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SUN/SHADE ACCLIMATION AND NITROGEN NUTRITION OF *TRADESCANTIA FLUMINENSIS*, A PROBLEM WEED IN NEW ZEALAND NATIVE FOREST REMNANTS

Summary: Growth, sun/shade acclimation and nitrogen nutrition were examined in *Tradescantia fluminensis* to gain greater understanding of why this species is so successful in New Zealand native forest remnants. Over a two year period, the rate of shoot extension of *T. fluminensis* in a New Zealand mixed mahoe (*Melicytus ramiflorus*) coastal forest remnant showed a similar pattern to monthly mean values for mean daily air temperature and day length. Growth at the shoot apex was balanced by death at the shoot base. During the first year, nitrate (NO_3^-) content of the plant in the field was always > 250 μmol g^{-1} dry weight. On high NO_3^- supply in pot experiments, in a glasshouse or outdoors, total plant dry weight increased with increased relative irradiance from 1 to 30-50% (open ground photosynthetically active radiation = 100% relative irradiance). Changes in shoot to root dry weight ratio (S:R), specific leaf area (SLA) and leaf chlorophyll, carotenoid and protein content associated with decreased irradiance from 50 to 1% were similar to those associated with increased distance into the forest remnant and are discussed in relation to shade acclimation. Values for S:R (>30:1) and SLA (≈900 cm^2 g^{-1} dry weight) were extremely high at low irradiance. These results support earlier conclusions that irradiance level is likely to be the primary factor limiting the extent of colonisation of forest remnants by *T. fluminensis*. Under glasshouse conditions, the growth response of *T. fluminensis* to different ammonium and NO_3^- concentrations was similar to that previously reported for herbaceous species capable of rapid growth. Leaf nitrate reductase activity was within the range previously reported for fast growing species. *Tradescantia fluminensis* accumulated substantial amounts of NO_3^- in shoots with no depression in growth. This NO_3^- was utilised when nitrogen became limiting to growth. An 'invasion strategy' of *T. fluminensis* into N.Z. native forest remnants is proposed.

Keywords: *Tradescantia fluminensis*; nitrogen assimilation; sun/shade acclimation; growth strategy; temperate forest remnant; weed; New Zealand.

Introduction

Tradescantia fluminensis Vell. is a perennial, herbaceous species native to tropical regions of Brazil and Argentina which has become established in many lowland native forest remnants of the North Island and northern South Island of New Zealand. Under certain conditions, *T. fluminensis* spreads rapidly to form a dense mat up to 60 cm in depth which can 'smother' ground cover species and prevent seedlings of canopy species from establishing, thus blocking the regeneration cycle (Esler, 1962, 1988; Kelly and Skipworth, 1984; Timmins and Williams, 1987; Ogle and Lovelock, 1989).

Tradescantia fluminensis is capable of growth under a wide range of irradiance levels. It can grow under a forest canopy at irradiance levels around 1% that of open ground (Kelly and Skipworth, 1984) and also in exposed conditions, e.g., amongst kikuyu grass (*Pennisetum clandestinum* Hochst. ex Chiov.) on stable sand dunes at Whatipu, West Auckland (Maule, *unpubl.*). Esler (1962) observed that *T. fluminensis* tends to invade forest remnants in which canopy degradation, through, for example, stock browsing and tree fall, has resulted in increased internal irradiance levels. In addition, Kelly and Skipworth (1984) found a close positive correlation between the regrowth of cleared areas of *T. fluminensis* and forest floor irradiance from 1 to 10% that of open ground. Level of irradiance during growth can affect the partitioning of dry matter to leaf, stem and root, leaf morphology, and leaf composition of many higher plants. In comparison with plants grown under high irradiance, plants grown under low irradiance often allocate more dry matter to leaves and have greater specific leaf area (SLA, area per unit dry weight leaf) and total

chlorophyll per unit dry weight, but their chlorophyll a to chlorophyll b ratio (chlorophyll a:b) and protein content per unit area are usually lower (Björkman, 1981; Givnish, 1988). These features of plants grown under low irradiance tend towards those of shade adapted plants and, in general, are considered to be mechanisms of acclimation to low irradiance and hence of benefit to the plant (Boardman, 1977; Björkman, 1981; Lichtenthaler, 1985; Evans, 1988; Givnish, 1988).

Ogle and Lovelock (1989) reported vigorous growth of *T. fluminensis* in a forest remnant with high soil nutrient levels, but little is known of the nutrition of this plant. Nitrogen is often the main soil nutrient limiting plant growth in most environments. In undisturbed forest soil, nitrogen levels are usually low and ammonium (NH_4^+) and amino acids are likely to be the main forms of nitrogen available to plants (Russel, 1973; Haynes *et al*., 1986). Disturbance of forest soils through, for example, tree fall, is likely to increase plant available nitrogen, especially nitrate (NO_3^-) levels (Haynes *et al*., 1986; Stewart, Hegarty and Specht, 1988). Herbaceous species capable of rapid growth, such as many weed and annual crop species, are usually also capable of high rates of NO_3^- assimilation and respond to soil NO_3^- concentrations above 1 mol m^{-3}, which are likely to occur only in nitrogen-fertilised or disturbed soils (Lee, Woodin and Press, 1986; Andrews *et al*., 1984b, 1992b). Often, they can store high concentrations of NO_3^- in shoots; this NO_3^- is utilised when external nitrogen supply becomes limiting to growth.

In the present study, growth rate and NO_3^- content of individual *T. fluminensis* plants were monitored in swards in a New Zealand native forest remnant. Also, SLA and leaf photosynthetic pigment and protein content were examined in *T. fluminensis* sampled at different distances into the forest remnant. Findings were compared with more detailed studies of sun/shade acclimation and nitrogen nutrition conducted under controlled conditions. The specific objectives of the study were 1: to determine seasonal growth rates of *T. fluminensis* within a forest remnant; 2: to determine if *T. fluminensis* shows mechanisms of acclimation to different irradiance levels similar to those of higher plants in general; 3: to determine if *T. fluminensis* shows characteristics of nitrogen nutrition similar to those of fast growing species; and 4: to assess the importance of irradiance and nitrogen as factors limiting the extent of colonisation of forest remnants by *T. fluminensis*. The overall objective of the study was to gain greater understanding of why this species is so successful in New Zealand native forest remnants.

Methods

Field studies

The population of *T. fluminensis* studied is located in Shuttleworths Bush, 0.8 ha of largely undisturbed mixed mahoe (*Melicytus ramiflorus* Forst. et Forst. f.) coastal forest at Akaroa, Canterbury, New Zealand. (National grid reference NZMS 260 N36, Akaroa 076113). The forest remnant is situated on a south facing valley side with the Wai-iti stream at its base. *T. fluminensis* is present along almost the entire length of the forest remnant edge. The two *T. fluminensis* swards studied are situated on the extreme east and west sides of the remnant and lie on the north stream bank penetrating the remnant 3-5 m. Plants used in the study of seasonal growth rates occurred 2-4 m into the remnant where relative irradiance levels (midday approximately) ranged from 1-5% full sunlight. Open ground photosynthetically active radiation (PAR) determined with a Li-cor LI-188B quantum sensor (Lincoln, Nebraska, USA) was defined as 100% relative irradiance. Details of temperature during the field study were obtained from the meterological station at Akaroa which is within 1 km of the field site. Daylength datum is mean monthly daylength for Christchurch.

Individual *T. fluminensis* plants within the swards are usually comprised of one main vertical leaf-bearing stem of about 60 cm preceded by a horizontal leafless stem of 30-150 cm with roots at the nodes. The root system is small and only penetrates the leaf litter and humus layers immediately below the sward. Rates of shoot extension were determined from 3 August 1989 to 11 June 1991 by tagging stems of six plants in each sward at the 3rd, 5th and 10th nodes from the apex. The first root usually occurred at or about the 10th node. At approximately monthly intervals in the first year and two monthly intervals in the second year, stem length from the apex to the top tag and between tags was measured for all plants. Usually, two tagged plants and five untagged plants were then removed from each sward for total length and dry weight determination and a further two plants were recruited into each of the tagged groups. All plants were separated into ten leaves (laminae), upper stem (stem and petioles above and including the 10th node) and lower stem (stem and roots below the 10th node), dried at 70 ^{o}C for 96 hours, then weighed. Dried material was ground and an aqueous extract of a 0.1 g sample analysed for NO_3^- as described in MacKereth, Heron and Talling (1978). On 21 March 1991, all plants within six 0.09 m^2 quadrats placed near the centre of each sward were harvested for biomass and shoot to root dry weight ratio (S:R)

determination. Soil NO_3^- levels were determined on one occasion (28 September 1991). Four soil cores of 5 cm depth were sampled at the streamside and at the sward inner edge, 0.1 and 4-5 m into the forest remnant, respectively. Samples were also taken at 15 m into the forest remnant. Soil NO_3^- was extracted into 2 M KCl (Blakemore, Searle and Daly, 1987) and determined as described in MacKereth *et al.* (1978).

On 16 January 1991, shoots were sampled at 0.5, 2.0 and 3.5 m along five transects from the stream edge into the forest remnant. The relative irradiance levels (1100 - 1300 h) at the sampling points were approximately 20, 5 and 1% respectively. A repeat study was carried out on 27 August 1991. Leaves (laminae) from the 3rd to 5th nodes behind the main stem apex of each plant were detached for protein analysis (Bradford, 1976) and SLA and photosynthetic pigment determination (Andrews *et al.*, 1984a; Andrews, Love and Sprent, 1989). Chlorophyll a, chlorophyll b and carotenoids were determined spectrophotometrically (Shimadzu UV-160A spectrophotometer, Tokyo, Japan) using the equations given in Strickland and Parsons (1972). Chlorophyll standards (Sigma Chemical Co., St. Louis, USA) with chlorophyll a:b in the range 1 to 5 were prepared. Carotenoid content is in milli specific pigment units which approximate to mg (Strickland and Parsons, 1972). On 18 January 1992, SLA was measured in ten leaves from plants sampled at 4 - 5 m into the forest remnant.

Sun/shade acclimation experiments

In experiment 1, shoot cuttings comprising five or six nodes plus apex, were rooted in distilled water for 10 days. Six plants were then sampled for determination of initial dry weight. The remaining 30 plants were transferred to 100 mm diameter, 200 mm tall pots (one plant per pot) filled with vermiculite/perlite (1:1) soaked in basal nutrient solution (Andrews *et al.*, 1989) containing 5.0 mol m^{-3} NO_3^- added as potassium nitrate. Plants were grown in a glasshouse during spring/summer in an initial experiment and late summer/autumn in a repeat experiment. The photoperiod was 12-14 hours and the temperature was maintained between 15 and 30 °C although it was rarely above 25 °C. There were six light regimes: 1, 3, 8, 26, 48 and 90% relative irradiance. The relative irradiance level within the glasshouse was 90%. The remaining irradiance levels were obtained by using different layers of shade cloth. All pots were flushed with nutrient solution every 2 days. Plants were harvested 89-90 and 60-61 days after planting in the initial and repeat experiments respectively. Leaves from the 3rd to 5th nodes behind the main stem apex of each plant were detached for protein, SLA and photosynthetic pigment determination as in the field study. Plants were then separated into leaves, stem (stem plus petioles) and roots for dry weight determination.

Experiment 2 was carried out as for experiment 1 except that plants were grown outdoors during late summer/autumn and from autumn to spring in the initial and repeat experiments respectively. Relative irradiance levels were 1, 3, 9, 28, 53 and 100%. Plants were harvested 53-54 and 177-178 days after planting in the initial and repeat experiments respectively. Plants grown under 100% irradiance showed considerable wind damage and, in the repeat experiment, frost damage also, and were not included in the analysis.

Nitrogen nutrition experiments

Experiments 3-5, which examined nitrogen nutrition of *T. fluminensis*, were carried out in a glasshouse under natural daylight during late summer/autumn. The photoperiod was 12-14 hours and the temperature was maintained between 10 and 25 °C. Shoot cuttings were rooted then transferred to pots as for experiment 1. All pots were flushed every two to three days with basal nutrient solution containing the appropriate nitrogen treatment added as potassium nitrate or ammonium sulphate. In all treatments, potassium concentration was maintained at 23.6 mol m^{-3} by the addition of potassium sulphate as necessary. In experiment 3, all plants were supplied 0.5 mol m^{-3} NO_3^- for 45 days then transferred to 0.1, 0.5, 1.0 or 5.0 mol m^{-3} nitrogen as NO_3^- or NH_4^+. Plants were harvested 34 days later, and dry weight of leaves, stem and root determined. In experiment 4, plants were supplied 0.1, 0.5, 1.0, 5.0 or 20 mol m^{-3} NO_3^- throughout. Plants were harvested 54 days after planting and leaf, stem and root dry weight, nitrate reductase activity (NRA) and NO_3^- content determined (Andrews *et al.*, 1984b, 1992b). In experiment 5, plants were supplied 5.0 mol m^{-3} NO_3^- for 43 days then divided into four groups. One group was harvested to determine initial leaf, stem and root dry weight and NO_3^- content. The remaining three groups were supplied with 0, 0.5 or 5.0 mol m^{-3} NO_3^- for 23 days before determination of dry weight and NO_3^- content of the component plant parts.

Experimental design and data analysis

All experiments were of completely randomised design with five replicates per treatment. All measurements were carried out on all replicates. An analysis of variance was carried out on all data. All effects discussed have a probability $P<0.01$. All

experiments were carried out at least twice and effects discussed were also obtained in the repeat experiments. Variability quoted in the text is S.E.

Results

In the field study, the rate of shoot extension showed a similar pattern to monthly mean values for mean daily air temperature and daylength (Fig. 1A). In general, shoot extension rate was 0.2-0.3 cm day^{-1} in the summer months and 0.04-0.06 cm day^{-1} in winter. The shoot extended 60-70 cm yr^{-1}. Mean length and dry weight of individual shoots fluctuated throughout the two year study period but for both, values were similar at the beginning and end of the study (Fig. 1B, C). Nitrate content of the plant was always greater than 250 μmol g^{-1} dry weight over the first year of study. Usually, levels decreased with tissue in the order upper stem > leaves > lower stem (Fig. 1D). Biomass of the swards on 21 March 1991 was 477 ± 177 g dry weight m^{-2} (303 ± 19 stems m^{-2}); S:R was 33 ± 4. Soil NO_3^- levels on 28 September 1991 were 0.53 ± 0.08, 1.08 ± 0.18 and 0.28 ± 0.02 mol m^{-3} NO_3^- at 0.1, 4-5 and 15 m into the forest remnant respectively.

Specific leaf area and leaf chlorophyll and carotenoid content increased 50-75% with increased distance from 0.5 to 3.5 m into the forest remnant on 16 January 1991 (Table 1). The chlorophyll a:b ratio

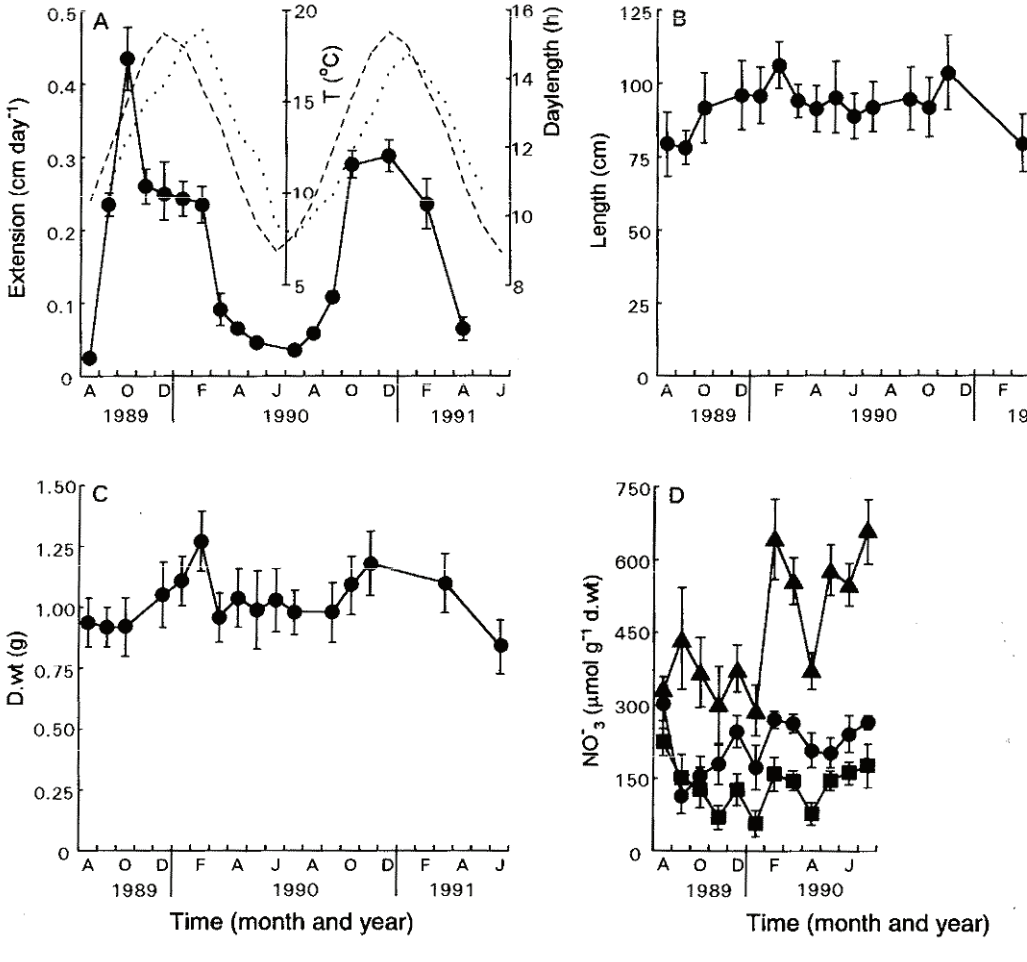

Figure 1: *Seasonal changes in extension rate, length and dry weight (d.wt) of shoots and nitrate (NO_3^-) content of leaves (●), upper stem (▲) and lower stem (■) of* Tradescantia fluminensis *in a New Zealand native forest remnant. Dotted line on (A) indicates monthly mean values for mean daily air temperature (T), dashed line indicates mean monthly daylength. Vertical bars indicate ± SE.*

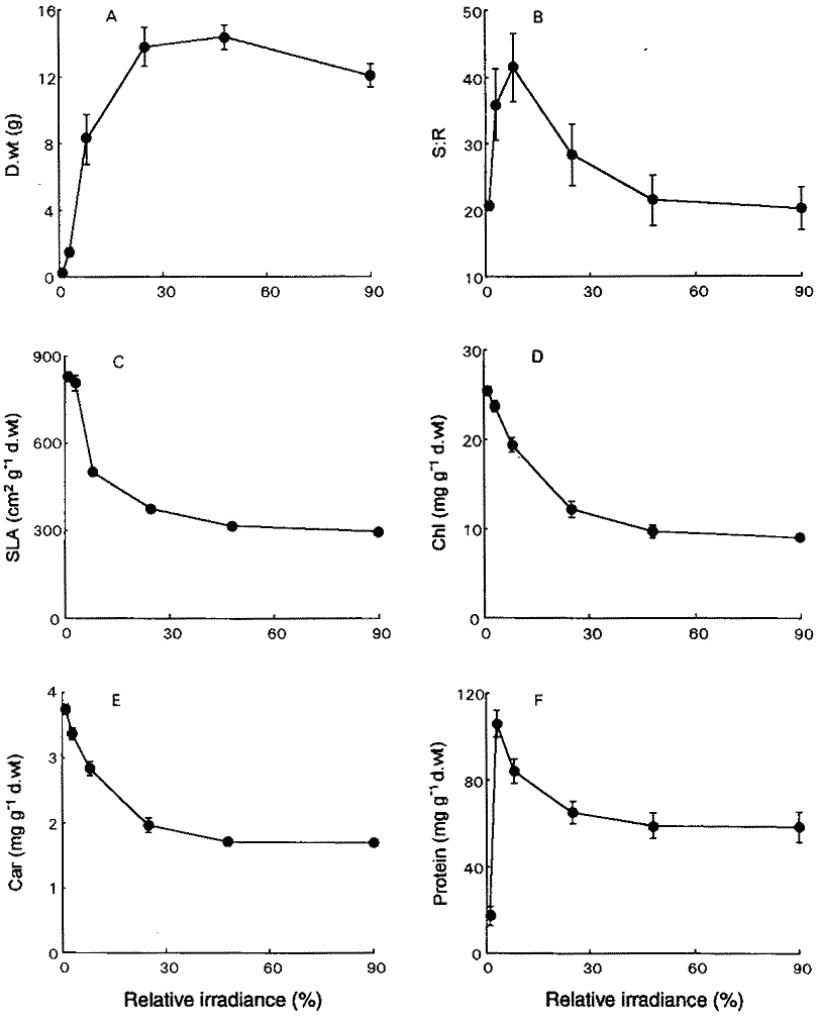

Figure 2: *Effect of irradiance level on total plant dry weight (d.wt), shoot to root dry weight ratio (S:R), specific leaf area (SLA), leaf chlorophyll content (chl), leaf carotenoid content (car) and leaf soluble protein content of* Tradescantia fluminensis *under glasshouse conditions. Vertical bars indicate ± SE.*

Table 1: *Specific leaf area (SLA), chlorophyll (chl), carotenoid (car) and soluble protein content of leaves of* Tradescantia fluminensis *sampled at different distances from the edge into a New Zealand forest remnant. Irradiance is % open ground photosynthetically active radiation. Variability is SE.*

Distance (m)	Irradiance (%)	SLA (cm^2 g^{-1} d.wt)	Chl (mg g^{-1} d.wt)	Chl a:b	Car (mg g^{-1} d.wt)	Protein (mg g^{-1} d.wt)
0.5	20	354±27	13.3±1.2	3.08±0.07	2.08±0.16	55.1±8.9
2.0	5	489±30	21.7±0.6	2.75±0.06	3.23±0.08	14.7±4.4
3.5	1	536±16	23.2±0.2	2.54±0.01	3.48±0.02	8.1±0.9

decreased steadily with increased distance into the forest remnant while the chlorophyll:carotenoid ratio was greater at 2.0 and 3.5 m (6.73 ± 0.04 and 6.68 ± 0.02 respectively) than at 0.5 m (6.37 ± 0.10). Leaf protein content decreased by 85% with increased distance into the forest remnant. Chorophyll and carotenoids per unit area changed little with distance into the forest remnant but protein per unit area decreased from 1.54 ± 0.20 g m^{-2} at 0.5 m to 0.14 ± 0.01 g m^{-2} at 3.5 m. On 18 January 1992, SLA of leaves sampled at 4-5 m into the forest remnant was 886 ± 34 cm^2 g^{-1}.

At planting in experiment 1, total plant dry weight was 0.15 ± 0.01 g. Regardless of irradiance, total plant dry weight increased during the course of experiment 1 (Fig. 2A). At harvest, total plant dry weight increased fifty fold with irradiance levels of 1 to 26%, then changed little with increased irradiance thereafter. The major changes in all parameters measured occurred over the range in which irradiance affected growth and are described in relation to decreased irradiance for ease of comparison with the field study (Table 1). The S:R increased sharply with decreased irradiance from 48 to 8% then decreased sharply with decreased irradiance 3 to 1% but was always greater than 20 (Fig. 2B). The partitioning of dry matter between leaves and stems was not significantly affected by irradiance level. Specific leaf area and leaf chlorophyll and carotenoid content approximately doubled with decreased irradiance 48 to 1% (Figs. 2C, D, E). Also, the chlorophyll:carotenoid ratio increased from 6.19 ± 0.07 to 6.77 ± 0.04 with decreased irradiance 48 to 1% but the chlorophyll

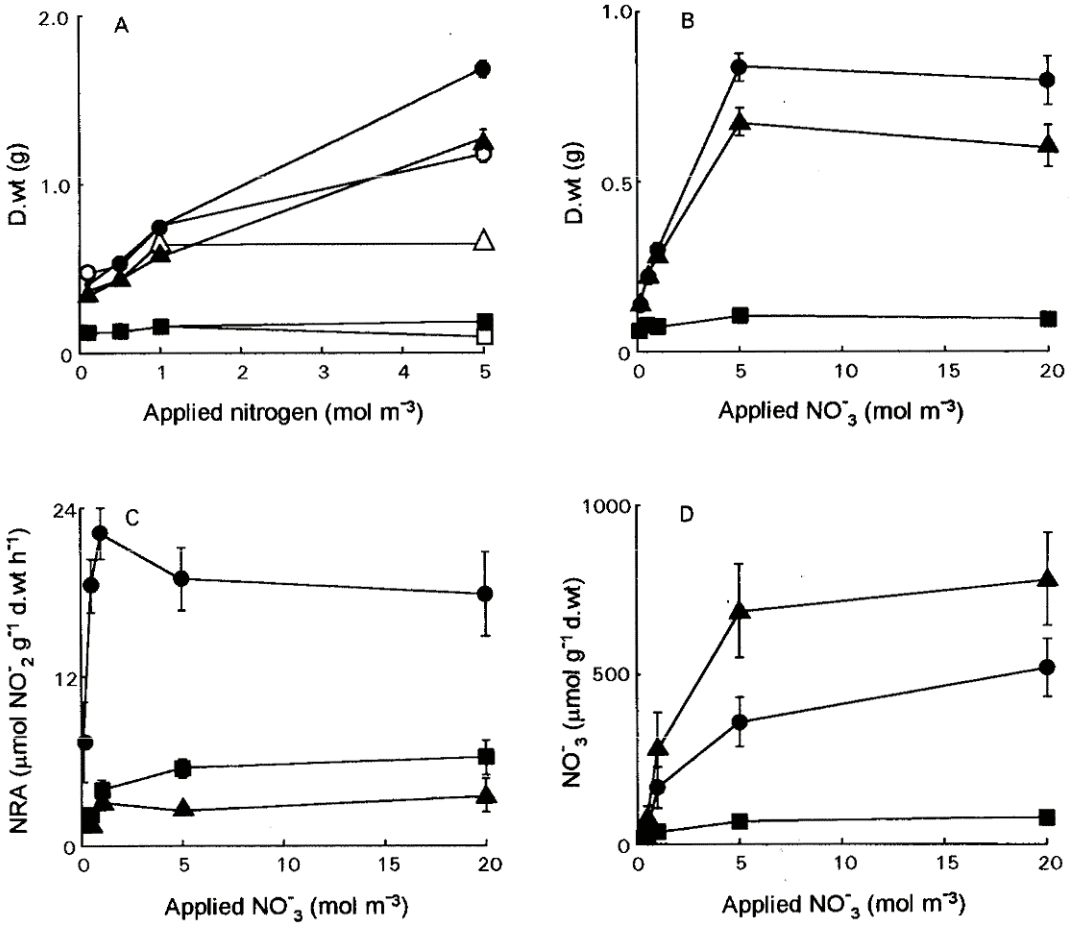

Figure 3: *Effects of different concentrations of applied ammonium (open symbols) on dry weight (d.wt) and different concentrations of applied nitrate (NO_3^-) on d.wt, nitrate reductase activity (NRA) and NO_3^-content of leaves (●), stem (▲) and root (■) of* Tradescantia fluminensis. *Vertical bars indicate ± SE.*

Table 2: *Effect of different concentrations of applied nitrate (NO_3^-) on dry weight (d.wt) and total plant NO_3^- of* Tradescantia fluminensis. *Variability is SE.*

Applied NO_3^- (mol m^{-3})	Dry weight (g)			Total plant NO_3^-(µmol)		
	Leaf	Stem	Root	Leaf	Stem	Root
Pre-Treatment						
5.0	0.32±0.03	0.25±0.02	0.07±0.01	140±17	209±15	10±2
Treatment						
0	1.24±0.09	1.48±0.09	0.19±0.03	2±1	14±5	1±0.7
0.5	1.41±0.12	1.59±0.13	0.20±0.02	6±5	42±4	4±0.8
5.0	2.18±0.07	2.17±0.12	0.27±0.02	136±29	425±51	28±3

a:b ratio was not affected by irradiance and was always within the range 2.85-3.00. Leaf protein content was similar to S:R in that it increased with decreased irradiance from 48 to 8% then decreased sharply with decreased irradiance 3 to 1% (Fig. 2F).

In experiment 2, which was carried out outdoors, effects of varying irradiance (1 to 53%) on growth, dry matter partitioning to leaf, stem and root, SLA and leaf photosynthetic pigment and protein content were as in experiment 1 except that the chlorophyll a:b ratio increased from 2.72 ± 0.02 to 3.31 ± 0.06 with increased irradiance level 1 to 53%.

In experiment 3, total plant dry weight increased with increased applied NH_4^+ or NO_3^- concentration from 0.1 to 5.0 mol m^{-3}, mainly due to increases in shoot material (Fig. 3A). At concentrations of 0.1 to 1.0 mol m^{-3}, growth was similar with NH_4^+ or NO_3^- but at 5.0 mol m^{-3}, plants supplied NO_3^- showed greater growth. Plants supplied 5 mol m^{-3} NH_4^+ had necrotic patches on their leaves. In experiment 4, total plant dry weight increased with increased applied NO_3^- from 0.1 to 5.0 mol m^{-3} (as in experiment 3) then changed little with increased NO_3^- thereafter (Fig. 3B). For all tissues of *T. fluminensis*, NRA increased with increased NO_3^- supply to 1.0 mol m^{-3} then changed little with increased NO_3^- thereafter (Fig. 3C). The greater proportion of total plant NRA occurred in the leaves. Nitrate content of all tissues increased with increased NO_3^- supply to 20 mol m^{-3} with no depression in growth (Fig. 3 B, D). In experiment 5, plants given 5.0 mol m^{-3} applied NO_3^- were either maintained on this treatment or transferred to zero or 0.5 mol m^{-3} applied NO_3^-. In all treatments, plants showed growth during the course of the experiment (Table 2). Leaf, stem and root dry weight were greater in the 5.0 mol m^{-3} NO_3^- treatment than with 0 or 0.5 mol m^{-3} NO_3^-, which were similar. In comparison with pre-treatment plants, plants maintained on 5.0 mol m^{-3} NO_3^- showed increased total plant NO_3^- while plants given 0 and 0.5 mol m^{-3} NO_3^- showed a substantial decrease in total plant NO_3^-. In all cases, total NO_3^- was greatest in the stem. Total plant NO_3^- was more than 10 times greater with 5.0 mol m^{-3} NO_3^- than with either 0 or 0.5 mol m^{-3} NO_3^-.

Discussion

Seasonal growth

At 1-5% relative irradiance level in the forest remnant, growth of *T. fluminensis* showed a seasonal pattern similar to that for monthly mean values for mean daily air temperature and day length (Fig. 1A). It is likely that these factors have an influence on growth rate. However, other factors are likely to have been involved. For example, irradiance level would have shown a similar pattern to temperature but was not measured. Nitrate appears to accumulate in *T. fluminensis* only under conditions of high NO_3^- availability and stored NO_3^- will be used if nitrogen availability is limiting growth (Fig. 3D, Table 2). As tissue NO_3^- content throughout the first year was high (Fig. 1D), it was concluded that nitrogen availability was not limiting growth. Soil NO_3^- concentration, measured on 28 September 1991, was greater at the swards' inner edge than at the streamside; therefore it is unlikely that soil nitrogen levels are limiting further encroachment of *T. fluminensis* into this remnant. Although the stem extended 60-70 cm yr^{-1}, individual shoot length and dry weight were similar at the beginning and end of the two year study period. In the swards, individual *T. fluminensis* plants consist of one major stem with little occurrence of branching. Growth occurs at the stem apex. The vertical stem grades into a horizontal stem, the end of which is decaying (Kelly and Skipworth, 1984). Over the two year study period in the field, apical growth was balanced by basal decay. It is likely that this growth strategy is a self pruning mechanism utilised to cope with high light attentuation within a stand (Andrews *et al.*, 1984a).

Sun/shade acclimation

Tradescantia fluminensis has been described as an obligate shade plant (Esler, 1988). However, in experiments 1 and 2, it was shown that *T. fluminensis* can grow at irradiance levels from 1 to 90% normal daylight over most of the year. In the glasshouse during spring/summer, total plant dry weight increased sharply with increased irradiance 1 to around 30% then changed little with increased irradiance thereafter (Fig. 2A). Thus, *T. fluminensis* is best described as a facultative shade plant. The major changes in all parameters measured in pot experiments occurred over the irradiance range which affected growth (Figs. 2A-F). Changes associated with increased distance into the forest remnant are likely to have been due to decreased irradiance level as they were similar to those obtained with decreased irradiance in experiments carried out in the glasshouse and outdoors (Table 1; Figs. 2A-F). Also, values for chlorophyll, carotenoid and protein content were similar at 3.5 m into the forest remnant and at 1% irradiance in experiments while SLA was around 900 cm^2 g^{-1} dry weight at 4-5 m into the forest remnant. Plants with these characteristics growing at 1% irradiance showed an extremely low growth rate. For example, in experiment 1, total plant dry weight increased only 65% during the twelve week period experimental period. This is strong evidence that irradiance level is the primary factor limiting the extent of colonisation of the forest remnant by *T. fluminensis* as concluded by Kelly and Skipworth (1984).

Usually, plants respond to low irradiance by increasing their capacity for light absorption per unit dry weight. This can be achieved by greater allocation of dry matter to photosynthetic tissue (Björkman, 1981; Adamson *et al*., 1991). At 1-5% relative irradiance in the field, approximately 97% of total plant dry weight of *T. fluminensis* was in the shoot. This value is extremely high in comparison with most values published for herbaceous species (e.g., Andrews *et al*., 1984b, 1992a, b; Andrews, 1993). In the glasshouse, the proportion of total plant dry weight in the shoot increased with decreased irradiance from 48 to 8% but decreased with decreased irradiance from 3 to 1% and was always greater than 95% (Fig. 2B). It is possible that the high S:R obtained for plants in the sward could have been due to root loss during sampling. However, similar results were obtained in pot experiments in which we are confident that root loss was minimal. Therefore, it is concluded that *T. fluminensis*, consistantly, has an unusually high S:R. Also, the partitioning of shoot dry matter between stem and leaves was not affected by irradiance. Therefore, increased partitioning of dry matter to photosynthetic tissue at the expense of non-photosynthetic tissue was of little importance with regard to shade acclimation of *T. fluminensis* in this study (cf. Adamson *et al*., 1991). Although a high S:R is likely to be advantageous to *T. fluminensis* under low irradiance conditions, in open ground it could lead to excess water loss and is likely to be a factor limiting this species to sheltered habitats (Wyman, 1977; Ivens and Taylor, 1985).

A second mechanism by which plants can increase their capacity for light absorption per unit dry weight is to increase SLA. For *T. fluminensis*, SLA increased from 300 to 800 cm^2 g^{-1} dry weight with decreased irradiance from 90 to 1% in the glasshouse (Fig. 2C). In the field, SLA increased from 354 to 536 cm^2 g^{-1} dry weight with increased distance 0.5 to 3.5 m into the forest remnant (Table 1) and at 4-5 m was around 900 cm^2 g^{-1} dry weight. Values of SLA > 500 cm^2 g^{-1} dry weight are extremely high (e.g., Björkman, 1981; Andrews *et al*., 1992a). The effect of increased SLA on light absorption and photosynthetic rate (CO_2 fixation) per unit area is dependent on how photosynthetic pigments, especially chlorophyll, and photosynthetic enzymes change on an area basis. In the field and in the glasshouse, chlorophyll per unit area changed little with decreased irradiance; thus the capacity for light absorption per unit area was maintained (Table 1; Fig. 2D). Changes in levels of photosynthetic enzymes per unit area can be inferred from changes in total soluble protein per unit area (Björkman, 1981; Givnish, 1988). For *T. fluminensis*, protein per unit area decreased with increased SLA (Table 1; Fig. 2C, F). Under high irradiance conditions, decreased protein per unit area is likely to lead to decreased photosynthetic rate per unit area (Field and Mooney, 1986), but under low irradiance conditions, effects on photosynthesis should be less and outweighed by the greater area per unit dry weight for light absorption due to increased SLA (Givnish, 1988). Reports on irradiance effects on protein per unit dry weight are not consistent (Björkman, 1981; Lichtenthaler, 1985; Givnish, 1988). For *T. fluminensis*, protein per unit dry weight increased with decreased irradiance 48 to 3% in the glasshouse (Fig. 2F). Increased protein per unit dry weight with decreased irradiance over this range may have been due to reduced allocation of carbon to carbohydrates which accumulate under high irradiance conditions (Lichtenthaler, 1985). However, protein per unit dry weight decreased by around 85% with decreased irradiance from 3 to 1% in the glasshouse or with increased distance from 0.5 to 3.5 m into the forest remnant (Table 1; Fig. 2F). Under conditions where irradiance level is severely restricting growth, low protein per unit dry weight

would be essential for survival as any possible advantage of maintaining high protein content would be outweighed by its high energetic costs of production and maintenance (Björkman, 1981; Andrews, 1993).

For higher plants in general, the chlorophyll a:b ratio decreases with decreased irradiance but *T. albiflora* (which is closely related to *T. fluminensis*) has been reported to be an exception (Adamson *et al*., 1991; Chow, Adamson and Anderson, 1991). As most, if not all, of the chlorophyll b in higher plants is found in light harvesting complexes (LHC), a decrease in chlorophyll a relative to chlorophyll b reflects a decrease in photosystems (PS)/reaction centres relative to LHC (Anderson, 1986; Di Paulo, Peruffo and Bassi, 1990). In the field and in pot experiments outdoors, the chlorophyll a:b for *T. fluminensis* decreased with decreased irradiance but under natural daylight in the glasshouse, values did not change with irradiance. This difference between experiments was not due to low irradiance levels in the glasshouse as 90% of photosynthetically active radiation penetrated the glass. The glasshouse glass absorbs the greater proportion of light of wavelengths 300-350 nm which are in the UV range and the possibility that UV light affects chlorophyll a:b in *T. fluminensis* is being tested. Several benefits have been proposed for increased chlorophyll b/LHC relative to chlorophyll a/PS under low irradiance conditions (Björkman, 1981; Evans, 1988). Evans (1988) argued that the reduced protein cost of complexing chlorophyll in LHC in comparison with PS/reaction centres is likely to be of greatest importance. Findings for *T. fluminensis* and *T. albiflora* show that changes in chlorophyll a:b are not essential for survival under a wide range of irradiance levels. Although irradiance effects on chlorophyll a:b were not consistent across experiments, the chlorophyll:carotenoid increased with decreased irradiance under all conditions (Table 1; Fig. 2D, E). Carotenoids are involved in light harvesting but they also have a protective function in that they dissipate excess light energy (Rau, 1988; Demmig-Adams *et al*., 1989). The likelihood of photodamage will decrease with decreased irradiance and thus decreased investment in carotenoids relative to chlorophyll may be of benefit to the plant. However, in view of the magnitude of the change in protein per unit dry weight in comparison with all other parameters measured and the likelihood that protein production and maintenance is energetically expensive relative to overall plant metabolism, it is proposed that a decreased protein content linked to an efficient system of internal recycling of nutrients (Table 2) is the primary mechanism of acclimation of *T. fluminensis* to low irradiance.

Nitrogen nutrition

Total plant dry weight for *T. fluminensis* increased with increased applied NO_3^- from 0.1 to 5.0 mol m^{-3} then changed little with increased NO_3^- thereafter (Fig. 3B). This growth response to NO_3^- is similar to that shown by a range of annual crops and weeds grown under similar conditions (e.g., Andrews *et al*., 1984b, 1992b). Growth was greatest at a NO_3^- concentration which, under non-agricultural conditions, is likely to occur only in disturbed soils. At concentrations of 0.1 to 1.0 mol m^{-3}, growth was similar with NH_4^+ or NO_3^- but at 5.0 mol m^{-3}, plants supplied NO_3^- showed greater growth (Fig. 3A). Plants supplied 5.0 mol m^{-3} NH_4^+ had necrotic patches on their leaves. Similar results have been obtained for a wide range of herbaceous species (Maynard and Barker, 1969; Raven and Smith, 1976; Mehrer and Mohr, 1989). In longer term experiments, plants supplied 1 mol m^{-3} NH_4^+ also showed leaf damage. Thus, *T. fluminensis* shows no unusual ability to utilise NH_4^+. Data in the literature are consistent in that the root is the main site of NH_4^+ assimilation in higher plants (Andrews, 1993). If NH_4^+ is translocated to the shoot it can cause damage (Raven and Smith, 1976). In comparison with many other herbaceous species, *T. fluminensis* has a very small root system relative to shoot system (Fig. 3B); this would limit its capacity for NH_4^+ assimilation. These findings are consistent with observations that *T. fluminensis* shows vigorous growth in fertile sites and tends to invade disturbed remnants where soil NO_3^- levels are likely to be high (Esler, 1962; Timmins and Williams, 1987; Ogle and Lovelock, 1989).

Nitrate reductase is the first enzyme in the pathway of NO_3^- assimilation. It is a substrate induced enzyme and thus NRA usually reflects NO_3^- assimilation in the plant. Plant species which respond to high soil NO_3^- concentrations are capable of high rates of NO_3^- assimilation, especially in the shoot. This is reflected by high shoot NRA (Andrews, 1986; Lee *et al*., 1986; Stewart *et al*., 1988). For all tissues of *T. fluminensis*, NRA increased with increased NO_3^- supply to 1.0 mol m^{-3} then changed little with increased NO_3^- thereafter (Fig. 3C). The greater proportion of total plant NRA occurred in the leaves. The level of NRA in leaves was within the range previously reported for fast growing crop and weed species using similar assays (e.g., Andrews *et al*., 1984b, 1992b). This explains in part how *T. fluminensis* can respond to high NO_3^- concentrations. Some species which respond to high external NO_3^- concentrations can also accumulate high concentrations of NO_3^-, especially in shoot tissue, with no depression in growth (Lee *et al*., 1986). This NO_3^- can be utilised when nitrogen

supply becomes limiting. For *T. fluminensis*, NO_3^- content of all tissues increased with increased NO_3^- supply from 1 to 20 mol m^{-3} without a decrease in plant dry weight (Fig. 3B, D). Nitrate content was substantially greater in shoot than in root tissue. In experiment 3, it was shown that *T. fluminensis* will utilise this NO_3^- when nitrogen becomes limiting to growth as plants showed a substantial increase in dry weight after transfer from 5.0 to 0.5 or 0 mol m^{-3} NO_3^- and this increase was associated with a substantial decrease in stored NO_3^- (Table 2). It is concluded therefore that *T. fluminensis* shows characteristics of nitrogen nutrition typical of species capable of rapid growth.

Proposed 'invasion strategy' of *T. flumimensis* into New Zealand forest remnants.

Tradescantia fluminensis shows characteristics of nitrogen nutrition typical of species capable of rapid growth (Table 2; Fig. 3). However, it also shows many features atypical of species capable of rapid growth such as a complete reliance on vegetative reproduction (Kelly and Skipworth, 1984), the ability to acclimate to very low irradiance levels (Table 1; Fig 2) and longevity associated with low growth rate (Fig. 1). It is proposed that it is the combination of these features which accounts for the success of *T. fluminensis* in New Zealand forest remnants.

Breaks in the forest remnant canopy (e.g., through wind damage or natural death of canopy trees), accompanied by disturbance of the ground cover (e.g., through uprooting of trees or animal browsing) result in increased forest floor irradiance and soil NO_3^- levels. This enables *T. fluminensis* already present on the remnant edge to rapidly colonise the disturbed sites, and while doing so, accumulate a substantial store of nitrogen and other nutrients in tissues. If the canopy break is then closed by the surrounding trees and the remnant returns to a low internal irradiance/low nutrient state, *T. fluminensis* can successfully acclimate to the decreasing irradiance and utilise its store of accumulated nutrients. If no further disturbance occurs, the established sward will then reach an equilibrium biomass, turning over slowly as production of new tissue at the shoot apex is balanced by death and decay of old tissue at the shoot base. The finely reticulated root system penetrates the leaf-litter and humus layers immediately below the sward. A large part of these layers is made up of decomposing *T. fluminensis* material; thus, the sward as a whole is likely to possess an efficient system of internal recycling of nutrients. Efficient recycling of nutrients within the sward coupled with the low natural input of nutrients into the system will allow *T. fluminensis* to occupy a site for an indeterminate period.

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