Effects of Light Intensity and Defoliation on the Receptiveness for Primary Induction in Festuca Pratensis Huds

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ABSTRACT
Seedlings of *Festuca pratensis Huds*. (cv. Salten) were raised at three different light intensities (141, 85 or 28 (mol $m^{-2}s^{-1}$) for 7 weeks after emergence and then either left uncut or defoliated 40 or 80% of total leaf area, before transfer to primary induction (6°C, natural short days) for 12, 15 or 18 weeks. Percentage of heading plants was more affected by the duration of primary induction than by light intensity and defoliation prior to induction. The results lend no support to the existence of a juvenile stage in seedlings of *Festuca pratensis*. Defoliation had less influence on the number of panicles per plant than light intensity and, in particular, the duration of primary induction. An additional tagging experiment revealed that even some tillers developed after primary induction became reproductive.

KEYWORDS
Defoliation, *Festuca pratensis*, flowering, induction, juvenility, light intensity, meadow fescue

INTRODUCTION
Seedlings and tillers of many temperate grasses must pass through a juvenile stage before they can be induced to flower. The juvenile stage has often been described by leaf number and leaf area (e.g. Bean, 1970) or by accumulation of carbohydrates within the plant (Wellensiek and Higazy, 1961).

The objective of the present research was to obtain some more information about the juvenile stage in *Festuca pratensis* and to determine how different intensities of light and degrees of defoliation prior to primary induction influence plant growth during induction and subsequent flowering.

MATERIALS AND METHODS
The experiment was carried out at the NCRI, division Landvik and the Ås phytotron during August 1994 through April 1995. Seedlings of 'Salten' (origin 67°N) were raised at three different light intensities (141 (L_1), 85 (L_0.6 ; 60% of L_1) or 28 ($L_{0.2}$; 20% of L_1) µmol $m^{-2}s^{-1}$, 18-20°C) for 7 weeks after emergence. Before transfer to primary induction, plants from each light intensity were divided into three equal groups, which were either left uncut (D_0) or defoliated 40 ($D_{0.4}$) or 80 ($D_{0.8}$) per cent of total leaf laminae.

Primary induction was accomplished in a phytotron compartment (6°C) with natural daylight supplemented with 115 (µmol $m^{-2}s^{-1}$ for 8 hr per day. After 0, 12 and 18 weeks of primary induction 8 plants from each combination of light intensity and defoliation treatment were destructively sampled and tiller number, leaf area, tiller base diameter and carbohydrate content were measured.

Plants not subjected to destructive sampling were transferred to secondary induction at 15°C and continuous light (200 (µmol $m^{-2}s^{-1}$) after 12, 15 or 18 weeks of primary induction. (3 light intensities * 3 defoliation treatments * 8 replicates = 72 plants per length of primary induction treatment.) Per cent flowering plants and the number of panicles per plant were used as the main criteria for flowering, while the number of days to heading of the first panicle was used as a criterion for the rate of flower development.

An additional experiment in which newly emerged tillers on 15 plants from each of the three light intensities (5 from each defoliation treatment) were tagged at the start of, midway through and at the end of a 12 weeks treatment, was carried out simultaneously with the main experiment.

RESULTS
Plant status prior to primary induction. At the start of primary induction, plants grown at the highest light intensity (L_1) had approximately 35 and 85 per cent more tillers than plants grown at medium ($L_{0.6}$) or low irradiance ($L_{0.2}$), respectively (Fig.1). While an increase in light intensity from $L_{0.2}$ to $L_{0.6}$ dramatically increased leaf number and leaf area per plant, differences between $L_{0.6}$- and L_1-plants were generally less conspicuous. The average tiller number for $L_{0.2}$-, $L_{0.6}$- and L_1-plants at the start of induction was 4.3, 16.9 and 26.0 and the leaf area was 21.1, 103.6 and 122.8, respectively. The concentration of water soluble carbohydrates also increased, both in shoots and roots, with increasing light intensity (data not shown).

Plant growth during primary induction. Plants which had received low irradiance (L0.2) prior to induction continued to have the lowest tiller number per plant throughout the induction treatment. The lowest proportion of small tillers (< 2 mm) was always found in L0.2-plants (Fig. 1). Defoliation of 40% of leaf area before induction reduced the number of big tillers (> 2 mm) after 12 and 18 weeks of primary induction (Fig. 1).

Flowering. Per cent heading plants was lower after 12 than after 18 weeks of induction (Table 1). The number of panicles also increased with increasing duration of primary induction. Panicle production was lowest in plants which had received low light intensity (L0.2) and/or were defoliated prior to induction.

Prolonged duration of primary induction from 12 to 18 weeks decreased the time to heading with approximately 6 days (Table 1). The shortest period to heading was usually recorded in the smallest $L_{0.2}$-plants.

Tagging experiment. Approximately 51, 22 and 3 per cent of reproductive tillers had emerged before, during or after primary induction, respectively. Tillers emerging prior to induction headed, on average, 3 days earlier than tillers emerging during and 8 days earlier than tillers emerging after induction.

DISCUSSION
Bean (1970) suggested that seedlings of *Festuca pratensis* required a leaf area of at least 25 cm^2 leaf area in order to respond to inductive stimuli. This is in clear contrast to the present experiment in which per cent heading plants were hardly affected by either light intensity or defoliation prior to primary induction (Table 1). In accordance with Havstad (1996), the duration of primary induction seems to be more critical than plant age or plant size at the onset of induction. These results lend no support to the existence of a juvenile stage in seedlings of *Festuca pratensis*.

Apart from the increase in per cent heading plants, longer exposure to inductive conditions also enabled more tillers to enter a generative development (Table 1). A high proportion of big tillers (> 2 mm) at the end of primary induction explains the relatively high panicle production in uncut plants and in plants receiving high light intensity ($L_{0.6}$- and L_1-plants) during plant raising (Table 1; cf. Fig.1). However,

as a main effect, defoliation had less effect on panicle production than light intensity prior to induction and, in particular, the duration of the primary induction treatment.

The tagging experiment revealed that a few tillers which emerged after the primary induction treatment became reproductive. Generative development of tillers unexposed to induction was also observed by Hare (1993, 1994) in *Festuca arundinacea*. Since *Festuca pratensis*, has an extreme induction requirement (16-20 weeks at 6°C in 10 h photoperiod, Heide, 1988), these tillers must have been induced while still in the leaf sheath or as very young buds at the base of the parent shoot (Kleinendorst, 1974). Alternatively, transmission of flowering stimuli from mother to daughter tillers, as further discussed by Havstad (1996), may have occurred. These results support earlier suggestions (Havstad, 1996) that tillers of *Festuca pratensis* lack or have an extremely short juvenile stage. In any case, juvenility in seedlings or tillers of *Festuca pratensis* can hardly be related to leaf area or carbohydrate status at the onset of primary induction.

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Table 1

Main effects of length of primary induction (12, 15 and 18 weeks), light intensities (28 ($L_{0.2}$), 85 ($L_{0.6}$) and 141 (L_1) (µmol $m^{-2}s^{-1}$) and defoliation (uncut (D_0), cut 40 % of D_1 ($D_{0.4}$) and cut 80 per cent of D_1 ($D_{0.8}$)) prior to induction on the percentage of heading plants, panicles per plant and days to heading. Means of 72 plants per treatment. Main effects of length of primary induction (12, 15 and 18 weeks), light intensities (28 ($L_{0.2}$), 85 ($L_{0.6}$) and 141 (L_1) (µmol $m^{-2}s^{-1}$) and defoliation (uncut (D_0), cut 40 % of D_1 ($D_{0.4}$) and cut 80 per cent of D_1 ($D_{0.8}$)) prior to induction on the percentage of heading plants, panicles per plant and days to heading. Means of 72 plants per treatment.

	Duration of primary induction (weeks)			Light intensity			Defoliation			
	12	15	18	$L_{0.2}$	$L_{0.6}$	L_1	$D_{0.8}$	$D_{0.4}$	D_0	$LSD_{0.05}$
% heading plants	86	93	97	89	93	94	94	93	89	8.7
Panicles per plant	6.2	7.9	13.0	6.4	10.4	10.1	8.4	8.6	10.1	1.4
Days to heading[1])	39	34	33	34	36	35	35	35	35	1.7

1) Days to heading after transfer to secondary induction

Figure 1

Increase in total tiller number per plant as affected by a) light intensity (28 (L 0.2), 85 (L 0.6) and 141 (L1) (mol m-2s-1) and b) defoliation (uncut (D0), cut 40 % of D1 (D0.4) and cut 80 per cent of D1 (D0.8)) prior to primary induction. Bars represent 1 SE for total tiller number.