Interactive effects of root-zone temperature and irrigation volume on banana vegetative growth in two environments

C Ramcharan
Agriculture Experimental Station
University of Virgin Islands
RR02, Box 10000
Kingshill, Saint-Croix
US Virgin Islands 00850
USA

DL Ingram
Department of Horticulture and Landscape Architecture
University of Kentucky
N-318, Agricultural Science Building-North
Lexington, KY 40546
USA

TA Nell
JE Barrett
Environmental Horticulture Department
IFAS, University of Florida
Gainesville, FL 32611
USA

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ABSTRACT
Tissue-cultured 'Grande Naine' banana plantlets were subjected to root-zone temperatures (RZT) of 28, 33, 38 and 43°C for 6 hours daily and two irrigation volumes daily in two growing environments for 6 to 10 weeks. Plant height, shoot dry weight, leaf length and leaf number did not differ with RZT or irrigation volume but leaf width and leaf area were reduced by the 38 and 43°C RZT treatments in greenhouse and growth room environments. Increased RZT generally resulted in decreased root dry weight. The 43°C RZT caused root injury and this was aggravated by increased irrigation volume in the greenhouse experiment. Roots of plants at 43°C were brown, suberized and lacking root tips. The RZT-induced reduction in leaf area, due specifically to reduced leaf width and not leaf length, was not offset by increased irrigation volume.
A RZT-induced, hormone-mediated response associated with the loss of root tips at the high RZT was postulated.

Effets de la température du sol et de l'irrigation sur la croissance du bananier.

RÉSUMÉ
Des racines de vitroplants du cv Grande naine ont été soumises à des températures (RZT) de 28, 33, 38 et 43°C pendant 6 h/j et à deux volumes d'irrigation/j dans deux milieux de croissance différents pendant 6 à 10 semaines. La hauteur des plants, le poids de matière sèche des racines (PMS), la longueur des feuilles et leur nombre ne sont influencés ni par RZT, ni par la dose d'irrigation ; cependant, en conditions de serre ou en chambre de culture, la largeur et la surface (SF) des feuilles ont été réduites dans les traitements pour lesquels RZT = 38 et 43°C. D'une façon générale, l'accroissement de RZT entraîne la diminution de PMS. La valeur RZT = 43°C a provoqué dans certaines conditions des dégâts aux racines. La réduction de SF induite par certaines valeurs de RZT n'a pas été compensée par l'augmentation du volume d'irrigation. La plante répondrait aux fortes valeurs de RZT par synthèse d'une hormone, associée à la perte de l'extrémité de ses racines.

Efectos de la temperatura del suelo y de la irrigación sobre el crecimiento del banano.

RESUMEN
Las raíces de plantones de bananos del cv Grande naine, procedentes de cultivo *in vitro*, fueron expuestas a unas temperaturas (RZT) de 28, 33, 38 y 43 °C durante 6 h / día y a dos volúmenes de irrigación / día en dos medios de crecimiento diferentes durante seis a diez semanas. La altura de los plantones, el peso de materia seca de las raíces (PMS), la longitud de las hojas (LF) y su número no son influenzados ni por RZT ni por la dosis de irrigación. Sin embargo, en condiciones de invernaderos o en cámara de cultivo, la anchura y la superficie (SF) de las hojas fueron reducidas en los tratamientos para los que RZT = 38 y 43°C. De una manera general el crecimiento de RZT ocasiona la disminución de PMS. El valor RZT = 43°C provocó en algunas condiciones daños en las raíces. La reducción de SF inducida por ciertos valores de RZT no fue compensada por la aumentación del volumen de irrigación. La planta respondería a los fuertes valores de RZT por síntesis de una hormona, asociada a la pérdida de la extremidad de sus raíces.

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KEYWORDS
Musa, leaves, dimensions, rhizosphere, soil temperature, drought stress.

MOTS CLÉS
Musa, feuille, dimension, rhizosphère, température du sol, stress dû à la sécheresse.

PALABRAS CLAVES
Musa, hojas, dimensión, rizosfera, temperatura del suelo, estres de sequía.

introduction

High temperature and water stress often occur simultaneously in crop situations and alleviating the latter is often considered a remedy for the former. Although many drought tolerant plants are also heat tolerant (LEVITT, 1980), interactions and sometimes negative correlations occur between heat and drought stress effects (OGUNLELA and SULLIVAN, 1974). Research has tended to concentrate on water and temperature stress effects separately with little emphasis on defining or separating the characteristics of these two stresses.

Suboptimal root-zone temperature (RZT) (BROWN and BLASER, 1970; BARLOW *et al*, 1976; BARLOW *et al*, 1977) and temperate plant species (BABALOLA *et al*, 1968; KAUFMANN, 1977) have been used in most of the reported investigations that involve RZT and soil moisture interactions. BARLOW *et al* (1976) found that increased shoot carbohydrate under reduced soil moisture conditions was offset by increasing RZT in corn seedlings. KAUFMANN (1977) found that soil water deficits directly affected leaf water potential and transpiration in 'Monterey' pine seedlings but RZT had no consistent effects on other parameters. Water stress, independent of RZT, has been shown to affect growth (RYLSKI *et al*, 1976; DANIELLS, 1984), yield, water use efficiency (GHAVAMI, 1974; BHATTACHARYYA and RAO, 1984) and physiological responses (SHMUELI, 1953; CHEN, 1971) in banana (*Musa* spp AAA). Relatively fewer studies have been reported on temperature stress effects on banana (TURNER and LAHAV, 1983, 1985; INGRAM *et al*, 1986).

With the development of tissue-cultured banana, a containerized phase in which irrigation and RZT are critical aspects has been interjected into banana production schemes. This study investigated the effects of four RZTs and two irrigation volumes on growth and carbohydrate status of 'Grande Naine' banana in greenhouse and growth room environments.

materials and methods

plant materials and general cultural procedures

Ten to twelve cm tissue-cultured 'Grande Naine' banana plants were obtained from a commercial nursery. Plants were hardened in intermittent mist (6 s/min) under 80% light exclusion for one week and then moved to 40% light exclusion for another week. Plants were transplanted to 6.5 cm diameter x 25.0 cm high conical containers (555 cm^3) using Metro-Mix 300 growth medium (WR Grace and Co, Cambridge, MA, USA). Plants were then moved to the experimental greenhouse or growth room where they were irrigated daily with 120 ± 5 ml of water and allowed to acclimatize for one week prior to the initiation of experiments.

greenhouse experiment

An experiment was initiated in August 1985 in an air-conditioned, glass greenhouse in which photosynthetic photon flux on a typical cloudless day was 120 µmol/m^2/s at 800 hours, increasing to 800 µmol/m^2/s by midday then decreasing after 1400 hours to 150 µmol/m^2/s by 1800 hours. Air temperatures were 25 to 30°C during the day and 18 to 21°C at night. Relative humidity varied from 40 to 80%, fluctuating inverse to daily light fluctuations. The CO_2 concentration during the day was 325 ± 30 mg/l.

Two irrigation volumes and four RZT treatments were factorially combined in a split plot experimental design. Plants received 50 ± 5 ml (W1) or 100 ± 10 ml (W2) of water per container (555 cm^3) at 2200 HR daily through drip tubes using a battery-operated controller (Water Watch Corp, Seattle, WA, USA). The 100 ml treatment restored the media moisture content to near container capacity each day. Irrigation volume treatments have proven to be effective in applying water stress in banana (RAMCHARAN *et al*, 1990). Plants were fertilized weekly with the appropriate volume of water and concentrations of 20 N/8.8 K/16.6 P fertilizer (Peters 20-20-20, WR Grace and Co) to apply 250 mg N/container each week.

RZT treatments of 28, 33, 38 and 43 ± 1°C were established in air-bath boxes as described previously (Ingram *et al*, 1986). Each of the 12 temperature boxes contained six banana plants to which the irrigation treatments W1 and W2 were assigned randomly. The experiment was arranged in a split plot design with three blocks (four boxes per block) in which RZT treatments were main

plots and irrigation treatments represented subplots. There were three plants per experimental unit. A general linear model analysis was performed to determine the variation explained by treatments with the residual error used to test sample effects, the subplot error used to test irrigation effects and the RZT by irrigation volume interactions, and the main plot error was used to test effects of RZT. There were no significant block or sample unit effects on any measured parameter. Standard errors were calculated.

Plant height, leaf area, leaf number and stem diameter were recorded weekly. Plant height was considered the distance from the soil surface to the leaf apex and stem diameter was measured at pot rim level. Leaf numbers were derived from the number of fully developed, green functional leaves and emerging leaves which were assigned a value of 0.25, 0.50 or 0.75 depending on the fraction of the leaf lamina fully exposed.

Ten weeks after the initiation of the experiment, leaf and root samples were collected for carbohydrate analysis. The third leaf and a 5 to 7 g composite sample of carefully washed roots was used for carbohydrate analysis. Plants were then separated into leaves, stems and roots and dried for at least 48 h in a forced-air oven at 70°C prior to recording dry weights. Ethanol-soluble sugars and starch were determined according to procedures used by STAMPS (1984). Free sugars were extracted from a 50 mg sample, with 80% ethanol and starch determined from the resulting centrifuged pellet.

growth room experiment

To further monitor growth responses of banana to RZT and irrigation treatments under more precisely controlled environmental conditions, the greenhouse experiment was repeated in a walk-in growth room (RAMCHARAN *et al*, 1990) in August and September, 1986. Irradiance of 1100 µmol/m^2/s photosynthetic photon flux density was supplied at canopy height from 600 to 1830 hours by 1000 W phosphor-coated metal-arc HID bulbs (GTE Sylvania Corp, Manchester, NH, USA). Air temperatures of 28°C during the day and 21°C at night and a relative humidity of 65 to 70% were maintained. Similar plant materials and cultural procedures were used as described earlier, except plants were first transplanted for one week into 4 mm 7.5 cm diameter x 22.5 cm high clear plastic bags (1200 cm^3) which were inserted into similar sized sections of PVC pipe. One week prior to the initiation of treatments, the plastic bags were transferred to root heating tubes in the growth room. Irrigation volumes of 75 ± 8 ml (W1) and 150 ± 15 ml (W2) per container were applied daily at 2200 hours. RZT treatments of 28, 33, 38 and 43 ± 0.8°C were applied daily from 1000 to 1600 hours, using electronically controlled root heating tube containers (INGRAM *et al*, 1990). The four RZT and two irrigation treatments were factorially combined in a randomized complete block design with three blocks and two plants per experimental unit. After 6 weeks, later growth data and samples for carbohydrate analysis were taken and analyzed as described in the greenhouse experiment. A general linear analysis of variance was performed using the residual error to test for treatment and interactive effects.

results

greenhouse experiment

growth responses

RZT and irrigation treatments interacted to affect root dry weight but not other measured parameters. Plant height, leaf number, stem diameter and leaf length did not differ with RZT or irrigation treatments, but width and area of the third newest leaf after 10 weeks were affected by RZT (table I). Effects of RZT became evident as early as two weeks after initiation of treatments with reductions in leaf area expansion by the 38 and 43°C RZT across irrigation volume treatments.

Shoot dry weight was not influenced by RZT or irrigation treatments (table I). However, effects of RZT on root dry weight were altered by irrigation treatments (table II). Although the effects of irrigation volume were similar for plants at the 28, 33 and 38°C RZT treatments, the higher irrigation volume was detrimental in terms of root dry weight in plants at the 43°C RZT. Root dry weight was increased by the 38 and 43°C RZT under the W1 treatment, but only by the 38°C RZT in the W2 treated plants (table II). Root morphology was also influenced. Roots were lack-

ing distinct tips and were brown and less succulent in plants at the 38 and 43°C RZTs compared to plants at 28 and 33°C. By the end of the 10-week experiment, plants were somewhat pot-bound and roots were located mainly in the upper portion of the container. Due to the 1.0°C gradient within containers, as noted previously (INGRAM *et al*, 1986), these roots may have been exposed to the lower limits of each RZT treatment.

Table I
Growth parameters and dry weights in Grande Naine banana measured after 10 weeks at four root-zone temperatures (6 h/day) and two irrigation volumes (W1:50 ± 5 ml or W2: 100 ± 10 ml/container/day) under greenhouse conditions.

Stress treatments	*Plant height (cm)*	*N° of leaves*	*Stem diam (cm)*	*Leaf lenght (cm)*	*Leaf width (cm)*	*Leaf area (cm^2)*	*Shoot dry weight (g)*
Root-zone temperature (°C)							
28	44.0	11.6	2.6	23.7	10.1 ± 0.2	155.9 ± 6.4	20.1
33	43.6	11.5	2.4	22.8	10.5 ± 0.1	155.7 ± 3.1	17.9
38	43.2	11.9	2.6	23.3	9.8 ± 0.1	148.4 ± 2.0	20.3
43	43.7	12.2	2.6	21.2	9.2 ± 0.1	126.7 ± 3.1	18.5
Irrigation volume							
W1	42.6	11.6	2.6	22.6	9.9	145.4	19.3
W2	44.2	11.8	2.5	22.9	9.8	145.9	19.1
Significance[z]							
Temperature	NS	NS	NS	NS	Q*	Q*	NS
Irrigation	NS	NS	NS	NS	NS	NS	NS

[z] Statistical differences between treatments resulting from orthogonal comparisons. Best fit models were quadratic (Q). Interactions between temperature and irrigation volume treatments were nonsignificant for parameters in this table and data were combined for calculation of main effect means. Standard errors are presented for parameters affected by treatments.
*, NS refer to significance at the 5% probability level and nonsignificant, respectively.

Table II
Effect or root-zone temperature and irrigation volume on root dry weight in Grande Naine banana after 10 weeks under greenhouse conditions.

Root-zone	*Low irrigation volume (50 ± 5 ml daily)*	*High irrigation volume (100 ± 5 ml daily)*
28	5.8 ± 0.44[z]	5.8 ± 0.16
33	5.1 ± 0.21	5.0 ± 0.27
38	9.0 ± 0.51	8.9 ± 0.29
43	10.0 ± 0.73	4.2 ± 0.71

[z] Standard errors.

carbohydrate analysis

Shoot carbohydrate content was not influenced by the treatments, but there were significant RZT effects on root sugar (table III). Root sugar content was greatest in plants grown at the 33 and 38°C RZT in both irrigation treatments. Root starch content was not influenced by treatment.

growth room experiment

growth responses

Plant height, leaf number and leaf length were not affected by RZT or irrigation treatments, but stem diameter was increased and leaf width and area were decreased by increased RZT (table IV). Shoot dry weight was not altered by RZT or irrigation volumes but root dry weight was affected independently by RZT and irrigation volume treatments. Root dry weight was reduced linearly by increased RZT with the lower irrigation volume causing additional reduction. As was true in the greenhouse experiment, root tips of plants at the 43°C RZT were absent and roots were brown and less succulent at the 38 and 43°C RZT compared to plants at 28 and 33°C RZT.

Leaf area was also decreased by the higher RZT treatments in this study as a function of reduced leaf width (table IV). There was no RZT effect on plant height, which in reality is a measure of total leaf length in the banana plant. Since leaf area was decreased but leaf dry weight (data not shown) was not altered by increased RZT, smaller, thicker leaves in response to high RZT were assumed.

carbohydrate analysis

Shoot sugar and starch content were not affected by treatments (table V). Root starch content decreased with increasing RZT and there were interactive effects of RZT and irrigation volume on root sugar content. There was a trend of decreased root sugar concentration with increased RZT except at 43°C RZT where the higher irrigation volume resulted in greater root sugar than the lower irrigation volume (table VI).

discussion

The reduced leaf width but not leaf length observed in both experiments suggest a RZT-induced effect on cell expansion and/or division rather than on cell elongation. Anatomical studies of the unfolding banana leaf revealed that increases in leaf width were mainly through expansion of groups of meristematic cells within the leaf lamina (SKUTCH, 1927). Inhibition of leaf expansion by the 38 and 43°C RZT treatments in the greenhouse and growth room could have involved physiological mechanisms not entirely associated with leaf water deficits. DE LANGHE *et al* (1983), examining endogenous hormonal patterns in developing plants, demonstrated that root tips were a major source of cytokinins in banana. Reduced leaf expansion simultaneous with loss of root tips observed in the high RZT-treated plants under both environmental conditions studied may imply a RZT-stimulated, hormonal role in leaf expansion. Since leaf width and not leaf length was affected by high RZT, it may be hypothesized that root-synthesized cytokinin was limiting in plants subjected to the higher RZT treatments. This hypothesis is further supported by the observation that when adult banana plants are cut at the soil level in the field, thus removing the sink but not the primary source of cytokinins, suckers with abnormally wide leaves emerge (personal observations).

Modification of root dry weight by RZT and irrigation volume without an accompanying effect on shoot dry weight or shoot sugar or starch content in both environments indicate that root maintenance and growth were not at the expense of shoot carbohydrate status or growth. The effect of RZT on translocation of sugars from shoots to roots has been shown to differ with plant species (INGRAM *et al*, 1986).

The general RZT-induced increase in root dry weight of the greenhouse-grown banana plants receiving the lower irrigation volume contradicted the decrease in root dry weight found in the growth room experiment and reported by others (FRANCO, 1958; COOPER, 1973; JOHNSON and INGRAM, 1984; GOSSELIN and TRUDEL, 1986). The relatively small container volume and the precision (± 1°C) of RZT treatment application could help explain this difference. Reduction in root dry weight by increased RZT in the growth room was moderated by increased irrigation, but increased irrigation volume was actually detrimental to root dry weight of plants at the 43°C RZT in the greenhouse experiment. The 43°C RZT in the W2 treatment could have disrupted the absorptive capacity of banana roots and the higher irrigation volume in the greenhouse resulted in excessive soil moisture under the higher irrigation volume, thus, additional restriction of root growth. A similar condition was reported for well-watered, container-grown eggplants (*Solanum melongena* L) grown at 40°C RZT, resulting in decreased root dry weight (RYLSKI *et al*, 1976). The suberization and browning of roots for plants at 43°C were evident in both environments. Suberization of roots at high RZT (22 to 35°C) was observed in ryegrass (Poa *pratensis* L) (DARROW, 1939), peach (*Prunus persica* Batch) (NIGHTINGALE and BLAKE, 1934), and rose (*Rosa* sp L) (SHANK and LAURIE, 1949).

Table III
Carbohydrate distribution in Grande Naine banana measured after 10 weeks at four root-zone temperatures (6 h/d) and two irrigation volumes (W1: 50 ± 5 ml and W2: 100 ± 10 ml/container/day) under greenhouse conditions.

Stress treatments	*Shoot sugar (% dwt)*	*Shoot starch (% dwt)*	*Root sugar (% dwt)*	*Root starch (% dwt)*
Root-zone temperature (°C)				
28	3.5	3.8	2.0 ± 0.3	3.9
33	3.1	3.4	3.3 ± 0.3	3.2
38	3.0	3.5	3.4 ± 0.2	3.5
43	3.6	3.3	1.5 ± 0.3	3.0
Irrigation volume				
W1	3.3	3.7	2.4	3.7
W2	3.3	3.3	2.6	3.1
Significance[z]				
Temperature	NS	NS	Q**	NS
Irrigation	NS	NS	NS	NS

[z]Statistical differences between treatments resulting from orthogonal comparisons. Best fit models were quadratic (Q). Interactions between temperature and irrigation volume treatments were nonsignificant for parameters in this table and data were combined for calculation of main effect means. Standard errors are presented for parameters affected by treatments.
**, NS refer to significance at the 1% probability level and non significant, respectively.

Table IV
Growth parameters and dry weights in Grande Naine banana measured after 10 weeks at four root-zone temperatures (6 h/day) and two irrigation volumes (W1:50 ± 5 ml or W2: 100 ± 10 ml/container/day) under growth house conditions.

Stress treatments	*Plant height (cm)*	*N° of leaves*	*Stem diam (cm)*	*Leaf lenght (cm)*	*Leaf width (cm)*	*Leaf area (cm^2)*	*Shoot dry weight (g)*	*Root dry weight (g)*
Root-zone temperature (°C)								
28	37.7	10.0	2.2 ± 0.08	21.3	9.9 ± 0.14	137.4 ± 3.2	17.9	7.6 ± 0.6
33	39.1	10.2	2.5 ± 0.04	20.7	9.9 ± 0.15	133.5 ± 4.4	19.7	6.4 ± 0.5
38	36.5	9.9	2.8 ± 0.06	20.9	8.4 ± 0.23	114.5 ± 6.4	18.7	5.3 ± 0.6
43	36.2	9.8	3.2 ± 0.13	20.7	8.2 ± 0.32	110.5 ± 6.2	19.9	4.1 ± 0.4
Irrigation volume								
W1	36.7	9.8	2.6	21.1	9.3	127.4	18.4	5.0 ± 0.4
W2	37.7	10.2	2.7	20.8	9.1	122.0	19.4	6.8 ± 0.4
Significance[z]								
Temperature	NS	NS	L**	NS	L**	L**	NS	L**
Irrigation	NS	NS	NS	NS	NS	NS	NS	L**

[z] Statistical differences between treatments resulting from orthogonal comparisons. Best fit models were linear (L). Interactions between temperature and irrigation volume treatments were nonsignificant for parameters in this table and data were combined for calculation of main effect means. Standard errors are presented for parameters affected by treatments.
**, NS refer to significance at the 1% probability level and nonsignificant, respectively.

The reduction in root sugar content by the 43°C RZT compared to the 33 and 38°C RZT in both environments further reveals that this RZT was above optimum for banana growth and development. The reduced root sugar content without a change in shoot sugar or starch content could indicate that a smaller portion of synthesized carbohydrates were translocated to the roots and/or more of the translocated sugars were utilized for maintenance at the higher RZT treatments. Increased root respiration or membrane damage in plants at the 43°C RZT treatment may have caused increased utilization of sugars or leakage of photosynthates from the roots (RUTER and INGRAM, 1990). The higher root sugar content stimulated by the higher irrigation volume in plants at 38 and 43°C RZT in the growth room experiment, with a corresponding decrease in root dry weight, implies that higher soil moisture levels may have further decreased the utilization of available sugars. TURNER and LAHAV (1983) reported significant shifts in assimilate partitioning as reflected by dry weights in banana plants subjected to increasing air temperatures in a growth room.

The observed interactions between RZT and irrigation volume could have important implications in the nursery phase of banana production. If growth medium temperatures are 33 to 38°C, maintaining relatively high soil moisture levels in a porous medium would apparently be beneficial in terms of root carbohydrate status. Control measures would be essential if medium temperatures approached 43°C, since this RZT was shown to be supraoptimal under both environmental conditions investigated. Irrigation of plants exposed to this high RZT should be closely regulated since heat stress effects could be enhanced by increased irrigation.

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Table V
Carbohydrate distribution in Grande Naine banana measured after 10 weeks at four root-zone temperatures (6 h/d) and two irrigation volumes (W1: 75 ± 8 ml and W2: 100 ± 15 ml/container/day) under growth room conditions.

Stress treatments	*Shoot sugar (% dwy)*	*Shoot starch (% dwt)*	*Root starch (% dwt)*
Root-zone temperature (°C)			
28	4.9	4.9	8.3 ± 0.43
33	4.0	4.4	8.0 ± 0.30
38	4.0	4.6	7.7± 0.40
43	3.7	4.0	6.8 ± 0.34
Irrigation volume			
W1	3.9	4.3	7.6
W2	4.3	4.7	7.8
Significance[z]			
Temperature	NS	NS	L**
Irrigation	NS	NS	NS

[z]Statistical differences between treatments resulting from orthogonal comparisons. Best fit models were linear (L). Interactions between temperature and irrigation volume treatments were nonsignificant for parameters in this table and data were combined for calculation of main effect means. Standard errors are presented for parameters affected by treatments.
**, NS refer to significance at the 1% probability level and nonsignificant, respectively.

Table VI
Effect of root-zone temperature (6 h/d) and two irrigation volumes (W1: 75 ± 8 ml and W2: 150 ± 15 ml/container/day) on root sugar content in Grande Naine banana after 10 weeks under growth room conditions. The interaction is significant at the 0.001 level.

Root-zone temperature (°C)	*Low irrigation volume (50 ± 5 ml daily)*	*High irrigation volume (100 ± 5 ml daily)*
28	6.5 ± 0.39[z]	6.5 ± 0.69
33	6.6 ± 0.13	4.5 ± 0.48
38	3.8 ± 0.94	5.0 ± 0.43
43	1.3 ± 0.02	5.9 ± 0.43

[z]Standard errors.

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