Introduction

Tea is amongst the most popular beverages in the world. In addition to the provision of phenolic compounds (mostly flavonoids of the catechin group), it is an important source of caffeine and trace elements. The quality of green tea (GT) in terms of commerce and trade is merely governed by the ratio of polyphenols (PP) to free amino acids (AA), in addition to numerous further compounds determining the flavour characteristics. The concentration of free AA is positively associated with GT quality and accounts for 10-50 mg g^{-1} dry matter in marketed GT. Free AA principally contribute to the freshness and mellowness of the infusion and their profile is dominated by the rare amino acid theanine (N^5-ethyl-glutamine). The flavonoids in GT, which comprise 20-40% of dry matter of young tea shoots are dominated by catechins (flavan-3-ol), accounting for 10-30 % of the dry matter.

Provision of nitrogen (N) has far-reaching consequences for the performance of plants at the biochemical, ecophysiological and ecosystem level. Nitrogen strongly affects the use of environmental resources (water, light), and in many cases a competition has been observed between N and carbon (C) allocation, which also led to the development of theoretical concepts, like the protein competition model and the carbon/nutrient balance model addressing the functional relationship between these pools. Green tea represents an ideal model system to study such interaction both from an ecophysiological and applied point of view.

Results and Interpretation

Increasing N supply significantly raised total biomass production and the yield of young shoots (‘two and a bud‘), although this was solely attributed to an increased number of young shoots. The level of N supply induced substantial alterations in the N and C economy of tea plants. Total N concentration increased and C/N ratio continuously decreased with increasing N supply. The concentrations of soluble carbohydrates in roots and mature leaves were significantly reduced in response to excessive N supply, due to the demand for assimilates for nutrient uptake, assimilation and growth.

The accumulation of **AA** in young shoots depended largely on the N status, and decreased significantly in plants supplied inadequately with N. Graphical vector analysis (GVA, Koricheva, 1999, Oecologia 119, 467-473), allowing the contribution of growth-induced dilution and concentration effects on phytochemical concentration to be elucidated, indicated that increasing provision of N led to a genuine increase of AA synthesis, and this relation was particularly explicit when analysed on a ‘per shoot basis’. Theanine always remained the predominant free AA, supporting its importance in long-distance N transport in tea plants. However, while its molar share of the total AA contents initially increased from 24 to 47 % with increasing provision of N, under conditions of excessive N supply its share was reduced to 38 %. A concomitant raise of the relative contribution of glutamine and arginine that increased to 20 and 15 % of the total free AA concentration, respectively, accompanied this change, which has also been observed in previous experiments (Ruan et al., 2007, J. Sci. Food Agric 87, 1505-1516). The accumulation of these amino acids, characterised by lower C/N ratios (theanine [7/2], glutamine [5/2], arginine [6/4]), most likely stems from metabolic adjustments to improve the C economy, as frequently observed in other woody plants. The higher demand for C skeletons under such conditions is further supported by an increasing PEPC activity.

The major **catechin** was epigallocatechin gallate, followed by epigallocatechin, epicatechin gallate and epicatechin. Catechin was only present at low concentrations, similar to gallic acid (1-2 mg g^{-1}). Overall, individual catechins exhibited a uniform response to the N treatments imposed; hence their profile was not significantly affected. Highest concentrations of catechins were detected at intermediate N supply, while a strong reduction was noted at the highest level of N supply that also led to maximal N concentrations and lowest C/N ratios. This response has also been observed in other plant species and discussed in relation to the protein competition model (e.g. Strissel et al., 2005, Plant Biol. 7, 677–685) and the carbon/nutrient balance (e.g. Bryant et al., 1983, Oikos 40, 357-368). GVA clearly indicates that the total content of PP per plant increased regardless of declining PP concentrations under abundant N supply, suggesting that a dilution effect due to biomass growth is involved. Indeed, as the yield (number of shoots) was strongly increased at excessive N supply, the PP accumulation on a 'young shoot basis' was strongly diminished. With respect to substrate availability and energy the C status has been discussed as a critical factor for the accumulation of phenolic compounds (Rühmann et al., 2002). Diverting the C flux to N metabolism is therefore an important factor contributing to the observed reduction in PP accumulation, and the declining availability of carbohydrates is also analogue to substantially increased concentrations of AA, which is further supported by enhanced activities of (anapleurotic) PEPC and glutamine synthetase (GS) under abundant N supply.

The precursor of the phenylpropanoid pathway, free phenylalanine (Phe), increased in young shoots in response to increasing N supply, but the magnitude of this increase was much smaller than that of the major amino acids mentioned above. Surprisingly, activity of leaf phenylalanine-ammonia lyase (PAL), the key enzyme of the phenylpropanoid pathway, increased with external N supply and plant N status, and the relation of polyphenols accumulation to the activity of PAL was negative (-0.60). In fact, activities of PAL and GS were highly correlated (r^2 = 0.85), which is interpreted as a positive influence of N supply on overall metabolic activity, rather than a mechanistic link between PAL activity and the accumulation of polyphenols. Nonetheless, elucidating the relationships among N supply, the accumulation of flavonoids, and the activity of enzymes involved in their biosynthesis in tea awaits further investigations.

The results indicate that the balance between growth and secondary metabolism in tea plants is shifted toward increasing synthesis of growth-related compounds such as amino acids and proteins, while investment of C into secondary metabolites is not changing proportionally. The quality index PP/AA decreased curvilinearly with increasing N status and the C/N ratio in young shoots. While a high GT quality is associated with a low PP/AA ratio, the accumulation of free arginine in response to excessive N supply needs particular attention due to the adverse taste notes attributed to this amino acid.