At northern latitudes (40 to 50°), light and energy consumption are the most important factors which limit productivity and profitability of greenhouse crops (Tooze and Klapwijk, 1985). Covering materials with better energy savings and lower initial investment are used increasingly by growers, and might influence the microclimate of the greenhouse by changing several climatic factors simultaneously (Blom and Ingratta, 1985; Cockshull, 1992). Greenhouse air temperature, humidity, and leaf temperature can be affected by light transmittance of the covering material and its insulating property (Noble and Holder, 1989; Noble and Holder, 1992). Corning materials with better energy savings and lower initial investment are used increasingly by growers, and might influence the microclimate of the greenhouse by changing several climatic factors simultaneously (Blom and Ingratta, 1985; Cockshull, 1992). Greenhouse air temperature, humidity, and leaf temperature can be affected by light transmittance of the covering material and its insulating property (Noble and Holder, 1989; Noble and Holder, 1992). Corning materials with better energy savings and lower initial investment are used increasingly by growers, and might influence the microclimate of the greenhouse by changing several climatic factors simultaneously (Blom and Ingratta, 1985; Cockshull, 1992). Greenhouse air temperature, humidity, and leaf temperature can be affected by light transmittance of the covering material and its insulating property (Noble and Holder, 1989; Noble and Holder, 1992).
investigation was to study the influence of three covering materials with or without SL on growth, early yield (first 4 weeks of harvest in spring), photosynthesis, and diurnal changes in leaf carbohydrate accumulation in a spring tomato crop (December to March). This study was conducted in mini-greenhouses covered with glass, D-poly, or acrylic with three replications of each greenhouse covering material.

Materials and Methods

**PLANT MATERIAL AND EXPERIMENTAL DESIGN.** The experiment was conducted under low solar radiation (Dec. 1995 to Mar. 1996) (Fig. 1). Seeds of ‘Trust’ tomato were sown in Pargro rockwool blocks (3.8 × 3.6 × 4.0 cm) (Pargro, Inc., Orillia, Ontario, Canada) on 31 Oct. 1995. After emergence, seedlings were transplanted to larger Pargro rockwool blocks (7.5 × 7.5 × 7.5 cm). On 7 Dec. 1995, at the appearance of the seventh true leaf, seedlings were transplanted to 10-L pots (one seedling/pot) filled with clay pellets (Zwart Systems, Grimsby, Ontario, Canada) and placed in greenhouses. The experimental design was a split plot in a 3 × 3 latin square. Nine identical mini-greenhouses (6.2 m long × 7.2 m wide × 3 m high) were covered with D-poly (0.15 mm), acrylic (16 mm), or single-layered glass (3 mm) as the main plot. Twin-wall polycarbonate panels (8 mm thick) were used to glaze the north side-wall of all the greenhouses. The pots were arranged in double rows at 2.5 plants/m² and divided into two subplots; one under natural light (nonsupplemental lighting, nonSL) and the other one with natural light + supplemental lighting (SL) of 65 µmol·m⁻²·s⁻¹ at 1 m from the ground, providing a 16 h photoperiod. The SL was provided by 400 W high pressure sodium (HPS) lamps [P.L. Light System Canada, Grimsby, Ontario, Canada (54 W·m⁻² installed capacity)]. Only the central six plants in each experimental unit were used for collecting experimental data; the other six plants were treated as guards.

The plants were fumigated according to standard recommendations of Agriculture and Agri-Food Canada (Papadopoulos, 1991), controlled by a Harrow Fertigation Manager, a computerized multi-fertilizer injection system (Papadopoulos and Liburdi, 1989). Pure liquid CO₂ was used to enrich the atmosphere of all nine greenhouses during the light period to a concentration of 1000 µmol·mol⁻¹. A PRIVA environmental computer (PRIVA Computers, Inc., Vineland, Canada) controlled the climate in all greenhouses. Day and night heating air temperatures were set at 21 °C and 17 °C, respectively, according to sunrise and sunset; ventilation temperature was set at 24 °C. Day and night temperature, water vapor pressure deficit (VPD), and CO₂ concentration in greenhouses covered with the three different cover materials are reported in Table 1. The light transmitted (PAR) under the three covers to the plants at a 2 m height in the greenhouses is shown in Fig. 1.

**GROWTH MEASUREMENTS.** Plant height, leaf, fruit and flower number were measured every 2 weeks for 8 weeks on four plants randomly sampled from each experimental unit (total of 18 experimental units; total of 12 plants per treatment). Leaf area of the fifth youngest leaf from the apex was measured with a leaf area meter (LI-3100, LI-COR, Inc., Lincoln, Nebr.) on four plants

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Table 1. Mean day and night temperature, water vapor pressure deficit (VPD), and greenhouse CO₂ concentration (±SE) under three different greenhouse covering materials.

| Covering material | Temp (°C) | VPD (kPa) | CO₂ concn (µmol·mol⁻¹) |
|-------------------|-----------|-----------|------------------------|
|                   | Day       | Night     | Day                    | Night      | Day                    | Night      |
| Glass             | 21.3 a (0.06) | 17.5 a (0.04) | 1.1 a (0.02) | 1.0 a (0.02) | 922 a (7.0) | 549 a (4.1) |
| D-poly            | 21.5 a (0.04) | 17.7 a (0.03) | 0.9 c (0.02) | 0.8 b (0.02) | 982 a (4.2) | 563 a (3.9) |
| Acrylic           | 21.6 a (0.10) | 17.9 a (0.03) | 1.0 b (0.03) | 1.0 a (0.02) | 927 a (5.2) | 525 a (3.5) |

^Means ± SE are the averages of three greenhouses over 84 d.

^Mean separation within columns by LSD, P ≤ 0.05.
per experimental unit. Leaf dry weight (DW) was determined after drying at 65 °C for 1 week and specific leaf weight calculated (leaf biomass/leaf area). Fruits were first harvested on 14 Feb., 1996. Two times per week fruit were harvested and graded according to specifications of the Ontario Ministry of Agriculture (1987). Harvest index was calculated as [(fruit DW/total above ground plant DW) × 100].

Gas exchange and chlorophyll measurements. Gas exchange was measured under winter (15 Jan.) and spring (14 Mar.) growing conditions. Measurements were made with a portable photosynthesis system (LI-6200, LI-COR, Inc.) on the fifth youngest leaf from the apex of four plants per experimental unit (total of 12 plants per treatment) between 1100 to 1400 hr on sunny days. Photosynthetic rates were measured at 1000µmol·mol⁻¹ CO₂. Total chlorophyll (chl) concentration for each experimental unit was measured using a leaf chl meter (SPAD-502; Minolta, Osaka, Japan) on the fifth youngest expanded leaf of four plants per experimental unit (total of 12 plants per treatment). Ten readings were taken from each leaf and averaged as one observation. A standard curve from leaf chl extraction (Leegood, 1993) was plotted to quantify the total chl concentration in each treatment.

Carbohydrate determination. Samples for leaf carbohydrate concentration were collected five times a day (every 2 h from 0800 to 1600 hr every 2 weeks for a period of 2 months). Tissues from the fifth youngest expanded leaf from the apex of four plants per experimental unit (total of 12 plants per treatment) were ground in liquid nitrogen, and carbohydrates were extracted with 80% ethanol at 80 °C. The ethanol soluble fraction (sucrose, fructose, and glucose) was separated and quantified by high-performance liquid chromatography (HPLC) (Waters 600E System Controller, Waters Co., Milford, Mass.; Sugar-PAK column 6.5 × 300 mm). The pellet remaining (ethanol insoluble) was homogenized and the starch was solubilized with 0.02 N NaOH overnight using 2 units of amylglucosidase/µL (EC 3.2.1.3) (Sigma Chem. Co., St. Louis), and released glucose measured by a biochemistry analyzer (model 2700 select; Yellow Springs Instrument, Inc., Yellow Springs, Ohio). Starch content was expressed as milligrams of glucose released per gram of leaf fresh weight (FW).

Data analysis. Data were analyzed using GLM procedures in the SAS 6.12 package (SAS Institute, Inc. Cary, N.C.). Differences between treatment means were determined using Fisher’s least significant difference (LSD). For each parameter measured, no interaction (P < 0.05) between covering material and light treatments was observed.

Results

Plant growth and development. In both January and March, plants grown without SL under acrylic covering (96.3 ± 6.7 and 194.3 ± 17.0 cm, respectively) had similar heights (P ≤ 0.05) than D-poly (93.5 ± 1.8 and 184.6 ± 0.7 cm, respectively) but were higher (P ≤ 0.05) than plants grown in glasshouses (83.7 ± 1.3 and 174.6 ± 4.6 cm, respectively) (data not presented). During the experiment, covering materials did not influence (P ≤ 0.05) leaf and flower numbers per plant (data not presented). On the other hand, SL increased the number of leaves (March) by 15% (P ≤ 0.05) in glasshouses, but had no effect on plant height, and flower number per plant compared to nonSL treatment (data not presented).

Leaf area of the fifth expanded leaf from the apex in all treatments decreased (P < 0.05) in March compared to January (Fig. 2A, B, and C) as the natural PAR increased (Fig. 1). This decrease (35% to 40%) was greater for plants grown under SL than nonSL. As expected, specific leaf weight increased in March compared to January (Fig. 2D, E, and F). No significant effect of the covering material on specific leaf weight was observed under nonSL growing conditions. After 18 weeks of growth, however, specific leaf weight was 33%, 31%, and 19% greater (P < 0.05) under D-poly, acrylic, and glasshouse, respectively, with the use of SL compared to nonSL.

Productivity and harvest index. Both D-poly and acrylic covering increased (P < 0.05) the number of fruit per plant by 13% compared to glass under SL while under nonSL only D-poly yielded higher fruit number (17%) than glass (Table 2). Across all light treatments, D-poly covering had higher (P < 0.05) marketable yield than glass (15% to 16%), while plants under D-poly produced a higher marketable yield (P < 0.05) than plants in acrylic (Table 2) under nonSL. Use of SL increased by 23% (P < 0.01) the marketable yield of plants grown under acrylic houses. There was no significant difference in the percentage of total fruit graded as no. 1 due to the three different covering materials or light treatments (Table 2). However, plants grown in D-poly houses under non SL produced a significantly (P < 0.05) higher percentage of extra large fruit compared to those grown in acrylic houses, while glass increased (P < 0.05) the percentage of large fruit compared to D-poly. Use of SL in acrylic houses increased production of extra large fruit by 19% (P < 0.05) compared to nonSL but did not affect the percentage of large or small fruit. No significant effect of covering material or light treatment was observed on the percentage of small fruit. The harvest index was

![Fig. 2](image-url)
Results were observed for the leaf chl concentration. Not significant except for the acrylic houses under SL. Similar growth under nonSL. The decrease in carbon exchange rate was acrylic and 15% in glass and D-poly houses after 2 months of

\[ \text{Photosynthetic rate of plants decreased (} \] 

3. On the other hand, SL in glasshouses increased the gas exchange rate (P ≤ 0.01) of the fifth youngest leaf in March by 22%, and their chl concentration by 16% compared to nonSL (P ≤ 0.01) (Table 3). SL also increased (P ≤ 0.01) leaf chl concentration in D-poly (March) and acrylic (January and March) houses. The photosynthetic rate of plants decreased (P ≤ 0.05) by 18% in acrylic and 15% in glass and D-poly houses after 2 months of growth under nonSL. The decrease in carbon exchange rate was not significant except for the acrylic houses under SL. Similar results were observed for the leaf chl concentration.

Carbohydrate determination. Starch. Diurnal changes in starch concentration were measured in the fifth youngest leaf (Fig. 3). Irrespective of the covering material, SL increased (P ≤ 0.05) leaf starch accumulation compared to nonSL conditions (Fig. 3). In January, diurnal changes of leaf starch accumulation followed a similar trend in all houses. Leaf starch concentration was highest between 1400 and 1600 hr, and lowest at 0800 hr (Fig. 3A, B, and C). Starch accumulation was highest in plants grown under acrylic houses (26 mg glucose/g FW) (Fig. 3C) followed by those grown in glasshouses (20 mg glucose/g FW) (Fig. 3A), and D-poly houses (15 mg glucose/g FW) (Fig. 3B).

In March, average starch accumulation across the entire day tripled (Fig. 3D, E, and F) with a maximum concentration of 80 mg glucose/g FW in D-poly houses (Fig. 3E). Most of the increase in starch concentration in the daylight hours occurred between 0800 and 1200 hr with only a small increase between 1200 and 1400 hr. This pattern was similar for all treatments but starch concentration was higher under SL (Fig. 3D, E, and F).

Sucrose and hexoses. Sucrose concentration was very variable under all growing conditions (data not presented). Consequently, it was difficult to distinguish treatment effects. The overall pattern of diurnal accumulation of hexoses (glucose and fructose) followed a similar trend as starch (Fig. 4). Generally, leaf hexose accumulation increased with time reaching its maximum values between 1200 and 1600 hr. SL however, seems to have had a negligible effect on diurnal hexose accumulation under the different growing conditions. The concentration of hexoses decreased by half in March (Fig. 4).

Discussion

Plant Growth and Development. Regardless of light regimes, the marketable yield and the number of fruit per plant were significantly improved in D-poly houses compared to glasshouses, but yield in the acrylic house was higher than in glass-
houses only under SL (Table 2). The insulation value of these covering materials is likely due to their higher diffusibility to transmitted PAR which enhances uniformity of light in the greenhouse and also affects plant growth and development (Zhang et al., 1996). Nevertheless, light transmission at a 2 m height was 60% and 61% in D-poly and acrylic houses, respectively, compared to 70% in glasshouses (Fig. 1). Use of SL which increased photosynthesis in March (Table 3), combined with better light diffusibility under D-poly and acrylic houses (Papadopoulos and Hao, 1997a,b), compensated for reduced light transmission. Decreased leaf area and increased specific leaf weight (Fig. 2) are typical responses to the global solar radiation increase from January to March and plant growth in an enriched CO₂ atmosphere. The higher number of leaves in acrylic houses without SL provided an overall larger photosynthetic and PAR interception area, which could compensate for the lower availability of PAR in these houses and the reduction of leaf area in March. Plant growth and productivity are determined not only by photosynthesis, but also by the way in which the end products of photosynthesis are allocated and used during growth and development. Lawlor (1995) reported that crop yield is more related to total leaf area and photoassimilate distribution than photosynthesis. However, we observed no effect of either covering materials or SL on harvest index (Table 2). Results herein suggest that light conditions in both D-poly and acrylic houses are more favorable for tomato growth and development than glasshouses, particularly under SL. Except for a lower water vapor pressure deficit under D-poly covering material, day and night temperatures, and CO₂ greenhouse concentration were similar under the three covering materials and could not explain the growth and yield variations observed under different covering materials. These results are in agreement with previous research reported by Papadopoulos and Hao (1997a, 1997b). For cucumber (Cucumis sativus L.), which has a lower light requirement than tomato, growth and yield were also higher in D-poly and acrylic houses, and a 30% energy saving was reported (Papadopoulos and Hao, 1997a, 1997b). Considering the actual heating cost (10% to 25% of the production cost) and the initial investment, D-poly covering material seems an excellent choice for North American greenhouse tomato growers.

**PHOTOSYNTHETIC CAPACITY AND CARBOHYDRATE ACCUMULATION.** Our results have clearly shown that the covering material did not affect the photosynthetic capacity and the chl concentration of tomato leaves. On the other hand, SL enhanced photosynthetic rate in March irrespective of the covering materials. The increase in total chl content could explain in part this effect. However, despite the SL effect, a reduction of photosynthetic capacity occurred after 2 months of growth in CO₂ enrichment, expressed by a reduction in CO₂ assimilation rate and chl concentration. Under our growing conditions, the decline in stomatal conductance could not explain the reduction of photosynthesis as no significant decrease was observed (data not presented). The decrease in photosynthesis was faster and more pronounced for

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**Fig. 3.** Daily variations of starch accumulation on (A, B, C) 21 Jan. in the fifth youngest leaf of 'Trust' tomato plants grown under (A, D) glass, (B, E) D-poly, or (C, F) acrylic coverings, and (D, E, F) 45 d later in March with (❖) or without (❑) supplemental lighting. Vertical bars ±SE (n = 12).

**Fig. 4.** Daily variations of hexose accumulation on (A, B, C) 21 Jan. in the fifth youngest leaf of 'Trust' tomato plants grown under (A, D) glass, (B, E) D-poly, or (C, F) acrylic coverings, and (D, E, F) 45 d later in March with (❖) or without (❑) supplemental lighting. Vertical bars ±SE (n = 12).
all plants grown under nonSL conditions compared to SL (Table 2), even if the leaf carbohydrate accumulation was higher for plants grown under SL.

Significant starch accumulation occurred in March under all coverings throughout the photoperiod. Similarly, a high specific leaf weight (Fig. 2) and a significant decrease in photosynthesis (Table 3) were observed in agreement with recent studies (Ayari et al., 2000a, 2000b; Dorais et al., 1996). Previous reports have shown that end-product accumulation might limit photosynthesis when plants are grown at high partial pressures of CO₂ (Harley et al., 1992; Socias et al., 1993) and extended photoperiod (Logendra et al., 1990). In a fully expanded leaf, the rate of starch accumulation is proportional to the net photosynthesis rate and it is influenced by the photoperiod as well as the translocation of photosynthetic products (Grange, 1985). Hence, leaf starch synthesis is determined by both the prevailing net photosynthesis and the carbon export from the leaf. Under our conditions, starch levels in all plants followed the natural lighting and the PAR increase provided by HPS lamps within the canopy (Fig. 3). The high level of starch accumulation at the beginning (March) and the end of diurnal cycle might suggest that carbon export to the sink organ and photosynthesis were not in balance. On the other hand, since the rate of photosynthesis under all houses remained relatively higher under SL, starch accumulation could be attributed to a limitation in carbon metabolism, but could not explain the photosynthesis reduction observed in spring. Dorais et al. (1996) suggested that this limitation in carbon metabolism could be explained by a low activity of sucrose phosphate synthase considered as a key enzyme in sucrose synthesis.

Conclusions

D-poly and acrylic covering materials in conjunction with application of SL provided the best environment for spring tomato growth and productivity in Ontario, Canada. Tomato plants reacted to the different covering materials by increasing plant height, fruit number and yield. On the other hand, use of SL in greenhouse tomato production resulted in increased leaf number, specific leaf weight, photosynthetic rate (March) and chl concentration as well as yield. Large accumulation of starch in the leaf was observed in March under SL and high CO₂ levels suggesting that tomato plants are unable to distribute efficiently additional photoassimilates to the fruit.

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