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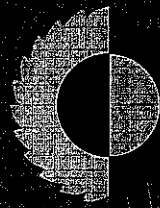
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Do carbohydrates contribute to winter survival of white clover ?

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Summary

The aim of this paper was to investigate whether or not the carbohydrates accumulated in stolons during autumn contributed to the overwintering of white clover. Relationships between plant morphogenesis, carbohydrates and meteorological data were established outdoors over three consecutive years winter/spring periods in the North-East of France. The results showed that leaf appearance rate was not solely dependent on the mean air temperature and that there was no clear relationship between the relative growth rate of leaves and the amount of starch in the stolons. Starch continued to accumulate in the stolons up to a threshold of 300° C day (established from the day of the last defoliation in autumn). The starch was then hydrolysed during the winter but the decrease in starch was influenced by parameters other than temperature sum. There was no clear relationship between the fate of starch and plant morphogenesis.

Keywords: carbohydrates, low temperature, morphogenesis, overwintering, starch, white clover.

Introduction

White clover is the most abundant forage legume found in grazed temperate pastures, contributing significantly to the quality of the pasture. The lack of persistence of white clover during winter is a major problem with respect to its spring yield and the management of its association with grasses. Starch accumulates in stolons during autumn as part of the hardening process, but it is not clear how these compounds enhance the tolerance of white clover to low temperature (Bertrand & Paquin, 1991). The aim of this paper is to investigate the relationships between plant morphogenesis, carbohydrate compounds and meteorological data during winter and spring, under the semi-continental climate of the North-East of France.

Materials and Methods

White clover (cv. Huia) was sown in association with ryegrass (cv. Preference) in May 1991, at the experimental station of INRA-SAD at Mirecourt (280 m above sea, 850 mm rainfall). During three winter periods (1992-1993; 1993-1994; 1994-1995), the following parameters were determined for white clover at monthly intervals from

October to May: leaf appearance rate, leaf relative growth rate and stolon length (mm^{-2}). Leaf relative growth rate was calculated as the difference between leaf appearance rate and leaf death rate on a stolon axis as described by Maitre *et al.* (1985). Stolons were sampled during winter, immediately frozen in liquid nitrogen and then freeze-dried, weighed and ground for further biochemical analyses. Starch was analysed after hydrolysis with B amyloglucosidase at 55°C and enzymatically determined as described by Bergmeyer *et al.* (1974). Data were statistically evaluated by analysis of variance using 'Proc GLM' and by regression analysis using 'Proc REG' of SAS (SAS Institute Inc., 1987). The mean air temperature (2m above the soil) was measured at the experimental site. T sum above 0°C was calculated from the date of the last cut in autumn until the beginning of May.

Results

Leaf appearance rate was low during winter and was not well correlated with the mean air temperature (Figure 1). A curve could be fitted to the points such that those along the boundary line were correlated with the mean air temperature but points below this line were not solely dependent on the mean air temperature. A relationship between the starch content of the stolons and the sum of temperatures above 0°C (from the day of the last cut) could be drawn (Figure 2). This relationship indicated that from the beginning of winter starch accumulated in the stolons until a threshold above 300°C day. Above this threshold, starch was hydrolysed during the winter, but accumulated again in the stolons when the temperature sum reached 600°C day in early Spring. The relative growth rate (RGR) of leaves was not always positive during winter. Negative RGR indicated that leaf death was greater than leaf production. No clear relationship could be determined between the relative growth rate of leaves and the amount of starch in the stolons during the three winters (Figure 3).

Discussion

This experiment was conducted in the field over a period of 3 years in order to determine the relationships between plant morphogenesis, the amount of starch in stolons and air temperature. Our results showed that the mean air temperature during winter was not the only climatic factor limiting leaf appearance rate. Other parameters such as minimum air and soil temperature and global radiation may also influence the morphogenesis of white clover during winter (Sackville Hamilton & Harper, 1989). Stolon starch content decreased during winter as already shown by many authors (Vez, 1961; Guckert *et al.*, 1983; Volenec *et al.*, 1991; Bertrand & Paquin, 1991). Starch hydrolysis is assumed to provide free sugars which may act as cryoprotectants and maintain high osmotic pressure in the cells, thus enhancing cold tolerance (Tronsmo *et al.*, 1993; Yelenosky & Guy, 1989). Our results indicate that the hydrolysis of starch was dependent on the temperature sum during winter but the relationship was not linear. This suggests that other factors influence the decrease in starch in the stolons during winter. No clear relationship was observed between morphogenesis during winter and the fate of starch. This result indicates that morphogenesis of white clover during winter is not directly related to the fate of starch in the stolons.

Figure 1. Leaf appearance rate during three winters (from 1992 to 1995) versus the mean air temperature. Each point represents a measurement.

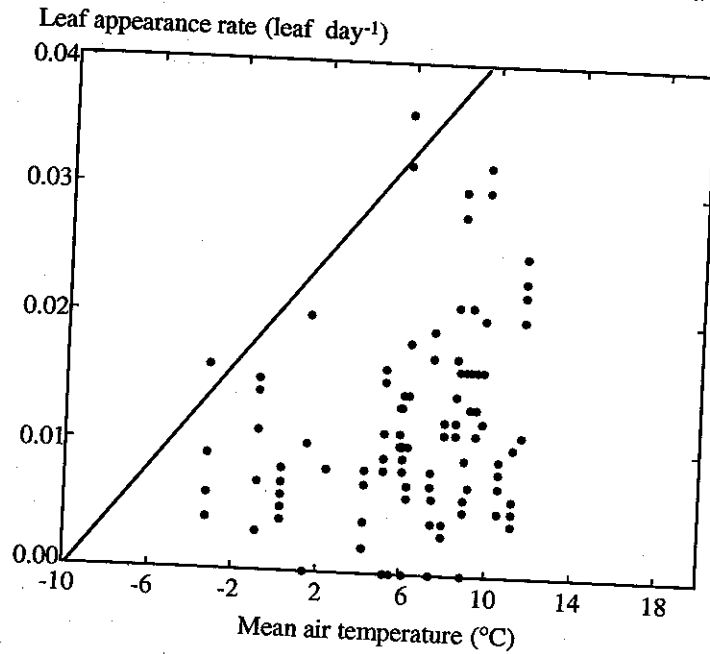
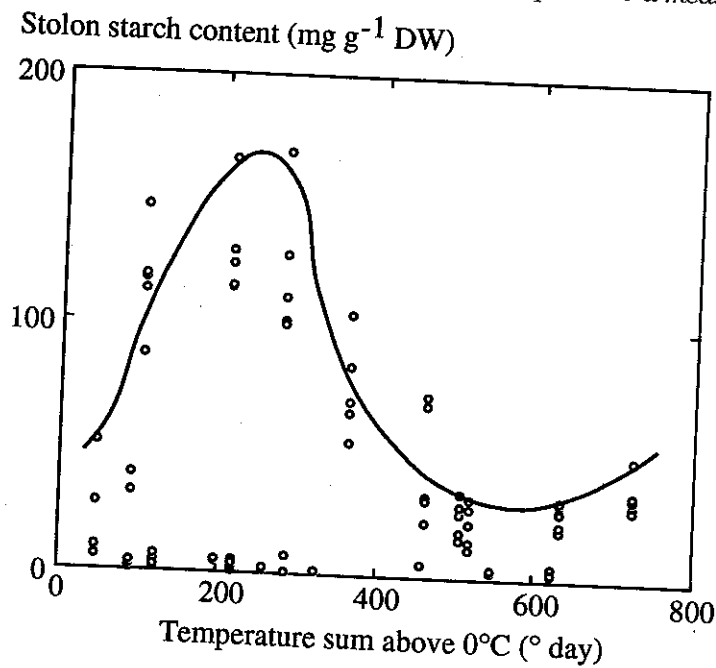


Figure 2. Stolon starch content during three winters (from 1992 to 1995) versus the temperature sum above 0°C. Each point represents a measurement.

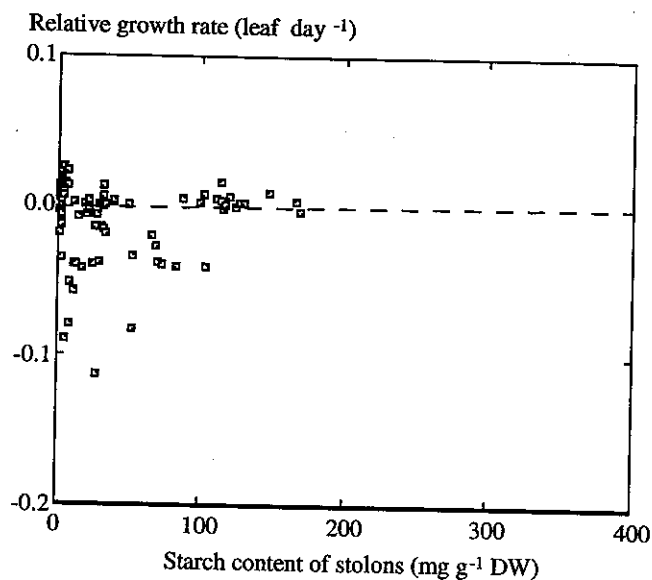


growth rate and stolon length difference between leaf appearance rates described by Maitre *et al.* were frozen in liquid nitrogen for biochemical analyses. Starch was extracted at 55°C and enzymatically hydrolysed. Data were statistically evaluated using regression analysis using 'Proc Mixed' procedure (temperature (2m above the ground) and temperature (2m above the ground) were calculated from May to May).

Starch content was not well correlated with the mean air temperature but was correlated to the points such that the sum of temperatures above 0°C (Figure 2). This relationship was simulated in the stolon starch content until the temperature sum reached a value where starch hydrolysis was not always complete. The relative growth rate was greater than leaf appearance rate during the three winters.

Starch content was measured over a period of 3 years in order to determine the amount of starch in the stolon as a function of the mean air temperature and the leaf appearance rate. Other factors such as global radiation may influence starch content (Sackville Hamilton winter as already shown by Bertrand *et al.*, 1991; Bertrand & Bertrand, 1991). Our results indicate that the temperature sum during winter is a major factor influencing the starch content. This result indicates that starch content is directly related to the fate of

Figure 3. Relationship between the relative growth rate (RGR) and the amount of starch in the stolons during the three winters (from 1992 to 1995). Each point represents a measurement.



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THE EUROPEAN UNION CAP REFORMS HAVE CAUSED FUNDAMENTAL CHANGES IN EUROPEAN FARMING SYSTEMS AND NEW TECHNICAL STRATEGIES AND SOCIO-ECONOMIC FACTORS NEED TO BE INCREASINGLY TAKEN INTO ACCOUNT BY FARMERS. GRASSLAND WILL CONTINUE TO HAVE A CENTRAL ROLE IN OBTAINING HIGH-QUALITY ANIMAL PRODUCTS. NEVERTHELESS, THE INCREASING USE AND INTEGRATION OF GRASSLAND FOR SET-ASIDE, AMENITY AND OTHER NON-FOOD PRODUCING ROLES IS BECOMING MORE IMPORTANT FOR ITS SUCCESSFUL OVERALL USE. DIFFERENT ASPECTS OF GRASSLAND BREEDING, PRODUCTION, GRAZING, CONSERVATION, ALTERNATIVE USES AND ENVIRONMENTALLY FRIENDLY MANAGEMENT IN THE DIFFERENT LAND USE SYSTEMS OF EUROPE ARE PRESENTED IN THIS VOLUME.

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