Flowering Dynamics in Monoecious and Dioecious Hemp Genotypes

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ABSTRACT. Flowering is a crucial phase in hemp cultivation. It influences both stem and seed yield. A uniform and short flowering duration

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in hemp is desirable, because it favors uniform crop development. Moreover, flowering is often taken as a reference point for harvesting, and very long durations of flowering might mislead the operator in judging the proper time for mowing. In this article, a large dataset of flowering time and duration for different monoecious and dioecious varieties was studied and the effect of sowing time and genotype on flowering duration is discussed. Minimal flowering duration was observed when the time from emergence to flowering was short. This, was related however, to low yields. Dynamics of flowering was accurately described by a bi-logistic curve that indicates the presence of two underlying logistic processes.

KEYWORDS. Hemp, *Cannabis sativa*, flowering, bi-logistic, genotype

INTRODUCTION

Flowering is generally considered a crucial moment for the determination of hemp yield both in terms of quantity (van der Werf, Haasken, and Wijlhuizen, 1994; van der Werf, Mathijssen, and Haverkort, 1996; Struik et al., 2000) and quality (Keller, Leupin, Mediavilla, and Wintermantel, 2001; Mediavilla, Leupin, and Keller, 2001; Amaducci, Müssig, Zatta, and Pelatti, 2005). When hemp cultivation is not intended for seed production, harvesting is normally carried out at flowering (Venturi and Amaducci, 1999). Prediction of flowering in a given environment and for a given genotype would therefore be useful to select varieties adapted to specific conditions, and to plan and organize sowing and harvesting. Two phenological models for hemp are available (Lisson, Mendham, and Carberry, 2000; Amaducci, Colauzzi, Bellocchi, and Venturi, 2007), that aim at predicting when 50% of flowering occurs, i.e., when 50% of plants have visible pedicillate male or stigmatic female flower structures. Limited information is provided on the dynamics of the process and on the time elapsed from the onset to the end of flowering. In Amaducci et al. (2007), flowering data from a large data set were presented and among the combinations of genotype and sowing date studied a large variation in the duration from the appearance of the first flower to the last one (from 4 to 99 days) was apparent, but it was not discussed. At flowering, stems normally cease their elongation (Sankari and Mela, 1998; De Meijer and Keizer, 1994) and as a consequence, a large variation in flowering time decreases crop homogeneity, which is normally already low in hemp (Sankari and Mela, 1998; van der Werf et al., 1994). An improved crop homogeneity is desired, however, to facilitate the mechanization of harvesting and industrial processing (Amaducci, 2003; Venturi and Amaducci, 2004; Ranalli and Venturi, 2004; Mediavilla et al., 2001). Moreover, harvesting time is usually set at flowering, and as a consequence long flowering duration and uneven flowering times can mislead farmers and researchers on the proper moment to mow the crop (Amaducci et al., submitted). The objective of this article is to analyze a selection of the data presented by Amaducci et al. (2008) and to discuss the dynamics of flowering in monoecious and dioecious hemp genotypes.

MATERIAL AND METHODS

Phenological Data

Phenological datasets were collected in the years 1997–1998 and 2003–2005 from separate field trials (Table 1), conducted as part of both national (Ranalli, 2002) and international (Cromack, 1998; Amaducci, 2003) studies. All trials were carried out at Cadriano Experimental Station of the University of Bologna, Italy (latitude: 44° 33′ north; longitude: 11° 21′ east; altitude: 32 m a.s.l.).

The crops were planted both before and after the summer solstice, thus encountering either increasing or decreasing day lengths. The minimum sub-sub plot size was 50 m^2. Details on the field trials are provided in Amaducci, Errani, and Venturi (1998, 2002). De Meijer (1995) reviews the origin, breeding history, registration, availability, and agronomic features of the cultivars used in this study.

Counts of flowering plants were carried out on 20 to 50 plants per plot. A minimum of one count per week was made, while frequency was increased near and during flowering up to a count every 2 days. For both monoecious and dioecious genotypes, a plant was recorded as flowering when at least one anther and/or stigma was visible. Flowering percentage corresponds to the percentage of flowering plants. Flowering duration was computed as the difference between the date of the last and the first flowering plant in the same plot.

Flowering duration differed between trials (up to 99 days from the appearance of the first to the last flower). As discussed in Amaducci et al. (2007), the date when 50% of plants had visible flowers was defined as "flowering date." In 2005, the flowering observations of dioecious

TABLE 1. Experimental years, cultivars, and sowing dates for field trials carried out at Cadriano (BO, Italy) and used for collecting information on hemp phenology

Years	Cultivars	Sowing Dates
1997	Carmagnola	29/4
	Felina 34	29/4
	Fibranova	29/4
	Futura 77	28/3–18/4–29/4–6/5–4/6–24/6–16/7
1998	Carmagnola	2,9,23,30/3–2,6,14,20/4–11/5–4/6–30/6–4/8
	Felina 34	2,9,23,30/3–2,6,14,20/4–11/5–4/6–30/6–4/8
	Fibranova	2,9,23,30/3–2,6,14,20/4–11/5–4/6–30/6–4/8
	Futura 77	2,9,23,30/3–2,6,14,20/4–11/5–4/6–30/6–4/8
2003	Carmagnola	16/4–29/4–12/5–28/5–1/7
	Felina 34	16/4–29/4–12/5–28/5–1/7
	Fibranova	16/4–29/4–12/5–28/5–1/7
	Futura 75	16/4–29/4–12/5–28/5–1/7
2004	Carmagnola	23/3–1/4–6/4–23/4–7/5–9/6–20/7
	Felina 34	23/3–1/4–6/4–23/4–7/5–9/6–20/7
	Fibranova	23/3–1/4–6/4–23/4–7/5–9/6–20/7
	Futura 75	23/3–1/4–6/4–23/4–7/5–9/6–20/7
	Tiborszallasi	23/3–1/4–6/4–23/4–7/5–9/6–20/7
2005	Futura 75	6/4–22/4–10/5
	Carmagnola	6/4–22/4–10/5
	Fibranova	6/4–22/4–10/5

genotypes (Fibranova and Carmagnola) were carried out separately for male and female plants; in all other years these observations were pooled.

Logistic and Bi-Logistic Equation to Analyze Flowering Dynamics

The dynamics of flowering of both male and female plants (dioecious plants) can be described by the following equation:

$$yc = \frac{a_1}{1 + \exp(-b_1(t - c_1))}$$

where ***yc*** is the estimated percentage of flowering plants (upper limit); ***t*** is the independent variable, time, expressed as day of year (DOY); $\boldsymbol{a_1}$ is the maximum percentage of flowering; $\boldsymbol{b_1}$ regulates the shape of the curve (the speed at which the maximum value is reached); c_1 represents the abscissa for the point of inflection of the curve (DOY) when $t = c_1$.

Estimation of parameters a_1, b_1, and c_1 was carried out using the fitting procedure “LSQCurveFit” available in the MATLAB environment. For the procedure, the fitting of two logistic curves was adopted—one for male data and one for female data. Curves were then added together and plotted to analyze the overall dynamics of flowering of monoecious plants.

For dioecious plants that, in most cases, show a bi-phasic flowering dynamic, data were fitted using a bi-logistic equation:

$$yc = \frac{a_1}{1+\exp(-b_1(t-c_1))} + \frac{a_2}{1+\exp(-b_2(t-c_2))}.$$

The meaning of the parameters of the above equation is the same as that described for the logistic equation with the difference that it shows two inflexion points, respectively, when $t = c_1$ and $t = c_2$.

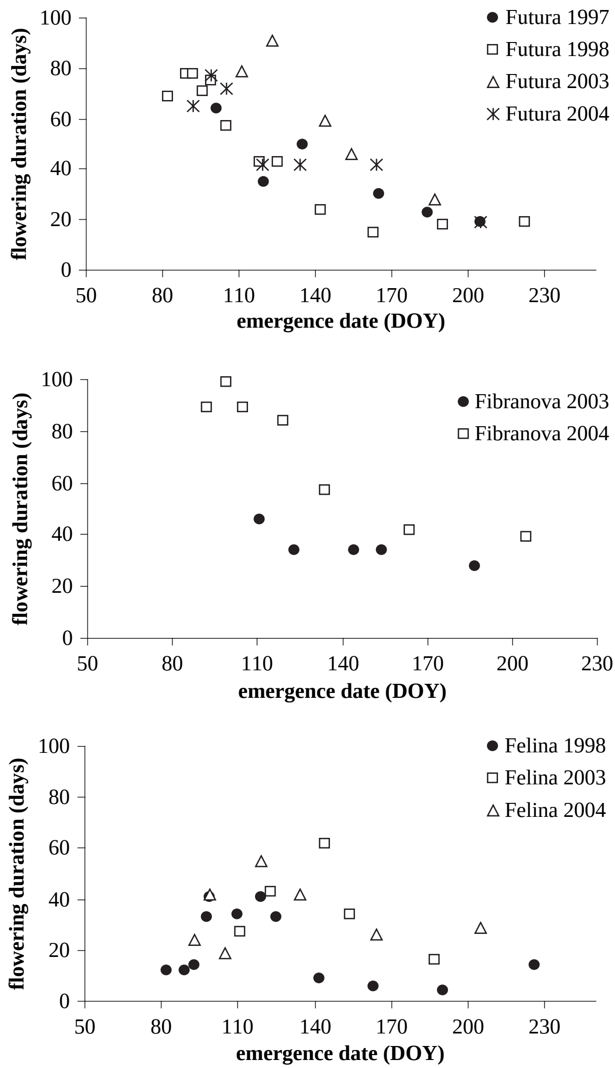
RESULTS

In Figure 1, the number of days from onset to the end of flowering as a function of day of emergence are presented for all monoecious and dioecious genotypes. A large difference in flowering duration among genotypes is evident, as is also true for individual genotypes sown at different times. The shortest flowering duration observed was 4 days, for the cultivar Felina sown on 1 July 1997; the longest flowering duration was for Fibranova after the second sowing in 2004 (99 days).

In most cases, postponing sowing time, and thus emergence time, resulted in shorter flowering durations. The exception to this was observed in Felina which had a peculiar flowering pattern. Flowering duration was relatively short after the earliest sowing times; it then increased, reaching its maximum (40–50 days) when emergence was within the first half of May, and decreased after subsequent sowings.

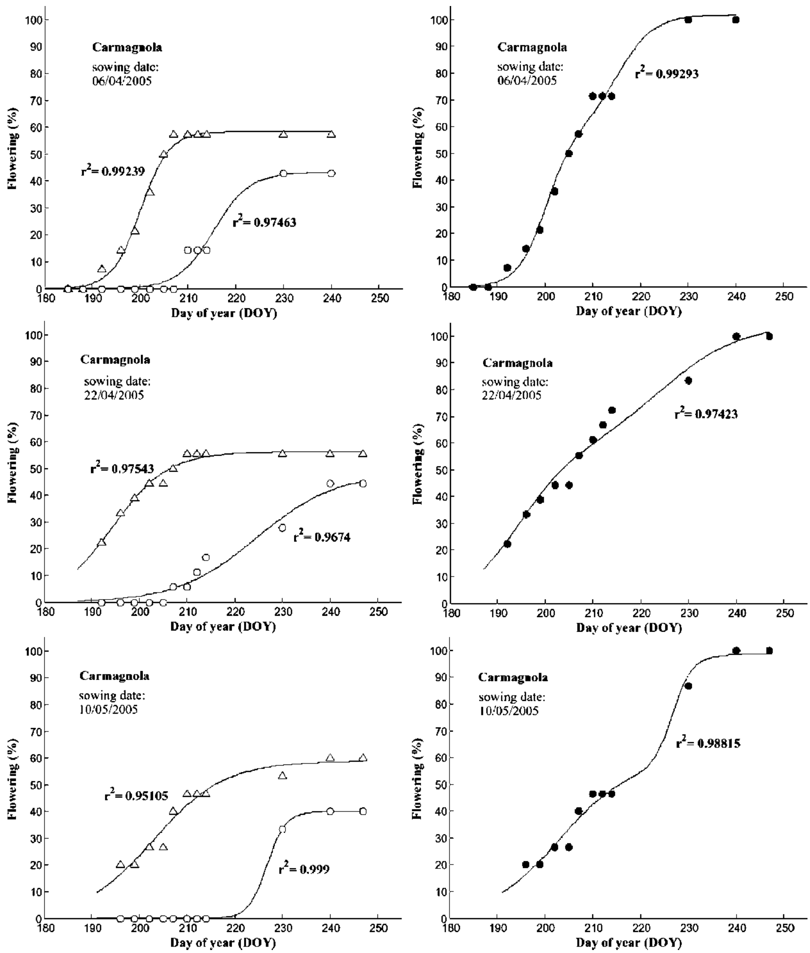
Data on flowering dynamics for the monoecious Futura (in 1997 and 2005) and the dioecious Carmagnola and Fibranova (in 2005), are presented together with fitted logistic curves in Figures 2 to 5. Values of the curve parameters and the coefficient of determination (r^2) are presented in Table 2. The flowering data of the two dioecious genotypes are presented both separately for the male and female plants (left panels of Figures 2 and 3) and as the sum of plants of both sexes (right panels of Figures 2 and 3). It

FIGURE 1. Flowering duration (number of days between the beginning and the end of flowering) for hemp cultivars Futura, Fibranova, and Felina observed in the years 1997–1998 and 2003–2004.



is clear that the logistic curve fitted the female flowering data well and the bi-logistic function (sum of the two logistic ones) accurately described the overall flowering data. The male flowering data are also well described by

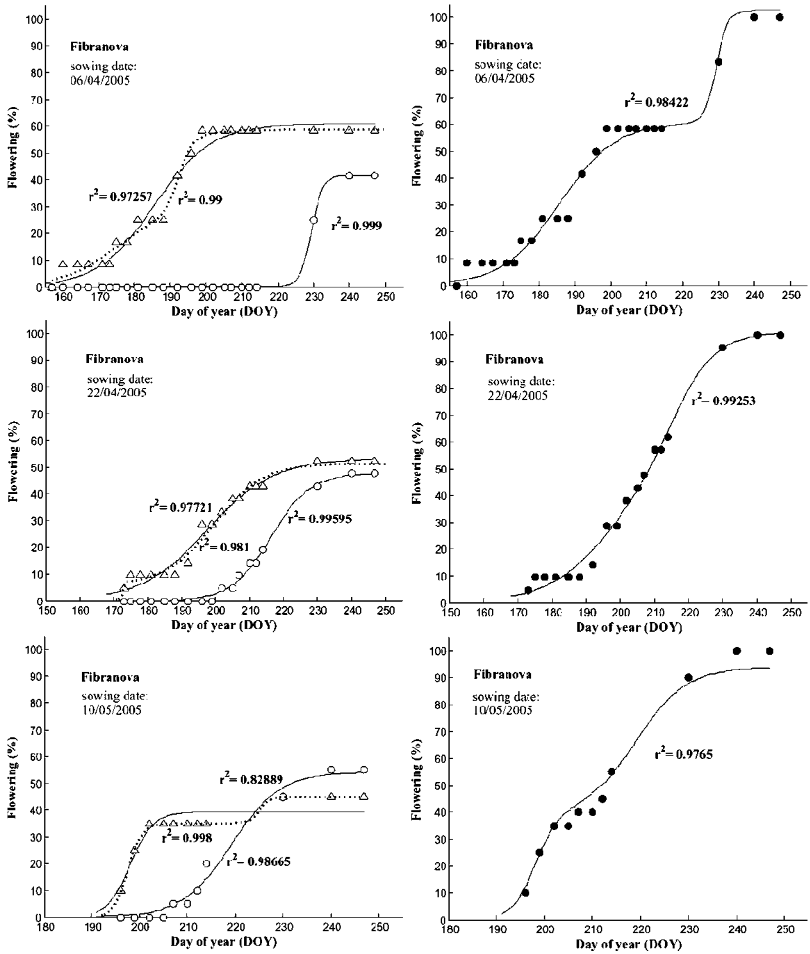
FIGURE 2. Observed (symbols) and computed (continuous line) flowering data from 2005 for cultivar Carmagnola obtained with successive planting dates. The graphs on the left with empty symbols (triangles and circles) represent, respectively, data of the male and female populations. Full circles on the right-hand-side of the figure represent pooled data.



the logistic function, though in Fibranova the fitting worsens at later sowing times and flowering data were better described by a bi-logistic curve.

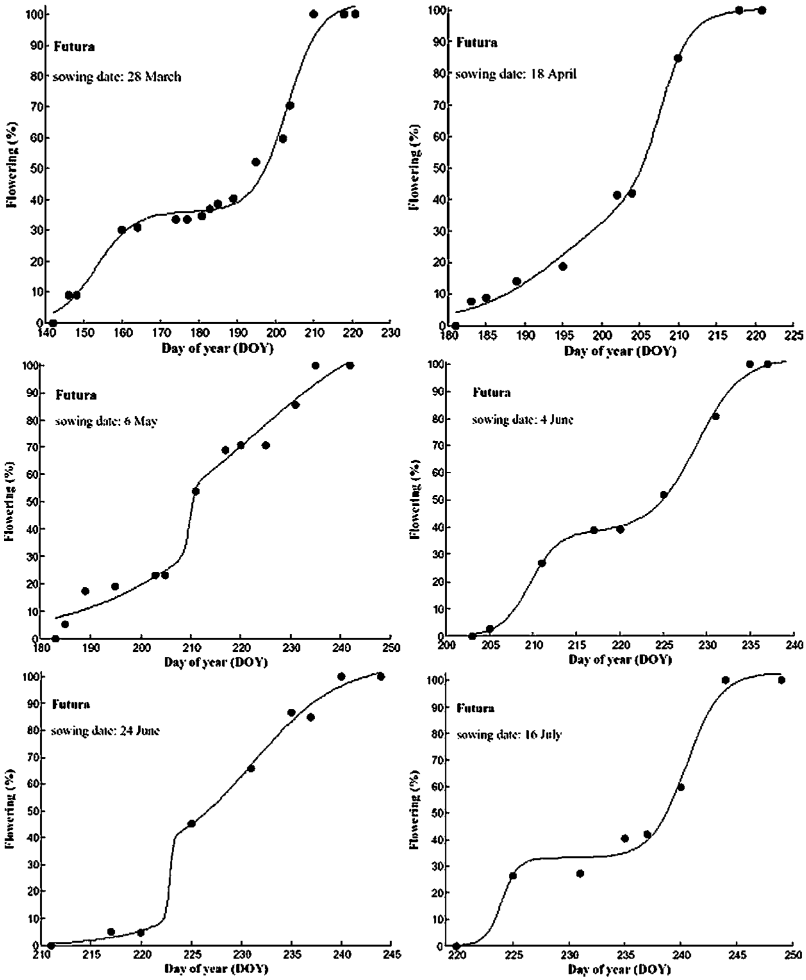
Both dioecious genotypes revealed their proterandry. In Carmagnola, the male plants anticipated female flowering by approximately 20 days. In Fibranova, proterandry was more pronounced

FIGURE 3. Observed (symbols) and computed (continuous line) flowering data from 2005 for cultivar Fibranova obtained with successive planting dates. The graphs on the left with empty symbols (triangles and circles) represent, respectively, data of the male and female populations. Full circles on the right-hand-side of the figure represent pooled data. The dashed lines in the left graphs are bi-logistic curves fitted to the male plants (see text for explanation).



with earlier sowings: the first male flower anticipated females by 60 days in the first sowing, 30 days in the second, and 15 days in the third.

FIGURE 4. Observed (symbols) and computed (continuous line) flowering data from 1997 for cultivar Futura obtained with six successive planting dates.



In the case of the monoecious Futura, data were only fitted with the bi-logistic curve, that also in this case proved to be valuable in describing the dynamics of flowering.

FIGURE 5. Observed (symbols) and computed (continuous line) flowering data from 2005 for cultivar Futura obtained with three successive planting dates.

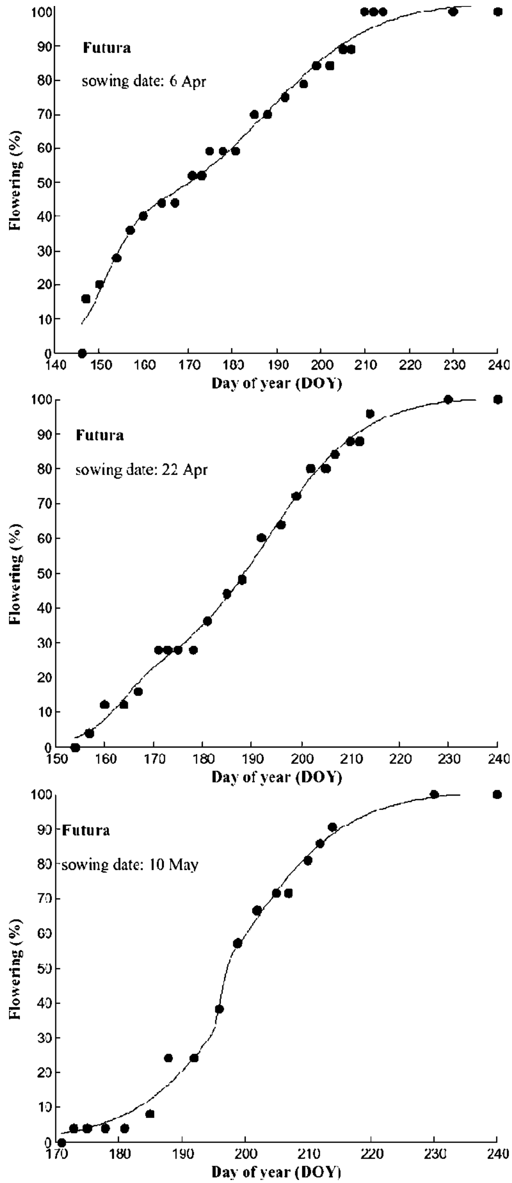


TABLE 2. Parameters of the bilogistic equation estimated for different cultivars and years and flowering duration computed as the difference between the date of the last and the first flowering plant

Cultivar	Year	Sowing Date	Parameters of the Bilogistic Equation							
			a_1	b_1	c_1	a_2	b_2	c_2	r^2	Duration (Days)
Futura	1997	28/3	36.1	0.2	153.31	67.51	0.23	203.25	0.987	64
		18/4	47.68	0.16	195.72	53.49	0.54	207.74	0.995	35
		6/5	23.77	1.87	209.87	99.94	0.06	222.21	0.984	50
		4/6	45.56	0.38	210.71	54.44	3.26	230.81	0.998	30
		24/6	30.14	6.19	222.83	75.06	0.23	231.17	0.996	23
		16/7	33.1	1.35	224.01	69.85	0.64	240.51	0.989	19
	2005	6/4	37.79	0.28	151.51	65.64	0.08	187.94	0.987	63
		22/4	18.12	0.28	163.23	82.92	0.1	193.15	0.995	57
		10/5	14.6	2.52	196.33	86.37	0.12	199.6	0.994	41
			Male			Female				Duration (Days)
			a_1	b_1	c_1	a_1	b_1	c_1	r^2	
Carmagnola	2005	6/4	58.5	0.33	200.13	43.22	0.27	215.44	0.992	38
		22/4	56.36	0.17	194.35	48.2	0.12	224.58	0.974	52
		10/5	58.87	0.13	203.02	40.04	0.5	226.82	0.988	44
Fibranova	2005	6/4	60.95	0.13	185.62	41.71	0.63	229.36	0.984	83
		22/4	53.32	0.1	197.65	47.82	0.17	216.3	0.992	67
		10/5	42.03	0.2	198.33	54.37	0.19	219.17	0.976	44

DISCUSSION

A short flowering duration in hemp is desirable because it favors uniform crop development (Venturi, 1969). Moreover, flowering is often taken as a reference point for harvesting and very wide periods of flowering might mislead the operator in judging the proper time for mowing. In these experiments, we observed a large variation in flowering duration, that was influenced by time of emergence in all genotypes (Figure 1). Amaducci et al. (2007) showed that in dioecious varieties (i.e., Carmagnola and Fibranova) time from emergence to 50% flowering decreased when postponing sowing, because of the long basic vegetative phase (BVP) and the high sensitivity to the photo period. Due to this combination of parameters, crops sown earlier at low temperatures have a long BVP that ends when the photo period is long and not favorable for flowering. On the contrary, when sown later, BVP is completed sooner and flowering induction is favored by a progressively shorter photo period. In monoecious varieties, in particular Felina, but also Futura, a shorter BVP and a lower sensitivity to the photo period results in early flowering in early sowings because BVP is completed when the photo period is still short and inductive. With later sowings, 50% flowering is progressively delayed (because of increasing photo periods) until a maximum time from emergence to flowering is reached; thereafter, the time to flowering decreases again when the photo period shortens after the summer solstice. Flowering duration, as reported in this article, seemed to follow the same pattern: it decreased when emergence was delayed in the dioecious varieties, while it increased until a maximum duration for plants emerged in the beginning of May and it progressively decreased for later emergences in the monoecious Felina. In Futura, a tendency to increase the flowering duration was only observed between the first and the second crop emerged in 1998, 2003, and 2004 (Figure 1). This confirms the intermediate behavior of Futura in terms of cycle length (Amaducci et al., 2007).

The similarity between flowering duration and time to 50% flowering as influenced by sowing time suggests that the same underlying mechanism controls both parameters.

Carberry et al. (1992) found that in a kenaf variety cultivated outdoors in conditions of increasing photo periods, which completed the BVP close to the critical photo period, a number of plants were induced and flowered soon after BVP completion, while the rest of the plants kept vegetating and flowered only when the natural photo period became shorter than the critical one. This indicates that within the same genotype, two groups of individuals could be segregated on the base of the flowering time. Carberry et al. (1992) did not speculate on the reasons for this segregation, but it is possible to assume that the earlier plants had a slightly lower critical photo period or shorter BVP. As hemp, kenaf is a short-day plant, but with a qualitative response to photo period. This could explain why hemp flowering responses to changing photo periods were continuous and not determinate as in kenaf.

The goodness of the bi-logistic function to fit the flowering dynamic in both monoecious and dioecious genotypes indicates the presence of two underlying logistic processes (Meyer, 1994). In the case of dioecious genotypes, male flowering always preceded female flowering, confirming the proterandry of hemp (Crescini, 1930; Bonvicini, 1932), and clearly indicating that flowering in dioecious genotypes happens in two phases. In Fibranova, however, male flowering did not seem to closely follow a logistic pattern but it was more accurately described by a bi-logistic curve (Figure 3). This might indicate that the population of male plants in Fibranova could be composed of two groups of individuals with different flowering characteristics (for example, with different sensitivity to the photo period or critical photo period).

This same reasoning can be proposed to explain the bi-logistic pattern of flowering in the monoecious Futura (Figures 4 and 5). This is also supported by the work of Venturi (1969) who found that it was possible to distinguish two biotypes with different morphological characteristics and flowering patterns in each of three French monoecious cultivars. Another reason for the earlier flowering of some of the plants in Futura can be ascribed to the instability of the monoecious genotypes that after a few generations return to a natural dioecy (Venturi, 1967). It is therefore possible that within a monoecious genotype, early plants bring male, proterandric characters.

CONCLUSIONS

Flowering duration as well as flowering time in hemp depends on the combination of genotype and sowing time. A minimal flowering duration would be desirable for agronomic reasons, but a short flowering duration was observed when time from emergence to flowering was also short, something that is related to low yields (Cromack, 1998; Amaducci et al., 1998; Struik et al., 2000; Sankari, 2000). Breeding for genotypes with short and uniform flowering duration should improve the homogeneity of hemp crops.

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