ENVIRONMENTAL FACTORS AFFECTING TUBERIZATION

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SUMMARY

A review of literature of climatic and biotic factors affecting tuberization mainly of *Solanum* potatoes.

RESUME

Un apercu des données sur les facteurs climatiques et biotiques sur la déterminisme de la tubérisation chez la pomme et terre et quelques autres cultures.

RESUMEN

Repeso de literatura de clima y factores bioticos pateticos la producción de tuberculos lo principal de *Solanum tuberosum*.

INTRODUCTION

Tuberization in plants showing this special morphogenetic feature does not take place at the same rate and intensity in different environments. Both climatic and edaphic and biotic factors, including pathogens, affect this phenomenon. The most important factors are photoperiod, temperature, light (intensity and quality), mineral nutrition, water availability and viruses.

The physical environmental factors act by the synthesis, destruction, transport and activation of growth substances. Minerals, water balance and viruses are also known to alter growth-substance balance in plants and hence environmental factors affecting tuberization may be at least partly explained by their influences on the growth substance. By affecting the intensity and duration of photosynthesis and respiration, the environment may also affect the level of photosynthate available for storage in tubers. According to one theory on the mechanism of tuberization, surplus photosynthate is required for the process.

Inductive and non-inductive environmental conditions have been distinguished. Kopetz and Steineck[35] claimed that differences in tuberization found between different cultivars may be explained by differences in critical daylength requirements defined as the daylength above which tuberization did not occur. However, perhaps it is better to distinguish favourable from unfavourable conditions, since it is now recognized that effects are apparently often quantitative not qualitative. Moreover, optimal environmental conditions differ for tuber initiation, growth and maturation and between different plant species and cultivars.

This paper will review knowledge collected mostly from temperature plant species, but in the expectation that such information may lead to a better understanding of tuberization in tropical species. However, there is danger in uncritical transfer of information from one species to another, or even from one cultivar to another within a species. The genetically determined tuber-forming potential of a plant, including the control of reaction to environment, is the most important factor in tuberization. Nevertheless, a knowledge and understanding of the influences of environmental factors may help to improve the yield and/or efficiency of cultivation of root and tuber crops in the tropics.

Tuberization has been reviewed in other crops by Courduroux, Dupaigne, Gregory and Jolivet[14,16,24,33], but most work has been concerned with potatoes (*Solanum tuberosum* L.) only[5,41,50,59].

EFFECTS OF PHOTOPERIOD

On potatoes

Garner and Allard[23] reported that tuberization in *Solanum* potato was promoted by short-day conditions. Although differences were later found between different cultivars of potato, the promotional effect of short days was confirmed.[5,65] Slater[57] took account of the differences in total radiation as well as the shortening of daylength. Driver and Hawkes[15] demonstrated that many varieties of potato tuberize earlier in shorter than in longer days. Gregory[25,26], Chapman[9], Okazawa and Chapman[49], Madec[42] and Purohit[54]

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all provided evidence for a specific tuberization factor formed in short days. Van der Planck[51] pointed out that although final total tuber yield may be higher in long days than in short days, the yield per unit leaf area per unit of time is always higher in short days.

Short-day promotion of tuberization can be abolished by a short light interruption during the dark period, as for other photoperiodic phenomena. Thus, Slater[57] showed that tuber initiation in *Solanum tuberosum* was delayed for two weeks and in *Solanum demissum* did not occur at all, if a light break was applied in the middle of the dark period. Purohit[53] studied the photoperiodic reaction of four Indian potato cultivars in relation to tuberization and confirmed the existence of antagonism between vegetative growth and tuber formation. One cultivar appeared to be a quantitative short-day plant in relation to tuberization, while three were qualitative short-day plants in this respect.

Other crops

In most tuber-forming species other than the *Solanum* potato, short days either favour tuberization or have no effect on it. Positive influence of short-days was demonstrated by Nitsch[46] for *Dahlia* spp., *Begonia socotrana* and some cultivars of *Helianthus tuberosus.* Moser and Hess[45] proved that the phenomenon was one of photoperiodism in *Dahlia* spp. by application of a light break during the dark period. Zimmer[72] did the same for *Begonia* spp. Courduroux[12,13,14] reported different responses for different cultivars of *Helianthus tuberosus.* Some were day-neutral whilst others had either a short day or a long day response. According to Esashi and Nagao[19], underground tuberization in *Begonia evansiana* is daylength insensitive, but the formation of aerial tubers has a short day response. Exceptionally, for a few species, either continuous illumination or long days (more than 12 hours) may favour tuberization. Le Clerch[39] claimed this for a tuberizing variety of *Arrhenatherum elatius* (L.) Mert. and K., although effects of total daily irradiation cannot be excluded in this response.

In tropical root and tuber crops photoperiod may not play a major role since differences in natural daylengths within the tropical belt are rather small and daylength in general is short compared to that in the growing conditions of temperate climate summers. Nevertheless, it is possible that artificial shortening of the day might accelerate tuberization in some crops, without necessarily however improving final yield. According to Bautista and Cadiz[2] in the yam bean (*Pachyrrhizus erosus* L. Urb.) root production in the Philippines was greater in the cooler part of the year which also had shorter daylengths. Initiation of tuberization under the influence of daylength has been suggested for the same crop in Hawaii by Ezumah[20]. Bolhuis[6] suggested that optimal daylength for tuberous root formation in cassava (*Manihot esculenta* Crantz) was 12 hours, and cassava a short-day plant in this respect. Positive influence of short days on tuberization has also been found for yams (*Dioscorea* spp.) by Njoku[47] and cocoyams (*Colocasia antiquorum* Schott) by Tsukamoto and Inaba[64].

EFFECTS OF TEMPERATURE

On potatoes

Most of the information presently available on the influence of temperature on tuberization refers to potato. Both photosynthetic and morphogenetic processes mediate the effects of temperature on tuberization. Thus Burt[8] demonstrated that sink (tuber) initiation, as well as the use of carbohydrates for tuber growth were sensitive to temperature. Low temperatures promoted sink initiation, whereas high temperatures promoted storage of carbohydrates by the sinks.

Gregory[25], Went[67], Borah and Milthorpe[7] and others found that low temperatures, especially low night temperatures, promoted tuber formation. The temperature optimum for the process was 17°C (approx.) and tubers were seldom formed above 30°C. According to Bodlaender[4] the number of tubers per plant was higher at low air temperature, especially at low night temperature, but larger tubers were formed at higher temperature. Soil temperature also had a clear influence on tuber yield, this influence being greatest when air temperature was unfavourable for tuber growth. Epstein[17] and tuber development depended on the growth stage reached by the plant. Yamaguchi *et al.*[71] demonstrated that there was more starch in the tuber cortex at low than at high temperature. Epstein[18] confirmed Slater's[57] suggestion that tuber initiation occurred earliest in plants with a surplus of assimilates, by comparing the effect of soil temperatures of 5°C. and of 29°C. on the composition and morphology of the potato plant. At the high temperature, assimilates were used for root and shoot growth and there were only a few stolons and no tubers. At the low temperature, there was a surplus of assimilates, plants were smaller but flowered earlier and small tubers were formed.

Other crops

The positive influence of low temperature on tuberization has been demonstrated for several other species: e.g. *Helianthus tuberosus* by Courduroux[10,12,13,14] Stachys sieboldi Lagarde[37,38], *Ficaria renunculoides* by Couduroux[11], aerial tubers of *Begonia evansiana* by Esashi and Nagao[19] and *Ipomoea batatas* by Kim[34]. On the contrary, Dupaigne[16] reported that formation of aerial tubers on *Dioscorea batatas* was favoured by high temperatures.

INTERACTION BETWEEN DAYLENGTH AND TEMPERATURE

Sekioka[56] studied interrelationships between the temperature and various phases of translocation of carbohydrates in sweet potato. At low air temperatures (optimum at 15° C.) translocation to young leaves and growing points increased. The influence of the soil temperature was not clear. At high soil temperature, accumulation in the above ground parts was high, but accumulation in the underground parts was dependent on relative day/night temperatures. At low soil temperature, accumulation in the underground parts was also dependent on day/night temperatures.

EFFECTS OF LIGHT INTENSITY AND QUALITY

It might be expected that higher light intensity would lead to higher carbohydrate production and hence tuber yield. This was in fact demonstrated for *Solanum* potato by Bodlaender[5] and by Posthumus (unpublished results) for radish (*Raphanus sativus* L. var. *radicula*) under phytotron conditions. With illumination of four different light qualities, but with equal amounts of energy irradiated per unit area, we found that greatest tuberization in radishes occurred in red light. This may therefore be a photo-morphogenetic rather than a photosynthetic effect and needs more investigation.

In *Solanum* potato, illumination of the stolon' tips inhibits tuberization by converting these into leafy shoots. An instance of a negative influence of light on tuberization is the complete inhibition of tuber initiation in sweet potato that occurs by exposure of the root system to light[63].

The high light intensity in the tropics compared with that in temperate climates, should generate sufficient potential photosynthetic energy to produce abundant crop yields, through the process of tuberization.

EFFECTS OF MINERAL NUTRITION

Adequate supplies of macro and micro elements are of course required for optional growth and development. However, as Werner[68] reported, abundant supply of nitrogen will favour top growth (stem and leaves) and impair the process of tuberization by diverting more energy to such vegetative growth. Relatively low doses of N, on the contrary, can reduce vigorous top growth and hasten the process of tuberization. However, yield is a product of bulking rate and bulking time, and high N-levels could lead to high yield by causing late bulking at a high rate.

There are also considerable differences in effects of mineral nutrition in tuber yields between different species and varieties. For *Solanum* potato, mineral nutrition has been investigated rather thoroughly as indicated by Watson[66] and Holliday[29]. Tsuno and Fujise[51 – 63] studied dry matter product and distribution in sweet potato in relation to the absorption of mineral elements (N,P,K). Martin[43] discussed other tuber bearing crops in which nitrogen promoted juvenile growth until reduced N supply led to increases in the rate of starch storage.

Relatively few fertilizer experiments have been carried out with tropical root and tuber crops. Fujise and Tsuno[22] demonstrated that K was most important for the dry matter production in sweet potato. Samuels[55] studied the influence of nutrient ratios on sweet potato yields and concluded that adverse effects could result from applied nitrogen at low K levels. Too much N promoted shoot growth and inhibited tuber growth. The same was found by Wilson[69]. Effects of N, P and K on sweet potato yield were also studied by Liang Li[40]. Krochmal and Samuels[36] found that high N levels promoted top growth and prevented tuberization in cassava and that increasing P levels increased tuber yield quite considerably. Irving[30] applied sulphate of ammonia to yams (*Dioscorea* spp.) with favourable results. Ferguson and Haynes[21] studied the response of yams to N,P,K and organic fertilizers, and found a relatively small but positive response to nitrogen and organic matter. Reference was made to the importance of species and varietal differences in response potential, as indicated by Nye[48]. According to Plucknett[52] the aroids generally are very responsive to fertilizers, but little is known of their detailed nutritional requirements. Spence and Ahmad[58] described N,P,K.S.Mg, Ca and Fe deficiencies in *Xanthosoma saggitifolium*.

EFFECTS OF WATER REGIME ON TUBERIZATION

Water stress hastens tuberization in *Solanum* potato (Ito and Kato[31]). As a result of water stress-induced cessation of shoot and leaf growth, tubers are initiated much earlier but only grow slowly because of the much smaller productive leaf area.

Irrigation has been shown to be beneficial for tuber production in *Solanum* potato. Thus, Ivins[32] showed that irrigating at the time of early tuberization produced a higher yield than irrigating either earlier or later during the early-bulking period of the crop. On the other hand too much water due to inundation or excessive irrigation may prevent tuberization completely if it creates an anaerobic soil environment. Togari[60] showed the dependence of tuberization in sweet potato on adequate soil aeration. Haynes[28] explained the seasonality of sweet potato production in Trinidad by suggesting that the high soil moisture and the consequent low soil oxygen content during the wet season might inhibit tuberization. Wilson[70] found that growth of sweet potato plants with total root systems submerged, even in well-aerated water cultures, completely inhibited tuber initiation, and that tuber initiation only took place if the upper half of the root system was exposed to air.

EFFECTS OF PATHOGENS ON TUBERIZATION

Bald and Hutton[1] and later Harmey *et al*[27] reported that viruses, such as the leaf roll virus, may accelerate tuberization in *Solanum* potatoes. This phenomenon may be explained by alteration of the balance of hormones in the host by the pathogen, but may also be the result of the restricted growth of the plant top.

CONCLUSION

Based on the extensive work, mainly with *Solanum* potato, but also with some other tuber crops in temperate climates, it can be stated that photoperiod and temperature, especially night temperatures favour, but are not indispensable for, tuber formation in many crops. Tuberization is also influenced by, but not specifically dependent on light intensity and quality and on mineral nutrition and soil moisture. As a result of the higher photosynthetic activity induced, tuber yield is higher in higher light intensity, but light quality seems to have a photomorphogenetic effect on tuberization. As for all growth and develop-
light quality seems to have a photomorphogenetic effect on tuberization. As for all growth and develop-
ment phenomena, supply of water and minerals is a general pre-requisite for tuberization. But shortage of N-salts and water stress may cause accelerated tuber formation. The influence of a pathogen on tuberization is mentioned as an exceptional case. Thus, leaf roll virus in potato may hasten the tuberization process. But final yield in all these cases of precocious tuber formation is rather more dependent on the duration than on the intensity of the tuber bulking process.

As Milthorpe[44] stated at the first International Symposium on Tropical Root and Tuber Crops, many relevant aspects of the physiology and ecology of strictly tropical root crops are unknown. More precise experiments in controlled environments are necessary for understanding of the effects of environmental factors on tuberization in tropical root crops. More detailed studies on the response potential of different cultivars to N, P, K and organic matter are also necessary to improve the soil conditions so as to attain optimal yield in root crops.

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