to freezing temperature, is important in many crops. Some crops, e.g. maize, rice, cotton, cucumber and tomato, are commonly chilling-sensitive, due to their tropical and subtropical origin. When the temperature drops slightly below the growth optima, the photosynthesis rate decreases, and the critical chilling stress temperature leads to a marked reduction of photosynthesis (Wise and Naylor, 1987). In wintersown crops, such as cereals and oil seed rape, a cold hardening (acclimatization) takes place under natural conditions in the autumn when the temperature gradually decreases to 0 °C over several weeks. Temperatures of 2–5 °C and photoperiods of about 12 h are considered to be optimal for cold hardening. During cold acclimation a complex of responses in plants at the cellular, physiological and developmental levels take place. The adaptation processes related to frost resistance are regulated in a polygenic manner (Galiba et al., 2001). Freezing tolerance is composed of at least two independent genetic components, non-acclimated freezing tolerance and acclimation capacity (Stone et al., 1993). The strategy of adaptation consisting of autumn accumulation of reserves and their subsequent utilization during hibernation (wintersleep) may be considered common for even remote organisms. This becomes possible as a result of higher thermoresistance of photosynthesis, as compared to respiration, and low light requirements for photosynthesis saturation at low positive or negative temperatures (Klimov, 2003). Klimov (2003) also mentioned that the absolute values of the photosynthesis/respiration ratio in the hardened plants was 1.5–2 times higher than non-hardened plants.

Even in frost tolerant winter varieties a certain period of growth at low, but non-freezing temperature is required for the development of frost hardiness (Janda et al., 2003). This cold acclimation includes several physical and biochemical processes, including changes in membrane composition (Nishida and Murata, 1996) and the accumulation of protective compounds, such as carbohydrates, abscisic acid (ABA), free amino acid and polyamines (Racz et al., 1996). Studies on potato (*Solanum tuberosum* L.) (Stone et al., 1993) and *Brassica rapa* (Teutonico et al., 1995) showed that inherent and acclimation-specific freezing tolerance are under separate genetic control. This was also shown for oil seed rape (*Brassica napus* L.) (Hawkins et al., 2002).

During acclimation to drought stress, it has been demonstrated that several metabolic and physiological changes that may increase resistance to desiccation occur, and that some of these changes may be common to various adverse factors. An important common response to drought and cold stress seems to be the increased accumulation of sugars, for instance in oat (*Avena sativa* L.), rye (*Secale cereale* L.) and other crops (Alberdi et al., 1993; Koster and Lynch, 1992; Alberdi and Corcuera, 1991). Rapacz (1999) showed that the progress of the cold acclimation process may lead to an increase in soluble sugar content in oil seed rape. Proline and sucrose contents increased with stress duration, while the content of

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