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GROWTH AND SYMBIOTIC NITROGEN FIXATION OF AN EAST AFRICAN HIGHLAND CLOVER (TRIFOLIUM STEUDNERI S.)

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II SUMMARY

Trifolium steudneri Schweinfurt, an annual clover indigenous to the East African highlands, has shown potential as a nitrogen source for the crop-lands in the Ethiopian highlands. Due to its broad altitudinal distribution (1100 to 2800 m), it is exposed to a wide range of temperatures, radiation and rainfall. However, there is no information on how the species responds to different climatic and edaphic conditions. This study was undertaken to investigate the influence of environmental factors on the growth and symbiotic nitrogen fixation of this clover. Experiments were conducted both in the field and in growth chambers.

In a first group of trials, spaced plants and swards were grown in 1985 and 1986 on seasonally waterlogged shrink-swell clay soils (Vertisols) during the main cropping season at two altitudes (1850 and 2380 m) in the Ethiopian highlands. Growth was distinctly slower at the higher altitude and appeared to be limited by lower day temperatures and lower radiant exposure. The lower relative growth rate was mediated partly by a lower leaf area ratio, but more importantly by a lower net assimilation rate. Reduced leaf area expansion was the main factor responsible for lower sward yields. Marked differences in growth between the years were associated with the duration of inadequate soil aeration caused by waterlogging. Although extended periods of waterlogging (7 to 12 weeks) distinctly depressed productivity, swards still acquired an appreciable amount of biomass (2.3 to 3.8 t dry matter ha^{-1}) and a high proportion (81 to 93%) of their nitrogen from symbiotic fixation (^{15}N isotope dilution method). The amount of fixed nitrogen was closely associated with dry matter yield. Under favourable environmental conditions, Trifolium steudneri had a high yield (9.1 t dry matter ha^{-1}) and fixed a large quantity of nitrogen (165 kg ha^{-1}) in a relatively short period (104 days).

In a second group of experiments, spaced plants were grown in growth chambers at different day/night shoot (air) temperature combinations. In addition, they were exposed to two separate night root temperature regimes. Higher mean shoot temperatures in the range of 15 to 21°C stimulated the growth rate of Trifolium steudneri by promoting the activity of the shoot apices. The ensuing increase in the requirements for photosynthates and nitrogen prompted the plant to enhance its net assimilation rate and its nitrogen fixing ability. Faster growing plants had a higher proportion of nitrogen from fixation (^{15}N isotope dilution), a greater nodule mass and a greater total nitrogenase activity (acetylene reduction). Diurnal amplitudes of 6 and 18°C at a common mean temperature of 15°C did not differ in their influence on growth and nitrogen fixation. Night root temperature between 13 and 19°C had only a small effect on growth and nitrogen fixation. The clover appeared to compensate a lower night root temperature by increasing its specific nitrogenase activity (per unit nodule mass) during the daytime.

This study indicates that the productivity of Trifolium steudneri can be expected to be highest in a temperature range found in the lower belt of the East African highlands. At the same time, it seems to be adapted to large daily temperature amplitudes and to cool nights — conditions typical of tropical highlands. The results also suggest that the indigenous Rhizobia fixed nitrogen efficiently in symbiosis with the clover. Trifolium steudneri appears to be a promising nitrogen source for the cropped Vertisols, since in wet years it would tolerate waterlogging, while in drier ones it would be high yielding both in dry matter and quantity of fixed nitrogen.

ZUSAMMENFASSUNG

Trifolium steudneri Schweinfurt ist eine im ostafrikanischen Hochland heimische einjährige Kleeart, welche einen wichtigen Beitrag zur Stickstoffversorgung der Ackerböden im äthiopischen Hochland liefern könnte. Da diese Leguminose in Höhen zwischen 1100 und 2800 m über Meer gedeiht, ist sie innerhalb dieses Bereiches sehr unterschiedlichen Temperaturen, Einstrahlungs- und Niederschlagsmengen ausgesetzt. Diese Arbeit befasst sich mit der Frage des Einflusses der Umweltfaktoren auf das Wachstum und die symbiotische Stickstoff-Fixierung dieser Kleeart. Es sind Versuche im Feld und in Wachstumskammern durchgeführt worden.

In den Jahren 1985 und 1986 wurden in zwei Höhenlagen (1850 und 2380 m ü. M.) im äthiopischen Hochland auf saisonal vernässten Tonböden (Vertisole) während der Hauptregenzeit Einzelpflanzen und Bestände angebaut. Das Wachstum war eindeutig langsamer am höheren Standort und schien durch die tieferen Tagestemperaturen und die geringere Einstrahlung begrenzt worden zu sein. Die niedrigere relative Wachstumsrate war teilweise durch ein tieferes Blattflächenverhältnis verursacht, zur Hauptsache aber durch eine tiefere Nettoassimilationsrate. Für die geringeren Bestandeserträge war vorallem eine reduzierte Blattflächenentfaltung verantwortlich. Signifikante Wachstumsunterschiede zwischen den Jahren hingen mit der Dauer von Perioden ungenügender Bodendurchlüftung zusammen, verursacht durch stauende Nässe. Obwohl eine längere Nässeperiode (7 bis 12 Wochen) die Erträge deutlich verringerte, produzierten die Bestände eine beachtliche Menge an Biomasse (2.3 bis 3.8 t Trockensubstanz ha^{-1}) und wiesen einen hohen Anteil (81 bis 93%) an symbiotisch fixiertem Stickstoff auf (^{15}N-Verdünnungstechnik). Der Trockensubstanzertrag war der wichtigste Bestimmungsfaktor für die Menge des fixierten Stickstoffes. In einer verhältnismässig kurzen Wachstumsperiode

(104 Tage) lieferte Trifolium steudneri unter günstigen Umweltbedingungen hohe Erträge an Trockenmasse (9.1 t ha^{-1}) und fixiertem Stickstoff (165 kg ha^{-1}).

In einer zweiten Versuchsserie wurde der Einfluss von unterschiedlichen Tag/Nacht-Lufttemperaturen und von zwei Nacht-Bodentemperaturen auf das Wachstum und die Stickstoff-Fixierung untersucht. Höhere Temperaturmittel (zwischen 15 und 21°C) förderten die Wachstumsrate über eine Erhöhung der Aktivität der Vegetationsspitzen. Der höhere Bedarf an Photosyntheseprodukten und Stickstoff wurde durch eine höhere Nettoassimilationsrate und Stickstoff-Fixierungsfähigkeit gedeckt. Rascher wachsende Pflanzen hatten höhere Stickstoffanteile aus der Fixierung (^{15}N-Verdünnungstechnik), eine grössere Knöllchenmasse und eine höhere Gesamt-Nitrogenaseaktivität (Azetylen-Reduktion). Tag/Nacht-Temperaturschwankungen von 6 und 18°C bewirkten bei einem gemeinsamen Temperaturmittel (15°C) keine Unterschiede. Nacht-Bodentemperaturen (zwischen 13 und 19°C) wirkten sich nur geringfügig auf das Wachstum und die Stickstoff-Fixierung aus. Die Pflanzen schienen eine kühlere Nacht-Bodentemperatur mit einer erhöhten spezifischen Nitrogenaseaktivität (Aktivität pro Einheit Knöllchenmasse) am Tag zu kompensieren.

Die vorliegende Arbeit zeigt, dass wegen der höheren Temperaturen eine hohe Produktivität von Trifolium steudneri in den tieferliegenden Regionen des ostafrikanischen Hochlandes erwartet werden kann. Gleichzeitig schien die Pflanze gut an grosse Tag/Nacht-Temperaturunterschiede und tiefe Nachttemperaturen angepasst zu sein. Die Resultate zeigen auch, dass die einheimischen Rhizobien, in Symbiose mit dieser Kleeart, effiziente Stickstoff-Fixierer sein können. Trifolium steudneri scheint eine vielversprechende Stickstoff-Quelle für die bebauten Vertisole darzustellen. Sie tolerierte längere Nässeperioden in feuchteren Jahren und lieferte in trockeneren Jahren hohe Trockensubstanz- und Stickstoff-Erträge.

III GROWTH AND NITROGEN FIXATION AT TWO ALTITUDES IN THE ETHIOPIAN HIGHLANDS

1. ABSTRACT

Trifolium steudneri Schweinfurt, an annual clover indigenous to the East African highlands, has shown potential as a nitrogen source for the crop-lands in the Ethiopian highlands. The objective of this study was to assess the growth (functional growth analysis) and symbiotic nitrogen fixation (^{15}N isotope dilution method) of this clover at two altitudes (Debre Zeit (DZ) = 1850 m, Addis Ababa (AA) = 2380 m) in Ethiopia. Spaced plants and swards were grown in 1985 and 1986 on seasonally waterlogged shrink-swell clay soils (Vertisols) during the main cropping season (late June to October).

Eleven weeks after sowing, the spaced plants showed a 4 to 9-fold greater dry weight at DZ than at AA and a 33 to 41% higher mean relative growth rate (RGR). The higher RGR was mediated partly by a greater leaf area ratio, but more importantly by a greater net assimilation rate. A higher rate of leaf appearance on the primary shoot (38 to 58%) supported the greater RGR. The greater growth rate at DZ appeared to be associated with the higher day temperature and the higher radiant exposure at that site. At both altitudes, the spaced plants had a greater dry weight (2 to 5 times) and a higher RGR (33 to 41%) in 1986 than in 1985. Growth seemed to be limited in 1985 primarily by a longer duration of inadequate soil aeration (oxygen partial pressure below 7 kPa) due to waterlogging.

Growth analysis of swards grown in 1986 revealed that crop growth rate (CGR) at DZ reached a peak of 24.8 g m^{-2} d^{-1} 12

weeks after sowing, while at AA CGR was only 7.3 g m^{-2} d^{-1}. The main cause for this difference was a more rapid expansion of the leaf area at DZ, which resulted in a higher maximum LAI (6.0 at DZ versus 1.3 at AA).

Between 72 and 93% of the N yield of the swards was derived from symbiotic fixation. The amount of fixed N was closely associated with dry matter yield. Under favourable environmental conditions (at DZ in 1986 with no waterlogging), the swards produced 9.1 t above-ground dry matter ha^{-1} and fixed 165 kg N ha^{-1} in 104 days of growth. Although extended periods of waterlogging (7 weeks at DZ in 1985 and 9 to 12 weeks at AA) depressed productivity distinctly, the swards still yielded 3.8 t dry matter ha^{-1} at DZ in 1985 and 2.4 t at AA and fixed 80 and 61 kg N ha^{-1} respectively.

The results suggest that Trifolium steudneri is a herbaceous legume with a great potential for use on the cropped Vertisols in the warmer belt of the East African highlands. It is high yielding both in dry matter and fixed nitrogen and it tolerates waterlogging.