CHAPTER 8

GROWTH AND PRODUCTIVITY OF POTATO AS INFLUENCED BY CULTIVAR AND REPRODUCTIVE GROWTH: I. STOMATAL CONDUCTANCE, RATE OF TRANSPIRATION, NET PHOTOSYNTHESIS, AND DRY MATTER PRODUCTION AND ALLOCATION

8.1 ABSTRACT

The effect of cultivar and reproductive growth on leaf gas exchange, water relations, dry matter production and allocation in potato was the subject of investigation. Debudded, flowering and fruiting plants of cultivars Al-624, Al-436, CIP-388453-3(A) and CIP-388453-3(B) were evaluated under field condition of a sub-humid tropical highland of Ethiopia during 2003. Cultivars exhibited differences with respect to leaf stomatal conductance, rate of transpiration and photosynthetic efficiency. Cultivars Al-624 and CIP-388453-3(A) showed higher stomatal conductance and rate of leaf transpiration than CIP-388453-3(B) and Al-436. Cultivar CIP-388453-3(A) exhibited higher net photosynthesis than Al-624 while Al-436 is intermediate. Fruiting plants exhibited higher leaf stomatal conductance and higher rate of leaf transpiration and net photosynthesis. Fruit development promoted early plant maturity, and without affecting total dry matter production it reduced the amount partitioned to the leaves, stems, and tubers.

Keywords: Assimilate partitioning, berry set, Ethiopia; flowering, genotype, potato

8.2 INTRODUCTION

Potato (*Solanum tuberosum* L.) is an annual crop that can be propagated vegetatively from seed tubers or sexually using botanical seed. Flowering in potato occurs in various degrees depending on the cultivar and environmental conditions (Sadik, 1983; Lozaya-Saldana, 1992). Its expression is influenced by internal and external factors, including source-sink equilibrium, hormonal balance, physiological maturity and photoperiod (Lozaya-Saldana & Miranda-Verlazguez, 1987; Lozaya-Saldana, 1992). Generally, *Solanum tuberosum* ssp *andigena* flowers regardless of the day length although flowering increases under short days, while *Solanum tuberosum* ssp *tuberosum* does not flower under short days (Sadik, 1983).

In Ethiopia most of the cultivars produce profuse flowers and some of them set berries. For commercial potato production seed tubers are mainly used and the use of true potato seed is limited to breeding activities at research institutions. Fruit formation is an undesirable quality because the berries have no subsidiary uses.

The assimilation of dry matter and its distribution within the plant are important processes determining crop productivity. A higher investment to the vegetative organs may give high total biomass and a relatively low proportion may be used for the production of storage organs, especially if the maintenance requirements of the vegetative organs are high (Van Heemst, 1986). Studying the pattern of dry matter allocation amongst plant parts, the variability of this pattern among cultivars, and the effect of environmental conditions on the process can help in maximizing productivity and selection of a cultivar for a particular purpose. The presence of plant organs with a net demand for assimilates can strongly influence the pattern of dry matter production and distribution (Gifford & Evans, 1981). Developing fruit has a considerable effect on the growth of other plant organs in such a way that with increasing fruit load the growth of

roots, shoots and leaves are often reduced (Marcelis, 1992; Heuvelink, 1997). Net photosynthesis, gauged either by growth analysis or by direct measurements of gas exchange, is higher in plants with actively growing fruit (Lenz, 1979; Eckstein *et al*., 1995). The effect of flowering and berry set on the photosynthetic efficiency and rate of transpiration of potato has not been well investigated. There are reports indicating that the distribution of assimilates among sinks is primarily regulated by the sinks themselves (Ho *et al.*, 1989; Marcelis, 1996).

The suppressing effects of reproductive growth on vegetative growth have been reported in cucumber (Marcelis, 1992), tomato (Heuvelink, 1997), banana (Eckstein *et al*., 1995), dandelion (Letchamo & Gosselin, 1995) and chestnut (Famiani *et al*., 2000). Very little research has been done regarding the effect of reproductive growth on biomass production and allocation in potato. This chapter reports on the effect of cultivar and reproductive growth on leaf stomatal conductance, rate of transpiration, net photosynthesis, dry matter production and assimilate distribution in potato. The effect of cultivar and reproductive growth on tuber yield and yield components, specific gravity, dry matter content and nutrient compositions is presented in the following chapter (Chapter 9).

8.3 MATERIALS AND METHODS

8.3.1 Experimental site description

The study was conducted during February to June 2003 on the Research Farm of Alemaya University, Ethiopia. The experimental site is located at 42° 3'E longitude, 9° 26'N latitude and at an altitude of 1980 m above sea level. It is situated in the semi-arid tropical belt of eastern Ethiopia and characterized by a sub-humid climate with an average annual rainfall of about 790 mm, annual mean temperatures of 17 ℃ with mean minimum and maximum temperatures of 3.8 and 25 ℃, respectively. During the study period, the mean maximum temperature was 26 ℃ (ranging from 20.5 to 29 ℃) and minimum temperature 11.4 ℃ (ranging from 7.8 to 16.4 ℃). During the growing period a total of 177 mm precipitation was received and supplementary irrigation was applied. Mean sunshine hours were 9.7 per day, along with a relative humidity of 41% (ranging from 19 to 71%). The soil of the experimental site is a well-drained deep alluvial that contains 14 g kg^{-1} organic carbon, 1.4 g kg^{-1} total nitrogen, 0.01 g kg^{-1} available phosphorus, 0.47 g kg^{-1} total potassium, and a pH of 7.2.

8.3.2 Cultivars

To obtain a range of genotypes from comparatively light to profusely blooming types, and from light to heavy fruit setting, cultivars with different floral and berry development behaviour were selected. The four selected cultivars were CIP-388453-3(A), CIP-388453-3(B), Al-624, and Al-436, all with a determinate growth habit (Figure 8.1).
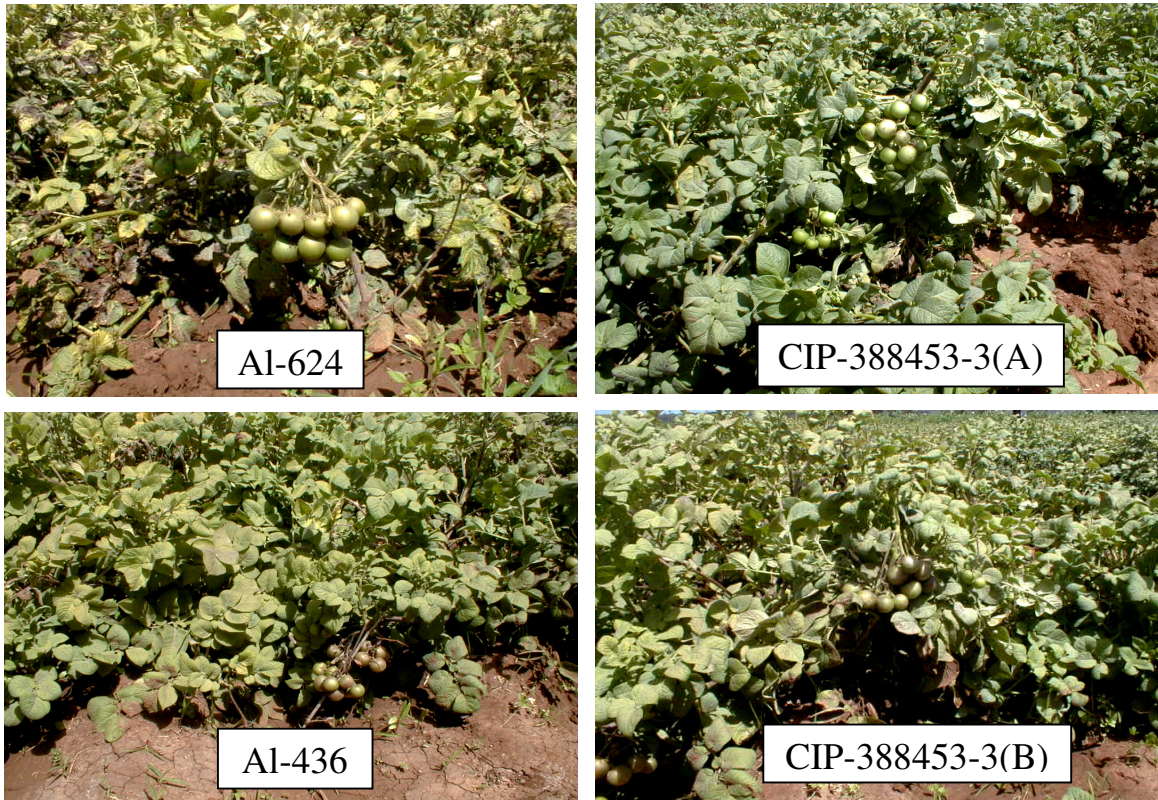
Figure 8.1 Cultivars used for the study

8.3.3 General field procedure

The experimental plots were arranged in a split-plot design in a randomised complete block design replicated three times. The four cultivars were assigned to the main plots and the three reproductive growth manipulation treatments to the sub-plots. Forty-nine medium sized and well-sprouted tubers of each cultivar were planted in seven rows of a sub-plot (size = 11.025 m^2) at a spacing of 75 x 30 cm. Sub-plots within the main plots were arranged continuously without board rows, and the end plots were bordered by two rows of potato plants. Phosphorus was applied as diammonium phosphate at planting time at a rate of 150 kg P ha^{-1} and nitrogen was side dressed after full emergence at a rate of 100 kg N ha^{-1} in the form of urea. All other cultural practices were applied according to the regional recommendation (Teriessa, 1997). No major disease and insect pest incidences were encountered.

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8.3.4 Treatments

The study was designed to grow plants of the four cultivars by providing the following three different types of treatments:

1. **Non-flowering plants (debudded plants)**: Flower clusters were nipped off at bud emergence stage at two-day intervals (Figure 8.2A).

2. **Flowering plants**: The plants were permitted to flower but not to set fruit. The flowers were removed after anthesis. This process was repeated every two days (Figure 8.2B).

3. **Fruiting plants (control)**: Plants were allowed to flower and set berries (Figure 8.2C).

Figure 8.2 Non-flowering (A), flowering (B), and fruiting (C) treatments applied to cultivar CIP-388453-3(B)

8.3.5 Data recorded

Gas exchange

Two, four, and six weeks after debudding commenced, leaf stomatal conductance, rate of transpiration and net photosynthesis were measured using a portable LCA-4 photosynthesis system (Analytical Development Company, Bio Scientific Ltd., UK). From each sub-plot, three plants were randomly selected and the measurements were taken on the terminal leaflets of the three youngest fully expanded leaves. During the measurements the photon flux density incident at the level of the leaf in the cuvette ranged between 1995 and 2644 μmolm^{-2}s^{-1}. The external carbon dioxide concentration varied between 342 and 354 μmolmol^{-1}. Since the cultivars varied with respect to days to flowering, gas exchange measurements were taken on different days for the different cultivars.

Assimilate partitioning

Eight weeks after debudding of a specific cultivar commenced, three randomly selected plants per sub-plot were sampled and separated into different parts. The samples were oven dried at 72 °C to a constant mass. Dry matter partitioning to the different organs was expressed as a percentage of the total biomass. Days elapsed to reach physiological maturity were recorded when about 50% of the leaves senesced.

8.3.6 Statistical analysis

The analyses of variance were carried out using MSTAT-C statistical software (MSTAT-C 1991). Means were compared using least significant differences (LSD) test at 5% probability level. Correlations between parameters were computed when applicable.

8.4 RESULTS

The cultivars differed greatly with respect to the degree of berry production. The ranking of the cultivars in decreasing order of fresh berry mass is Al-624 (275 g hill^{-1}), CIP-388453-3(B) (226 g hill^{-1}), Al-436 (209 g hill^{-1}), and CIP-388453-3(A) (81 g hill^{-1}). Cultivar Al-624 produced 26 berries per hill, followed by CIP-388453-3(B), Al-436, and CIP-388453-3(A) with respective mean berry numbers of 22, 19, and 14.

Leaf stomatal conductance was influenced by cultivar and pruning treatments independently. Cultivar means pooled over treatments showed that during all measurements, the stomatal conductance of Al-624 and CIP-388453-3(A) was higher than that of Al-436 with CIP-388453-3(B) intermediate (Figure 8.3A). At all measurement phases, fruiting plants had consistently higher stomatal conductance than flowering and non-flowering plants (Figure 8.3B).
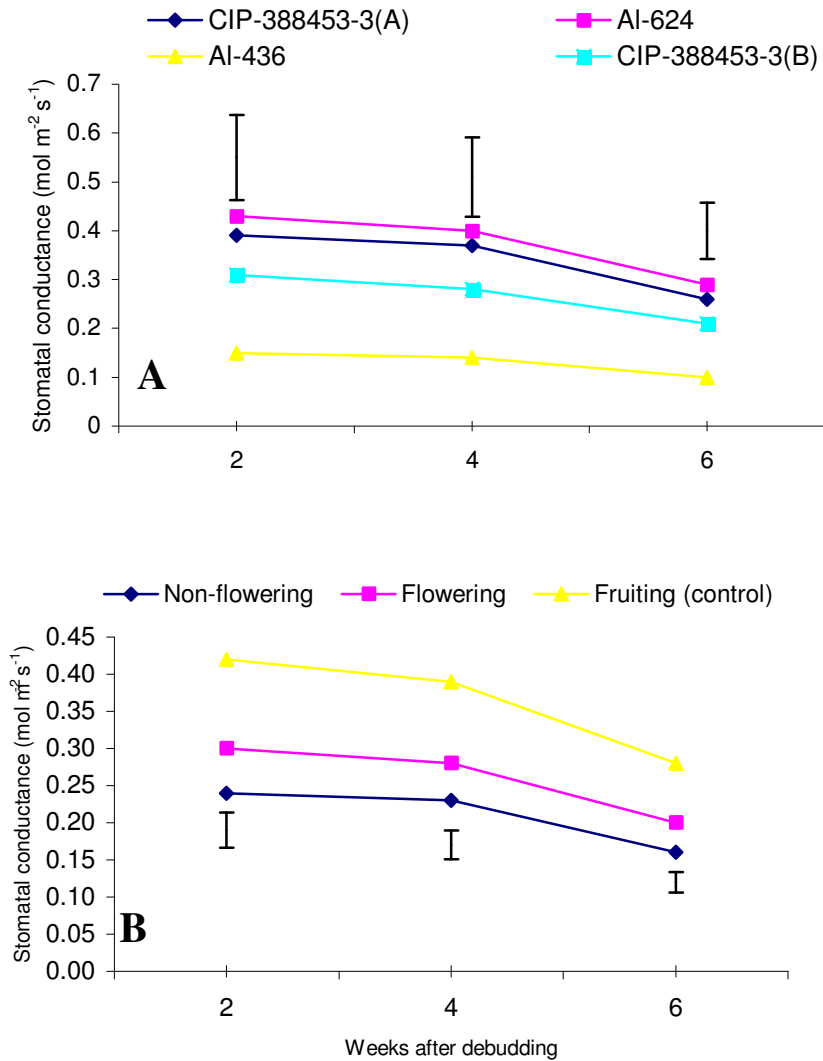
Figure 8.3 Leaf stomatal conductance of potato as affected by cultivar (A) and reproductive growth (B). The vertical bars represent least significant differences at P < 0.05

Distinct differences among cultivars were exhibited with respect to rate of leaf transpiration as shown in Figure 8.4A. The leaf transpiration rate of Al-624 and CIP-388453-3(A) was higher than Al-436 and CIP-388453-3(B). During the three observation periods (two, four, and six weeks after debudding) higher leaf transpiration rates were recorded on fruiting plants than on flowering and non-flowering plants (Figure 8. 4B).
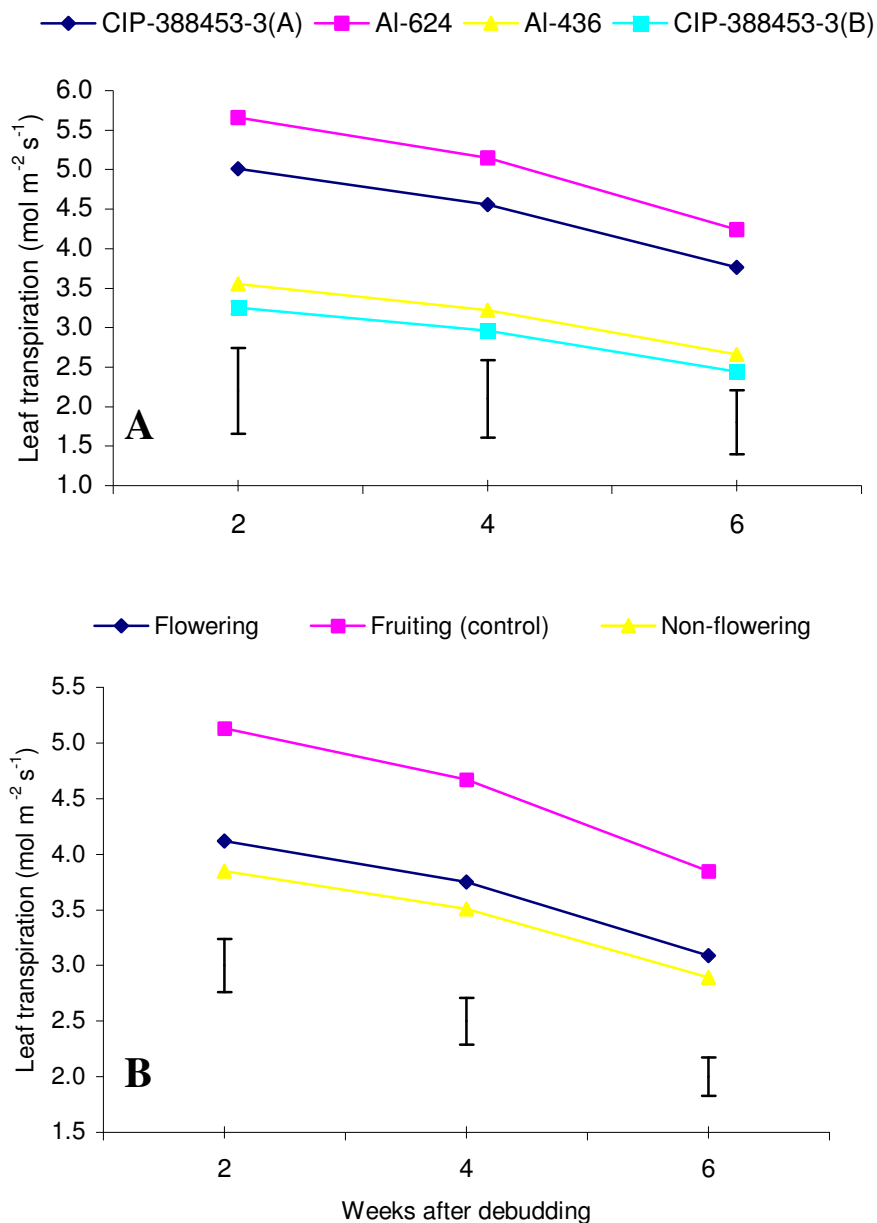
Figure 8.4 Leaf transpiration of potato as influenced by cultivar (A) and reproductive growth (B). The vertical bars represent least significant differences at P < 0.05

During the observation periods, the net photosynthetic rate of cultivar CIP-388453-3(A) was consistently higher than Al-624, with Al-436 intermediate (Figure 8.5A). Like stomatal conductance and rate of transpiration, the fruiting plants had higher photosynthetic rates than the other two groups (Figure 8.5B). The overall trend showed that leaf stomatal conductance, rate of

transpiration and net photosynthesis tended to decline from two weeks after debudding until last monitoring, six weeks after debudding..
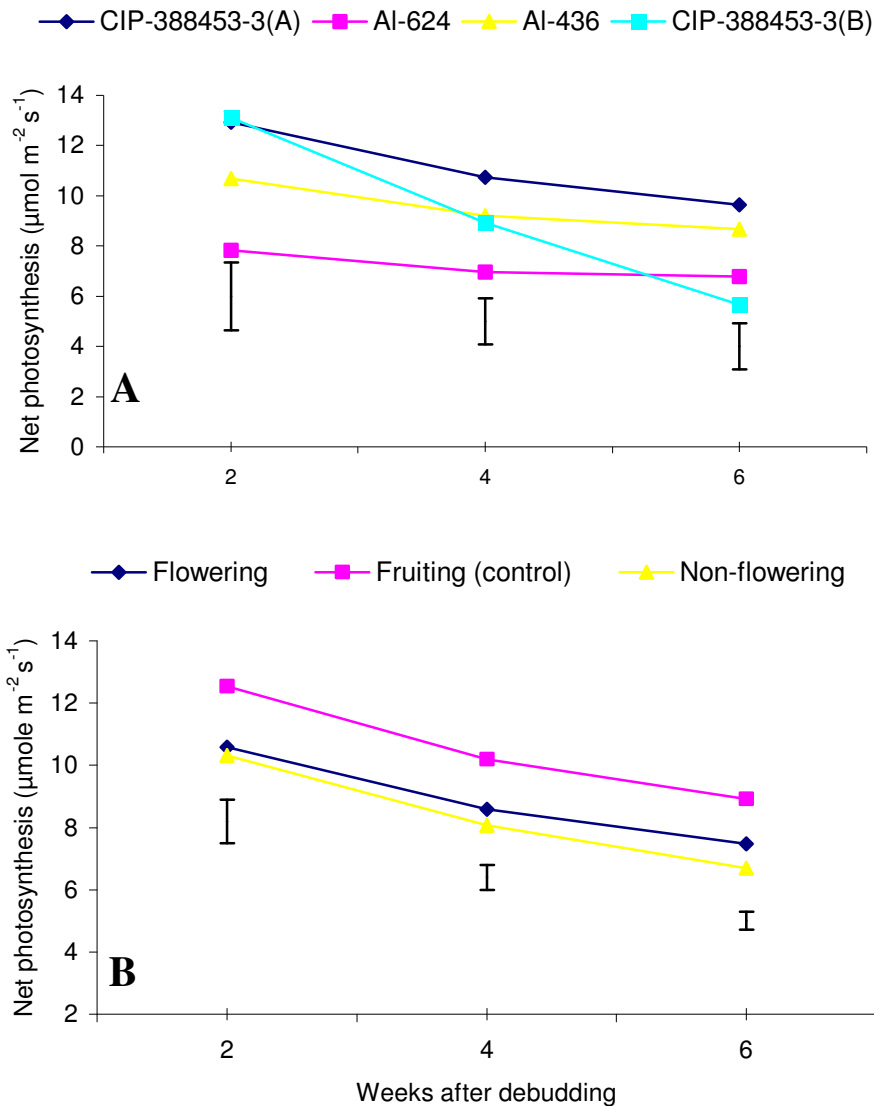

Figure 8.5 Net photosynthesis of potato as influenced by cultivar (A) and reproductive growth (B). The vertical bars represent least significant differences at P < 0.05

The dynamics of growth as measured by dry matter accumulation two, four, six and eight weeks after debudding showed that cultivar CIP-388453-3(A) produced a higher total biomass than Al-436, CIP-388453-3(B), and Al-624 (Figure 8.6A). Flowering and berry set slightly but significantly affected total biomass production at all sampling periods (Figure 8.6B).

During the second sampling period, debudded plants produced the highest biomass (223 g), followed by fruiting (216 g) and flowering plants (209 g). During the third and fourth sampling period, the fruiting and debudded plants produced a higher biomass than the flowering plants.
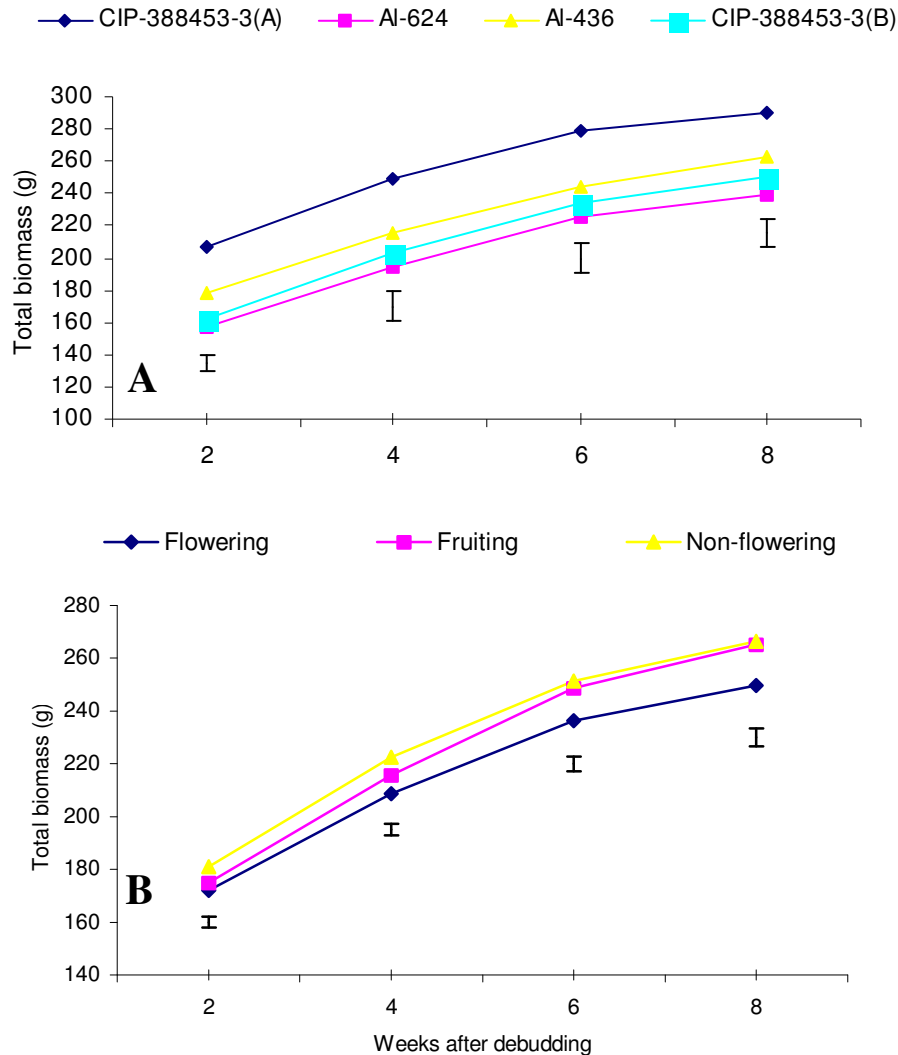

Figure 8.6 Total biomass yield of potato as affected by cultivar (A) and reproductive growth (B). The vertical bar represents least significant differences at P < 0.05

The fraction of dry matter partitioned amongst plant components eight weeks after debudding is presented in Figure 8.7A. Cultivar Al-624 had diverted more dry matter to the leaves than CIP-388453-3(A) and CIP-388453-3(B), while Al-436 was intermediate. CIP-388453-3(A) partitioned a larger fraction of the dry mass to the stems than the other cultivars. Al-624 and CIP-

388453-3(B) partitioned more assimilates to the developing fruit than CIP-388453-3(A) and Al-436. Of the total carbon fixed, the cultivars partitioned about 4% to the roots. CIP-388453-3(A), Al-436, and CIP-388453-3(B) allotted about 36% of the total dry matter to the tubers, which is higher than that partitioned by Al-624 (31%). The effect of reproductive growth on assimilate partitioning is indicated in Figure 8.7B. Fruiting plants utilised 9% of the assimilates for the production of berries, and partitioned less to the leaves, stems, and tubers than flowering and non-flowering plants.
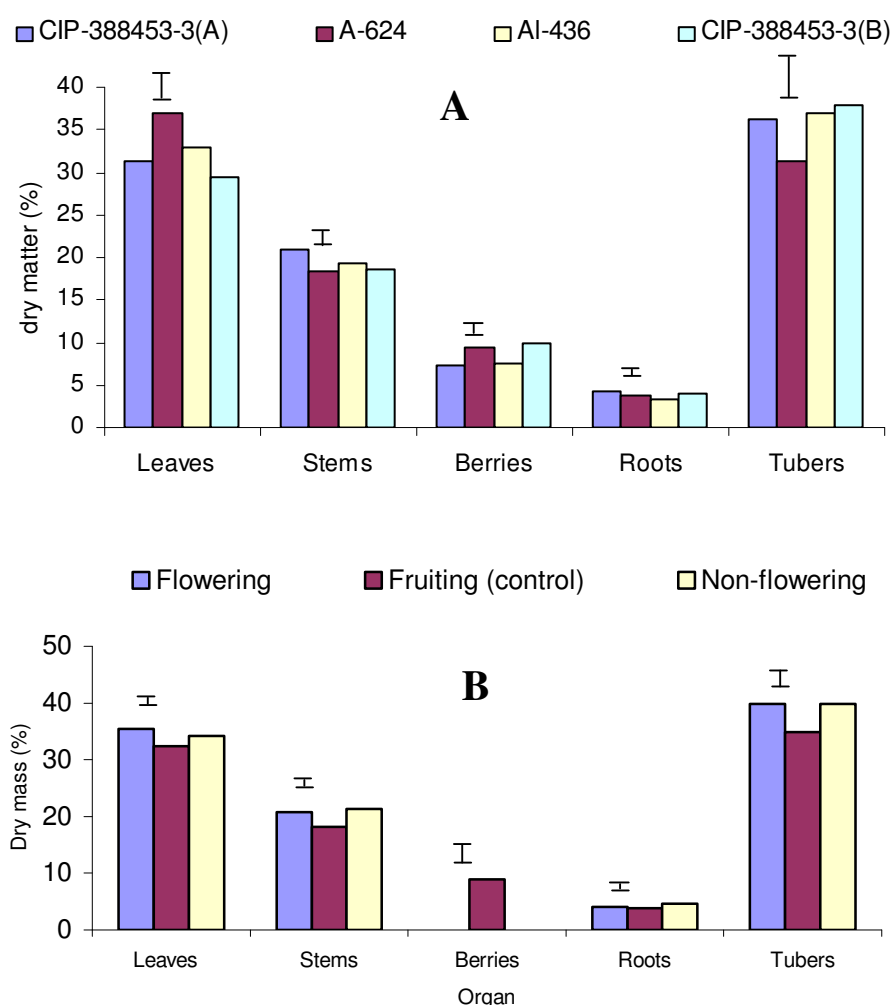

Figure 8.7 Dry matter distribution (% of the total dry mass) among organs of potato as influenced by cultivar (A) and reproductive growth (B) (eight weeks after flower bud initiation). The vertical bar represents least significant differences at P < 0.05

A significant variation in days to maturity occurred among cultivars (Figure 8.8A). Cultivar CIP-388453-3(A) required about 110 days to reach maturity. On the other extreme, cultivar Al-624 attained maturity within 92 days after planting. The presence of reproductive growth accelerated the onset of senescence in potato (Figure 8.8B). Fruiting plants showed the onset of senescence a week before the non-flowering plants.
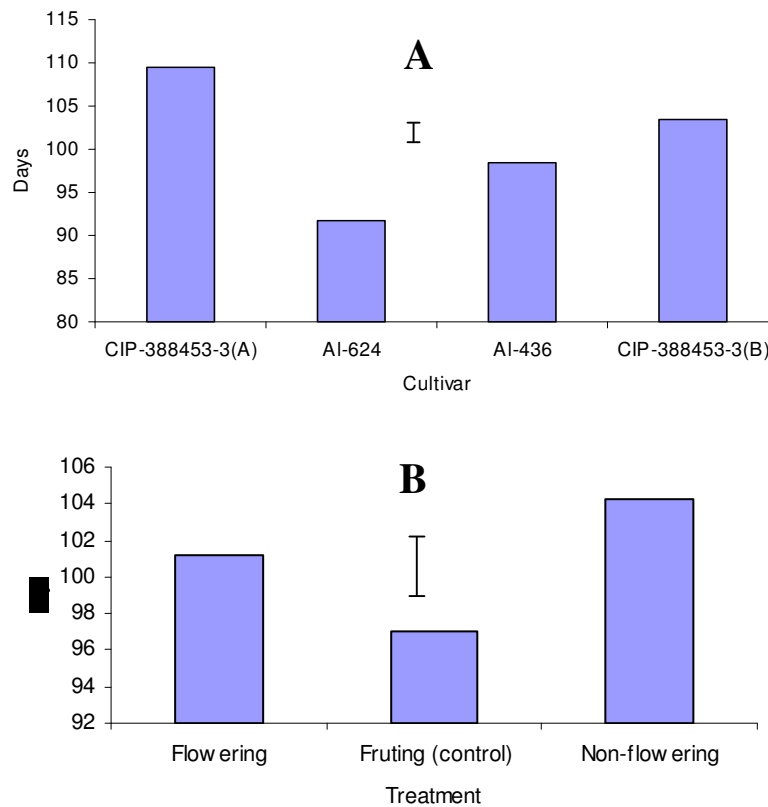

Figure 8.8 Physiological maturity of potato as affected by cultivar (A) and reproductive growth (B). The vertical bar represents least significant differences at P < 0.05

8.5 DISCUSSION

The cultivars Al-624 and CIP-388453-3(A) exhibited higher leaf stomatal conductance and rates of transpiration than the other cultivars. Dwelle *et al.* (1981b) reported the existence of genotype differences in potato regarding stomatal diffusive resistance and stomatal conductance. This may be linked to the variation in abscisic acid accumulation, which is an important trait to improve yield in a water-limited environment. The presence of berries increased leaf stomatal conductance and rate of transpiration. It is postulated that the developing fruit decrease the level of endogenous ABA and thereby increase leaf stomatal conductance, and concomitantly the rate of transpiration. ABA regulates the opening and closing of stomata (Salisbury & Ross, 1992). ABA causes stomatal closure and stimulates the uptake of water into roots (Hartung & Jeschke, 1999). Luckwill (1975) reported that leaves in close proximity to developing fruit contain much less ABA and have lower stomatal resistance than leaves more distant from the fruit. Similarly, Loveys & Kriedmann (1974) from their investigations with many plant species reported an increased level of ABA and phaseic acid in response to fruit removal. Removing the growing pod in soybean decreased the level of IAA-esters moving to the source leaf and increased ABA concentration in the leaves, suggesting that the leaves may be the source of ABA present in the seeds (Hein *et al.*, 1984).

Photosynthesis is probably the most important metabolic event on earth and is certainly an important process to understand in order to maximize potato productivity (Dean, 1994). It is not the absolute rate of photosynthesis that is important, but rather the relationship between photosynthesis and respiration, identified as the photosynthetic rate. Selection of cultivars with high net photosynthetic rates should result in higher yield if all other factors are equal (Dwelle,

1985). The cultivar CIP-388453-3(A) showed higher rates of leaf net photosynthesis compared to the other tested cultivars. In a field trials Dwelle *et al*. (1981b) screened 17 potato clones and found that clone A6948-4 showed a significantly greater gross photosynthetic rate than the others. The observed genotype differences in relation to photosynthetic efficiency could be a major factor explaining the variation in growth rate and total biomass production. The strong positive association between leaf net photosynthesis and total biomass yield (r = 0.95*) substantiate the postulation. Wilson & Cooper (1970) also observed a positive correlation between shoot dry matter yield and photosynthetic capacity for genotypes of *Lolium perenne*. On the other hand, Werf (1996) reported that although there is much variation among species and genotypes in the rate of photosynthesis per unit leaf area, this variation hardly explains the difference in growth rate between species at similar growth stages. Generally, higher crop yield may not be associated with a higher photosynthetic capacity according to Hay & Walker (1989) because so many canopy characteristics affect productivity.

Fruiting plants showed higher net photosynthetic rates than the flowering and debudded treatments. This may partly be attributed to an increase in assimilate demand. The requirements of the sink organs for photoassimilates regulate the rate of photosynthesis (Ho, 1992). Numerous reports on various crops have shown that increased sink demand results in increased source output (net CO_2 fixation); and decreased sink demand decreased source output (Geiger, 1976; Hall & Milthorpe, 1978; Peet & Kramer, 1980). Pammenter *et al*. (1993) also suggested that low sink demand causes a build-up of assimilates in source leaves and this, in turn, decrease the rate of photosynthesis. A reduced rate of photosynthesis as a consequence of carbohydrate accumulation in leaves was reported in wheat (Azcon-Bieto, 1983) and peanut (Bagnall *et al*., 1988). The observed lower net photosynthetic rate of flowering plants compared to fruiting plants revealed that the growth rate of berries affects the demand for assimilate. Ho (1984) from

his study on the priority of assimilate partitioning in tomato, reported that depending on the availability of assimilates the weaker sinks may or may not receive sufficient assimilates. An initiating inflorescence of tomato is a weaker sink than the shoot apex or roots (Ho *et al.*, 1989). The strength of fruit to attract assimilates depends strongly on the developmental stage of the fruit (Heuvelink & Marcelis, 1989; De Koning, 1994).

The photosynthetic efficiency of the leaves of fruiting and non-fruiting plants is regulated by current demand for assimilates and regulatory mechanisms such as hormonal influence, and assimilate concentration (Lenz 1979). Since fruit has relatively high concentrations of phytohormones (Luckwill, 1975; Nitsch, 1970), it has been suggested that hormones deriving from the fruit regulate photosynthesis by directly activating ribulose diphosphate carboxylase (Wareing, 1968). Some experiments have shown that auxin, cytokinin and GA can stimulate the rate of photosynthesis. GA enhanced the activity of ribulose diphosphate carboxylase in leaves (Treharne & Stoddart, 1970; Huber & Sankhla, 1973). Tamas *et al.* (1972) reported that IAA increased photosynthesis of chloroplast through enhancing photophosphorylation. Furthermore, Hoad *et al.* (1977) reported that a change in GA and cytokinin level in grape was observed in response to fruit removal, and ultimately the rate of photosynthesis was altered.

Dry matter production and distribution are crucial processes in determining crop productivity. Cultivars differed with respect to total dry matter production and in the amount allocated to the developing fruit. The cultivar CIP-388453-3(A) produced higher total biomass yield while Al-624 produced the least. A strong correlation between total dry matter yield and net photosynthesis (r = 0.95*) was exhibited, indicating that the variation in photosynthetic efficiency among cultivars substantially contributed to total biomass yield differences. Other researchers also reported the existence of cultivar differences with respect to photosynthetic

efficiency and dry matter production (Hammes & De Jager 1990; Gawronska *et al.,* 1990). Analysing the differences among cultivars with respect to dry matter allocation to the different organs indicated that cultivar Al-624 is less efficient in allocating dry matter to the tubers. The cultivar allotted about 37% of the total dry matter to the leaves and 9.5% to the developing berries and this could be the reason for reduced tuber dry mass. Meyling & Bodlaender (1981) reported that intervarietial differences in tuber yield of the four late cultivars were due largely to differences in the distribution of dry matter. On the other hand, Rijtema & Endrodi (1970) observed a linear relationship between total dry matter, and tuber dry matter and only small differences were observed between cultivars.

The development of berries reduced the partitioning of assimilates to the leaves, stems and roots. Since berries are strong sinks, the reduction may be attributed, at least in part, to the higher assimilate demand for their growth and development. Bartholdi (1940) reported reduced vegetative growth due to flowering and fruiting in potato. Starck *et al*. (1979) observed an increased dry mass of tomato stems and leaves in response to deflowering. Cockshull (1982) reported that the terminal inflorescence buds of C*hrysanthemum morifolium* are stronger sinks for assimilates, and removal of the terminal buds increased the diversion of assimilates to the vegetative organs, particularly to the leaves and roots. Investigating the effect of defoliation and debudding on the root growth of *Taraxacum officinale*, Letchamo & Gosselin (1995) obtained a higher root biomass from debudded than from flowering plants, indicating that flowering has a depressing effect on root growth. The inhibitory effects of reproductive growth on vegetative growth have been reported in tomato (Heuvelink, 1997), apple (Schupp *et al.,* 1992) and chestnut (Famiani *et al*., 2000). Furthermore, the results of many studies on the movement of ^{14}C-assimilates from leaves treated with $^{14}CO_2$ have indicated the capacity of reproductive parts to act

as strong sinks and depress vegetative growth (MacRae & Redgwell, 1990; Eckstein *et al*., 1995; Cruz-Aguado *et al*., 2001).

There is evidence indicating that after fertilization the developing seed and fruit structures are strong sinks and gain priority over vegetative organs in the partitioning of assimilates (Ho, 1988; Ho *et al.*, 1989). This dominance may be mediated by phytohormones as developing seeds and fruit are rich sources of several plant hormones including cytokinins, IAA, ABA and GA_3, although their absolute concentration varies from tissue to tissue within the fruit and is influenced by fruit growth stage (Hedden & Hoad, 1985; Brenner, 1987). Morris (1996) hypothesized that hormones produced by the developing seeds or other fruit parts are exported to other parts of the plants where they induce physiological changes. In soybean, removing the growing pods reduces the level of IAA-esters moving to the source leaf and causes ABA to accumulate in the leaves, suggesting that these may be the source of ABA present in seeds (Hein *et al*., 1984). Brenner (1987) reported IAA stimulates the opening of stomata and IAA protects stomatal closure induced by ABA (Mansfield, 1987). It is believed that developing seeds and fruit can act as a source of auxin for the leaves and sink for leaf produced ABA and thereby regulate assimilate production by promoting CO_2 exchange (Brenner, 1987).

Debudded plants produced a higher aboveground biomass than flowering and fruiting plants. This is due to the production of more lateral branches and expanded leaves in response to removing the flower buds. Salisbury & Ross (1992) reported the existence of apical dominance in the stem of most plant species and pinching off the terminal buds favours the growth of lateral buds and thereby increases branching.

The differences in the growing period of the cultivars may have contributed to the differences in total biomass yield. The observed positive correlation between days elapsed to maturity and total biomass yield (r = 0.84) and maturity period and tuber dry mass (r = 0.99**) support the hypothesis. Iwama *et al.* (1983) also reported that increasing the growing period of potato increased the dry mass of the leaves, stems and roots. Biomass production depends upon leaf canopy size and the duration over the growing season to intercept radiant energy (Van der Zaag, 1984). Allen & Scott (1980) reported that earliness in potato is accompanied by a lower yield. Similarly, Almekinders (1991) reported that the earlier maturing potato variety, Atzimba, produced the least biomass.

Fruit development accelerated the onset of senescence that could be attributed to a competition for nutrients among vegetative and reproductive organs. Developing flowers and fruit are strong sinks for sugar and amino acids and accelerate senescence due to a corresponding decrease in the amounts present in the leaves, according to Salisbury & Ross (1992). They also noted that reproductive organs may produce substances that are transported to vegetative tissue, where they promote senescence.

8.6 CONCLUSION

This study provided evidence that there are cultivar differences with respect to stomatal conductance, rates of leaf transpiration and net photosynthesis. Cultivars also exhibited differences in total biomass yield and allocation among plant organs. Compared to debudded and flowering plants, plants with berries exhibited a higher stomatal conductance and enhanced rate of leaf transpiration that may increase crop water demand and may limit its productivity under water deficit conditions. Although fruit development increased

photosynthetic efficiency, without affecting total dry matter yield, it accelerated plant maturity and decreased the partitioning of assimilates to the leaves, stems and tubers.