

Wild Relatives as a Source for Sub-Optimal Temperature Tolerance in Tomato

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Abstract

Greenhouse tomato cultivation often requires a high energy input to maintain set-point temperatures. If set-point temperatures could be lowered by a few degrees this would reduce energy consumption significantly. However, this can only be applied when new, more energy-efficient cultivars are developed, i.e. cultivars that can be cultivated at sub-optimal temperatures without loss of production or quality. As variation for temperature response within the current elite tomato cultivars is limited, it is important to look for other sources of variation. One option are wild relatives which originate from South America, where they grow at altitudes up to 3300 m. In this study we examined the effects of temperature (12-24°C) on growth of young vegetative tomato plants of the cultivar 'Moneymaker' and two wild relatives (*L. hirsutum* LA 1777 and *L. pennellii* LA 716). The aim was to elucidate the physiological and morphological parameters which underlie interspecific differences in growth response to sub-optimal temperatures. During a 28-day period five destructive measurements were carried out in which total dry weight, including root weight, leaf area and leaf dry weight were measured in order to calculate growth parameters. Even though 'Moneymaker' had a higher relative growth rate (RGR) over a large temperature range (16-24°C), RGR of 'Moneymaker' was severely reduced below 20°C, while RGRs of *L. hirsutum* and *L. pennellii* were only decreased below 16°C. At 12°C RGR of 'Moneymaker' was reduced by 41% compared to 20°C, while in *L. pennellii* and *L. hirsutum* this decrease was only 27 and 18%, respectively. This decrease in RGR in 'Moneymaker' was mainly a result of a decreased leaf area ratio (LAR), caused by a 35% decrease in specific leaf area (SLA). In contrast, the decrease in RGR in *L. pennellii* and *L. hirsutum* was a result of a decreased net assimilation rate (NAR) of 24 and 14%, respectively. This study illustrates that wild tomato species provide possibilities for the breeding of more energy-efficient tomato greenhouse cultivars.

INTRODUCTION

The high yield level in Dutch greenhouses requires high energy inputs for heating the greenhouses during the dark and cold winter months. However, as energy prices and public concern about the environmental problems relating with the combustion of fossil fuel are increasing, it is important that energy efficiency (kg of tomatoes produced per m³ of natural gas) is increased. Over the last 25 years there has been a large increase in energy efficiency mainly as a consequence of increasing production levels, while the absolute amount of energy per m² greenhouse area was hardly reduced. A lowering in set-point temperature by a few degrees could contribute significantly to a reduction in energy consumption. It is therefore important that new cultivars are developed that can be cultivated at (slightly) lower temperature set-points. But breeding for equal production and quality at lower temperatures is hampered by the limited genetic variation for temperature response between elite tomato cultivars (Van der Ploeg and Heuvelink, 2005).

The variation in cold tolerance that exists among related *Lycopersicon* species could potentially be useful for the development of cultivars with increased energy efficiency (Venema et al., 2005). These *Lycopersicon* species are native to western South

America, where they grow in a wide range of habitats, from sea level up to 3300 m a.s.l. (Rick, 1995) and some of the high-altitude species (e.g., *L. hirsutum*, *L. peruvianum*) are known to be chilling tolerant (Wolf et al., 1986). However, they might also contain traits that make them grow better at moderately low or suboptimal temperatures: temperatures above chilling but below the current optimum for tomato growth.

The present work aims at determining possible differences in growth and development of young vegetative tomato plants (*L. esculentum*) cv. Moneymaker and two wild relatives (*L. pennellii* and *L. hirsutum*) in response to temperature (12-24°C). Furthermore we elaborate on what physiological and morphological parameters could explain these possible differences, which could be useful for selection criteria during breeding programs.

MATERIALS AND METHODS

Plant Material and Growth Conditions

Seeds of *L. hirsutum* LA 1777, *L. pennellii* LA 716 and *L. esculentum* cv. Moneymaker were sown in seed trays in a greenhouse. Seeds of 'Moneymaker' were sown one week later than seeds of *L. hirsutum* and *L. pennellii*, because of the faster germination rate of 'Moneymaker'. Three weeks later soil was removed from the roots and the seedlings were transferred to 12 cm diameter pots containing expanded clay grit (range 6-8 mm). To allow acclimation to the new root environment, the pots were placed on greenhouse benches in a 2 cm water layer for one week. At the start of the experiment, the plants were transferred to four identical growth chambers (2.5 m × 3.5 m). Within each chamber there were six trolleys. Each trolley contained 16 plants of one species so that within each growth chamber there were two trolleys of each species. The pots were continuously standing in a layer of standard nutrient solution, covered with white plastic to prevent algae growth, and this solution was refreshed weekly.

Each chamber had a constant temperature (12, 16, 20 or 24°C). Fluorescent tubes (Philips TL 58W, color 84) were used during 12 hours, providing 128 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation at plant level. Plants were grown under ambient CO₂ (growth chamber continuously ventilated) and at a relative humidity of 55%.

Measurements

The first destructive harvest of 10 plants of each species was taken when the plants were transferred to the climate chambers. Subsequently, for the duration of 4 weeks, there were weekly destructive harvests of 4 plants per trolley. After each destructive measurement plants were redistributed so that they could grow without mutual shading. Leaf area (LI-COR Model 3100 Area Meter), leaf, stem and root fresh and dry weight (105°C for at least 10 hours), stem length and number of leaves (> 5 mm) were determined in each destructive measurement.

A growth analysis was conducted according to the functional approach (Hunt, 1990). The best fitting polynome for the relation between natural logarithms of total (root and shoot) dry mass (TDM), leaf dry mass (LDM) and leaf area (LA) with time was calculated by using the ordinary "least squares estimate". In all cases polynomials of degree 2 were found to be necessary and sufficient. To exclude ontogenetic effects the growth parameters relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA) and leaf weight ratio (LWR) were compared on the basis of a TDM interval instead of a time interval. The TDM interval is 20.5-92.5 mg, because this was the largest possible interval in these experiments not requiring extrapolation of data.

Results were statistically analyzed as split-plot design with two replications (trolleys were taken as replications) for temperature. Temperature was the main factor and species the split factor. Analysis of variance was conducted. Mean separation was done by the Least Significant Difference (LSD) based on Student *t*-test ($P = 0.05$). The statistical software package Genstat 8.1 was used.

RESULTS

Growth

At the end of the experiment, the accumulated total dry mass (TDM) was significantly influenced by the interaction between species and temperature ($P < 0.001$; Fig. 1A). In all species TDM was significantly lower at 12°C than at 20°C and 24°C but the difference was much larger in ‘MoneyMaker’ than in the two wild *Lycopersicon* species. TDM in ‘MoneyMaker’ was reduced by 83% at 12°C, while this reduction was 63 and 51% for *L. pennellii* and *L. hirsutum*, respectively. *L. pennellii* and *L. hirsutum* had a significantly lower TDW than ‘MoneyMaker’ at 16, 20 and 24°C, while at 12°C there were no significant differences between the species.

In order to explain differences in temperature response of biomass accumulation between species, a growth analysis was conducted (Fig. 2). At 16, 20 and 24°C ‘MoneyMaker’ clearly showed a higher RGR than the two wild species (Fig. 2A). However ‘MoneyMaker’ also exhibits a severe decrease in RGR below 20°C, while *L. pennellii* only showed a decrease in RGR below 16°C and an even smaller decrease in RGR with temperature was found for *L. hirsutum*. At 12°C RGR of ‘MoneyMaker’ was reduced by 41% compared to 20°C, while in *L. pennellii* and *L. hirsutum* this decrease was only 27 and 18%, respectively. The decrease in RGR for ‘MoneyMaker’ was associated with a large decrease in LAR (Fig. 2B) while NAR (Fig. 2C) only showed a very small decrease with decreasing temperature. On the other hand, LAR of *L. pennellii* and *L. hirsutum* was unaffected by temperature. The decrease in RGR in *L. pennellii* and *L. hirsutum* was thus a result of a decrease in NAR. For *L. pennellii* and *L. hirsutum* NAR at 12°C was reduced by 24 and 14%, respectively. The decrease in LAR in ‘MoneyMaker’ is a consequence of a large decrease in SLA (Fig. 2D), which in both wild species was unaffected by temperature. In all species LWR only showed a very small decrease with decreasing temperatures.

Leaf dry matter content (LDMC) was influenced significantly by the interaction between species and temperature ($P = 0.008$; Fig. 1B). LDMC of *L. hirsutum* was not affected by temperature, while in *L. pennellii* LDMC showed a small increase at 12°C but LDMC in ‘MoneyMaker’ was even more increased at 12°C. In contrast to both wild tomato species, LDMC of ‘MoneyMaker’ revealed a significant increase below 20°C.

Development

Stem length of all species increased with temperature but this increase was less pronounced in *L. pennellii* compared to the other two species (Fig. 3). Neither the number of leaves ($P = 0.724$) nor leaf appearance rate ($P = 0.465$) did show an interaction between temperature and species. Leaf appearance rate increased with temperature and was higher in ‘MoneyMaker’ than in the two wild species (Table 1).

DISCUSSION

Both growth and development were influenced by temperature and species. Leaf appearance rate and therefore stem length are well known to increase with temperature, but changes in development rate in response to temperature showed a similar trend for all three species, whereas growth related traits clearly showed different temperature responses between the cultivated and the wild species.

Even though TDM accumulation was much higher for ‘MoneyMaker’ over a large temperature range (16-24°C), the reduction in TDM production at sub-optimal temperatures (12-16°C) was much lower in both wild *Lycopersicon* species. A growth analysis can be a helpful tool in explaining differences in growth between species. RGR can be separated into an assimilatory component (NAR) and a morphological component (LAR), which in turn is the product of SLA (total leaf area per unit leaf mass) and LWR (leaf biomass per unit total plant mass). The large decrease in RGR at sub-optimal temperatures as a consequence of a decrease in SLA (increasing leaf thickness) and subsequently LAR as reported in this study for ‘MoneyMaker’ (Fig. 1), has previously

been reported for several commercial greenhouse tomato cultivars (Hoek et al., 1993; Paul et al., 1984; Venema et al., 1999). Furthermore leaves of ‘Moneymaker’ showed a large increase in dry matter content at sub-optimal temperatures which suggests an inhibition of carbon translocation to sink tissues. Tomato cultivar ‘Abunda’ showed a large increase in starch content when grown at 16/14°C D/NT compared to 25/20°C D/NT, while this increase was much smaller in *L. hirsutum* (Venema et al., 1999). Both *L. pennellii* and *L. hirsutum* showed a considerable smaller reduction in RGR at lower temperatures than ‘Moneymaker’. Furthermore, contrary to ‘Moneymaker’ decreasing RGR in both wild relatives was not caused by a reduction in LAR but solely resulted from a reduction in NAR. More research is needed to elucidate the underlying mechanism(s) why carbohydrates accumulate so strongly at lower temperatures in the cultivated tomato, thereby decreasing SLA, in contrast to the wild species. As growth of *L. pennellii* and *L. hirsutum* is less temperature sensitive and SLA is hardly affected, both species are definitely interesting sources for the breeding of new greenhouse cultivars with improved energy efficiency.

Although growth of *L. pennellii* and *L. hirsutum* stays behind on ‘Moneymaker’ at optimal temperatures (and even at 16°C), they still have possibilities of being used in breeding programs to improve vegetative growth rate (at decreased greenhouse temperatures). Growth and ultimately yield are complex traits, which involve several genes. Among numerous ‘unfavorable’ genes in the wild *Lycopersicon* species it possibly contains a few favorable genes. With molecular linkage maps it is possible to identify, map and study the effect of individual loci that control quantitatively inherited traits (Tanksley and McCouch, 1997). In fact, in an introgression line (IL) population of *L. pennellii* in a processing tomato variety a number of ILs were found that increased yield by 7-13% compared to the same variety without introgressions (Eshed et al., 1996). An ideal energy-efficient tomato cultivar, with a broad temperature optimum, would combine the level of growth at optimal temperature of commercial elite greenhouse cultivars with the limited response to temperature of the wild *Lycopersicon* species.

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Tables

Table 1. The effect of temperature and species on leaf appearance rate. Different letters indicate significant differences for temperature ($P < 0.001$) and species ($P = 0.006$), respectively.

Species	Temperature (°C)				
	12	16	20	24	
<i>L. esculentum</i> cv. Moneymaker	0.181	0.303	0.358	0.391	0.308 ^b
<i>L. pennellii</i>	0.152	0.232	0.258	0.309	0.238 ^a
<i>L. hirsutum</i>	0.143	0.221	0.316	0.370	0.263 ^a
	0.159 ^a	0.252 ^b	0.311 ^c	0.357 ^d	

Figures

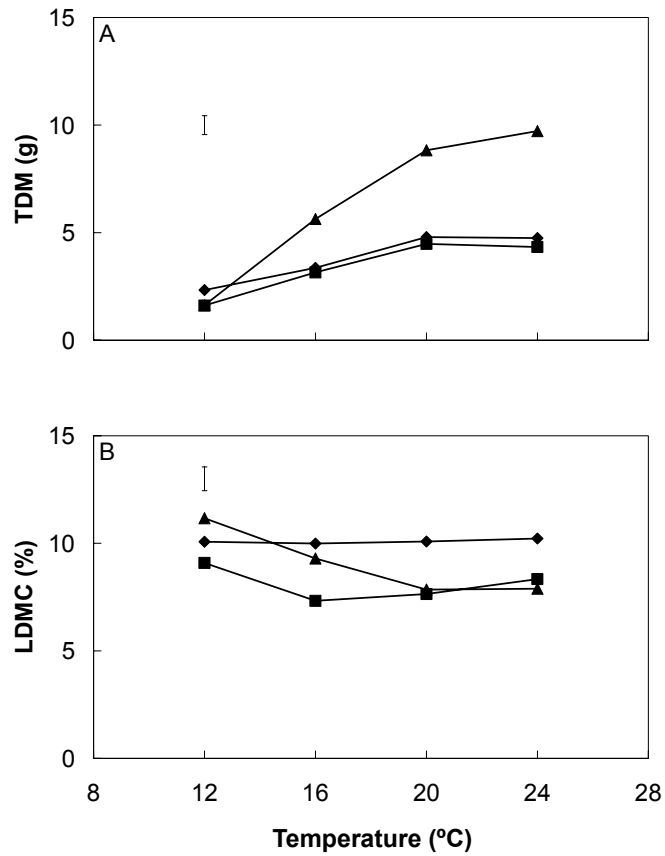


Fig. 1. The effect of temperature on total dry mass (TDM) (A) and leaf dry matter content (LDMC) (B) of *L. esculentum* cv. Moneymaker (▲), *L. pennellii* (■) and *L. hirsutum* (◆) after four weeks of temperature treatment. Vertical bars indicate LSD = 0.87 (A) and LSD = 1.1 (B).

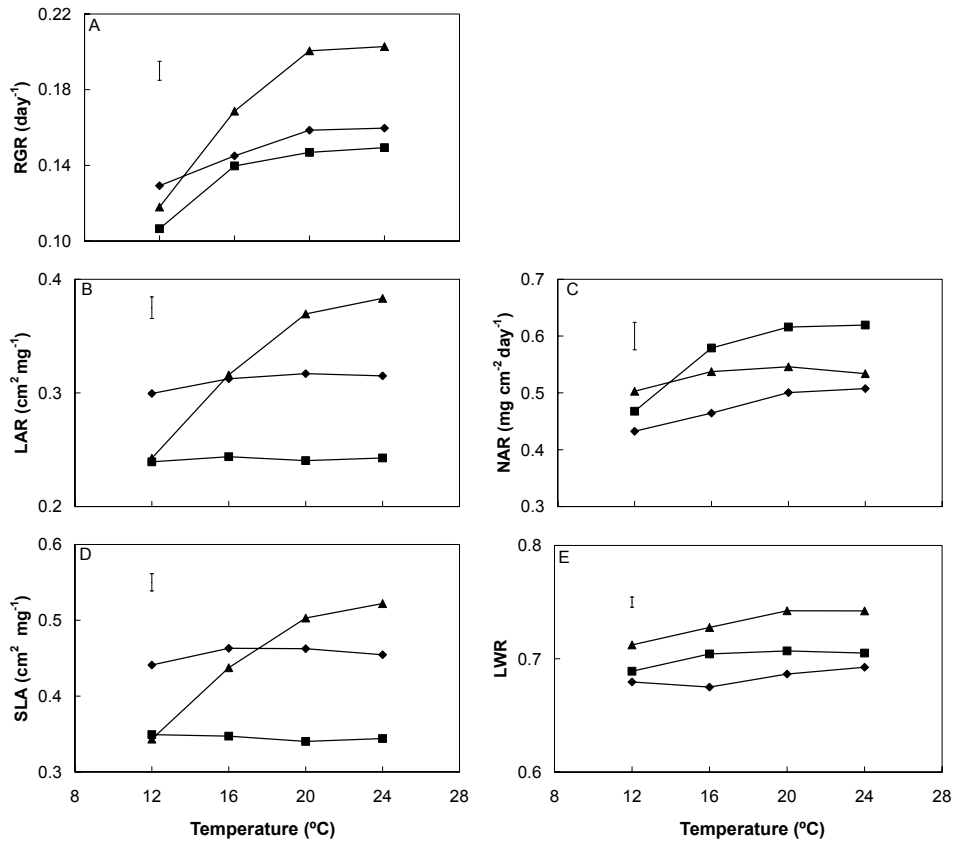


Fig. 2. The effect of temperature on RGR (A), LAR (B), NAR (C), SLA (D) and LWR (E) of *L. esculentum* cv. Moneymaker (▲), *L. pennellii* (■) and *L. hirsutum* (◆). Vertical bars indicate LSD = 0.010 (A), LSD = 0.019 (B), LSD = 0.048 (C), LSD = 0.023 (D) and LSD = 0.009 (E).

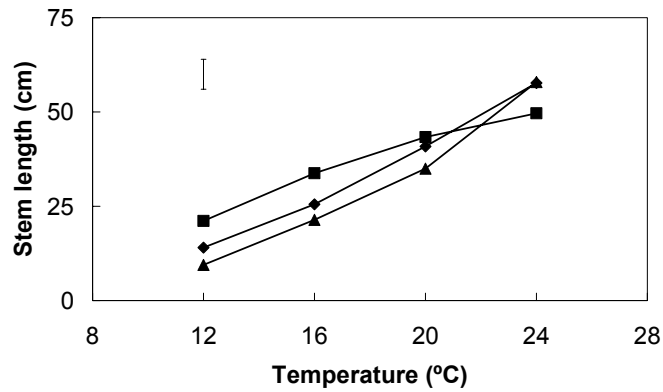


Fig. 3. The effect of temperature on stem length of *L. esculentum* cv. Moneymaker (▲), *L. pennellii* (■) and *L. hirsutum* (◆). The vertical bar indicates LSD = 7.9.

