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Elevated CO_2 Coupled with Mineral N Supply Enhanced Lateral Branch Development in Common Pea

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Abstract: The effect of elevated CO_2 (1000 μmol mol^{-1}) on the development of lateral branches in nodulating and non-nodulating (supplied with mineral N) common pea (*Pisum sativum* L.) was studied. The time of emergence (in relation to the growth stage of the parent plant) and phenological growth of lateral branches on cultivated plants under ambient and elevated CO_2, with or without nitrogen supply depending on plant nodulation state, were observed throughout the life span of the plants. Lateral branching was only evident in plants (nodulating or non-nodulating) supplied with mineral N and was more prominent (98-100%) in both nodulating and non-nodulating plants under elevated CO_2. The higher incidence of lateral branching under elevated CO_2 was linked to differential allocation of excess dry mass produced under elevated CO_2 and a possible reduction in lateral bud growth inhibitor. Lateral branches attained full maturity (reproductive stage) only under elevated CO_2 and where mineral N is supplied and nodules are absent.

Key words: Ambient CO_2, elevated CO_2, common pea, lateral branches, lateral branching, nitrogen, N, nodulating, non-nodulating

INTRODUCTION

With the current estimated rate of 1.8 μmol mol^{-1} increase in atmospheric CO_2 concentration [CO_2] per year (Houghton *et al*., 1990), [CO_2] has been estimated to likely double the pre-industrial level of 280 μmol mol^{-1} in the next century. However, the atmospheric carbon dioxide concentration [CO_2] by the year 2002, had already risen variably and above 360 μmol mol^{-1} and with an unchanged energy policy the atmospheric carbon dioxide meter will point towards 1200 μmol mol^{-1} in a hundred years from now. (van der Galiën, 2002).

According to Murray (1995), the doubling of [CO_2] has the potential to increase the yield of many crops, as both vegetative and reproductive structures may benefit. The reason for these can be found in the report of Robertson and Leach (1995) and Mesle (2000) that elevated CO_2 stimulates cell production and expansion in most plants. Ade-Ademilua and Botha (2004) have reported that non-nodulated common pea plants (*Pisum sativum* L.) do better under elevated CO_2 than nodulated ones. The authors pointed that unlike in nodulated plants where assimilates are being shared by the plant as well as by the nodules, non-nodulated plants can make full use of the increase in the production of photosynthates under elevated CO_2 to improve their canopy.

Daepp *et al.* (2001) have reported that high growth rate under high nutrients availability promotes a strong response to elevated CO_2. In addition various experiments have demonstrated that the strong growth effects of elevated CO_2 on legumes, relative to effects seen in non-legume species, are obtained only in the presence of high mineral nutrient supply (Körner, 1995; Pritchard *et al*., 1997). Ade-Ademilua and Botha (2004) reports have shown that common pea has an opportunity to enhance its canopy under CO_2 levels as high as 1 000 μmol mol^{-1}, only when soil N is adequate and better still, when nodules are absent.

The study is a report on the effect of elevated CO_2 (at 1000 μmol mol^{-1}) on the lateral branching characteristics of nodulating and non-nodulating common pea plants, supplied with mineral N.

MATERIALS AND METHODS

Plant culture: Plants were grown according to the method of Ade-Ademilua and Botha (2004). Sterilised (3.5% m/v sodium hypochlorite solution to prevent nodulation; Rivière-Rolland *et al*., 1996) and non-sterilized seeds of common pea (*Pisum sativum* L var. Greenfeast) were sown in sterilized and non-sterilized potting soil, respectively (Greenfingers, South-Africa). Upon germination, six

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seedlings were transplanted per pot. Five gram of slow-releasing fertilizer (NPK 2:3:2; Wonder Horticultural Products, Johannesburg, South Africa) was added to the soil in pots (185×185, 165 mm deep) prior to transplanting seedlings. Twelve plants were used per treatment. Pots were irrigated with either full strength complete (with 6 mM nitrogen) or nitrogen-free Long Ashton nutrient solution (Hewitt, 1966) depending on treatment group. Plants were grown in growth chambers under same environmental conditions as described by Ade-Ademilua and Botha (2004). Twelve plants made up a treatment population and the experiments were repeated four times.

Plant growth parameters: Treatments were based on six controlled parameters: elevated CO_2 (E, 1000 μmol mol^{-1}) and ambient CO_2 (A, 380 μmol mol^{-1}); non-nodulating (r) and nodulating (R); irrigation with nutrient solution containing mineral N (N) and irrigation with nitrogen-free nutrient solution (n). Following Ade-Ademilua and Botha (2004) grouping, pots were assigned symbols as described below:

The group, non-nodulating supplied with N-free nutrients solution were left out of the experiments because according to Ade-Ademilua and Botha (2004), preliminary tests under both controlled and greenhouse conditions show that without nitrogen supply, non-nodulating pea seedlings display highly retarded growth and plants die within a few weeks of seedling germination.

RESULTS

Figure 1 shows a common pea plant bearing lateral branch in its node 1 (A) and another common pea plant under a different growth condition without lateral branch in its node 1 (B) while, Table 1 shows the observations on lateral branch emergence in plants under all treatment conditions.

Lateral branches did not emerge on nodulating plants supplied with N-free nutrient solution either under elevated (REn) or ambient (RAn) CO_2 throughout the life span of the plant. Lateral branches emerged from node 0 in all nodulating plants supplied with mineral N under elevated CO_2 (REN) shortly before flowering of the mother

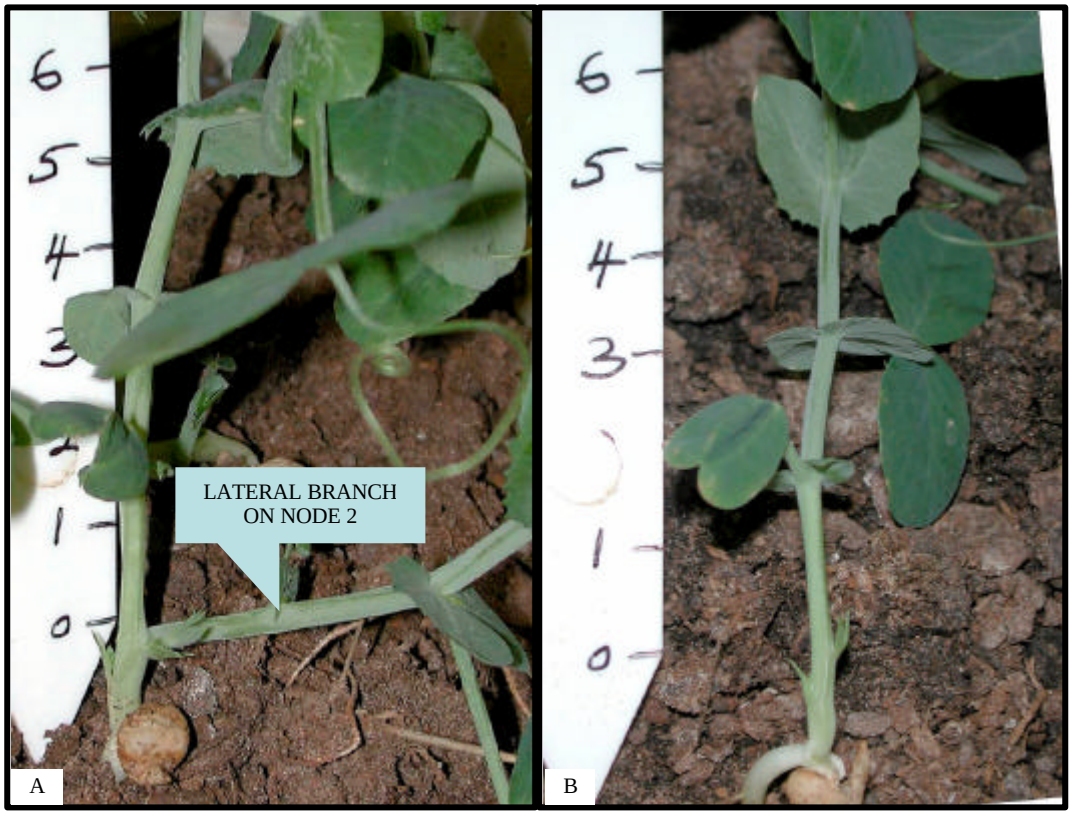

Fig. 1: Basal portion of non-nodulating plants supplied with mineral N show (A, left) lateral branch on node 2 under elevated CO_2 (rEN); (B, right) no lateral branch on node 2 under ambient CO_2 (rAN)

Table 1: The characteristics of lateral branches that emerged on common pea plants under the different growth conditions

Growth condition	Average % of plants with lateral branches per population n = 12)	Growth stage of mother plants by lateral branch emergence	Morphology of lateral branch	Reproductive state of lateral branch by the end of life span
REn	Nil	Nil	Nil	Nil
REN	98	Vegetative	Like mother plant	Nil
rEN	100	Flowering	Like mother plant	Flowered and fruited
RAn	Nil	Nil	Nil	Nil
RAN	16.67	Fruiting	Miniature stalk with minute leaves	Nil
rAN	25	Fruiting	Like mother plants	Flowered and fruited

Nodulating plants supplied with N-nutrient solution under elevated (REn) and ambient (RAn) CO_2; nodulating plants supplied with N+ nutrient solution under elevated (REN) and ambient (RAN) CO_2 and non-nodulating plants supplied with N+ nutrient solution under elevated (rEN) and ambient (rAN) CO_2

plants. They were morphologically similar to the mother plants, which bore them but they did not produce flowers throughout their life span which ended along with that of the mother plants. Lateral branches also emerged in very few (about two per population) nodulating plants supplied with mineral N under ambient treatment (RAN) only after the mother plants had produced pods. The lateral branches were however miniature stalks with minute size leaves. Lateral branches emerged from node 0 of non-nodulating plants supplied with mineral N under elevated CO_2 (rEN) during vegetative stage. These lateral branches were not just morphologically similar to the mother plants but they also produced flowers and fruits, shortly after the mother plants; though at a lower node than the mother plants. Lateral branches only emerged on three non-nodulating plants supplied with mineral N under ambient CO_2 (rAN) after the mother plants had reached pod-filling stage, grew morphologically like the mother plant but did not produce flowers.

DISCUSSION

The formation of lateral branches in non-nodulating and nodulating plants supplied with N shown in my experiments support the concept of a reduction in apical dominance in the plants under elevated CO_2. Experiments have shown that decapitation of apical bud in common pea result in growth of lateral buds on lower nodes (Stafstrom, 1995). This has been linked to a reduction in the lateral bud growth inhibitor, indole-3-aldehyde in peas with decapitated or aborted shoot tips (Nakajima *et al*., 2002). Lateral branch shoot morphology in common pea was influenced by the nodal position of the bud from which it was derived, developmental stage of the plant at the time when the bud was stimulated to grow, hormonal signals from the plant and nutrient availability (Stafstrom *et al*., 1993). This explains the difference in the morphology of lateral branches noticed under the different treatments in this experiment and could account for the differences in the growth of lateral branches, which emerged on plants under elevated CO_2 during vegetative stage to those which appeared at the flowering stage in nodulating plants grown under elevated CO_2 and even more so, in those that appeared at fruiting stage in plants grown under ambient CO_2. The difference between lateral branches that appear at the fruiting stage in both non-nodulating plants and nodulating plants under ambient CO_2 may be due to the availability of nutrients (nitrogen)-more so in non-nodulating plants than in nodulating plants and this reason could also apply to plants under elevated CO_2. It is not surprising that lateral branches on non-nodulating plants grown under elevated CO_2 produced flowers at nodes lower than was the case in the mother plants, experiments have shown that the node of floral initiation of lateral branch shoots differ from that of the main shoot in the pea plant. The morphology of the main shoot and lateral branch shoot are different with regard to the number of primodia initiated by their apical meristems prior to the onset of reproductive development (Stafstrom and Sussex, 1988, 1992; Stafstrom *et al*., 1993; Stafstrom, 1995). Lateral branching may also be linked to changes in biomass allocation as have been reported to occur in loblolly pine seedlings under elevated CO_2 (Tissue *et al*., 1997). Stitt and Krapp (1990) have proposed an involvement of nitrogen supply. Alternatively, nitrogen fixing plants may compensate by fixing more C, or fixing it at higher rate (Paul and Kucey, 1981), thereby increasing the total amount of C available to fill sinks. This should enable lower priority sinks to be filled sooner in nodulating than they would be in non-fixing plants (Arnone and Gordon, 1990). The results of these experiments show that in common pea, there was greater likelihood of allocation of dry matter more to nodules than to the lower priority sink like the stem in nodulating plants, while the absence of nodules in non-nodulating plants promoted allocation of excess dry mass to the stem. Mineral N supply to nodulating plants definitely aided the allocation of dry mass to the stem after the mother plant had flowered but at a lower rate compared to non-nodulating plants.

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