

Crop physiology of fibre hemp (*Cannabis sativa* L.)



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MN08201, 1810

Ontvangen
28 JUNI 1994
UB-CARDEX

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Crop physiology of fibre hemp (*Cannabis sativa* L.)

Proefschrift

ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
dr. C. M. Karssen,
in het openbaar te verdedigen
op donderdag 30 juni 1994
des namiddags te vier uur in de aula
van de Landbouwuniversiteit te Wageningen

ISBN 177267

CIP-GEGEVENS KONINKLIJKE BIBLIOTHEEK, DEN HAAG

Werf, Hayo van der

Crop physiology of fibre hemp (*Cannabis sativa* L.)/

Hayo van der Werf. - [S.l. : s.n.] - Ill.

Proefschrift Wageningen. Met lit. opg. -

Met samenvatting in het Nederlands.

ISBN 90-9007171-7

Trefw.: hennepcultuur/vezelhennep; fysiologie.

BIBLIOTHEEK
LANDBOUUNIVERSITEIT
WAGENINGEN

Stellingen

1. De efficiëntie van lichtbenutting voor de produktie van drogestof is lager in hennep dan in suiker- of zetmeelproducerende C₃-gewassen. Dit is het gevolg van de vlakke bladstand van het gewas, de energierijkdom van de lignine in de stengel en de snelle veroudering van het bladapparaat na de bloei.
Dit proefschrift.
2. De stengelopbrengst van de momenteel beschikbare Franse en Hongaarse vezelhennepcultivars wordt sterk beperkt door hun vroege bloei. In een veredelingsprogramma dat gericht is op opbrengstverhoging van vezelhennep dient geselecteerd te worden op late bloei.
Dit proefschrift.
3. Het aandeel van de bast in de stengel is het belangrijkste kwaliteitskenmerk voor hennep bestemd voor papierpulp. Dit bastaandeel neemt af tijdens de groei van de hennepplant, een hogere stengelopbrengst leidt tot een lager bastaandeel. Cultivars verschillen voor de grootte van deze afname.
Dit proefschrift.
4. In vezelhennep benadert de zelfdunningslijn het verband tussen de opbrengst en het optimale plantgetal: naarmate de opbrengst hoger is, ligt het optimale plantgetal lager.
Dit proefschrift.
5. Hogere stikstofgiften leiden tot meer zelfdunning in vezelhennep.
Dit proefschrift.
6. De vraag naar duurzaam geproduceerde vezels voor textiel en papier neemt toe en derhalve zal het wereldareaal vezelhennep, dat de afgelopen eeuwen gestaag is afgenomen, weer toe gaan nemen.
Riddlestone et al. 1994. Bioregional fibres, the potential for a sustainable regional paper and textile industry based on flax and hemp. Bioregional Development Group, Carshalton, Surrey, UK.
7. Opname van vezelhennep in een vruchtwisseling is een duurzame onkruidbeheersingsmethode.
Heuser 1927. Hanf und Hartfaser. Julius Springer Verlag, Berlin.
Lotz et al. 1991. Reduction of growth and reproduction of *Cyperus esculentus* by specific crops. Weed Research 31: 153-160.

Stellingen

8. Op basis van een dunne voorstudie heeft het Nederlandse Hennepprogramma zich op een smalle markt gericht.
9. In kringen van marihuana gebruikers worden de mogelijkheden van vezelhennep sterk overschat.
Herer J, 1990. Hemp & the marijuana conspiracy: The emperor wears no clothes. HEMP publishing, Van Nuys, California, USA.
10. In berekeningen omtrent de haalbaarheid van energieproductie uit biomassa is de gewasopbrengst vaak sluitpost.
Lysen et al. 1992. De haalbaarheid van de productie van biomassa voor de Nederlandse energiehuishouding. NOVEM, Apeldoorn.
11. Mee willen doen met de "Grote Jongens" is een belangrijke drijfveer in de wetenschap.
12. Wat vroeger "zonde" was, is nu "slecht voor het milieu".

Stellingen behorende bij het proefschrift van Hayo van der Werf:
"Crop physiology of fibre hemp (*Cannabis sativa* L.)".

Wageningen, 30 juni 1994.

Dit papier bevat 95 % hennepvezel.

Abstract

Van der Werf, Hayo M. G., 1994. Crop physiology of fibre hemp (*Cannabis sativa* L.). Doctoral thesis, Wageningen Agricultural University, Wageningen, the Netherlands, 152 pp, English and Dutch summaries.

Fibre hemp (*Cannabis sativa* L.) may be an alternative to wood as a raw material for the production of paper pulp. The effects of environmental factors and cultural measures on the functioning, yield and quality of fibre hemp crops in the Netherlands were investigated.

Until flowering (generally in August), the radiation use efficiency (RUE, above-ground dry matter accumulated per unit of photosynthetically active radiation intercepted) of hemp was 2.2 g MJ⁻¹, after flowering it dropped to 1.1 g MJ⁻¹. This reduction was mainly caused by senescence, resulting in a lower rate of canopy photosynthesis. When flowering was prevented by artificial daylength extension the RUE remained high throughout September, and stem dry matter yield was increased by 2.7 t ha⁻¹. Breeding late-flowering hemp seems a promising strategy to improve the stem yield potential of hemp.

Hemp grows at low temperatures, its base temperature is 1 °C for leaf appearance, and 2.5 °C for canopy establishment. Thermal time is a simple and accurate tool to describe leaf appearance and light interception in field-grown fibre hemp.

Hemp is grown at high plant densities to improve stem quality and to increase the allocation of above-ground dry matter to the stem. However, in dense hemp crops self-thinning (density-induced mortality) may occur, causing losses of dry matter. It was established that in fibre hemp optimum plant density is approximated by the highest density possible without inducing self-thinning. During self-thinning an increase in biomass is accompanied by a reduction in plant density, consequently, in fibre hemp optimum plant density is a function of yield.

N fertilization affected self-thinning: at similar above-ground dry matter, a higher plant density was sustained at 80 than at 200 kg N ha⁻¹. The reduced mortality at the low nitrogen level resulted from a shift from mainly competition for light, which enhances differences in plant size, to competition for nutrients, which does not give large plants a disproportionate advantage over small plants. Variability of both weight and height of hemp plants was higher at 200 than at 80 kg ha⁻¹ N, and more suppressed plants were present at 200 than at 80 kg ha⁻¹ N. Sexual dimorphism contributed to variability of height and weight, but the effects were smaller than those of nitrogen fertilization.

It is concluded that fibre hemp may be an interesting 'new' crop for arable farmers in the Netherlands: hemp may be profitable, its stems potentially have a large non-food market, the crop requires little or no biocide and suppresses weeds and some major soil-borne diseases.

Key words: allometry, base temperature, *Cannabis sativa* L., competition, daylength, dominance, dry-matter partitioning, fibre hemp, flowering, light interception, nitrogen fertilization, photoperiod, plant density, plant morphology, radiation-use efficiency, row width, self-thinning, sex expression, sexual dimorphism, size variability, stem yield, stem quality, suppression, thermal time

Aan Agnès, Aurélie en Charlotte

Woord vooraf

Dit proefschrift beschrijft een belangrijk deel van het onderzoek naar de gewasfysiologie en teelt van vezelhenneep dat van 1990 tot en met 1993 uitgevoerd werd op het DLO Instituut voor Agrobiologisch en Bodemvruchtbaarheidsonderzoek (AB-DLO, voorheen CABO-DLO) te Wageningen, de vakgroep Agronomie van de Landbouwniversiteit Wageningen en het Proefstation voor de Akkerbouw en de Groenteteelt in de Vollegrond (PAGV) in Lelystad.

Ik heb het een buitenkans gevonden te mogen werken aan een veelzijdig en veelbelovend gewas als hennep, temeer daar dit onderzoek zich afspeelde in een levendige en stimulerende omgeving: het AB-DLO, de vakgroep Agronomie en het PAGV. Een groot aantal mensen heeft een bijdrage geleverd aan het onderzoek en aan dit proefschrift.

Mijn co-promotor, Anton Haverkort, ben ik zeer dankbaar voor zijn uitgebreide, snelle en nauwgezette commentaar op de manuscripten. Van zijn stimulerende suggesties ten aanzien van structuur en inhoud van de concept-artikelen heb ik veel geleerd. De samenwerking met mijn promotor, Paul Struik, was zeer leerzaam en plezierig. Zijn snelle reacties op mijn manuscripten waren van grote waarde en het is mij een eer bij hem te mogen promoveren. Mijn dank gaat ook uit naar Bert van Arkel, voor zijn begeleiding en inzet in de beginfase van het onderzoek.

Willem Meijer en Els Mathijssen hebben mij ingewerkt op het AB-DLO. Tijdens het hele onderzoek hebben wij zeer aangenaam samengewerkt en hebben zij mij met raad (Willem) en daad (Els) bijgestaan. Dat de "eindsprint" voorspoedig verliep is mede te danken aan de ruime hulp die Els verleende.

Tijdens de eerste twee jaar van het onderzoek heeft Marjoleine ten Cate een belangrijk deel van de proeven op het AB-DLO uitgevoerd en verwerkt. Ik zal haar enthousiasme en kritische houding niet gauw vergeten. Hans Tick nam in die periode, op zijn eigen behoedzame wijze, veel van het werk op het PAGV voor zijn rekening. Ik denk met plezier terug aan onze samenwerking.

Tijdens de tweede helft van het project heb ik op het AB-DLO prettig samengewerkt met Marian Wijlhuizen. Zij nam op voortreffelijke wijze een groot deel van de uitvoering van de proeven, van de verwerking van de vele gegevens en van het maken van figuren voor haar rekening. Op het PAGV voerde Willem van Geel in die periode een belangrijk deel van de proeven en van de verwerking van de gegevens uit. Zijn energieke aanpak en nauwkeurige werk heb ik zeer gewaardeerd.

Ik ben de directie van het AB-DLO, mijn collega's en met name mijn afdelingsgenoten dankbaar voor het stimulerende werkklimaat en de gezellige sfeer op het instituut. Peter Kooman was altijd bereid om hulp te bieden bij het modelleren, en Bert Schnieders bleek een waardevolle gesprekspartner op zelfdunningsgebied. De medewerksters van de afdeling tekstverwerking van het AB-DLO wil ik hartelijk bedanken voor de plezierige samenwerking. Tijdens de eindfase verzorgde Rina Kleinjan op professionele wijze de layout van dit proefschrift. Deskundige en uiterst significante bijstand op statistisch gebied werd geboden door Wim van den Berg (PAGV) en Jacques Withagen, ik ben hen zeer dankbaar.

Gillian Marsh corrigeerde de tekst van de hoofdstukken 7 en 8, Joy Burrough-Boenisch corrigeerde de overige hoofdstukken en gaf leerzame aanwijzingen ten aanzien van de structuur van de teksten. Ik heb veel van hen beiden geleerd. Dankzij Erik van der Werf staan er 9 fouten minder in dit proefschrift.

De experimenten waarop dit proefschrift gebaseerd is, werden uitgevoerd in het fytotron van de vakgroep Agronomie, op proefboerderij De Bouwing in Randwijk, op het PAGV proefbedrijf in Lelystad, en op proefboerderij Het Kompas in Valthermond. Mijn dank aan de medewerkers en bedrijfsleiding van deze proefaccomodaties voor hun onmisbare bijdrage.

De studenten: Anne-Marie Bouma, Kor Brouwer, Bart van Gils, Erik Haasken, Harald van der Hoek, Maarten van Mensvoort, Jeroen de Schutter, Mariët de Vries en Frederik Wanink hebben meegewerkt aan het onderzoek en zorgden voor extra leven in de brouwerij. Hun inspanningen hebben veel extra resultaat opgeleverd.

De samenwerking met de collega's binnen het Hennep Onderzoeksprogramma was vaak plezierig. Met name Jan Egbert Harsveld van der Veen, Sebastiaan Hennink, Wim Huisman, Eddie de Maeyer, Etienne de Meijer en Gert Jan van Roekel wil ik bedanken voor de vruchtbare discussies en samenwerking. In deze categorie valt ook Paul van den Brink, het was altijd een genot te praten met een echte hennepkenner.

Fibre hemp is an unknown crop in the Netherlands, so contacts with hemp researchers from abroad were most valuable. I want to thank Ivan Bócsa ('the apostle of hemp') of the GATE Agricultural Research Institute in Kompolt, Hungary, who shared his enthusiasm and knowledge. Un grand merci également à Jean-Paul Mathieu de la FNPC au Mans, France, pour ses explications et ses conseils concernant le chanvre. I am grateful to Pavel Goloborodko and his colleagues of the Institute of Bast Crops at Glukhov, Ukraine, for their hospitality and readiness to share their knowledge on the agronomy of hemp.

A new, somewhat less orthodox generation of hemp enthusiasts is emerging, discussions and correspondence with Robert Clarke, Chris Conrad, Allan Dronkers, Marcel Hendriks, Andrew Katelaris, David Pate, Sue Riddlestone, Ed Rosenthal and David Watson were valuable and enjoyable. David Watson allowed one of his *Cannabis* illustrations to be reproduced as part of the cover of this thesis, Robert Clarke allowed one of his drawings to be used for the figure on page 5.

Ik heb veel aan mijn ouders te danken, die mij altijd gestimuleerd hebben en mijn eigen gang lieten gaan. Agnès, jou wil ik zeer hartelijk danken, je hebt deze hele onderneming op zijn tijd weten te relativeren, merci!

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CHAPTER 1

INTRODUCTION

INTRODUCTION

Within the European Union, the prices of many arable crops have fallen in recent years, and subsidies for food crops have been reduced in an attempt to combat the production surpluses. As a result, crop rotation on Dutch arable farms is increasingly restricted to a few crops which are relatively profitable (potato, sugar beet) or agronomically indispensable in the rotation (cereals). This narrow crop rotation has increased the incidence of diseases, in particular via the occurrence of soil pathogens, and has lowered yields. It has also led to greater use of biocides, in particular of soil fumigants. This is a worrying development, as it is generally agreed that arable farming should become more sustainable, and use less biocides.

The identification and development of a 'new' crop, to be introduced into the current rotations, might help solve the problem described above. The new crop should be profitable, produce for a large non-food market, require little or no biocide and help reduce disease incidence in the current crop rotations. Fibre hemp, to be grown for the production of stems for the paper pulp industry, was proposed as such a crop in the early 1980s (Du Bois 1982). Its yield was reported to be high, and it was said to improve soil structure. Furthermore, hemp was claimed to suppress weeds effectively, and to be virtually free from diseases or pests. During the 1980s preliminary research was conducted into the best ways of growing, harvesting and pulping fibre hemp in the Netherlands. The results were encouraging, and in January 1990 a comprehensive 4-year study, the Hemp Research Programme, was started to investigate the potential of fibre hemp as a new raw material for the pulp and paper industry and to establish whether the production of fibre hemp for paper pulp would be economically attractive. The major research disciplines within the programme were: plant breeding, crop physiology and agronomy, plant pathology, harvest and storage technology, pulp technology, and economics and market research. This thesis reports on a major part of the research into the crop physiology and agronomy of fibre hemp carried out in the Netherlands prior to and within the Hemp Research Programme. The results of the entire Hemp Research Programme are summarized in Van Berlo (1993).

The history of hemp

Hemp (*Cannabis sativa* L.) is grown for the production of fibre (Rabelais 1546), cannabinoids (Beaudelaire 1860) or seed. *Cannabis* originates from Central Asia but has been cultivated from the Equator to the Polar Circle (Vavilov 1926). Human use of hemp goes back at least 6,000 years and it may be one of the oldest non-food crops (Schultes 1970). For thousands of years, hemp bast fibre has been used to manufacture rope, fabric and paper. Cannabinoids have been used for medical, spiritual and recreational purposes, whereas the seed has been produced mainly for its oil. Hemp oil has been used as a food oil, and for paint, soap, lubricants and cosmetics, and the seed cake has been used as animal feed.

From the sixteenth to the eighteenth century hemp and flax were the major fibre crops in Russia, Europe and North America (Pounds 1979, Abel 1980). However, the large-scale cultivation of cotton, jute and other tropical fibres caused the world area of fibre hemp to decline in the nineteenth century (Conrad 1993). This decline has continued, due to the advent of synthetic fibres and because the cultivation of hemp has been made illegal in many countries (Herer 1992). Since the second world war, the main areas of fibre hemp production have been in China, the Soviet Union and Eastern Europe. In 1992 there were 260,000 ha under fibre hemp in the world (FAO 1993).

In the Netherlands, commercial hemp cultivation peaked during the seventeenth and eighteenth centuries, when hemp was in great demand for making ropes, sails and fishing nets (Hoogendoorn 1993). In the nineteenth century the hemp area decreased; in 1870 it was 1483 ha, in 1915 only 29 ha (Ten Rodengate Marissen 1919). After world war I no hemp was grown, but during world war II the crop briefly revived, and about 100 ha was grown for several years (De Jonge 1944).

In the twentieth century fibre hemp all but disappeared from North-west Europe. Only in France was it never completely abandoned: the area decreased from 176,000 ha in 1840 to 2000 ha in 1961 (Mathieu 1980), but in 1993 was 6000 ha. The survival of fibre hemp in France seems to be due to a timely change in the use of the bast fibres. In the 1960s the textile industry gradually stopped using hemp fibre, while the specialty paper industry started using hemp as a raw material (Mathieu 1980).

The botany of hemp

Cannabis sativa L. is a tall, vigorous annual of the *Cannabaceae* family. Hemp seedlings have two sessile seed leaves; all subsequent leaves have a petiole. Both leaves of the first pair of true leaves have a single narrowly elliptic blade with serrate margins (Stearn 1970). A leaf from the second pair of true leaves has three serrate leaflets radiating from the tip of its petiole; a leaf from the third pair of leaves has five leaflets and so on, up to 9 to 13 leaflets. In young hemp plants phyllotaxis is opposite, but as flowering begins, phyllotaxis changes from opposite to alternate and the number of leaflets per leaf declines (Heslop-Harrison & Heslop-Harrison 1958).

The stem of the hemp plant is grooved or furrowed to varying degrees, and hollow; when grown at a high plant density the stems are almost unbranched. At maturity the stem is 1 to 5 m high, depending on cultivar and growing conditions.

Hemp is a short-day plant: flowering is hastened by short days and delayed by long days. Hemp is normally dioecious, but monoecious cultivars have been bred. The two sexes are morphologically indistinguishable before flowering. The first sign of a transition to flowering is the formation of undifferentiated flower primordia. Soon the males can be identified by the

differentiation of round pointed flower buds having five radial segments. The females are recognized by the enlargement of a symmetrical tubular bract or calyx (Clarke 1980).

In a dioecious crop, male and female plants are generally present in roughly similar numbers, but, depending on cultivar and growing conditions, there may be up to 50 % more female plants than male plants (Hoffmann 1957). The inflorescence of male plants is strongly branched, with few or no leaves; the inflorescence of female plants is leafy, stocky and unbranched. Male plants die soon after anthesis, whereas female plants live 3 to 5 weeks longer than male plants, until the seed is ripe. The female flower has a small green organ, the bract, completely enclosing the ovary from which two stigmas protrude (Figure 1). This sheath is covered with slender hairs and stalked circular glands secreting resin containing cannabinoids (Stearn 1970).

The seed of commerce is an achene fruit, i.e. it contains a single seed with a hard shell, tightly covered by the thin wall of the ovary. It is ellipsoid, slightly compressed, smooth, 2 to 6 mm long and 2 to 4 mm in maximum diameter. The seed is light brown to dark grey, in some cases mottled, containing about 35 % oil and 25 % protein.

The anatomy and chemical composition of hemp stems

Hemp stems can be separated into two components: the stem tissues outside the vascular cambium (bark) and the stem tissues inside the vascular cambium (core).

The bark consists of the epidermis, the cortex and the phloem. In the phloem are sieve tubes and primary bast fibres, arising from the prodesmogen. The phloem may contain secondary bast fibres arising from the cambium (Kundu 1942). The length of primary bast fibres has been found to vary between 3 and 55 mm (Kundu 1942, Catling & Grayson 1982); according to Hoffmann (1957) mean length is about 20 mm. The mean length of secondary bast fibres is about 2 mm (Kundu 1942). Kundu (1942) found primary fibres (34 μm) to be wider than secondary fibres (17 μm).

The core consists of the pith and the xylem. The xylem consists of vessel members, ray and paratracheal parenchyma cells and libriform fibres (Esau 1965). Libriform fibres are 0.5 to 0.6 mm long and about 25 μm wide (Bosia 1976).

Bark and core differ in their chemical composition: Bedetti & Ciaralli (1976) reported 67 % cellulose, 13 % hemicellulose and 4 % lignin in the bark of an Italian hemp cultivar harvested in October. Its core contained 38 % cellulose, 31 % hemicellulose and 18 % lignin. Bosia (1976) presented similar results.

Fibre length and the contents of cellulose and lignin are important quality parameters for raw materials for paper. The strength of paper increases with fibre length. Cellulose content is important, because in chemical pulping the pulp yield corresponds to the cellulose content of

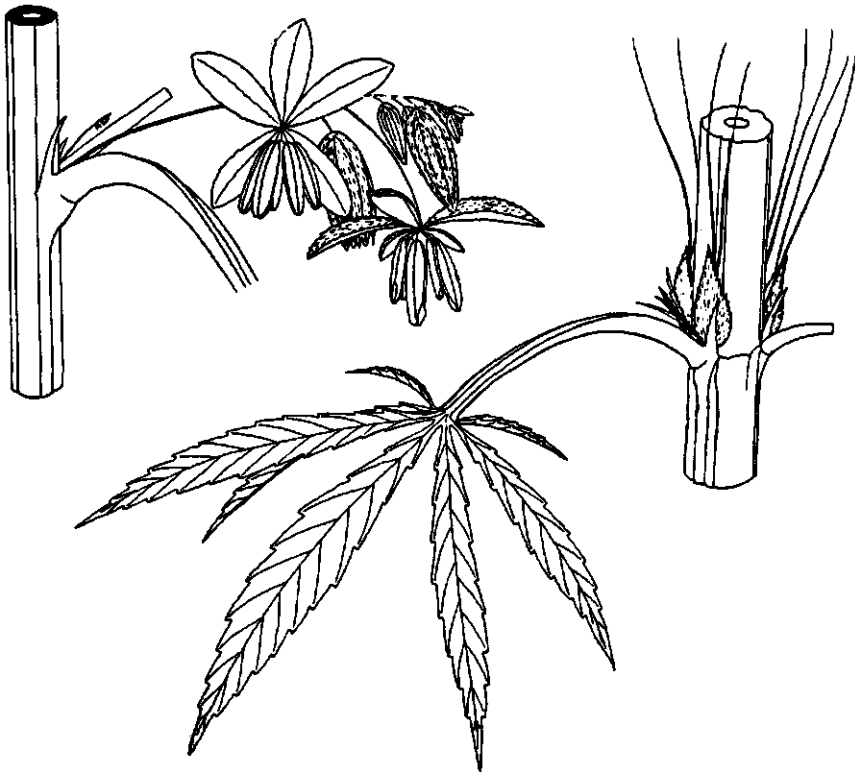


Figure 1. Sections of hemp stems, left bearing male flowers, right bearing female flowers and a leaf, from Clarke (1980).

the raw material. As lignin is removed by environmentally unfriendly procedures, a low lignin content is desirable. In bark, fibres are longer, cellulose content is higher, and lignin content is lower than in core. As a result, bark is more valuable as a raw material for paper than core.

Pulp and paper production

Paper was invented in China in the first century B.C., with hemp bast fibre as one of its major components (Abel 1980). From the twelfth century onwards, paper mills using worn-out ropes and tissues made from flax and hemp were established in Europe (Conrad 1993). During the nineteenth century, new technologies were developed to process wood into paper pulp to satisfy the increasing demand for paper (Tucker 1969). World consumption of paper has

continued to increase in this century; in 1913 it was 14 million tonnes, in 1950 40 million tonnes and in 1989 230 million tonnes (FAO 1991). However, hemp and flax fibres have lost their former major role in pulp and paper making. In 1989 92 % of the virgin fibre used to manufacture paper came from wood, the remaining 8 % was from annual crops or crop residues (FAO 1991).

During recent decades the pulp and paper industry has been criticized for its negative impact on the natural environment: deforestation, or the replacement of old-growth forests by tree plantations (Postel & Ryan 1991), the emission of chemical waste, high energy use by pulp and paper mills, and the production of toxic and mutagenic waste products by chlorine bleaching (McDougall et al. 1993). Measures taken to tackle these problems include increased recycling of paper, more sustainable management of tree plantations and forests and a shift towards less harmful pulp and paper technologies.

A comeback of bast fibre crops as a raw material for paper may further contribute to the solution of some of these problems. Growing such annual crops on farmland obviously lessens the need to cut down forests. In addition, less energy is required to produce pulp from kenaf (Keto 1990) or hemp (personal communication, S J Lips, DLO Agrotechnological Research Institute) rather than from wood. Finally, the lignin content is lower in bast fibre crops such as kenaf and hemp than in wood, offering better opportunities for non-chlorine bleaching or the production of unbleached pulp (McDougall et al. 1993).

The state of knowledge on hemp crop physiology and agronomy prior to this research

In the absence of limitations due to lack of water or nutrients, pests, diseases, or other stresses, crop yield is determined by:

- a) the amount of light intercepted by the crop canopy during a growing season
- b) the radiation-use efficiency: dry matter produced per unit of light intercepted
- c) the harvest index: the fraction of the plant parts of economic value in the total dry matter

To explore the potential of fibre hemp in the Netherlands, preliminary field experiments were conducted in the 1980s, using French cultivars and cultural techniques generally recommended for fibre hemp. In these experiments, the period of full light interception by the canopy was rather short, suggesting that light interception might be increased. Further, even in optimal growing conditions, crop growth rate was low, indicating that the radiation-use efficiency could be improved. Finally, inflorescence dry matter was significant at final harvest, indicating that dry-matter partitioning was not fully compatible with the objective of maximizing stem yield. Dry-matter partitioning between bark and core and the chemical composition of these two components had not been measured and remained to be investigated.

In the preliminary experiments hemp was never sown before 10 April, because in the literature most authors agree that hemp should not be sown before the second half of April (Heuser 1927, De Jonge 1944, Senchenko & Demkin 1972, Mathieu 1980). The extent to which earlier sowing advances canopy establishment depends on early growth and development of hemp at low temperatures, but the effect of temperature on growth and development of hemp was never quantified.

The monoecious French fibre hemp cultivars used in the preliminary Dutch experiments flowered early in August. After flowering, stem growth slowed down, ceasing by early September. This probably resulted from the allocation of assimilates to the inflorescence and from subsequent senescence (Meijer & De Meijer 1990). Later flowering cultivars may yield more stem dry matter, as no assimilates are diverted to the inflorescence and senescence is delayed. However, the effect of flowering date on stem yield potential and on stem quality was never established in hemp.

Radiation-use efficiency (RUE) of non-stressed crops depends on crop gross photosynthesis, maintenance respiration and growth respiration (Charles-Edwards 1982). Losses of dry matter during the growing season may cause the RUE to be underestimated. In order to obtain a high stem yield containing a large proportion of bark, plant densities were high (100 to 400 or more plants m^{-2}) in the preliminary experiments, as recommended in the literature (Heuser 1927, Jakobey 1965). However, at these densities more plants died before the end of the growing season than reported from other European countries: even at the lowest densities investigated almost half of the plants had died before harvest in September (Meijer & De Meijer 1990). This suggests that the optimum plant density for fibre hemp is lower in the Netherlands than in Central and Southern Europe. The reason for this difference remained to be investigated.

These findings also raised the question to what extent cultural measures (e.g. the level of nitrogen fertilization, row width or sowing method) might reduce the proportion of plants that die during the growing season.

Finally, in the preliminary experiments it was observed that at harvest the height and weight of hemp stems varied greatly. Uniformity of plant height and weight in a hemp crop is desirable, as it allows more efficient defoliation at harvest and better fine-tuning of decortication equipment at processing. It was not clear to what extent cultural measures and sexual dimorphism affect crop uniformity.

Objectives of the present study

The main objective of the study reported in this thesis was to better understand the crop physiology of fibre hemp, by establishing the effects of environmental factors and cultural measures on the functioning of a fibre hemp crop. Furthermore, this research aimed at elucidating the factors and processes constraining the yield and quality parameters of fibre

hemp produced in the temperate maritime climate of North-west Europe. It was also intended to help define the specific cultural measures required to maximize the crop's potential in a given agro-ecological environment, and to yield results that might be useful in defining the most desirable characteristics of a fibre hemp cultivar grown for pulp production in North-west Europe.

Structure of the thesis

Results from the field experiments conducted from 1987 to 1989 provided the starting point for the crop physiology research reported in this thesis. In Chapter 2 the results from these experiments are analysed in detail, using the radiation-use efficiency of the crops as a central concept. The effect of cultural practices and genotype on the level of parameters of stem quality is reported in Chapter 3, where the most relevant parameters of stem quality are identified, and methods to measure them are recommended.

Early growth and development of hemp at low temperatures largely determine how early the canopy can be established. Experiments to study the effect of temperature on development and growth of hemp in the field and in growth chambers are reported in Chapter 4. It was already known that in hemp flowering is delayed by long days. This was studied further, by applying 24-hour days to prevent flowering. The effects on yield and quality of hemp stems are reported in Chapter 5.

Inter-plant competition is a major factor affecting the crop physiology of fibre hemp. Therefore plant density and self-thinning were investigated to ascertain their influence on the yield and quality of fibre hemp (Chapter 6). Here, optimum plant density was defined as a function of yield. To refine this, the effects of nitrogen fertilization and row width on inter-plant competition were studied. We investigated the effects of these factors on self-thinning and yield formation (Chapter 7) and on size variability (Chapter 8). The contribution of sexual dimorphism to size variability in hemp is quantified in Chapter 8, and the thesis concludes with an analysis of the potential yield of fibre hemp and of its value as an annual crop for paper pulp (Chapter 9).

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**CONSTRAINTS TO DRY MATTER PRODUCTION IN
FIBRE HEMP (*Cannabis sativa* L.)**

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EUROPEAN JOURNAL OF AGRONOMY (accepted)

ABSTRACT

Fibre hemp (*Cannabis sativa* L.) may be an alternative to wood as a raw material for pulp and paper production. Research was done to assess the potential productivity of fibre hemp and to identify constraints to that productivity. Growth analyses were done on hemp crops in three consecutive years, using several cultivars and seeding rates. In 1987 the crops suffered severely from fungal diseases; stem dry matter yields were 9.4 t ha⁻¹. In 1988 and 1989 fungicides were applied and stem dry matter yields were respectively 11.9 t ha⁻¹ and 13.6 t ha⁻¹. The number of living plants m⁻² ranged from 86 to 823 at emergence, depending on treatment, and from 38 to 102 at final harvest. Increased seeding rates led to earlier canopy closure and higher initial biomass production, but more plants died during the growing season and the stem yield at final harvest was not affected by seeding rate. Average radiation-use efficiency (RUE; above-ground accumulated dry matter divided by intercepted photosynthetically active radiation) for the entire growing season under favourable growing conditions was 1.9 g MJ⁻¹, which is low compared to other C₃ crops. Leaf photosynthesis rates at saturating light intensities, however, were high: 30 kg CO₂ ha⁻¹ h⁻¹. The light extinction coefficient of hemp canopies was high (0.96), which reduces canopy photosynthesis rate and RUE. The high lignin content of the stems, and the high fat and protein content in the seed, also reduced RUE. Dry matter invested in the tap root and in shed dead leaves was ignored. The RUE was also underestimated because an appreciable proportion of the biomass of plants that died during the growing season could not be collected. More research is needed to optimize cultural practices in fibre hemp.

KEY WORDS: *Cannabis sativa* L., fibre hemp, stem yield, dry matter partitioning, radiation-use efficiency, light interception, seeding density.

INTRODUCTION

Hemp (*Cannabis sativa* L.) is an annual fibre crop. It contains long thick-walled bast fibres in the phloem and short thin-walled libriform fibres in the xylem. For centuries hemp bast fibre was the principal fibre used for marine cordage and sails; it has also been used widely as a fine textile fibre (Dempsey 1975). In the course of this century, hemp has been largely replaced by cotton and synthetic fibres, and has lost its importance as a raw material for cordage and textile products.

In recent years, interest in hemp as a potential raw material for paper production has revived, because world paper consumption is increasing by about 4% annually and is further threatening forest resources (Postel & Ryan 1991). The comprehensive Dutch research

programme investigating the potential of fibre hemp as a raw material for paper production, under which the study described here was done, is evidence of this interest.

The economic feasibility of hemp as a raw material for paper largely depends on its yield. Reports on the yields obtained in Europe are scarce and refer to straw: field-dried stems containing 10-18 % moisture and remnants of the inflorescence and leaves. For Denmark, Nordestgaard (1976) reported straw yields of 9 t ha⁻¹, in Poland Jaranowska (1964) obtained 7 to 9 t ha⁻¹, Mathieu (1980) reported 8 to 10 t ha⁻¹ in France. In Italy higher straw yields were obtained, e.g. 15 t ha⁻¹ (Marras & Spanu 1979). In the Netherlands Aukema and Friederich (1957) obtained 10 to 13 t ha⁻¹ and Van der Schaaf (1966) 12 t ha⁻¹ of straw. The seeding rate appears to be a major factor determining yield and quality of fibre hemp; however its effect on stem yield and quality varies (Dempsey 1975). In hemp, the proportion of stem in the biomass and the content of the more valuable bast fibres in the stem increases with plant density (Jakobey 1965), therefore dense crops are usually desired.

No studies analysing the efficiency of dry matter production and the partitioning of dry matter in fibre hemp were found in the literature. This chapter reports the results of 3 years of research on the crop physiology of fibre hemp in the Netherlands. We analysed the main limitations to dry matter production of the current fibre hemp cultivars. We used the radiation use efficiency (RUE), the average value of dry matter production per unit of intercepted photosynthetically active radiation (PAR) over a period of time (Monteith 1977, Gosse et al. 1986, Kiniry et al. 1989) to analyse the productivity of our crops and to compare the biomass production of hemp to that of other species. This study therefore concentrates on leaf area growth, light interception and RUE as the basic factors determining biomass production under favourable growing conditions. In order to clarify the effect of plant density on hemp growth and yield, growth analyses were done on crops sown at different rates.

MATERIALS AND METHODS

Field experiments were carried out in 1987, 1988 and 1989. The experimental set-up was a splitplot with four replications (details in Table 1, next page). In 1987 the main plots were combinations of four seeding rates (20, 40, 80 and 140 kg ha⁻¹) and two cultivars, with harvest dates in the sub-plots. The French monoecious cultivar Fédrina 74 was grown at all seeding rates; another French monoecious cultivar Fédora 19 was grown at the seeding rates 40 and 80 kg ha⁻¹ only. In 1988 seeding rates (20 and 80 kg ha⁻¹) were in the main plots and harvest dates in sub-plots and the cultivar was Fédrina 74. In 1989 harvest dates were in the main plots and cultivars in sub-plots. Cultivars were Fédrina 74, Kinai unisexualis (a Hungarian cultivar consisting of female plants only) and Kenevir, a dioecious cultivar from Turkey. Seeding rate was 40 kg ha⁻¹. Crop management was aimed at optimizing growing conditions. Fertilization was based on soil sampling. Because literature data on hemp are scarce, phosphate and

Table 1. Experimental details of the field trials.

Parameter	Year		
	1987	1988	1989
Location	Swifterbant	Randwijk	Randwijk
Soil	light clay	heavy clay	heavy clay
Sowing date	23 April	20 April	10 April
day number	113	111	100
Row distance (cm)	25	12.5	24
Nutrients applied (kg ha ⁻¹)			
N	122	135	120
P ₂ O ₅	122	115	90
K ₂ O		300	150
Gross plot size (m ²)	12 x 2	6 x 3	6 x 3
Area harvested (m ²)	6 x 1	2 x 1	2 x 1

potassium fertilizers were applied at the recommended rate for highly productive winter wheat crops in the Netherlands. Based on experimental results in Italy (Marras & Spanu 1979), Denmark (Nordestgaard 1976) and the Netherlands (Aukema & Friederich 1957), and on recommendations for hemp fertilization in France (Mathieu 1980), it was estimated that 175 kg N ha⁻¹ minus the reserve of soil mineral nitrogen would allow optimal crop growth and yields of up to 15 t ha⁻¹ of above-ground dry matter. To prevent the crops from suffering water stress they were occasionally irrigated until the plants were two metres tall. At the last irrigation (just before the crop became too tall to be irrigated), the uppermost 70 cm of soil was irrigated to field capacity. From then on, crop growth depended on precipitation and on reserves of soil moisture (Table 2).

No herbicides were used, as weeds were adequately suppressed by the crop. The 1987 growing season was cold and wet, temperature and precipitation in the 1988 growing season were about normal and the 1989 growing season was relatively warm and dry (Table 2). In 1987 the crops suffered severe damage from *Botrytis cinerea* and *Sclerotinia sclerotiorum*. These diseases were controlled in 1988 and 1989 by spraying fungicides (alternating vinchlozolin at 0.5 kg ha⁻¹ and iprodion at 0.5 kg ha⁻¹) from June through August at 14-day intervals.

Table 2. Weather conditions from 50 % plant emergence until 1 September and available water (-0.1 to -5.0 bar) at field capacity of the upper 70 cm soil layer.

Parameter	Year		
	1987	1988	1989
Mean temperature (°C)	13.5	15.5	15.0
Global radiation (MJ m ⁻² d ⁻¹)	14.8	15.3	18.5
Precipitation (mm)	403	228	167
Irrigation (mm)	-	75	25
Soil water (mm) at field capacity	100	70	70
Potential evapotranspiration (mm)	334	379	467

At each harvest the above-ground fresh weight of all living plants and of standing dead plants was determined. Dead stems and leaves lying on the soil were not collected. The living plants of a 0.75 m² subsample were separated into four fractions: stem, green leaves, inflorescences and yellow and dead leaves. The dead plants in the subsample were separated into stem and leaves. The dry weight of all fractions was determined by drying at 105 °C for 24 h. In the 1988 experiment, plastic gutters were installed in the crops to intercept most of the falling leaves. These leaves were included in the analyses. In addition, in 1988 the dry weight of most of the tap root was determined.

Leaf area indices (LAI) were determined using a LI-COR 3100 (Lincoln, USA) area meter. From emergence until canopy closure the interception of PAR by the canopy was measured weekly with a line sensor (Technical and Physical Engineering Research Service TFDL-DLO, Wageningen, the Netherlands). Per plot, 10 measurements were taken above and below the canopy. The maximum photosynthesis rate at light saturation was measured on clear days in 1988 (13 June, 25 July, 8 August and 7 September) on 40 fully expanded and fully exposed leaves, using an LCA2 CO₂ analyser (Analytical Development Company, Hoddesdon, England). The canopy light extinction coefficient k was calculated by fitting an exponential curve to the relationship between the periodic measurements of LAI and the fraction of PAR intercepted by the canopy in the period from emergence to canopy closure according to Beer's law:

$$F = 1 - e^{-kL}$$

where F is the fraction of PAR intercepted by the canopy and L is the leaf area index.

Cumulative light interception until canopy closure was calculated using daily values of F and PAR. We calculated daily values of F according to Spitters (1990) by fitting a logistic function to the relationship between F and the temperature sum since emergence. This procedure copes with variations in plant density, and does not require daily values of LAI to be calculated, thereby facilitating future crop modelling:

$$F_t = \frac{1}{1 + ((1/Nf_0) - 1)e^{-R_0 t}}$$

where R_0 is the initial relative leaf area growth rate, N the plant density, f_0 the initial fraction of light intercepted per plant (the relative area of the cotyledons) and t the temperature sum. In these calculations the fraction of intercepted PAR was assumed to remain at its maximum from canopy closure until final harvest. Actually measured values, however, showed a slight decline in the fraction of intercepted PAR in the last weeks of the growing season. This will have negligibly decreased the amount of PAR intercepted by the canopy, as radiation was low during this period. The temperature sums were calculated from the means of the daily minimum and maximum air temperature with a base temperature of 0 °C.

RESULTS AND DISCUSSION

Production and partitioning of biomass

The number of living plants decreased during the growing season in each of the three years and for all treatments. A long period of rainy weather during June and July 1987 caused the crops to be severely infected with *Botrytis cinerea* and *Sclerotinia sclerotiorum*, resulting in very many dead plants, especially at the highest plant densities (Figure 1). Although more plants survived in the healthy crops of 1988 and 1989, many plants died from canopy closure onwards. At canopy closure in 1988 (day 166) there were about 350 living plants m^{-2} ; at final harvest about 80 remained (Figure 1). With similar cultivars at similar seeding rates Nordestgaard (1976) in Denmark, Jaranowska (1964) in Poland and Mathieu (1980) in France found from 200 to over 300 living plants m^{-2} at harvest. When diseases and herbivores are absent, mortality of vegetative plants during the growing season in dense crops generally results from self-thinning (Westoby 1984). The low numbers of plants surviving until harvest in our experiments were probably associated with the high biomass yields we obtained. The dynamics of plant density in hemp will be dealt with in Chapters 6 and 7.

In 1987 stem growth rate was reduced by fungal disease from early August (Figure 2). In 1988 and 1989 stem growth ceased at the end of August or early September (Figure 2).

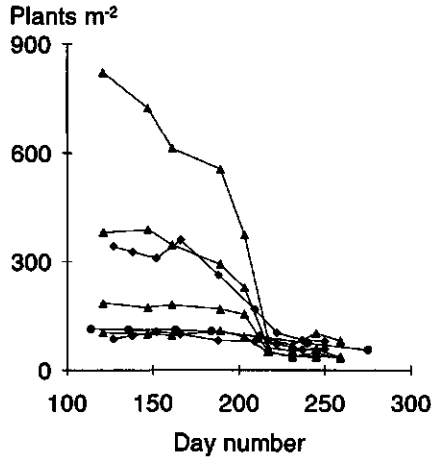


Figure 1. The number of living plants m⁻² of hemp crops sown at different rates, during the growing season in 1987 (triangles), 1988 (diamonds) and 1989 (circles) for Fédrina 74.

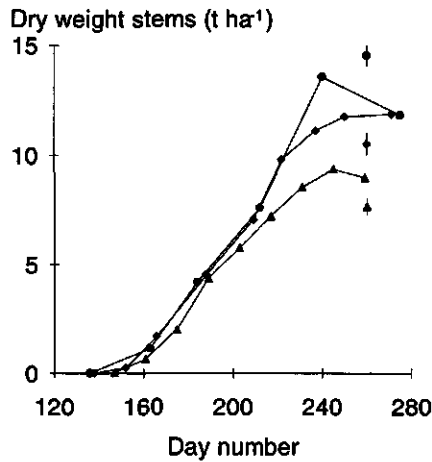


Figure 2. Total (living and dead) stem dry matter production for Fédrina 74. Plant density shortly after emergence 104 m⁻² in 1987 (triangles), 86 m⁻² in 1988 (diamonds) and 114 m⁻² in 1989 (circles). Vertical bars indicate standard deviations for the last three harvests.

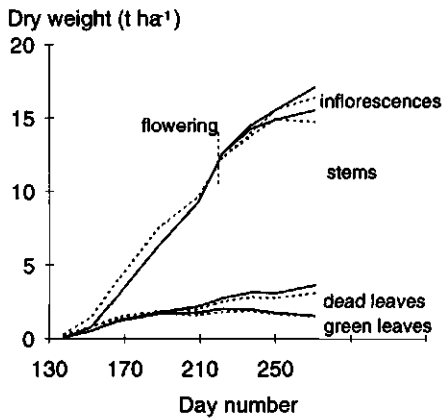


Figure 3. The seasonal pattern of above-ground dry matter production of hemp cultivar Fédrina 74 and the distribution of dry matter to the plant parts in 1988. Solid lines 86 plants m^{-2} , dotted lines 342 plants m^{-2} .

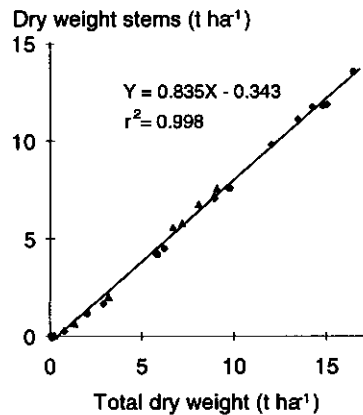


Figure 4. The relationship between total (living and dead) stem dry matter and total above-ground dry matter (living plants and dead stems) of hemp cultivar Fédrina 74. Plant density shortly after emergence 104 m^{-2} in 1987 (triangles), 86 m^{-2} in 1988 (diamonds) and 114 m^{-2} in 1989 (circles).

Cessation of stem growth coincided with the onset of dry matter accumulation in the inflorescence (Figure 3). Maximum stem yield was 11.9 $t ha^{-1}$ in 1988 and 13.6 $t ha^{-1}$ in 1989 (Figure 2). As 12 $t ha^{-1}$ of stem dry matter corresponds to about 14 $t ha^{-1}$ of straw, our yields were higher than those reported by Aukema & Friederich (1957) and Van der Schaaf (1966). In 1988, the high seeding density resulted in an earlier canopy closure and, initially, in a higher above-ground dry matter yield (Figure 3). Later on, the difference in above-ground dry matter yield between the two seeding densities (Figure 3) and the difference in plant density (Figure 1) disappeared. The higher death rate of plants growing at the 80 $kg ha^{-1}$ seeding rate was apparently the reason for the reduction in crop growth rate of this treatment. At final harvest no difference in yield was found between the two treatments (Table 3). In the 1989 experiment no differences in yield were found between the cultivars (Table 3).

During the first weeks after emergence most of the dry matter was partitioned to the leaves. Four weeks after emergence, about 50 % of above-ground dry matter consisted of stems. In Fédrina 74, the proportion of stem material in the above-ground dry matter increased rapidly to about 83 % in each of the three years (Figure 4). The proportion of stem in the above-ground dry matter was higher in Kinai unisexualis and Kenevir than in Fédrina 74 (Table 3).

In Fédrina 74 the proportion of stem in the above-ground dry matter was not affected by

flowering and seed filling: it remained constant until the end of the growing season (Figure 4). At final harvest the fraction of dry matter partitioned to the inflorescence was modest (Table 3) and was about as great as losses of leaves (Figure 3). The cultivar Fédrina 74 started flowering about two weeks earlier than the cultivars Kinai and Kenevir and therefore had a higher seed yield, though its stem yield was not affected (Table 3).

Light interception and radiation use efficiency

When crops are healthy and growing conditions are favourable, canopy photosynthesis (and indirectly, biomass production) is proportional to the amount of intercepted light. At an LAI

Table 3. Day number of maximum above-ground dry matter (DM) yield, number of living plants m^{-2} at emergence and at maximum above-ground DM (harvest), for four fibre hemp cultivars. Above-ground DM and DM of dead and living stems at maximum yield. DM yield of inflorescence (including seed) and of seed (1989 only) at final harvest (day number 259 in 1987, 271 in 1988 and 275 (Fédrina 74) or 296 (Kinai unisexualis and Kenevir) in 1989).

Year	Cultivar	Day number	Living plants m^{-2}		Maximum DM ($t ha^{-1}$)		DM at final harvest ($t ha^{-1}$)	
			Emergence	Harvest	Above-ground	Stem	Inflorescence	Seed
1987	Fédora 19	245	206	53	11.0	9.3	1.16	
			410	73	10.8	9.0	1.32	
	Fédrina 74	245	104	38	10.9	9.4	1.09	
			186	47	10.4	8.9	0.82	
			381	59	9.8	8.4	0.74	
	Fédrina 74		823	102	10.6	9.1	0.87	
	LSD (0.05)		66	11	1.7	1.4	0.50	
1988	Fédrina 74	271	86	42	15.0	11.9	1.57	
			342	71	14.9	11.6	1.67	
	LSD (0.05)		33	14	1.6	1.3	0.23	
1989	Fédrina 74	240	114	74	16.5	13.6	2.32	1.14
			Kinai unisexualis	123	86	15.7	13.7	1.24
	Kenevir		149	63	15.7	13.6	1.05	0.70
	LSD (0.05)		52	13	2.2	2.0	0.59	0.34

of 2 our crops intercepted about 90 % of PAR and at an LAI of about 4 interception was almost 100 % (Figure 5). The proportion of light intercepted by the canopy remained high during the growing season: at maximum above-ground dry matter yield (September) it was still above 95 % (data not shown).

Earlier canopy closure in spring, when incident PAR is high, will result in a considerably greater amount of light intercepted and in higher biomass production. As in many other crops, the increase of the fraction of PAR intercepted by the canopy was mainly affected by temperature and could be described by a logistic function (Spitters 1990). The course of light interception by the canopy for Fédrina 74 grown at about 100 plants m^{-2} was similar for the three years: 90 % interception of PAR was attained at 450-500 °Cd (base 0 °C) after emergence (Figure 6). Increased plant numbers accelerated canopy closure (Figure 6) resulting in a higher initial biomass production, but this advantage was lost later as a result of greater plant losses. Earlier sowing might be a more effective way of obtaining earlier canopy closure; however, potential yield gain must be balanced against the hazards of low temperature stress and late night frosts.

Data from both seeding densities in 1988 were used to calculate the regression of biomass on cumulative light interception (Figure 7a) resulting in an average RUE of 1.94 $g\ MJ^{-1}$. Growth during the 1988 season was considered optimal because no diseases were observed and soil moisture and regular precipitation preserved the crops from water stress. The RUE for 1987 was close to that of 1988 up to the point where fungal diseases affected the crop. The RUE for 1989 was below that of 1988, probably as a result of drought stress. From May to September

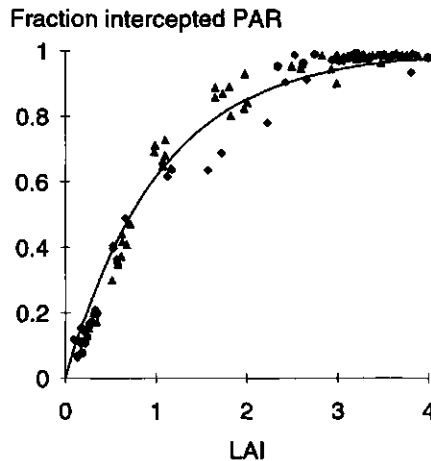


Figure 5. The relationship between the fraction of PAR intercepted by a hemp canopy and the leaf area index (LAI) of the different crops in the 1987 (triangles), 1988 (diamonds) and 1989 (circles) experiments.

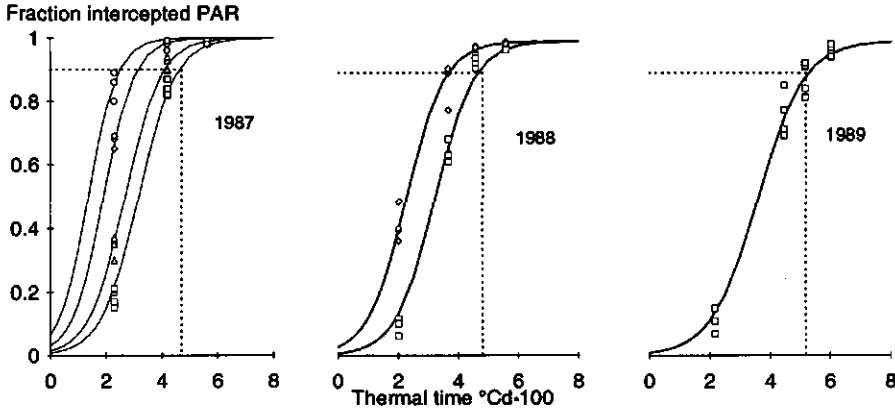


Figure 6. The fraction of PAR intercepted by a hemp canopy as a function of plant density and cumulative daily temperatures since emergence in 1987, 1988 and 1989 for Fédrina 74. Dotted lines indicate 90% interception. Plant densities (m⁻²) shortly after emergence were 104 (squares), 186 (triangles), 381 (diamonds) and 823 (circles) in 1987, 86 (squares) and 342 (diamonds) in 1988 and 114 in 1989.

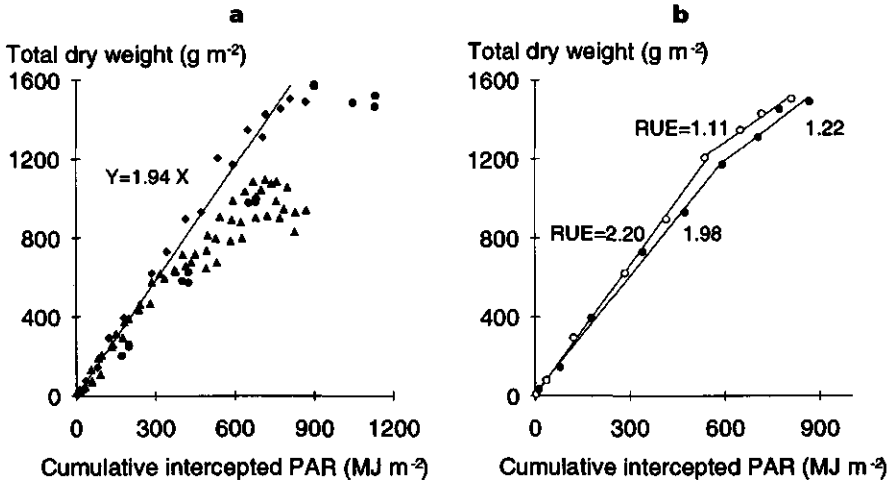


Figure 7. The relationship between above-ground dry weight of living plants and dead stems and cumulative intercepted PAR. (a) For the crops in 1987 (triangles), 1988 (diamonds and regression line) and 1989 (circles). (b) For Fédrina 74 in 1988 for two growth phases: from emergence to onset of flowering; from onset of flowering to final harvest. Open circles 86 plants m⁻², black circles 342 plants m⁻².

1989 rainfall was below average and potential evapotranspiration was high (Table 2). The low RUE in 1989 may also be attributable to the high level of incident PAR in 1989 (Table 2), which may have led to more frequent light saturation in the leaves at the top of the canopy. Closer examination of the 1988 data reveals a decrease in RUE after flowering (Figure 7b).

Dry matter losses and constraints to biomass production

In 1988 the RUE prior to flowering was 2.20 g MJ⁻¹ in the low-density hemp crop and 1.98 g MJ⁻¹ in the high-density hemp crop. (Figure 7b). These values are rather low, relative to the RUE values prior to flowering of 2.2 to 2.9 reported for other C₃ species such as sunflower, rice, wheat, potato, chicory and Jerusalem artichoke (Kiniry et al. 1989, Haverkort et al. 1992, Meijer et al. 1993). For the subtropical fibre crop kenaf a RUE of 2.4 g MJ⁻¹ was reported by Carberry & Muchow (1992). The RUE of hemp after flowering, (1.11 and 1.22 g MJ⁻¹, Figure 7b) was much lower than before flowering; the difference between seeding densities was not statistically significant. A low RUE may result from a low canopy photosynthesis rate, a high respiration rate, or a large proportion of the dry matter being lost during the growing season. These possibilities are examined below.

The constancy of the RUE of a species under non-limiting growing conditions is based on the assumption that canopy photosynthesis is not light saturated (Spitters 1990). Monthly measurements in the 1988 experiment showed leaf photosynthesis rates at saturating light of 30.8±1.6 kg CO₂ ha⁻¹ h⁻¹ in June, July and August and 27.2±1.1 kg CO₂ ha⁻¹ h⁻¹ in early September. These values are comparable to values of other C₃ species (Van Heemst 1988), making light saturation of canopy photosynthesis less probable. On the other hand, the mean light extinction coefficient of the hemp canopies we investigated was 0.96, which is at the upper end of the range reported for many other crops (Van Heemst 1988) and is caused by the planophile character of the hemp canopy (most leaves are nearly horizontal). During the first weeks after emergence the LAI of a hemp crop is low, and during this period a high extinction coefficient enhances canopy photosynthesis rate. However, over most of the season LAI is high and at high LAI a high extinction coefficient reduces canopy photosynthesis (Trenbath & Angus 1975). To quantify the influence of the relatively high extinction coefficient, the SUCROS model (Spitters et al. 1989a) was applied, using the 1988 crop and weather data. For 1988 an assumed extinction coefficient of 0.75 instead of 0.96 would have increased RUE and above-ground dry matter production by 2.6 % in the low-density crops and by 2.9 % in the high-density crops.

A low RUE is expected when the biomass contains much fat, protein or lignin. The costs and weight losses associated with the conversion of primary assimilates to these constituents are high compared to those associated with the synthesis of starch or cellulose (Penning de Vries et

al. 1974). Hemp stems contain about 15 % lignin (Bedetti & Ciaralli 1976), whereas the storage organs of carbohydrate-producing crops like wheat and sugarbeet contain 5 to 6 % lignin (Vertregt & Penning de Vries 1987). Because of the relatively high lignin content of its stems, hemp can form about 8 % less stem dry matter than wheat, potato or sugarbeet produce in their storage organs from the same amount of primary assimilates. This corresponds to a 6-7 % lower above-ground dry matter yield and a similar reduction in RUE.

The formation of about 1 t ha⁻¹ of seed (Table 3) containing 40 % oil and almost 30 % protein (Sinclair & de Wit 1975), reduces RUE after flowering. The primary assimilates required for 1 t of hemp seed could have yielded 1.4 t of dry matter in vegetative plants, thereby increasing above-ground dry matter production by 2.5 %. The large amount of assimilates required to synthesize oil and protein accounts for part of the low RUE over the final growth phase.

The RUE values reported in the literature for different species are not always comparable, for various reasons (e.g. below-ground and dead plant parts may or may not be included in biomass measurements). Like many tall plants, hemp forms a large tap root, which yielded about 1.1 t ha⁻¹ of dry matter at final harvest in 1988. This part of the plant may (Spitters et al. 1989b) or may not (Muchow 1992) be included in the biomass when RUE is calculated. We based RUE on measurements of above-ground standing dry matter only.

On average, about 15 green leaves were present per plant and over most of the growing period the average life span of a leaf was about 40 days (Figure 8). This is comparable to the life span of leaves reported for many other crops (Van Heemst 1988). A short life span of the leaves therefore does not help explain the low RUE of fibre hemp. Collecting shed leaves in the 1988

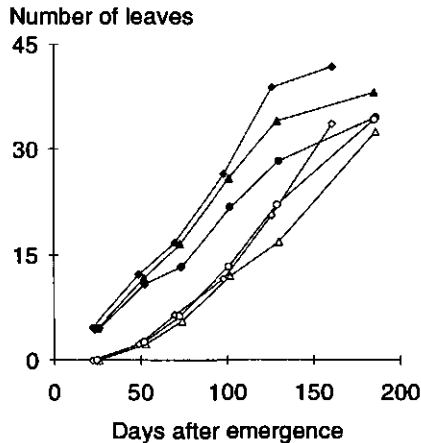


Figure 8. The increase in the total number of leaves per plant (black symbols) and the number of dead leaves (open symbols) during the growing season in 1989 for Fédrina 74 (diamonds), Kinai (circles) and Kenevir (triangles).

experiment yielded 1.5 to 2.0 t ha⁻¹ of dry matter at final harvest (Figure 9), but these data were not included in the RUE calculations. In hemp senesced leaves drop soon after turning yellow, and therefore a relatively large proportion of the leaf mass was not included in the biomass. This will have contributed to the low RUE.

Many plants died during the growing season, as a result of disease (1987) and self-thinning (1988 and 1989) (Figure 1). The plants that died early in the growing season did not represent a substantial amount of dry matter. In the second half of the growing season the dry matter of dead stems increased to 0.5 to 1.0 t ha⁻¹ (Figure 9). As a result of the time lapse between the death of a plant and the moment of harvest, measurements of the dry matter of dead stems in Figure 9 underestimate reality by an unknown amount, because part of the dry matter was lost by biotic or abiotic degradation. This effect becomes more pronounced at later harvest dates, as is suggested by the decline in dead stem matter observed at the high plant density (Figure 9). Dead biomass lost as a result of degradation before it was harvested was therefore another cause of the relatively low RUE during the later stages of crop growth.

In conclusion, the data presented here suggest that the relatively low dry matter production of fibre hemp per unit of intercepted radiation is the result of several factors. The rate of canopy photosynthesis was negatively affected by the high extinction coefficient of the hemp canopy. Dry matter production was reduced by 6-7% as a result of conversion losses during the synthesis of relatively large quantities of lignin in the stem. After flowering, dry matter production was reduced by the synthesis of fat and protein in the seed and the senescence of the canopy. Dead leaves were shed rapidly and not collected, and therefore an unknown proportion of the leaf mass escaped analysis. Furthermore, many plants died during the growing season; particularly at high seeding rates, their dry matter was only partially retrieved.

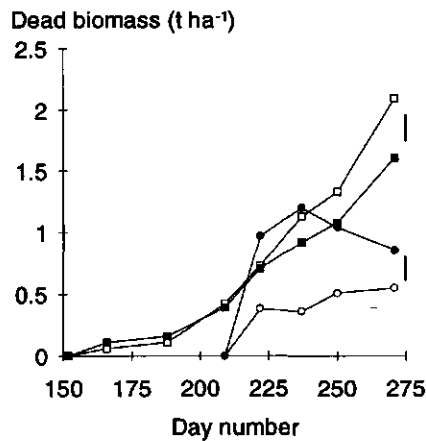


Figure 9. Losses of stem (circles) and leaf (squares) dry matter of hemp cultivar Fédrina 74 during the 1988 growing season. Open symbols 86 plants m⁻², black symbols 342 plants m⁻². Vertical bars indicate LSD (0.05) at final harvest.

IMPLICATIONS FOR FUTURE RESEARCH

This analysis indicates avenues that might lead to higher productivity of hemp. Earlier canopy closure may improve crop productivity by increasing the total amount of intercepted radiation during the growing season. Earlier sowing may be a more effective way of obtaining earlier canopy closure than high seeding densities. Experimental data, however, are needed to assess the benefit of yield gain against the risks of spring night frosts. Lower plant densities will decrease losses caused by plants dying during the growing season, but will increase the duration of the period between emergence and canopy closure. Further research is needed to determine the optimum plant density for growing conditions in the Netherlands.

Other cultural factors such as row width or rate of N supply may influence the number of plants that die during the growing season. The effect of such practices remains to be investigated.

Conversion losses can be reduced by breeding hemp varieties with a lower lignin content in the stem; this would also improve the quality of stem dry matter as a raw material for pulp and paper.

Using cultivars which flower later than the current ones would probably improve stem yield, as no assimilates would be invested in the inflorescence, and new leaves would continue to be formed, thereby prolonging the maximum photosynthetic capacity of the canopy.

ACKNOWLEDGEMENTS

The authors thank A J Haverkort and P C Struik for helpful comments on the manuscript.

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QUALITY OF HEMP (*Cannabis sativa* L.) STEMS AS A RAW MATERIAL FOR PAPER

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INDUSTRIAL CROPS AND PRODUCTS (in press)

ABSTRACT

Fibre hemp (*Cannabis sativa* L.) stems consist of high-cellulose low-lignin bark containing long fibres and low-cellulose high-lignin core containing short fibres. The bark, which contains a variable proportion of less valuable secondary bast fibre, is more valuable as a raw material for paper than the core. A study of the factors affecting the quality of hemp grown in the Netherlands for paper production is described. The bark content in the stem was determined by mechanically separating bark and core. The chemical composition of bark and core was determined according to procedures defined by the Technical Association of the Pulp and Paper Industry. The secondary bast fibre content was determined by manually separating primary and secondary phloem tissue after boiling in a 2 % NaOH solution. Bark content in the stem decreased during the growing season; at harvest in September it ranged from 30 % to 35 % depending on cultivar and plant density. The proportion of secondary bast fibre in the bast fibre fraction increased with stem weight, from 10 % to 45 %. Measurement of secondary bast fibre in a representative stem section allowed the proportion of this fibre in the bast fibre fraction of the entire stem to be estimated accurately. Differences in chemical composition within sets of samples of bark or core were small compared with the difference between bark and core. The bark of the French cultivars tested contained less cellulose than that of the Hungarian cultivars. Bark quality for paper making improved during the growing season because the cellulose content in the bark increased, whereas the content of lignin and extractives decreased.

KEY WORDS: *Cannabis sativa* L., fibre hemp, stem quality, bark, core, chemical composition, bast fibre, secondary bast fibre.

INTRODUCTION

The long bast fibres of hemp (*Cannabis sativa* L.) have been used since ancient times for spinning into cloth and cordage. This paper describes a study of the potential of hemp stems as a raw material for paper, which was conducted as part of a research programme investigating the potential of hemp as a new crop in the Netherlands.

The anatomy of the stem of hemp is crucial to its quality as a raw material for paper. The stem tissues outside the vascular cambium, the bark, contain primary bast fibres (about 20 mm long), arising from the prodesmogen, and may contain secondary bast fibres (about 2 mm long), arising from the cambium (Kundu 1942, Hoffmann 1957). The stem tissues inside the vascular cambium, the core, contain libriform fibres (Esau 1965) 0.5 to 0.6 mm long (Bosia 1976).

Bedetti & Ciaralli (1976) reported 67 % cellulose, 13 % hemicellulose and 4 % lignin in the bark of an Italian hemp cultivar harvested in October. Its core contained 38 % cellulose, 31 % hemicellulose and 18 % lignin. Bosia (1976) presented very similar results. Bedetti & Ciaralli (1976) also reported that the cellulose content of hemp bark increased from July to October, whereas that of the core did not change and the lignin content of bark and core hardly changed. Fibre length and the contents of cellulose and lignin are important quality parameters for raw materials for paper. The strength of paper increases with fibre length (Nelson et al. 1961). Cellulose content is an important parameter, because in chemical pulping the pulp yield corresponds to the cellulose content of the raw material. In paper making, lignin is removed by environmentally unfriendly pulping procedures. A low lignin content is advantageous in this respect as less polluting bleaching techniques may suffice to remove lignin (Rance 1984).

The bark and core of hemp differ in fibre length and chemical composition and, consequently, in value. In most cases, the stems of hemp and other bast fibre crops are separated into these fractions before pulping and the two components are processed separately. In France (a major user of hemp for paper making), the market price of dry bark of hemp in July 1992 was about 2500 FF t⁻¹, compared with 250 to 600 FF t⁻¹ for core (J P Mathieu, National Federation of Hemp Producers, personal communication). Stem value therefore primarily depends on the proportion of bark in the stem. To define stem quality in greater detail, the chemical composition of bark and core and the proportion of primary and secondary fibre in the bark must be ascertained.

The proportion of bark in the stem of hemp has been found to vary between 14 % and 48 % (Bredemann 1952, Arnoux et al. 1969), depending on genotype and plant height. We were unable to find any reports on the effect of cultural practices on the proportion of bark in the stem. The bast fibre content in the stem, which is strongly correlated with bark content (Bredemann 1952), has been found to increase with plant density (Heuser 1927, Jakobey 1965).

Bredemann et al. (1961) found that within the bast fibre fraction the proportion of secondary bast fibre increased (to a maximum of 45 %) with the dry weight of the stem. Horkay (1982) found that ratios of secondary bast fibre to primary bast fibre increased with increased bast fibre content in Hungarian high bast fibre cultivars. Breeding for high bast fibre contents tends to favour secondary fibre above primary fibre, unless genotypes with high secondary bast fibre contents are eliminated (Hoffmann 1957). Bedetti et al. (1979) found that the cellulose content in the bark was lower in the monoecious French cultivars than in the dioecious Italian cultivars.

Thanks to the favourable growing conditions, the stem yields of hemp in the Netherlands are up to 60 % higher than yields reported in the literature for most other European countries, and the plant densities at harvest are about one-third of those obtained elsewhere in Europe (Chapter 2). It is not known to what extent the stem quality of the French and Hungarian hemp cultivars currently grown in the Netherlands is affected by these differences in crop characteristics.

The study reported here had two aims: to determine the level of quality parameters of hemp stems grown in the Netherlands and to elucidate the effect of cultural practices and genotype on the quality of hemp stems.

MATERIALS AND METHODS

The hemp stems analysed in this study came from various hemp crops and field experiments which were part of the wider research programme investigating the potential of hemp as a new crop in the Netherlands.

The proportion of bark and the content of primary and secondary bast fibre

The stems analysed were obtained from field experiments conducted at Randwijk (near Wageningen) on a heavy river clay soil in 1990 and 1992. The 1990 experiments involved the monoecious French cultivar Fédrina 74 and the dioecious Hungarian cultivar Kompolti Hybrid TC, sown on 2 April and thinned to two densities, 10 and 90 plants m^{-2} , after emergence. Harvests took place at flowering (7 August for Fédrina 74, 28 August for Kompolti Hybrid TC) and at seed ripeness (18 September). During the growing season many plants died as a result of inter-plant competition ('self-thinning', Westoby 1984). On 18 September the densities were 10.3 and 36.3 plants m^{-2} for Fédrina 74 and 9.2 and 30.3 plants m^{-2} for Kompolti Hybrid TC. Samples of 20 (initial density 10 plants m^{-2}) or 40 (initial density 90 plants m^{-2}) plants were taken from each plot and used to determine the proportion of bark in the stem dry matter. A 3-plant sample was taken from each plot to determine the content of primary and secondary bast fibre. All plant samples were dried at 25 °C on a drying floor. The plants were defoliated and all branches were removed. The 20- and 40-plant samples were separated into bark and core by means of a flax breaker consisting of 7 pairs of fluted rollers. Stems were passed through the breaker three to five times, this broke the core into fragments 2 cm long or less. Shaking the tangled bark mass liberated most of the core fragments; the remaining core was removed by hand. Stems in the 3-plant samples were cut into 10 sections of equal length, which were numbered 1 (base) to 10 (top) and dried at 70 °C to constant weight. Then each section was submerged in a test tube containing 300 ml of a solution of 2 %

NaOH in water. The test tubes were placed in a 95-100 °C water bath for 20 minutes, after which the stem sections were rinsed with tap water. The primary bast tissue was carefully lifted from the stem section and thus separated from the secondary bast tissue which adhered to the xylem. Then the secondary bast tissue was removed from the xylem. Samples of primary and secondary bast tissue were macerated according to Jagels et al. (1982), and the fibre length of both tissues was determined with a microscope. Primary and secondary bast tissue were put into test tubes containing 75 ml of 2 % NaOH, which were placed in a 95-100 °C water bath for two hours and then put on a 0.5 mm sieve and the non-fibre material was removed using a strong jet of water. The dry weight of the primary and secondary fibre was determined after drying at 105 °C for 24 hours.

The 1992 experiment involved the cultivar Kompolti Hybrid TC, sown at five plant densities (0.3, 10, 30, 90 and 230 plants m⁻²) on 24 April. On 1 July, 3 and 31 August 2 plants from each plant density were harvested, defoliated and their stems manually separated into bark and core, which were dried at 105 °C. During the growing season many plants died from self-thinning at the two highest densities, on 10 August densities were 78 (initial density 90 plants m⁻²) and 140 (initial density 230 plants m⁻²).

Chemical composition of bark and core

The chemical composition of bark and core was determined in stems of French and Hungarian cultivars grown at various locations in the Netherlands in various years. The French cultivars were Fibrimon 56 (grown in Wageningen in 1987) and Fédora 19 (grown in Randwijk in 1989) and the Hungarian cultivars were Kompolti Sárgaszárú (grown in Randwijk in 1989 and in Nagele in 1990) and Kompolti Hybrid TC (grown in Randwijk in 1990). Plant density at harvest varied between 40 and 100 plants m⁻². At harvest the top metre of the plant was cut off and discarded. The leaves were removed and the stems were then dried on a drying floor at 25 °C. A 50 g sample of dry stem was separated manually into bark and core. Bark and core material was analysed according to TAPPI standards (TAPPI 1988). The samples were pretreated (T-257, codes in brackets refer to TAPPI procedures); a Wiley-type mill equipped with a 0.5 mm round hole screen was used for grinding. The milled material was used to determine the 1 % NaOH solubility (T-212), which is a measure of the proportion of readily degradable material (e.g. parenchyma cells), and has been shown to correlate with the proportion of non-fibre material in the bark (De Meijer & van der Werf, 1994). The ground material was also used to determine the moisture content of the samples and to prepare extractive-free samples (T-264, ethanol/benzene-ethanol-hot water extractives) to be used for lignin and carbohydrate determinations. The total lignin content was calculated as the sum of the Klason lignin content (T-222) and the acid-soluble lignin content (T UM-250). Carbohydrates were determined as alditol-acetates of hydrolysed and reduced samples

according to T-249. In T-249 all carbohydrate contents are reported as if they were present in the homo polymer form: glucose as glucan, xylose as xylan etc. The glucose content is presented as cellulose content, disregarding the glucose derived from hemicellulose, this introduces an error of 1 % to 3 % (Harsveld van der Veen, unpublished results). Hemicellulose was calculated as the sum of the arabinan, xylan, galactan and mannan contents. This implies that hemicellulose content is underestimated (by about 1 % in the bark and 4 % in the core; Harsveld van der Veen, unpublished results), because formyl and acetyl groups are lost during hydrolysis. Components which were not determined will be referred to as "unspecified" and probably comprise proteins, pectins and other uronic acids, carbohydrates other than those measured, and formyl and acetyl groups lost during hydrolysis. In accordance with TAPPI procedures, the contents were determined in extractive-free material. Since the amount of EtOH/benzene-EtOH-hot water extractives varied, we expressed all contents on sample dry matter before extraction.

RESULTS AND DISCUSSION

The proportion of bark in the stem

In 1990 the proportion of bark in the dry matter of the stem ranged from 30 % to 35 % and depended on genotype, plant density and development stage at harvest (Table 1). These results partly confirm those of Bredemann (1952) on the effect of genotype and of Jakobey (1965) on the effect of plant density. Our findings, however, showed that there were interactions between development stage and plant density and between development stage and cultivar. In plants grown at an initial density of 10 m⁻², the proportion of bark in the stem was not affected by development stage; in plants grown at an initial density of 90 m⁻² the proportion of bark in the stem was greater at flowering than at seed ripeness. In Kompolti Hybrid TC the bark content was high at both harvests, in Fédrina 74 the bark content was lower at seed ripeness than at flowering. The effect of harvest date on the proportion of bark in the stem dry matter depended on plant density as well as on cultivar in this experiment.

In 1992 the proportion of bark in the dry matter of the stem of Kompolti Hybrid TC decreased from 42.7 % on 1 July to 36.6 % on 31 August (Figure 1). The absence of an effect of plant density on bark content in this experiment may have been the result of the small sample size (2 plants per density on each harvest date).

As discussed in the introduction, the proportion of bark is the principal quality parameter of the stem. Its assessment is essential, as it varies with crop age, cultivar and plant density.

Table 1. The effect of initial plant density, cultivar and development stage on the proportion of bark in the stem dry matter (%) in 1990.

Development stage	Plants m ⁻²		Cultivar	
	10	90	Hybrid TC	Fédrina 74
Flowering	31.9	34.1	34.7	31.2
Seed ripe	31.6	32.5	34.3	29.7

LSD (0.05) within plant density or cultivar is 0.7, LSD (0.05) for other comparisons is 1.1.

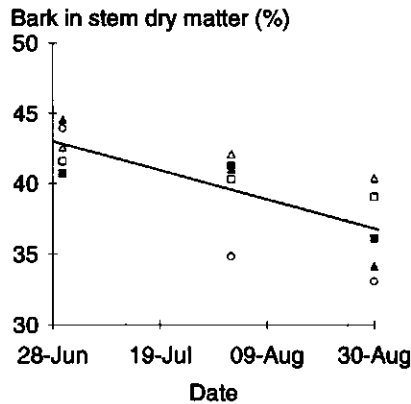


Figure 1. The proportion of bark in the stem of plants of the hemp cultivar Kompolti Hybrid TC grown at initial densities of 0.3 (open circles), 10 (open triangles), 30 (black triangles), 90 (open squares) and 230 (black squares) plants m⁻² and harvested on three dates in 1992. Data are averages of two plants.

Regression equation: $y = 61.0 - 0.100x$ ($p < 0.001$, 40.3 % of variance accounted for)

Bast fibre content and the proportion of secondary bast fibre

In both cultivars and at both plant densities the dry weight of the 10 sections into which the stem had been divided decreased from the base (section 1) to the top (section 10) of the plant. The difference between the lower and the upper sections was greater at 10 plants m⁻² than at 90 plants m⁻² (Table 2). These results agree with those of Bredemann (1940). In section 1, the bast fibre content was lower than the mean bast fibre content of the entire stem, but in sections 3, 4, and 5 it was higher. From sections 6 to 10 the bast fibre content decreased (Table 2). These results agree with those of Kraus & Biltz (1922) and Bredemann (1940), but contradict those of Heuser (1927) and Arnoux et al. (1969) who found that bast fibre content increased from the base to the top of the plant.

In the primary bast tissue the fibres were longer than 5 mm, in the secondary bast tissue they were about 2 mm. The proportion of secondary bast fibre in the total bast fibre was highest at the base of the plant and decreased towards the top of the plant (Table 2) confirming results obtained by Senchenko & Tarakan (1970) and Farago (1971). No relation was found between stem bast fibre content and stem weight or stem diameter (data not shown). Linear regression showed that stem weight accounted for 55.7 % of the variance in secondary bast fibre content. The proportion of secondary bast fibre in the total bast fibre increased from 10 % at a stem weight of 10 g to 45 % at a stem weight of 170 g (Figure 2). Stem diameter accounted for

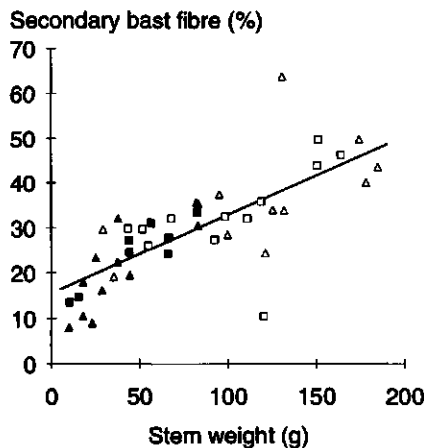


Figure 2. The relationship between the proportion of secondary bast fibre in the total bast fibre of the stem and stem dry weight of plants of the hemp cultivars Fédrina 74 (squares) and Kompolti Hybrid TC (triangles) grown at initial densities of 10 (open symbols) and 90 (black symbols) plants m⁻² in 1990.

Regression equation: $y = 15.5 + 0.174 x$ ($p < 0.001$, 55.7 % of variance accounted for)

Table 2. Proportion of total stem dry weight, bast fibre in stem dry matter (g/kg) and secondary fibre in bast fibre dry matter (g/kg) in 10 stem sections. Stems were divided in 10 sections of equal length. Section 1 is the base and 10 is the top of the plant. Data from two hemp cultivars grown at initial densities of 10 and 90 plants m⁻² in 1990.

Cultivar	Plant density (m ⁻²)	Observation	Stem section							Whole stem				
			1	2	3	4	5	6	7	8	9	10		
Hybrid TC	10	% of total stem	22.4	16.7	14.2	12.2	10.4	8.6	6.9	4.8	2.8	1.0		
		Bast fibre	222	245	246	248	244	231	202	168	156	117	229	
	90	Secondary fibre	633	392	322	277	274	265	218	141	48	0	365	
		% of total stem	18.8	15.7	14.0	12.5	11.1	9.4	7.6	5.6	3.7	1.6		
Fédrina 74	10	Bast fibre	219	233	252	255	254	249	233	205	172	133	236	
		Secondary fibre	517	256	174	148	121	110	88	54	4	0	214	
	90	% of total stem	20.4	16.2	13.9	12.3	10.9	9.2	7.3	5.5	3.2	1.1		
		Bast fibre	166	196	200	199	194	186	178	168	155	124	184	
90	Secondary fibre	647	371	297	261	214	199	196	163	77	0	329		
	% of total stem	18.6	15.5	13.3	11.9	10.8	9.8	8.2	6.0	4.1	1.8			
90	Bast fibre	158	186	207	208	209	207	200	191	158	125	190		
	Secondary fibre	572	339	190	164	156	153	159	110	25	0	245		

about 50 % of the variance in the proportion of secondary bast fibre in the total bast fibre (Table 3). An increase in the proportion of secondary bast fibre in the bark will reduce the mean length of the bark fibres, which might reduce the bark's value for paper making. Unfortunately, we were unable to find any reports quantifying the influence of secondary fibre content on paper making properties.

Bast fibre content in stem sections 3, 4 and 5 accounted for up to 95 % of the variance of bast fibre content in the entire stem (Table 3). Stem section 3 is the most appropriate sample to characterize secondary fibre, as it accounted for 92 % of the variance of secondary bast fibre in the bast fibre of the entire stem, which was more than any of the other sections accounted for (Table 3). This partly confirms findings of Arnoux et al. (1969), who measured only total bast fibre content and found the section situated between 30 % and 40 % of the height of the plant (section 4) to be most representative of the entire stem. Neither cultivar nor plant density affected the relationship between segment content and stem content of total bast fibre (Figure 3) or of secondary bast fibre (Figure 4).

In conclusion, when information on both total bast fibre content and secondary fibre content of hemp stems is needed, sampling the section between 20 % and 30 % of the height of the stem will give a good approximation of the contents in the entire stem.

Table 3. Percentages of variance accounted for by the regression of % bast fibre in stem dry matter (BF-stem) and % secondary bast fibre in total bast fibre (SEC-stem) on % bast fibre, % secondary bast fibre in total bast fibre and diameter of nine stem sections (BF-section, SEC-section and DIA-section, respectively). Hemp stems were divided in 10 sections of equal length, sections 1 and 10 are the base and the top of the plant. Data from two hemp cultivars grown at initial densities of 10 and 90 plants m⁻² in 1990.

Regression of	Stem section								
	1	2	3	4	5	6	7	8	9
BF-stem on BF-section	89.8	89.7	95.0	94.7	94.9	91.0	59.8	31.8	14.5
SEC-stem on SEC-section	73.4	86.5	92.1	88.2	85.9	77.6	63.5	59.5	36.3
SEC-stem on DIA-section	56.3	54.5	49.9	53.7	52.5	50.7	56.4	48.9	53.7

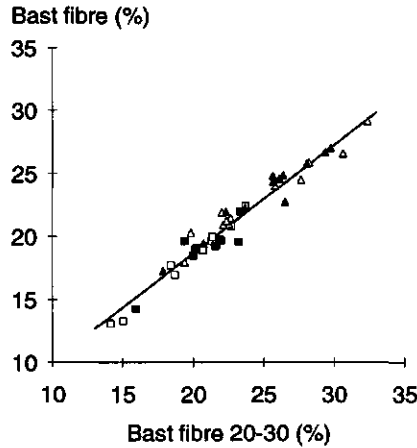


Figure 3. The relationship between the bast fibre content in the stem and in a stem section situated between 20 % and 30 % of the height of the stem of plants of the hemp cultivars Fédrina 74 (squares) and Kompolti Hybrid TC (triangles) grown at initial densities of 10 (open symbols) and 90 (black symbols) plants m^{-2} in 1990.

Regression equation: $y = 1.45 + 0.862 x$ ($p < 0.001$, 95.0 % of variance accounted for)

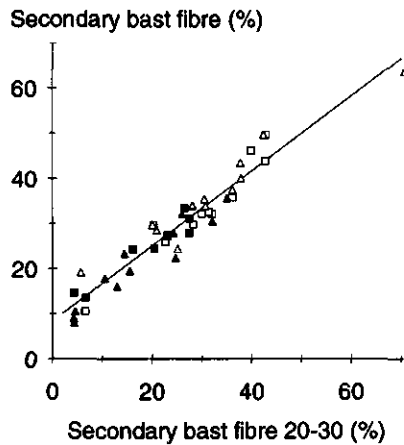


Figure 4. The relationship between the proportion of secondary bast fibre in the total bast fibre of the stem and in the total bast fibre of a stem section situated between 20 % and 30 % of the height of the stem of plants of the hemp cultivars Fédrina 74 (squares) and Kompolti Hybrid TC (triangles) grown at initial densities of 10 (open symbols) and 90 (black symbols) plants m^{-2} in 1990.

Regression equation: $y = 8.39 + 0.831 x$ ($p < 0.001$, 92.1 % of variance accounted for)

Chemical composition of bark and core

Bark and core showed different chemical compositions (Table 4). The mean cellulose content of bark was 64.8 %, of core it was 34.5 %. The mean hemicellulose and lignin contents were 7.7 % and 4.3 % in bark and 17.8 % and 20.8 % in core. In the French cultivars the content of unspecified (not determined) components was similar for bark and core, in the Hungarian cultivars it was higher in the core than in the bark. Our results for cellulose and lignin confirm those of Bedetti & Ciarelli (1976), but they found higher hemicellulose contents: 13 % in bark and 31 % in core. Bedetti & Ciarelli, however, defined hemicellulose as those components other than cellulose, Klason lignin and extractives, which make up a large proportion of the substances we did not specify. In our study the EtOH/benzene-EtOH-hot water extractives were higher in bark than in core. The 1 % NaOH solubility was somewhat higher in core than in bark, suggesting a higher content of readily degradable material in core than in bark.

The cellulose contents in the bark of the French cultivars Fibrimon 56 and Fédora 19 were 53.2 % and 58.6 % respectively; in the Hungarian Kompolti cultivars this content was between 68.2 % and 74.3 % (Table 4). This suggests a higher yield after chemical pulping from bark of the Kompolti cultivars. Bedetti et al. (1979) found that the cellulose content in the bark was lower in the cultivar Fibrimon 56 than in the Italian cultivars. As the Kompolti cultivars were selected from Italian hemp (De Meijer & van Soest 1992), our findings confirm those of Bedetti et al. (1979). The contents of hemicellulose and lignin in the bark varied, but were not affected by cultivar.

The cellulose content of the core (31.5 % to 37.4 %) was less variable than that of the bark (53.2 % to 74.3 %). The hemicellulose and lignin content in the core scarcely varied (Table 4). In Kompolti Hybrid TC the cellulose content of the bark increased during the growing season, reflecting the growth of the fibre cell walls. The increase in cellulose content coincided with a decrease of the 1 % NaOH solubility and of the content of extractives. The lignin content in the bark decreased in the course of the growing season. The contents of cellulose, hemicellulose and lignin of the core were lower in young plants of Kompolti Hybrid TC (harvested on 20 June) than in mature plants; extractives and 1 % NaOH solubility were higher in young plants than in mature plants.

In conclusion, bark and core differ greatly in chemical composition; this is reflected in all parameters measured here except for the 1 % NaOH solubility. Harvest date affected the chemical composition of bark and, to a lesser extent, of core. Cultivar affected the chemical composition of bark only. In terms of the cellulose content, hemp stems harvested after flowering yielded the most favourable raw material for paper making.

Table 4. Chemical composition of hemp bark and core (%).

Harvest date	Cultivar	Cellulose		Hemicellulose		Lignin		T-264 ¹⁾		T-212 ²⁾		Unspecified ³⁾	
		bark	core	bark	core	bark	core	bark	core	bark	core	bark	core
12-10 1987	Fibrimon 56	53.2	31.9	6.9	18.6	5.0	20.8	9.3	7.5	29.3	28.8	20.1	21.2
9-10 1989	Fédora 19	58.6	34.7	9.3	19.3	5.0	20.3	9.3	7.5	28.0	30.1	17.8	18.2
9-10 1989	Kompolti Sárgaszárú	69.2	31.5	8.5	16.8	5.5	20.1	9.3	7.5	27.4	29.4	7.5	24.1
15-08 1990	Kompolti Sárgaszárú	68.2	37.4	6.7	18.0	3.5	21.8	9.3	7.8	30.5	34.4	12.3	15.0
20-06 1990	Kompolti Hybrid TC	60.2	31.9	7.1	15.6	4.4	19.1	19.8	15.8	38.4	41.1	8.5	17.6
26-08 1990	Kompolti Hybrid TC	69.7	37.0	7.8	17.8	3.6	21.7	13.4	8.2	31.4	32.3	5.5	15.3
26-09 1990	Kompolti Hybrid TC	74.3	37.2	7.9	18.5	3.3	21.7	9.3	7.5	29.8	32.2	5.2	15.1
Mean		64.8	34.5	7.7	17.8	4.3	20.8	11.4	8.8	30.7	32.7	11.0	18.1
Standard deviation		7.5	2.7	0.9	1.2	0.9	1.0	4.0	3.1	3.7	4.3	6.0	3.5

1) EtOH/benzene-EtOH-hot water extractives

2) 1 % NaOH solubility

3) Not determined, calculated by difference of weight

CONCLUSIONS

Regarding the suitability for paper making, the following can be concluded. As a result of their large morphological and chemical differences, hemp bark and core differ greatly in quality and should be considered as two different types of raw material. As the bark content in the stem varies, to assess the quality of hemp stems breeders and agronomists must measure the proportion of bark in the stem. Determining the cellulose, hemicellulose and lignin content of bark and core using TAPPI procedures and determining the secondary fibre content of the bark yields further useful information on stem quality.

ACKNOWLEDGEMENTS

The authors thank P Kolster, A J Haverkort, P C Struik and W J M Meijer for helpful comments on the manuscript. We also gratefully acknowledge M J E M van Mensvoort, M de Vries, M Wijlhuizen and J C van der Kolk for their technical support.

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**THE EFFECT OF TEMPERATURE ON LEAF
APPEARANCE AND CANOPY ESTABLISHMENT IN
FIBRE HEMP (*Cannabis sativa* L.)**

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appeared. The pots were watered by hand from above the soil surface. Watering depended on evapotranspiration and it tended to be more frequent at higher temperatures.

The floor space of the growth chambers was 14 m², the light source in the chambers consisted of 18 Philips SON-T lamps and 18 Philips HPI-T lamps. Light intensity at plant level was about 110 (Exp. 1) and 90 (Exp. 2) W m⁻² (400-700 nm). The plants were grown under a 16/8 h (day/night) photoperiod and thermophase regime, relative humidity was maintained at 70%. Each chamber contained 30 pots, arranged in a rectangle of five by six pots. Plant density was about 60 (Exp. 1) or 40 (Exp. 2) m⁻². The pots on the outer edges of the rectangle were not used for measurements.

Experiment 1 had one constant temperature (19 °C) and three differential day/night temperature regimes (12/6, 19/10 and 26/14 °C), which corresponded to daily mean temperatures of 10, 16 and 22 °C. Experiment 2 had four constant temperatures (13, 19, 25 and 28 °C) and three differential day/night temperature regimes (12/6, 18/12 and 24/18 °C), theoretically corresponding to daily mean temperatures of 10, 16 and 22 °C. However, for the 18/12 °C temperature regime the night temperature was not controlled perfectly; on several occasions it was 17 °C instead of 12 °C. As a result, average daily mean temperature was actually 16.5 °C.

The experimental period extended from sowing to the 10-leaf stage (Exp. 1) or the 12-leaf stage (Exp. 2). The *n*-leaf stage is defined as the stage at which the leaves of the *n*th pair of leaves (not counting the cotyledons) are 1 cm long. In Experiment 1, plant height was measured in 12 plants at the 2-, 4-, 6-, 8- and 10-leaf stage; in Experiment 2 plant height was measured in 12 plants at all leaf stages from the 1- until the 12-leaf stage.

For each regime the rate of leaf appearance (RLA) was calculated as the slope of the linear regression of the cumulative number of leaf pairs on time. Logistic equations relating plant height to time were fitted to the data for each temperature, and weighted mean rates of stem elongation (RSE) were calculated from the parameters of the equations (Milford & Riley 1980). Temperature coefficients for RLA and RSE were calculated as the slopes of the regression of these parameters on temperature. Base temperatures for RLA and RSE were estimated by extrapolating the relationships to their intercepts with the temperature axis. Confidence intervals for base temperatures were calculated as in Sokal & Rohlf (1981).

Field experiments

The field experiments were carried out in 1990, 1991 and 1992 at Valthermond in north-east Netherlands on a peaty sand soil. The experimental set-up was a split-plot with three replications. Sowing dates were in the main plots, cultivars in sub-plots. The sub-plots were 14 m long and 3 m wide. The main plots were guarded on both sides by a 3 m-wide strip of hemp. The sowing dates were 19 March, 2 and 17 April and 1 May in 1990; 20 March, 9 and

25 April and 22 May in 1991; 25 March, 21 April and 6 May in 1992. On 29 May 1990 a -7 °C ground frost damaged the crops sown on 2 and 17 April, so data from these crops were not used in the analyses. On all sowing dates in each year except for 20 March 1991 three cultivars were sown: the French monoecious cultivar Fédrina 74 and the Hungarian dioecious cultivars Kompolti Hybrid TC and Kompolti Sárgaszárú. On 20 March 1991 only Fédrina 74 was sown; in 1992 the French monoecious cultivar Futura 77 (which is similar to Fédrina 74) was used instead of Fédrina 74.

P and K fertilizers were applied somewhat in excess of recommendations for arable crops, in order to avoid shortage of P and K limiting yields. N fertilizer was applied at rates of 100 kg ha⁻¹ in 1990 and 1991, and 120 kg ha⁻¹ in 1992. Herbicides were not used, as weeds were generally suppressed by the crop; when necessary, weeds were removed by hand. To prevent the occurrence of *Botrytis cinerea* and *Sclerotinia sclerotiorum* the crop was sprayed with fungicides (alternating vinchlozolin at 500 g ha⁻¹ and iprodion at 500 g ha⁻¹) at 14-day intervals during June, July and August. Crops were sown at 4 cm depth with a studded roller seed drill at 12.5 cm row width.

After sowing, the density of emerged plants was counted every two or three days, and the date of 50 % plant emergence was estimated by interpolation. For the crops sown on 1 May 1990, 25 April 1991 and 6 May 1992 50 % plant emergence had occurred before the first counting. For these crops, the date of 50 % plant emergence was estimated from the thermal time from sowing to emergence that had been required at the other sowing dates. In the 1- or 2-leaf stage the crops were hand thinned to a density of 64 plants m⁻². From thinning until canopy closure, leaf stage was determined at 7- or 14-day intervals. At those times the interception of photosynthetically active radiation (PAR) by the canopy was measured with a line sensor (Technical and Physical Engineering Research Service TFDL-DLO, Wageningen, the Netherlands). About five measurements were taken above and below the canopy per plot. Measurements of leaf stage and light interception continued until at least 95 % interception of PAR was reached. The last date on which measurements were taken was 4 July in 1990, 10 July in 1991 and 23 June in 1992.

The experimental period extended from the end of March (the earliest sowing date) until the end of June or the beginning of July (the last measurements). In 1990 this period was 0.6 °C warmer than normal (the 30-year average), in 1991 it was 0.7 °C colder than normal and in 1992 it was 1.8 °C above normal (Table 1, next page). In each of the three years, the crops sown on the first date (March) experienced lower temperatures than the crops sown on the last date (May): see Table 1. Average air temperatures over 10 days ranged between 4.7 and 20.6 °C. Daily mean air temperatures were calculated as the average of daily minimum and maximum air temperatures measured at Eelde meteorological station 35 km from the experimental site. Daily thermal time (t') was calculated as:

$$t' = \{(T_a - T_b); \text{ or } 0 \text{ if } (T_a < T_b)\}$$

where T_a is the daily mean air temperature and T_b is the base temperature. The base temperature for leaf appearance was estimated from the linear regression of leaf stage on

After an initial exponential phase, at all temperatures in both experiments stem length increased approximately linearly with time up to the last measurement (Figure 3). The weighted mean rate of stem elongation increased linearly with temperature between 10 and 28 °C (Figure 4). The estimated base temperature for stem elongation was 2.5 °C, with a 95 %-confidence interval from -3.7 to 6.7 °C.

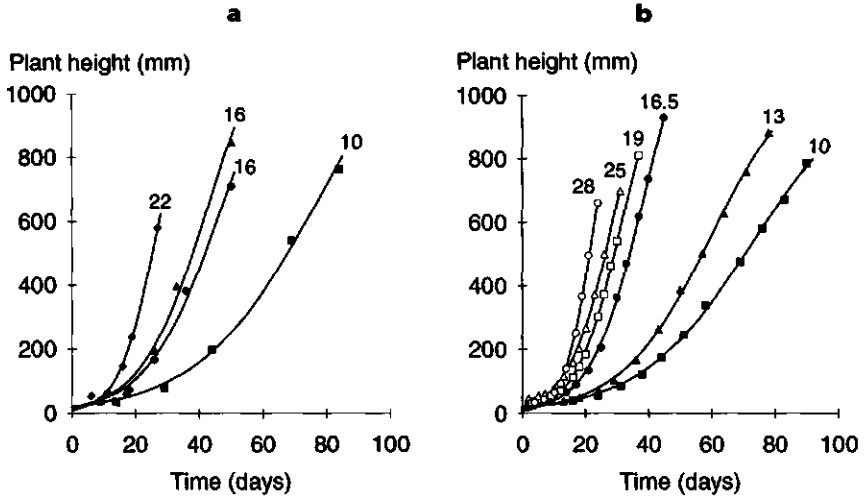


Figure 3. Stem length versus days from emergence for hemp plants grown at different temperatures, a) Exp. 1, b) Exp. 2. Mean temperatures (°C) are indicated for each curve.

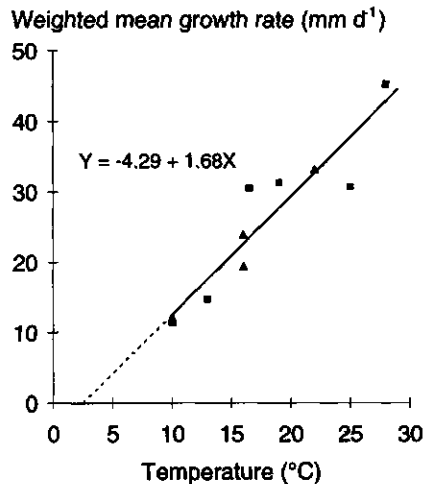


Figure 4. Weighted mean rate of stem elongation versus mean temperature. Triangles Exp. 1, squares Exp. 2, 85.3 % of variance accounted for.

Field experiments

The number of days between sowing and emergence ranged from 7 to 16; the average was 10.9 (Table 2). Thermal time (base 0 °C) between sowing and emergence ranged from 68 to 109.5 °Cd, the average was 88.3 °Cd. Results did not differ statistically significantly for the three cultivars. Coefficients of variation (CVs) were about 30 % for days between sowing and emergence, and were about half as large for thermal time between sowing and emergence (Table 2). For all three cultivars the CVs for thermal time between sowing and emergence were smallest at base temperatures 0 and 1 °C and greatest at higher base temperatures (Table 3).

Table 2. Days and thermal time (base 0 °C) between sowing and 50 % plant emergence for fibre hemp cultivars Fédrina 74, Kompolti Hybrid TC (HTC) and Kompolti Sárgaszárú (Sár.).

Year	Sowing date	Days to 50 % emergence			°Cdays to 50 % emergence		
		Fédrina	HTC	Sár.	Fédrina	HTC	Sár.
1990	19 March	13	12	14	97.1	87.0	109.5
1991	9 April	11	9	10	101.8	95.4	99.0
	22 May	7	7	7	68.0	68.0	68.0
1992	25 March	16	15	15	90.8	83.7	83.7
	21 April	9	9	10	88.0	88.0	96.4
Mean		11.2	10.4	11.2	89.1	84.4	91.3
Coefficient of variation		31.3	29.8	29.5	14.6	12.0	17.4

Table 3. The effect of base temperature on thermal time (°Cdays) between sowing and 50 % plant emergence and its coefficient of variation (CV) for 3 hemp cultivars.

Base temperature	Fédrina 74		Kompolti H. TC		K. Sárgaszárú	
	°Cdays	CV	°Cdays	CV	°Cdays	CV
0	89.1	14.6	84.4	12.0	91.3	17.4
1	77.9	14.4	74.0	13.1	80.1	18.2
2	66.8	15.4	63.6	16.1	68.9	20.1
3	55.9	18.3	53.5	21.0	58.0	23.1
4	45.4	24.6	43.5	28.7	47.3	28.5
5	36.1	33.2	34.7	37.8	37.8	35.5

After emergence, leaves appeared at an average rate of 0.152 pairs of leaves d^{-1} , which corresponds to one pair every 6.6 days (Figure 5a). However, rate of leaf appearance varied, e. g. at 40 days after emergence between four and ten pairs of leaves were present. Days from emergence accounted for 84.2 % of the variance in leaf stage, whereas thermal time from emergence (base 1 °C) accounted for 97.8 % of the variance in leaf stage (Figure 5b). Leaves appeared at a rate of 0.0149 pair of leaves $^{\circ}Cd^{-1}$. The thermal time required for the appearance of a single leaf (a phyllochron) was 33.5 $^{\circ}Cd$ (base 1 °C).

The base temperature that yielded temperature sums that best accounted for the variation in leaf number was 1.40 (± 0.50) °C for Fédrina 74, 0.78 (± 0.78) °C for Kompolti Hybrid TC and 1.28 (± 0.65) for Kompolti Sárgászárú. As the base temperatures of the cultivars did not differ statistically significantly, the data for the three cultivars were combined, and a base temperature of 1 °C was used, because it was an approximate average. For every cultivar the leaf stage was regressed on thermal time using a base temperature of 1 °C and, to allow comparison with the results obtained under controlled conditions, at a base temperature of 5.7 °C (Table 4). At a base temperature of 1 °C, regression accounted for about 98 % of the variance in leaf stage, compared with 93 to 94 % at a base temperature of 5.7 °C (Table 4). At both base temperatures the slope of the regression was steeper for Fédrina 74 and Kompolti Sárgászárú than for Kompolti Hybrid TC, i. e. phyllochron was larger for Kompolti Hybrid TC than for the other two cultivars (Table 4). For Kompolti Hybrid TC the phyllochrons were 35.1 $^{\circ}Cd$ (base 1 °C) and 22.6 $^{\circ}Cd$ (base 5.7 °C).

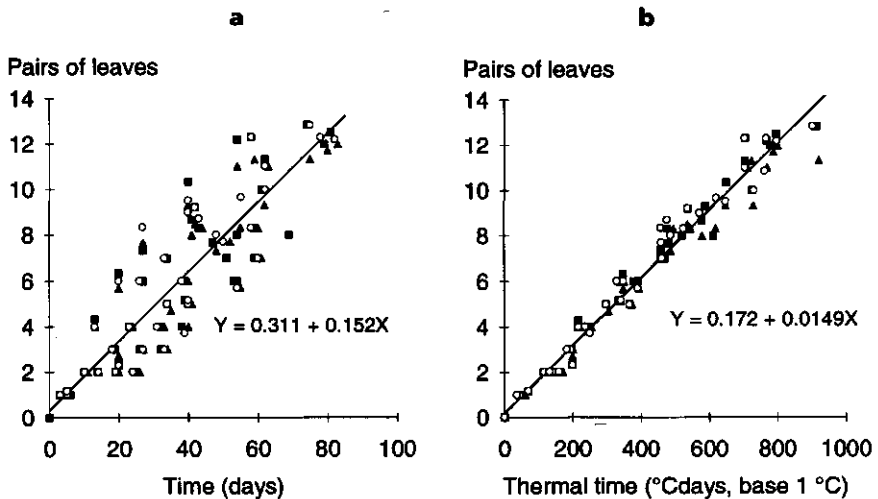


Figure 5. Pairs of leaves for hemp plants sown in the field in 1990, 1991, and 1992. a) versus days from emergence, b) versus thermal time from emergence (base 1 °C). Cultivars: Fédrina 74 (squares), Kompolti Hybrid TC (triangles) and Kompolti Sárgászárú (circles).

The number of days required from emergence to reach a closed canopy (> 90 % intercepted PAR) varied between 27 and 69; at 20 days after emergence the PAR intercepted by the canopy varied between 10 and 80 % (Figure 6). The days from emergence accounted for

Table 4. Linear regressions of pairs of leaves (y) on thermal time from emergence (x) with base temperatures 1 °C and 5.7 °C for hemp cultivars Fédrina 74, Kompolti Hybrid TC and Kompolti Sárgaszárú. Equations of the form $y = a + bx$, standard errors are shown in brackets.

Base	Cultivar	a	b	% of variance accounted for	Phyllochron (°Cd)
1 °C	Fédrina 74	0.125 (0.123)	0.0153 (0.0003)	98.2	32.7
	Kompolti H. TC	0.226 (0.134)	0.0143 (0.0003)	97.8	35.1
	K. Sárgaszárú	0.176 (0.138)	0.0152 (0.0003)	97.9	32.8
5.7 °C	Fédrina	0.752 (0.222)	0.0240 (0.0009)	93.3	20.8
	Kompolti H. TC	0.775 (0.222)	0.0222 (0.0009)	93.1	22.6
	K. Sárgaszárú	0.738 (0.219)	0.0237 (0.0009)	94.0	21.1

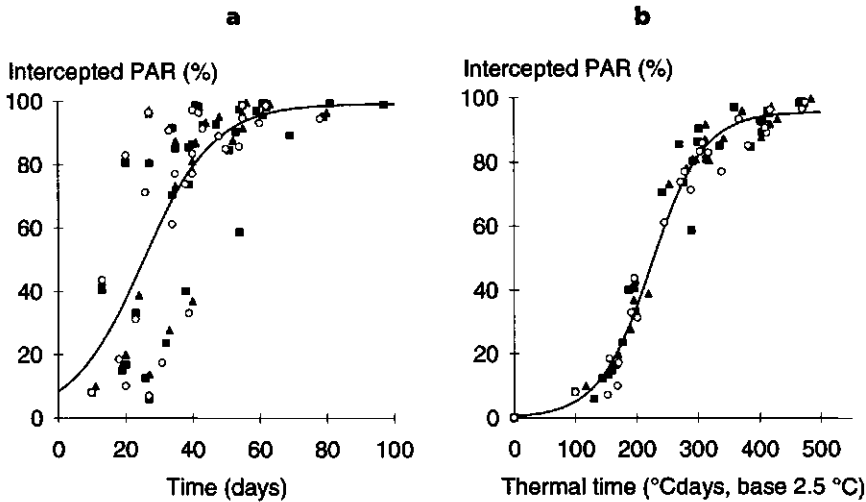


Figure 6. Percentage of photosynthetically active radiation (PAR) intercepted by the canopy of hemp crops sown in the field in 1990, 1991, and 1992. a) versus days from emergence, b) versus thermal time (base 2.5 °C). Cultivars: Fédrina 74 (squares), Kompolti Hybrid TC (triangles) and Kompolti Sárgaszárú (circles).

Table 5. Regressions of the percentage of photosynthetically active radiation intercepted by the canopy (y) on time (x = days) or thermal time (x = °Cdays) from emergence for hemp cultivars Fédrina 74, Kompolti Hybrid TC and Kompolti Sárgaszárú. Equations of the form $y = C/(1 + e^{-b(x-m)})$, standard errors are shown in brackets.

Cultivar	x	Base temperature (°C)	C (%)	b	m (°Cd or d)	Variance accounted for (%)
All three	d		99.3 (6.1)	0.0942 (0.0204)	25.3 (2.1)	53.5
	°Cd	0	96.0 (1.0)	0.0180 (0.0009)	299 (3.6)	97.7
	°Cd	2.50	95.6 (0.8)	0.0232 (0.0009)	224 (2.2)	98.6
Fédrina 74	°Cd	2.70	95.8 (1.5)	0.0232 (0.0023)	218 (14)	98.1
Kompolti H. TC	°Cd	2.23	96.5 (1.1)	0.0230 (0.0015)	229 (9)	99.2
K. Sárgaszárú	°Cd	2.57	94.5 (1.4)	0.0234 (0.0020)	225 (12)	98.7

53.5 % of the variance in % of PAR intercepted, compared with 97.7 % (base 0 °C) or 98.6 % (base 2.5 °C) for thermal time from emergence (Table 5). The thermal time required to reach 90 % interception of PAR was 465 °Cd (base 0 °C) or 340 °Cd (base 2.5 °C).

The base temperature which yielded the best fit for the regression of % PAR intercepted by the canopy on thermal time was 2.70 (\pm 0.47) °C for Fédrina 74, 2.23 (\pm 0.30) °C for Kompolti Hybrid TC and 2.57 (\pm 0.40) for Kompolti Sárgaszárú (Table 5). The three cultivars did not differ statistically significantly for base temperature, or with respect to the parameters of the logistic equation relating the percentage of intercepted PAR to thermal time (Table 5).

DISCUSSION

Base temperatures of 0 and 1 °C gave the smallest CVs for the calculation of thermal time from sowing to 50 % plant emergence in the field. This agrees well with the minimum temperature of 1-2 °C given by Haberlandt (1879) for the germination of hemp seed. On average, 88.3 °Cd (base 0 °C) was required from sowing to 50 % plant emergence; this is close to the value of 96 °Cd (base 0 °C) given by Tamm (1933) for the germination and emergence of hemp. For germination and emergence, therefore, our field trials confirm the few results available on the effect of temperature on hemp.

A base temperature for leaf appearance of 5.7 °C and a phyllochron of 21.9 °Cd were estimated from the growth chamber experiments for Kompolti Hybrid TC. From the field experiments, a base temperature for leaf appearance of about 1 °C and a phyllochron of 35.1 °Cd were estimated. Using a 5.7 °C base temperature, the field experiments yielded a

22.6 °Cd phyllochron. With regard to the thermal time required for the appearance of a leaf, the results obtained in the growth chambers agree closely with those obtained in the field, as phyllochrons were similar when the same base temperature was used. However, the estimated base temperature was much lower for the field data than for the results from the growth chamber experiments. As the relationship between temperature and development rate is sigmoid rather than linear, the estimate of the base temperature will depend on the range of temperatures investigated (Arnold 1959). Arnold (1959) and Angus et al. (1981) pointed out that a shift of the temperature range investigated from the linear middle section of the sigmoid curve towards the lower tail, will lead to a lower estimated base temperature. In our experiments, the plants in the field were exposed more to low temperatures (< 10 °C) and less to high temperatures (> 20 °C) than the plants in the growth chambers, and this probably caused the lower estimated base temperature. Clearly, the 1 °C base temperature estimated from the field trials will be most appropriate for describing development during canopy establishment in the cool spring weather of the Netherlands, because it accounted for more of the variance in leaf stage than other base temperatures. The base temperature estimated from the growth chamber experiments is not realistic, because it was obtained by linear extrapolation into a temperature range in which the relationship between temperature and development rate was probably curved rather than linear.

The comparison of field results and growth chamber results is straightforward for development (leaf appearance), but for growth the two sets of data cannot be simply compared. In the field, the course of PAR interception by the canopy was measured, whereas in the growth chambers stem elongation was measured. Nevertheless, the estimated base temperatures for canopy establishment in the field and for stem elongation in the growth chambers were both 2.5 °C.

In the growth chamber experiments, estimates of the base temperatures for growth and development were not statistically significantly different. In the field experiments the base temperature for growth (canopy establishment) was statistically significantly higher than the base temperature for development (leaf appearance), although the actual difference was not large (2.5 vs 1 °C). This result agrees with findings by Milford et al. (1985) for sugar beet: a base temperature of 3 °C for growth (leaf expansion), and of 1 °C for development (leaf appearance).

In the field experiments, thermal time, calculated with the appropriate base temperature, accounted for about 98 % of the variance in leaf stage and for 98.6 % of the variance in the proportion of PAR intercepted by the canopy. For both leaf appearance and PAR interception, days from emergence accounted for much less of the variance than thermal time. In earlier experiments (Chapter 2) 90 % interception of PAR was attained at 450 to 500 °Cd (base 0 °C) after emergence, in hemp crops grown at 86 to 114 plants m⁻². In the current experiments, plant density was 64 m⁻² and 90 % interception of PAR was attained on average at 465 °Cd after emergence. Thus the results of the earlier experiments are largely confirmed here and it can be concluded that thermal time is a simple and accurate tool for describing the course of leaf appearance and light interception capacity in field-grown hemp crops.

ACKNOWLEDGEMENTS

We thank J J Tick and W C A van Geel for help with collection and analyses of data. A J Haverkort and P C Struik are thanked for helpful comments on the manuscript.

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**THE EFFECT OF DAYLENGTH ON YIELD AND QUALITY
OF FIBRE HEMP (*Cannabis sativa* L.)**

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EUROPEAN JOURNAL OF AGRONOMY (in press)

ABSTRACT

Stem growth of the short-day plant fibre hemp (*Cannabis sativa* L.) decreases after flowering. In the Netherlands, the hemp cultivars currently available flower in August. In 1990 and 1991 the ambient daylength was compared with a 24-hour daylength in field experiments on two cultivars. Crop development, interception of photosynthetically active radiation, dry matter accumulation, stem yield and stem composition were recorded. The 24-hour daylength did not totally prevent flowering, but did greatly reduce the allocation of dry matter to floral parts. It enhanced the efficiency of post-flowering radiation use, and increased stem dry matter yield by 2.7 t ha⁻¹. The continued stem growth resulted in higher yields, which in one cultivar were accompanied by a lower bark content of the stem. At final harvest, the 1% NaOH solubility indicated a lower fibre content in the bark of plants from the 24-hour daylength. Breeding late-flowering hemp may be a promising strategy to improve the potential stem yield of hemp in the Netherlands, but the stem quality of such cultivars may be slightly poorer.

KEY WORDS: *Cannabis sativa* L., fibre hemp, photoperiod, daylength, flowering, stem yield, stem quality, radiation use efficiency.

INTRODUCTION

Photoperiodic induction of flowering was first shown by Tournois (1912) in hemp (*Cannabis sativa* L.) and Japanese hop (*Humulus japonicus* L.). Tournois demonstrated that flowering in hemp was hastened by short days and delayed by long days: hemp is a short-day plant.

Hemp is dioecious, but monoecious cultivars have been bred. The two sexes are morphologically indistinguishable before flowering. The first sign of a transition to flowering is the formation of undifferentiated flower primordia, which is accelerated by decreasing photoperiod, but occurs even under continuous illumination (Borthwick & Scully 1954, Heslop-Harrison & Heslop-Harrison 1969). In this respect hemp is a quantitative short-day plant. To produce open fertile flowers some cultivars require short days; in other cultivars flowering occurs in continuous light, but only after a protracted period of growth (Schaffner 1926, Borthwick & Scully 1954, Heslop-Harrison & Heslop-Harrison 1969). According to Borthwick & Scully (1954) the critical daylength may be longer for male plants than for female plants of the same cultivar.

In young hemp plants phyllotaxis is opposite, but as flowering begins phyllotaxis changes from opposite to alternate (Heslop-Harrison & Heslop-Harrison 1958). This change is considered to be the result of flower primordia interacting with leaf primordia at the apex (Bernier 1988).

Previous studies (Chapter 2) have shown that one of the factors limiting stem yield of fibre hemp in the Netherlands is the cessation of stem growth in early September in the currently available French and Hungarian cultivars. These cultivars flower in August, after which the

male plants die and in female and monoecious plants the assimilates are partitioned to the inflorescence. In France and Hungary precocious flowering is desired, as in these countries hemp is either harvested relatively early (August) or used for a dual purpose: stem and seed. In the Netherlands the aim is maximum stem yield, so a late genotype seems desirable.

We examined whether higher stem yields could be achieved from hemp crops which flowered later than normal. The results of this study will help in deciding on priorities in the fibre hemp breeding programme currently in progress in the Netherlands. The effect of delayed flowering on yield and quality of hemp was investigated by artificially prolonging daylength using halogen lamps.

MATERIALS AND METHODS

Field experiments were carried out in 1990 and in 1991. The experimental set-up was a split-split-plot with four replications. In 1991 one replication was discarded because poor soil structure had resulted in a patchy crop. Daylength treatments were in the main plots, cultivars in sub-plots and harvest dates in sub-sub-plots. The sub-sub-plots were 6 m long and 3 m wide; the centre 2 m x 1 m of each plot was harvested. Main plots were separated by 10 m of hemp serving as a buffer to ensure that artificial light did not affect main plots that received ambient daylength. The experiment was surrounded by a 6 m-wide buffer of hemp.

Daylength was prolonged by halogen lamps suspended above the canopy. The ratio of the photon fluence rate in the red to that in the far-red light of these lamps was 0.80. After sunset light intensity (400-700 nm) in the 24-hour daylength treatment was 1 to 1.4 W m⁻² at the top of the canopy. This corresponds to about 23 to 32 foot candles (ft.c.), which is well above the 0.03 ft.c. threshold light intensity required to inhibit flowering in hemp (Borthwick & Scully 1954). In 1990, daylength prolongation commenced on 2 July (interval between sunrise and sunset 16 h 38 min). Initially, daylength was prolonged to 18 h, as this did not completely prevent flowering, daylength was prolonged to 24 h on 13 August. In 1991 daylength was prolonged to 24 h from 22 June (interval between sunrise and sunset 16 h 44 min). In both years, lights were on during morning and evening twilight, and daylength prolongation continued until final harvest.

The 1990 growing season was warm, with May and August warmer than average; precipitation was normal. The 1991 growing season was of average temperature, but May and June were colder than average, whereas July was very warm, and August was warmer than average. In 1991 July was dry and August very dry.

Two cultivars were used: the French monoecious cultivar Fédrina 74 and the Hungarian dioecious cultivar Kompolti Hybrid TC. They were machine sown and manually thinned to a density of 90 plants m⁻² in the seedling stage. The sowing dates were 2 April 1990 and 17 April 1991 at the De Bouwing research farm at Randwijk, where the soil is a heavy river clay. Row width was 25 cm in 1990 and 12.5 cm in 1991. Plants were harvested at flowering

(first week of August for Fédrina 74 and last week of August for Kompolti Hybrid TC) and at seed ripeness (late September). In 1990 Fédrina was harvested on 7 August and Kompolti Hybrid TC on 28 August, and all treatments were harvested on 26 September. In 1991 all treatments were harvested on 6 August, 26 August and 23 September.

P and K fertilizers were applied somewhat in excess of recommendations for arable crops, in order to avoid P and K being yield-limiting. The mineral N content in the 0-60 cm soil layer in the last week of February was 72 kg ha⁻¹ in 1990 and 75 kg ha⁻¹ in 1991. In both years N-fertilizer was applied before sowing, at a rate of 135 kg ha⁻¹. Herbicides were not used, as weeds were adequately suppressed by the crop. To prevent the occurrence of *Botrytis cinerea* the crop was sprayed with fungicides (alternating vinchlozolin at 500 g ha⁻¹ and iprodion at 500 g ha⁻¹) at 14-day intervals during June, July and August.

Just before each harvest the interception of photosynthetically active radiation (PAR) by the canopy was measured using a line sensor (Technical and Physical Engineering Research Service TFDL-DLO, Wageningen, The Netherlands). Daily values for the fraction of PAR intercepted by the canopy were estimated using linear regression. Daily PAR interception by the canopy was calculated from the fraction of PAR intercepted and PAR measurements made at 5 km from the experimental site. Radiation use efficiency values were calculated as the ratio of dry matter production and intercepted PAR over a period of time.

At each harvest the above-ground fresh weight of all living plants was determined. A 16-plant subsample was separated into three fractions: inflorescence (including seed), green leaves, and stem; dead or yellow leaves were discarded. Leaf area was determined using a LI-COR 3100 (Lincoln, USA) area meter. The dry weight of all fractions was determined by drying at 105 °C for 24 h. A 40-plant subsample was dried at 25 °C on a drying floor. The plants were defoliated and separated into bark and woody core by means of a flax breaker. Any remaining core was removed from the bark by hand. The solubility of ground samples of bark and core in 1 % NaOH was determined according to TAPPI (1988) procedure T-212. Solubility in 1 % NaOH indicates the proportion of readily degradable material and correlates with non-fibre material in bark (De Meijer & van der Werf, in press).

Starting in August, a sample consisting of the top metre of 20 plants was taken once a week from the area bordering the 2 m² harvest area. These plants were classified as female (bearing one or more female flowers with visible stigmas), male (bearing one or more pedicellate male flowers), monoecious (bearing at least one male and one female flower) or non-flowering. The effect of daylength and cultivar on sex expression was analysed using a multinomial response model (McCullagh & Nelder 1989).

At final harvest the numbers of nodes with opposite and with alternate phyllotaxis and the number of leafless nodes were determined on 3 plants per plot. Nodes were classed as alternate if the leaf bases were more than 1 cm apart on the main axis after the full extension of the internode. Node numbers did not include the cotyledonary node.

RESULTS AND DISCUSSION

Flowering and sex expression

Prolonging the daylength reduced the proportion of flowering plants. In both years the reduction was greater in Kompolti Hybrid TC than in Fédrina 74 (Figure 1). In 1991 both cultivars flowered earlier than in 1990, and the reduction in the proportion of flowering plants was smaller (Figure 1). The exceptionally warm weather in July 1991 may have hastened flowering in 1991. Nelson (1944) found that high temperature accelerated flowering in hemp, and Heslop-Harrison & Heslop-Harrison (1969) showed that high temperature shortened the time from the formation of the first primordia to flowering more than it shortened the time required to form the first primordia.

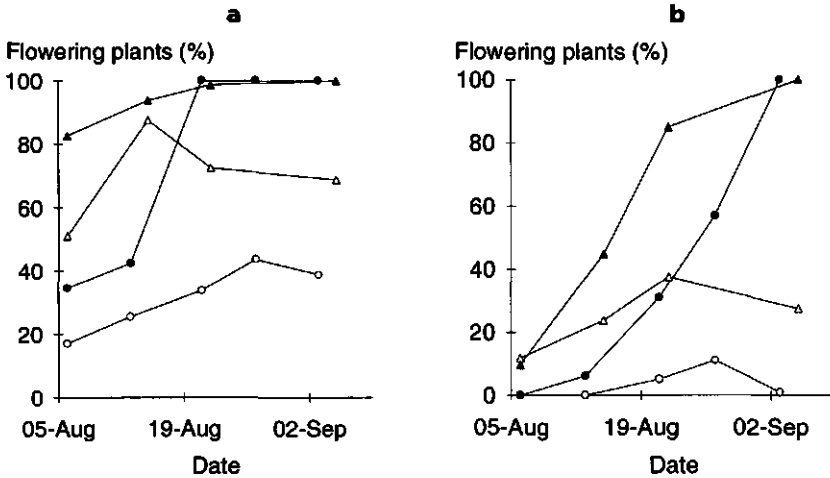


Figure 1. The proportion of plants bearing at least one male or female flower in hemp grown under ambient (black symbols) or 24-hour (open symbols) daylength in 1990 (circles) and 1991 (triangles): (a) the cultivar Fédrina 74; (b) the cultivar Kompolti Hybrid TC.

Long days did not affect the proportion of plants of female sex expression in either cultivar, but reduced the proportion of male or monoecious plants to zero (Table 1). Fédrina 74 had more female plants than Kompolti Hybrid TC, which explains why the 24-hour daylength reduced the proportion of flowering plants less in Fédrina 74 than in Kompolti Hybrid TC. Long days did not affect the proportion of plants bearing female flowers but did reduce the number of flowers per plant (data not shown).

Long days did not affect the number of nodes with opposite phyllotaxis (Table 2), indicating that this treatment did not prevent the change of phyllotaxis which usually accompanies the transition to flowering in hemp. In Kompolti Hybrid TC the number of nodes with alternate phyllotaxis was not affected by daylength, in Fédrina 74 it was greater under 24-hour daylength than under ambient daylength ($p = 0.09$). Flowering appeared to slow down the rate of node formation in Fédrina 74 but not in Kompolti Hybrid TC. Daylength prolongation did not affect the number of leafless nodes or plant height. On the whole, the daylength prolongation treatment we applied was only partially effective: it prevented flowering in male and monoecious plants but only reduced it in female plants, and had no effect on change in phyllotaxis.

This relative lack of response to artificial daylength prolongation contrasts with the significant delays or complete prevention of flowering that Schaffner (1926), Borthwick & Scully (1954) and Heslop-Harrison & Heslop-Harrison (1969) obtained by artificially prolonging daylength. The reason for this relative lack of response is not clear.

Dry matter accumulation and radiation use efficiency

At the harvest at the start of flowering, daylength had been artificially prolonged for at least 36 days for Fédrina 74 and for 57 days for Kompolti Hybrid TC. At that time, the crops grown under ambient or 24-hour days were very similar: neither above-ground dry matter, nor the proportion of the stem in the above-ground dry matter, nor leaf area index (LAI) were affected by daylength (Table 3). At final harvest, the LAI of hemp grown under long days was similar to or slightly less than LAI at flowering, whereas in hemp grown under ambient daylength it had decreased. Crop growth rates between flowering and final harvest were lower under ambient daylength than under long days. Differences in crop growth rate are often attributed to differences in the amount of intercepted PAR and/or the radiation use efficiency (RUE), i. e. the efficiency with which intercepted PAR is used in the production of dry matter. At final harvest, hemp grown under ambient or prolonged daylength differed much more in LAI than in the fraction of PAR intercepted by the canopy. Consequently, the amount of PAR intercepted between flowering and final harvest was only slightly less under ambient daylength than under long days (Table 3). The main cause of the low crop growth rate after flowering under ambient daylength was the low RUE (Table 3). In the period corresponding to the post-flowering stage in hemp grown under ambient daylength, RUE of hemp grown under long

Table 1. Percentage of female, male, monoecious and non-flowering plants on 22 August 1991 in cultivars Fédrina 74 and Kompolti Hybrid TC grown under ambient or 24-hour daylength. Standard errors are shown in brackets.

Cultivar	Daylength	Sex expression			
		Female	Male	Monoecious	Non-flowering
Fédrina 74	ambient	78.3 (11.4)	5.0 (2.9)	15.0 (5.0)	1.7 (1.7)
	24 hour	75.0 (11.2)	0.0	0.0	25.0 (6.5)
Kompolti H. TC	ambient	38.3 (8.0)	43.3 (8.5)	0.0	18.3 (5.1)
	24 hour	41.7 (8.3)	0.0	0.0	58.3 (9.9)

Table 2. Numbers of nodes and plant height at final harvest of cultivars Fédrina 74 and Kompolti Hybrid TC grown under ambient or 24-hour daylength. Means for 1990 and 1991.

Cultivar	Daylength	Number of nodes				Height (cm)
		Opposite	Alternate	Total	Leafless	
Fédrina 74	ambient	9.2	19.9	29.0	17.1	255
	24 hour	9.6	24.3	33.9	16.9	273
Kompolti H. TC	ambient	12.1	13.8	26.2	12.7	289
	24 hour	12.4	13.6	25.7	11.3	294
LSD (0.05)		1.7	5.5	5.5	4.2	34

Table 3. Above-ground dry matter and leaf area index (LAI), crop growth rate (CGR), daily interception of PAR (IPAR) and radiation use efficiency (RUE) of cultivars Fédrina 74 and Kompolti Hybrid TC grown under ambient or 24-hour daylength. Means for 1990 and 1991.

Cultivar	Daylength	Dry matter	LAI		Flowering to final harvest		
		flowering (t ha ⁻¹)	flowering	final harvest	CGR (kg ha ⁻¹ d ⁻¹)	IPAR (MJ m ⁻² d ⁻¹)	RUE (g MJ ⁻¹)
Fédrina 74	ambient	10.3	4.4	2.7	54	5.84	0.93
	24 hour	9.8	4.2	4.3	108	6.09	1.82
Kompolti H. TC	ambient	14.2	4.8	2.1	19	4.77	0.16
	24 hour	13.4	4.8	3.8	145	5.11	2.82
LSD (0.05)		1.2	0.8	1.4	64	0.47	1.47

days was similar to or higher than that measured before flowering (2.0 g MJ^{-1}) in previous experiments (Chapter 2), whereas the post-flowering RUE of hemp grown under ambient daylength was much lower (Table 3).

A low RUE after flowering had previously been found in hemp (Chapter 2) and in other crops, e.g. in sunflower (Trapani et al. 1992). The low post-flowering RUE in hemp has been attributed (Chapter 2) to the high energy costs of synthesizing oil and protein in the seed, the losses of dry matter invested in shed leaves and the lower rate of canopy photosynthesis resulting from leaf senescence. Assuming in our experiments that 50 % of the dry matter of the inflorescence consisted of seed containing 40 % oil and 30 % protein (Chapter 2), the primary assimilates required for the formation of 1 g of mature inflorescence could have yielded 1.19 g of stem dry matter (Vertregt & Penning de Vries 1987). Had all the assimilates invested in the inflorescence of the ambient daylength treatments been invested in stem material, the above-ground dry matter yield of Fédrina 74 and Kompolti Hybrid TC would have been increased by 0.2 and 0.1 t ha^{-1} respectively. The amount of dry matter invested in leaves shed after flowering can be estimated from the difference in leaf dry matter at final harvest between hemp grown at ambient or 24-hour daylength (Table 4); it amounts to 0.4 t ha^{-1} for Fédrina 74 and 0.5 t ha^{-1} for Kompolti Hybrid TC. Taken together, the high energy costs for the synthesis of oil and protein in the seed and the loss of the dry matter invested in shed leaves explain only a minor part of the difference in total above-ground dry matter yield between hemp grown under ambient or 24-hour daylength (Table 4). Given the small difference between the amount of light intercepted by the canopy under prolonged and ambient daylength (Table 3), it seems probable that a lower rate of canopy photosynthesis was the main reason for the low post-flowering RUE.

Dry matter distribution and stem quality

At final harvest the above-ground dry matter yield at long days exceeded that at ambient daylength by 2.2 t ha^{-1} for Fédrina 74 and by 2.8 t ha^{-1} for Kompolti Hybrid TC; the difference in stem yield was 2.7 t ha^{-1} of dry matter for both cultivars (Table 4). In both cultivars the inflorescence dry matter was about eight times less at long than at ambient daylength (Table 4), confirming that prolonging the daylength had largely prevented the allocation of dry matter to floral parts. Leaf dry matter yield was greater in the crops grown under prolonged daylength, reflecting accelerated leaf senescence at ambient daylength and/or the formation of more or larger new leaves at 24-hour daylength (Table 4). Prolonging the daylength increased the proportion of the stem in the above-ground dry matter more in Fédrina 74, in which the reduction in inflorescence yield caused by prolonging the daylength was greater (Table 4).

The above-ground dry matter yield of Kompolti Hybrid TC exceeded that of Fédrina 74 under both prolonged and ambient daylength, suggesting that the higher yield of Kompolti Hybrid TC was not the result of its later flowering date, but of some other characteristic of this

Table 4. Yield of inflorescence, green leaves, stem, total above-ground dry matter and the proportion of stem in the above-ground dry matter at final harvest of cultivars Fédrina 74 and Kompolti Hybrid TC grown under ambient or 24-hour daylength. Means for 1990 and 1991.

Cultivar	Daylength	Dry matter (t ha ⁻¹)				Stem in total
		Inflorescence	Leaves	Stem	Total	%
Fédrina 74	ambient	1.13	1.12	10.65	12.90	82.9
	24 hour	0.16	1.49	13.42	15.07	89.1
Kompolti H. TC	ambient	0.45	0.89	13.22	14.56	90.8
	24 hour	0.06	1.41	15.92	17.39	91.5
LSD (0.05)		0.20	0.48	1.4	1.7	2.8

Table 5. Dry matter yield of bark and core, the proportion of bark in the stem dry matter and solubility of bark and core in 1 % NaOH at final harvest of cultivars Fédrina 74 and Kompolti Hybrid TC grown under ambient or 24-hour daylength. Means for 1990 and 1991.

Cultivar	Daylength	Dry matter (t ha ⁻¹)		Solubility in 1 % NaOH (%)		Bark in stem (%)
		Bark	Core	Bark	Core	(%)
Fédrina 74	ambient	3.35	7.30	28.1	30.4	31.3
	24 hour	4.01	9.41	29.8	31.4	29.7
Kompolti H. TC	ambient	4.61	8.61	27.9	31.6	34.9
	24 hour	5.68	10.24	29.9	32.3	35.7
LSD (0.05)		0.43	1.05	2.1	1.1	1.6

cultivar. In 1991, when both cultivars were harvested on each harvest date, Kompolti Hybrid TC yielded 1.0 t ha⁻¹ of dry matter more than Fédrina 74 on 6 August (data not shown), indicating that the higher yield of Kompolti Hybrid TC was not the result of its later senescence.

Because of the large difference in the economic value of bark and core, the stem quality will primarily depend on the proportion of these two components in the stem (Chapter 3). Daylength prolongation did not affect the proportion of bark in the stem of Kompolti Hybrid TC, but in Fédrina 74 it reduced bark content (Table 5). In 1991 the bark content was determined not only at final harvest, but also at the harvests coinciding with the flowering dates of the two cultivars. In both cultivars and for both daylength treatments the bark content

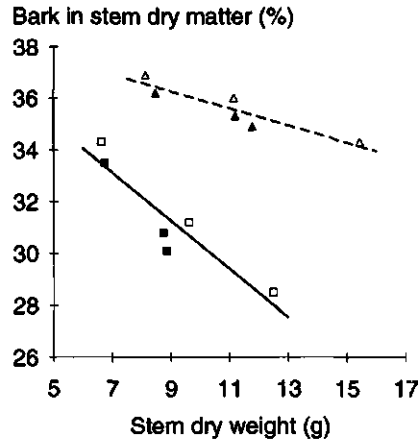


Figure 2. The relationship between the proportion of bark in the stem and stem dry weight for hemp cultivars Fédrina 74 (squares) and Kompolti Hybrid TC (triangles) grown under ambient (black symbols) or 24-hour (open symbols) daylength in 1991. Regression equations:

Kompolti Hybrid TC: $y = 39.24 - 0.331 x$ ($p < 0.01$, 81.7 % of variance accounted for)

Fédrina 74: $y = 39.63 - 0.930 x$ ($p < 0.01$, 81.9 % of variance accounted for)

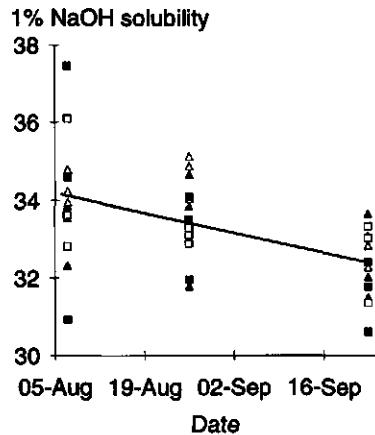


Figure 3. The solubility of core in 1 % NaOH in the course of August and September 1991 of hemp cultivars Fédrina 74 (squares) and Kompolti Hybrid TC (triangles) grown under ambient (black symbols) or 24-hour (open symbols) daylength. Regression equation:

$y = 42.14 - 0.037 x$ ($x = \text{Julian day number}$, $p < 0.002$, 22.9 % of variance accounted for)

decreased with stem dry weight; the decrease was slight for Kompolti Hybrid TC and larger for Fédrina 74 (Figure 2). Increased stem weights and lower bark contents have previously been found to be associated in hemp (Arnoux et al. 1969, Chapter 3) as well as in kenaf (Muchow 1979). The differential response of the two cultivars found here confirms our earlier findings (Chapter 3).

At final harvest the solubility of core and especially bark in 1 % NaOH was greater ($p < 0.10$) in hemp grown under long days (Table 5), indicating a higher content of readily degradable components and a lower fibre content in the bark (De Meijer & van der Werf, in press). In 1991 the solubility of bark and core was measured on each harvest date. Bark solubility was not affected by harvest date or daylength. Wood solubility decreased during August and September 1991 in both cultivars and in both daylengths (Figure 3). On the whole, quality of bark and core as measured by 1 % NaOH solubility, was less at long than at ambient daylength.

CONCLUSIONS

The light intensity of 1.0 to 1.4 W m⁻² at the top of the canopy supplied to prolong daylength was apparently too low to totally prevent the flowering of female plants and to impede the change to alternate phyllotaxis. However, the great reduction of flowering that was achieved did have the desired result: the allocation of dry matter to floral parts was greatly reduced by the long days.

Artificially prolonging daylength, resulting in the almost complete elimination of flowering, prevented the low RUE associated with the post-flowering period in hemp. The RUE of hemp in which flowering was prevented was similar to or higher than that measured in hemp before flowering. The prevention of flowering increased the dry matter yields of both total above-ground material and stem by 2 to almost 3 t ha⁻¹.

Previous research (Chapter 2) suggested that in the Netherlands the stem dry matter yield of currently available fibre hemp cultivars is limited by precocious flowering. The present experiments have shown that the yield potential of these cultivars can be increased by artificially delaying flowering, thus prolonging the vegetative growth phase and raising stem yield. The implication for hemp breeders is clear: there is scope for increasing the stem yield of fibre hemp by breeding late- or non-flowering cultivars.

ACKNOWLEDGEMENTS

The authors thank A J Haverkort, P C Struik and W J M Meijer for helpful comments on the manuscript. We thank M ten Cate, M J E M van Mensvoort and L J C van Gils for their technical support.

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**PLANT DENSITY AND SELF-THINNING AFFECT YIELD
AND QUALITY OF FIBRE HEMP (*Cannabis sativa* L.)**

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ABSTRACT

To ascertain the reasons for the high plant mortality in fibre hemp (*Cannabis sativa* L.) crops in the Netherlands changes in biomass yield, plant mortality and plant morphology were investigated in a hemp cultivar grown at initial densities of 10, 30, 90 and 270 plants m^{-2} . At 90 plants m^{-2} this cultivar was compared with a high bast fibre cultivar and a late-flowering cultivar. Rate of canopy establishment and early growth rate increased with increasing plant density. At 270 and 90 plants m^{-2} , plants died as a result of self-thinning. Self-thinning was associated with a reduced crop growth rate. In self-thinning stands, dry biomass (B , $g\ m^{-2}$) was related to density of surviving plants (D , m^{-2}) as $\log B = 3.81 - 0.304 \log D$. At the same crop growth rate, the rate at which plants died from self-thinning was higher in hemp than in other herbaceous dicots. The proportion of stem in the total dry matter increased with increasing plant density. Stem yield was maximum at 90 plants m^{-2} . Stem quality improved with increasing density as the bark content in the stem augmented, but self-thinning reduced the bark content in the stem. Optimum plant density was close to the density resulting after self-thinning. In hemp the relationship between yield and optimum plant density is approximated by the equation of its self-thinning line. The late-flowering cultivar yielded more than the other two cultivars because it grew faster during the latter part of the growing season.

KEY WORDS: *Cannabis sativa* L., fibre hemp, plant density, self-thinning, plant morphology, stem yield, stem quality

INTRODUCTION

Fibre hemp (*Cannabis sativa* L.) is generally grown for its bast fibres, which are used as a raw material for cordage and textile products. We studied the effects of plant density and self-thinning as part of a research programme investigating the potential of hemp stems as a raw material for paper pulp. Ideally, hemp grown for this purpose should have a high stem yield and a high proportion of bark in the stem (Chapter 3).

In annual crops the relationship between plant density and above-ground dry matter yield is described satisfactorily by a rectangular hyperbola (Willey & Heath 1969). At high plant density the positive effect of larger numbers of plants is cancelled out by the growth of each plant being reduced as a result of inter-plant competition, and hence in many experiments, at a certain point biomass yield has been found to stop increasing with increasing plant density. This has been called the "law of constant final yield" (Kira et al. 1953). Sometimes, even a slight decrease in total above-ground dry matter yield is found with increasing densities (Willey & Heath 1969).

The recommended seeding rates for fibre hemp vary between 40 and 150 kg ha⁻¹, which correspond to plant densities shortly after emergence of about 200 to 750 plants m⁻² (Dempsey 1975). Reports on the effects of low plant densities (below 80 m⁻²) on yield and stem quality of hemp are rare (Jakobey 1965). Plant densities between 80 and 400 m⁻² have been found to have little effect on stem dry matter yield (Jaranowska 1963, Jakobey 1965, Rynduch 1975, Marras & Spanu 1981, Chapter 2). The economically optimal plant densities of hemp grown for bast fibre, are higher than the lowest plant density that gives maximum stem dry matter yield, because plant density continues to improve stem quality when it no longer increases stem yield. With increasing plant density, bast fibre content in the stem tends to increase (Heuser 1927, Jakobey 1965), and the fineness of the bast fibres (an important aspect of fibre quality for spinning purposes) improves (Jakobey 1965). We were unable to find any reports on the effect of plant density on bark content in the stem, but in a preliminary experiment, comparing only two densities, we found that bark content was higher at 90 plants m⁻² than at 10 plants m⁻² (Chapter 3).

At very high plant densities, inter-plant competition may result in density-induced mortality: self-thinning (Weller 1987). In a self-thinning crop an increase in biomass yield is accompanied by a reduction of the plant density. These changes can be described by:

$$\log B = \log k - b \log D$$

where B is the dry weight of surviving plants (g m⁻²), D is the density (m⁻²) of survivors and k and b are constants. The value of b has been found to lie between 0.3 and 0.8, with an ideal value of 0.5, while log k varies between 3.5 and 5.0 (Lonsdale 1990). A collection of single-species self-thinning lines forms a band of slope -0.5 that extends over nine orders of magnitude of density, from mosses to sequoia trees (White 1985). So far, the self-thinning rule has been used to analyse yield-density dynamics in forestry and ecology (Weller 1987). It is used as a management tool in forestry, but it has not yet been applied in agronomy. Hence, the vast majority of the studies on self-thinning have been carried out either at densities of less than 5 plants m⁻² (forestry) or at densities above 200 plants m⁻² (ecology). The plant density of most dicot annual field crops is intermediate between these densities.

In most dicot annual crops the economically optimal plant density is not sufficiently high for self-thinning to occur. However, in a fibre hemp crop a considerable proportion of the plants present at emergence die before harvest. This proportion increases with plant density at emergence (Jaranowska 1963, Marras & Spanu 1979, Chapter 2). In experiments in the Netherlands, fibre hemp yield was high and fewer plants survived until the end of the growing season than reported from other European countries; even at the lowest densities investigated (about 100 plants m⁻²) almost half of the plants had died at harvest in September (Chapter 2).

Our objective was to establish the effects of a range of plant densities, including densities of less than 80 plants m^{-2} , on self-thinning, yield formation and stem quality. We therefore investigated changes in biomass yield, plant mortality and plant morphology during two growing seasons for four plant densities (ranging from 10 to 270 plants m^{-2}) of one cultivar. To broaden the research, at one density this cultivar was compared with a high-bast fibre cultivar and a late-flowering cultivar.

MATERIALS AND METHODS

Treatments and cultural methods

Field experiments were carried out at Randwijk, the Netherlands, on a heavy river clay soil in 1991 and 1992. The Hungarian cultivar Kompolti Hybrid TC was grown at 10, 30, 90 and 270 plants m^{-2} in 1991 and at 10, 30, 90 and 230 plants m^{-2} in 1992. These treatments will be referred to as 'TC10', 'TC30', 'TC90' and 'TC270' respectively. Kompolti Hyper Elite (a high bast fibre Hungarian cultivar) was grown at 90 plants m^{-2} in both years ('HE90'), Kozuhara zairai (a late-flowering Japanese landrace) was grown at 90 plants m^{-2} in 1991 and 65 plants m^{-2} in 1992 ('Kz90'). The experiment was set up as a randomized block design with four replications. In 1992 one replication was discarded because poor soil structure had resulted in severe drought stress.

P and K fertilizer were applied according to recommendations based on soil testing. Soil N between 0 and 60 cm was 70 kg ha^{-1} in February 1991 and 90 kg ha^{-1} in March 1992. In both years N fertilizer was applied before or shortly after sowing, at a rate of 140 kg ha^{-1} in 1991 and 120 kg ha^{-1} in 1992.

Hemp was sown with a precision seed drill on 20 April 1991 and on 24 April 1992. Row width was 25 cm for the treatments TC10 and TC30, 12.5 cm for the other treatments. The date of 50 % plant emergence was 1 May in 1991 and 2 May in 1992. In the seedling stage the crops were hand thinned to the desired plant density. No herbicides were used, as in most treatments weeds were suppressed by the crop. In treatments TC10 and TC30, weeds were removed by hand when necessary. The crops were sprayed with fungicides (alternating vinchlozolin at 500 g ha^{-1} and iprodion at 500 g ha^{-1}) at 14-day intervals during June, July and August. This prevented the occurrence of *Botrytis cinerea* in all treatments but TC10.

Data collection

The plots, which were 14 m long and 6 m wide, each contained four 1.5 m x 1 m sample areas, 2 m apart. The six plots making up a replication were separated from the next replication by a 3-m wide alley used for spraying. The experiment was surrounded by a 3 m-wide buffer of hemp. There were four harvests: 1) when TC270 approached complete interception of incident light, 2) when the Kompolti cultivars were flowering, 3) when Kz90 was flowering and 4) at the end of the growing season. Harvest dates were 10 June, 12 August, 16 September and 14 October in 1991 and 1 June, 10 August, 14 September and 12 October in 1992.

At each harvest all plants in the sample area were cut off flush with the ground. Above-ground fresh weight of the living plants was determined. At the first harvest, no dead plants were present; at the second harvest, dead plants represented a small amount of dry matter which was not measured. At the third harvest the dry weight of dead plants was determined separately. At the fourth harvest almost all the male plants of the Kompolti cultivars had completed their life cycle and were dead. In order to allow a meaningful comparison with Kz90, dead plants bearing an inflorescence were kept with the living plants at harvest 4. As a result of this, at the third and fourth harvests the fraction of dead plants consisted solely of plants without inflorescence, which had presumably died as a result of self-thinning. Shed leaves were not collected. Five (in TC10) or 10 (in the other treatments) plants from each sample area were separated into four fractions: stem, green leaves, senescent (yellow and dead) leaves, and other organs (inflorescence and branches). Area of green leaves was determined using a LI-COR 3100 (Lincoln, USA) area meter. All plant fractions were dried at 105 °C until constant weight. At the third harvest in 1991 and at the second and third harvests in 1992, 5 (in TC10), 10 (in TC30) or 20 (in the other treatments) plants per sample area were dried at 25 °C on a drying floor. The stems were separated into bark and core by means of a flax breaker; any remaining core was removed from the bark by hand. In 1991, shavings taken from a sample of core fragments were macerated, microscope slides were prepared and length and diameter of libriform fibres were determined. Solubility of ground samples of bark and core in 1 % NaOH, which is a measure of readily degradable material, was determined according to TAPPI procedure 212 (TAPPI 1988). Non-fibre components in the bark were determined according to Bredemann (1952).

On 12 August 1991 and 29 July 1992 the number of stem nodes was determined on 10 (in TC270) or 5 (in the other treatments) plants per sample area. Starting in August, once a week the tops of 10 plants per plot were classified as flowering or non-flowering (for methods see Chapter 5).

The interception of photosynthetically active radiation (PAR) by the canopy was measured about once a week using a line sensor (TFDL-DLO, Wageningen, The Netherlands).

Data analysis

Daily values for the fraction of PAR intercepted by the canopy (FPAR) were estimated using non-linear regression analysis. A logistic function described canopy establishment and the period during which FPAR remained at its maximum; the decrease of FPAR during senescence was described as a straight line. Daily PAR intercepted by the canopy was calculated from FPAR values and from PAR measurements made at 5 km from the experimental site. Crop growth rates were based on dry weight of living and dead plants. Radiation use efficiency values were calculated as the ratio of dry matter accumulation of living and dead plants and PAR intercepted over a certain period of time.

The effect of initial plant density on plant or crop parameters was investigated using regression analysis. The logarithm of the initial plant density was used to make plant densities equidistant, the significance of linear and quadratic components was determined.

In addition to the data from the experiments described in this Chapter, we used data from experiments carried out in 1988 and 1989 with the cultivar *Fédrina 74* (described in Chapter 2) to fit thinning lines. These were fitted by principal component analysis as the principal axis of logarithmically transformed measurements of above-ground dry matter of living plants (g m^{-2}) and number of living plants (m^{-2}) (Weller 1987). We estimated 95 % confidence intervals for the slopes of the thinning lines (Sokal & Rohlf 1981). To fit the thinning lines, data points from stands not undergoing crowding-dependent mortality were discarded (Weller 1987). In the experiments carried out in 1988 and 1989, data from early harvests where mortality was less than 20 % were excluded, and so were data from harvests in late September and October (because the crops were senescing). In the experiments described here, the harvests were less frequent than in the experiments carried out in 1988 and 1989, and the reduction in plant density was small for some of the crops grown at 90 plants m^{-2} . Data from the second and third harvests of treatment TC270 and from the third harvest of the treatments TC90, HE90 and Kz90 were used to fit the thinning line. Data from the fourth harvest were not used, as the Hungarian cultivars were already senescent.

RESULTS

Self-thinning

In all treatments except TC10 and TC30, the density of living plants decreased between the first and the third harvests. The reduction in plant density was greatest at the highest plant density (Table 1). At the third harvest the density of surviving plants was similar for the three cultivars. The number of surviving plants did not change between the third and fourth harvests, but note that dead male plants were included in the living plants at the fourth harvest (see materials and methods).

In all treatments, the dry matter yield of living plants increased from the first to the third harvest (Table 1). At the first harvest, dry matter yield was highest in TC270, at the second harvest, no density effects were observed. At the third harvest, TC30 and TC90 had similar yields; at the fourth harvest the yield of living plants was higher in TC30 than at the other plant densities; and for all treatments except Kz90, yield was lower at the fourth harvest than at the third. The yield of HE90 was similar to that of TC90 at all harvests, but Kz90 outyielded the other two cultivars at the fourth harvest.

Table 1. Number and above-ground dry matter of living plants as influenced by initial plant density and cultivar. Means of 1991 and 1992, see text for harvest (H) dates.

Parameter	Kompolti Hybrid TC				Regression		Hyper	Kozuhara	Cultivar
	Initial density (plants m ⁻²)						Elite	zairai	comp.
	10	30	90	270 ¹⁾	Linear	Quadratic	90 m ⁻²	90 ²⁾ m ⁻²	LSD (0.05)
Density (m⁻²)									
H 1	10.0	30.2	90.6	254.9	<0.001	<0.001	89.6	78.9	NS ³⁾
H 2	9.8	29.6	83.1	176.0	<0.001	<0.001	87.0	74.4	NS
H 3	9.6	28.7	70.7	111.2	<0.001	NS	74.9	72.4	NS
H 4	9.1	29.0	68.9	111.2	<0.001	NS	73.3	70.3	NS
Dry matter (t ha⁻¹)									
H 1	0.36	0.80	1.37	1.86	<0.001	NS	1.16	1.25	0.30
H 2	12.0	13.3	13.8	13.5	NS	NS	13.6	13.3	NS
H 3	13.8	17.4	17.5	15.1	NS	<0.001	17.5	18.4	2.2
H 4	12.3	16.6	16.0	15.3	0.006	<0.001	16.3	19.4	1.85

1) 230 in 1992, 2) 65 in 1992, 3) NS: p > 0.05

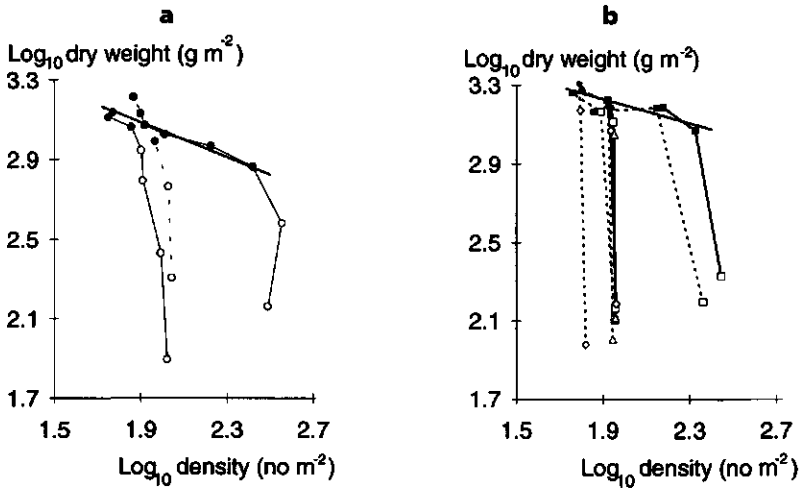


Figure 1. Changes in the number and the above-ground biomass of living plants with time. Black symbols indicate data points used for fitting the thinning line.

(a) Fédrina 74 in 1988 (solid lines) and 1989 (dotted line).

Thinning line: $\text{Log } B = 3.92 - 0.437 \text{ log } D$ (95% CI for slope: -0.240, -0.668).

(b) Kompolti Hybrid TC (squares), Kompolti Hyper Elite (triangles) and Kozuhara zairai (diamonds) in 1991 (solid lines) and 1992 (dotted lines).

Thinning line: $\text{Log } B = 3.81 - 0.304 \text{ log } D$ (95% CI for slope: -0.142, -0.482).

A graph of log biomass per unit area (log B) versus log density of surviving plants (log D) of three dense actively-growing hemp crops in 1988 and 1989 suggests that mortality was induced by crowding (Figure 1a). The paths of the 1988 crops approached and followed a straight line, but the path of the 1989 crop was steeper. Log B and log D of the subset of 10 stands where at least 20% of the plants had died correlated well ($r = 0.86$, $p < 0.01$). This is considered evidence of density-induced mortality: self-thinning (Weller 1987). For the relevant stands of the 1991-1992 experiments, log B and log D also correlated well (Figure 1b, $r = 0.83$, $p = 0.02$). Neither the slope nor the intercept (at density 1 plant m^{-2}) of this thinning line differed statistically significantly from those of the thinning line for the 1988-1989 data. However, the data were not pooled because the positions of the lines were different, i.e. at the median of the density range investigated here (around 100 plants m^{-2}) the intercepts differed statistically significantly.

Crop growth rate and radiation use efficiency

Crop growth rate (CGR) during three periods between emergence and harvest 3 was maximum ($182 \text{ kg ha}^{-1} \text{ d}^{-1}$) in period 2 (Table 2). During period 1, CGR increased with initial plant density, but during period 2 it was not affected by initial plant density. During period 3, the CGRs of TC30 and TC90 were higher than those of TC10 and TC270.

Mean daily intercepted PAR (IPAR) was maximum in period 2 (Table 2). In period 1, IPAR increased substantially with initial plant density; in period 2 it increased slightly with initial plant density. In period 3, IPAR was not affected by initial plant density. IPAR was always similar for the three cultivars.

Mean radiation use efficiency (RUE) for all treatments was maximum (2.21 g MJ^{-1}) in period 2 (Table 2). There was no difference in RUE between cultivars. During period 1 RUE decreased with increasing initial plant density. During period 2, it was not affected by initial plant density, and during period 3 the RUEs of TC10 and TC270 were lower than those of TC30 and TC90.

Table 2. Crop growth rate (CGR, $\text{kg ha}^{-1} \text{ d}^{-1}$) of total above-ground dry matter, intercepted radiation (IPAR, $\text{MJ m}^{-2} \text{ d}^{-1}$) and radiation use efficiency (RUE, g MJ^{-1}) as influenced by initial plant density and cultivar. Means of 1991 and 1992, see text for harvest (H) dates.

Parameter	Kompolti Hybrid TC				Hyper		Kozuhara	Cultivar	
	Initial density (plants m^{-2})				Regression		Elite	zairai	comp.
	10	30	90	270 ¹⁾	Linear	Quadratic	90 m^{-2}	90 ²⁾ m^{-2}	LSD (0.05)
Emerg. - H 1									
CGR	10.7	24.2	39.5	53.0	<0.001	NS ³⁾	33.3	35.2	NS
IPAR	0.45	1.18	2.29	3.49	<0.001	NS	2.15	2.02	NS
RUE	2.35	2.07	1.76	1.52	<0.001	NS	1.54	1.76	NS
H 1 - H 2									
CGR	174.9	189.0	187.2	174.6	NS	NS	186.0	180.9	NS
IPAR	7.82	8.30	8.35	8.40	0.05	NS	8.34	8.30	NS
RUE	2.24	2.28	2.25	2.07	NS	NS	2.22	2.17	NS
H 2 - H 3									
CGR	74.4	120.7	125.8	90.5	NS	0.043	118.9	146.8	NS
IPAR	6.44	6.41	6.58	6.60	NS	NS	6.59	6.57	NS
RUE	1.12	1.90	1.96	1.31	NS	0.023	1.81	2.29	NS

¹⁾ 230 in 1992, ²⁾ 65 in 1992, ³⁾ NS: $p > 0.05$

Canopy establishment, phenology and senescence

Leaf dry matter increased with initial density at harvest 1, and decreased with density at harvest 2, but at harvests 3 and 4 it was not affected by initial density (Table 3). Maximum leaf dry weight was reached at harvest 2 for all treatments except Kz90, which peaked at harvest 3. The greatest reduction in leaf dry weight from harvest 2 to harvest 3 was found in TC10. Specific leaf area of green leaves (SLA) increased with initial plant density at all harvests (Table 3). At harvest 2, SLA was maximum for all treatments, and the increase with density was also larger than at the other harvests. At harvest 2, SLA was lower for Kz90 than for the other two cultivars.

Table 3. Dry matter of green and yellow leaves, specific leaf area (SLA) and leaf area index (LAI) as influenced by initial plant density and cultivar. Means of 1991 and 1992, see text for harvest (H) date.

Parameter	Kompolti Hybrid TC				Regression		Hyper	Kozuhara	Cultivar
	Initial density (plants m ⁻²)						Elite	zairai	comp.
	10	30	90	270 ¹⁾	Linear	Quadratic	90 m ⁻²	90 ²⁾ m ⁻²	LSD (0.05)
Leaves (t ha ⁻¹)									
H 1	0.28	0.59	0.84	0.92	<0.001	0.019	0.71	0.75	0.13
H 2	2.45	2.31	2.03	2.01	0.025	NS ³⁾	1.96	2.41	0.44
H 3	1.84	2.05	1.85	1.76	NS	NS	1.75	2.61	0.40
H 4	0.77	0.76	0.71	0.71	NS	NS	0.65	1.99	0.36
SLA (cm ² g ⁻¹)									
H 1	213	200	253	313	<0.001	0.016	272	235	NS
H 2	232	266	343	387	<0.001	NS	372	288	57
H 3	192	201	255	299	<0.001	NS	238	235	NS
H 4	155	169	186	205	0.043	NS	229	191	NS
LAI (m ² m ⁻²)									
H 1	0.59	1.15	2.12	2.89	<0.001	NS	1.91	1.70	0.39
H 2	5.55	6.13	6.66	7.68	0.013	NS	7.29	6.84	NS
H 3	2.85	3.63	4.16	4.80	0.002	NS	3.77	5.80	1.24
H 4	0.86	1.06	1.05	1.08	NS	NS	1.14	3.40	0.67

1) 230 in 1992, 2) 65 in 1992, 3) NS: p > 0.05

Leaf area index (LAI) increased with initial plant density at all harvests except the fourth (Table 3). At harvest 1, the effect of initial density on LAI was particularly large, as both leaf dry weight and SLA increased with density. For all treatments, LAI was maximum at harvest 2. Rate of senescence, inferred from the decline of LAI between harvest 2 and 4, was not affected by initial density. It was much slower in Kz90 than in the other two cultivars.

At the onset of flowering, both the number of nodes with opposite phyllotaxis and the number of nodes with alternate phyllotaxis decreased with initial plant density (Table 4). The node numbers of the three cultivars did not differ. Date of flowering, as indicated by the proportion of plants flowering at harvests 2 and 3, was similar for TC10 and TC30, later for TC90 and even later for TC270. HE90 was flowering less than TC90 at harvest 2. For TC90 the date of 50 % flowering coincided with harvest 2; one month later, at harvest 3, Kz90 had almost reached 50 % flowering (Table 4). At harvests 2, 3 and 4 the proportion of light intercepted by the canopy increased with initial plant density (Table 4). At harvest 2 it was high (> 97 %) for all treatments, at harvest 3 it was still above 90 % for all treatments except TC10, and at harvest 4 it was below 90 % for all treatments except Kz90.

Table 4. Nodes with opposite phyllotaxis, nodes with alternate phyllotaxis (12 August 1991 and 29 July 1992), plants flowering and PAR intercepted by the canopy as influenced by initial plant density and cultivar. Means of 1991 and 1992, see text for harvest (H) dates.

Parameter	Kompolti Hybrid TC				Regression		Hyper	Kozuhara	Cultivar
	Initial density (plants m ⁻²)						Elite	zairai	comp.
	10	30	90	270 ¹⁾	Linear	Quadratic	90 m ⁻²	90 ²⁾ m ⁻²	LSD (0.05)
Nodes with phyllotaxis (no.)									
Opposite	13.3	12.4	10.9	9.2	<0.001	NS ³⁾	10.6	9.8	NS
Alternate	11.6	9.1	3.4	2.1	<0.001	NS	5.1	5.1	NS
Plants flowering (%)									
H 2	69.6	76.4	49.4	37.9	<0.001	NS	24.6	11.7	15.3
H 3	98.0	93.8	84.9	77.3	<0.001	NS	87.2	44.9	11.6
PAR intercepted (%)									
H 2	97.4	98.6	98.8	98.9	0.005	NS	98.8	99.0	NS
H 3	88.9	93.0	96.3	97.3	<0.001	NS	96.5	97.1	NS
H 4	62.1	70.9	81.8	87.6	<0.001	NS	83.6	91.0	7.7

1) 230 in 1992, 2) 65 in 1992, 3) NS: p > 0.05

Yield and yield components

At harvest 3 the dry matter of living plants was similar in TC30 and TC90 and lower in TC10 and TC270 (Table 5). Yield of the inflorescence and yield of dead leaves decreased with increasing initial density. Yield of green leaves was not affected by initial plant density, but was higher for Kz90 than for the other two cultivars. Dry matter yield of living stems was higher at TC90 than at the other densities. The dry matter yield of dead plants at harvest 3 was highest for TC270 and lowest for TC30. At TC10, 0.8 t ha⁻¹ of dead material was present, although the number of living plants had not declined much. Only in this treatment did an appreciable part of this dead material consist of branches shed from the lower nodes of the plants. Furthermore, about 15 % of the plants at TC10 showed *B. cinerea* lesions on the stem, which started at the scars left by abscised leaves. Some of these plants were dead at harvest 3. The dry matter weight of dead plants of KZ90 was lower than that of TC90.

Table 5. Above-ground dry matter (t ha⁻¹) of living plants, of the inflorescence, of the green leaves, of the dead leaves attached to the plant, of the stem, and of dead plants as influenced by initial plant density and cultivar. Means of 1991 and 1992, see text for harvest dates.

Parameter	Kompolti Hybrid TC				Regression		Hyper	Kozuhara	Cultivar
	Initial density (plants m ⁻²)				Regression		Elite	zairai	comp.
	10	30	90	270 ¹⁾	Linear	Quadratic	90 m ⁻²	90 ²⁾ m ⁻²	LSD (0.05)
Harvest 3									
Living plants	13.8	17.4	17.5	15.1	NS ³⁾	<0.001	17.5	18.4	NS
Infloresc.	1.16	0.84	0.58	0.45	<0.001	NS	0.50	0.41	NS
Green lvs	1.46	1.80	1.64	1.65	NS	NS	1.60	2.49	0.44
Dead lvs	0.38	0.24	0.21	0.11	<0.001	NS	0.15	0.12	NS
Stem	10.8	14.5	15.1	12.9	0.03	<0.001	15.2	15.4	NS
Dead plants	0.82	0.34	0.70	1.65	0.005	0.002	0.38	0.11	0.60
Harvest 4									
Living plants	12.3	16.6	16.0	15.3	0.006	<0.001	16.3	19.4	1.8
Infloresc.	1.54	1.38	1.06	1.00	0.004	NS	0.82	0.78	NS
Green lvs	0.56	0.62	0.54	0.55	NS	NS	0.50	1.80	0.31
Dead lvs	0.21	0.15	0.17	0.16	NS	NS	0.15	0.19	NS
Stem	10.0	14.5	14.3	13.6	<0.001	<0.001	14.8	16.6	1.8
Dead plants	1.08	0.21	0.47	1.08	NS	NS	0.30	0.08	NS

1) 230 in 1992, 2) 65 in 1992, 3) NS: p > 0.05

The Hungarian cultivars reached the highest yield at harvest 3, but Kz90 reached its highest yield at harvest 4 (Table 5). At harvest 4, the dry matter of living plants and of living stems was highest at TC30 (Table 5). The yield of the inflorescence decreased with increasing initial density; neither the yield of green leaves nor the yield of senescent leaves was affected by initial plant density. Kz90 outyielded the other two cultivars for all plant components except the inflorescence and dead leaves. The dry matter of dead plants was lower at the fourth harvest than at the third in all treatments except TC10, where it had increased.

Plant morphology and quality parameters

At harvest 1, plant height increased with increasing initial plant density; at harvests 2 and 3 it decreased with increasing density (Table 6). At all three harvests, plant slenderness

Table 6. Plant height, plant height/weight (slenderness), proportion of stem in the above-ground dry matter and proportion of bark in the stem as influenced by initial plant density and cultivar. Means of 1991 and 1992, see text for harvest (H) dates.

Parameter	Kompolti Hybrid TC				Regression		Hyper	Kozuhara	Cultivar
	Initial density (plants m ⁻²)						Elite	zairai	comp.
	10	30	90	270 ¹⁾	Linear	Quadratic	90 m ⁻²	90 ²⁾ m ⁻²	LSD (0.05)
Plant height (cm)									
H 1	22.8	25.2	34.2	36.4	<0.001	NS ³⁾	32.3	37.5	NS
H 2	355	304	253	199	<0.001	NS	238	229	NS
H 3	386	352	293	254	<0.001	NS	287	251	23
Slenderness (cm g ⁻¹)									
H 1	6.4	9.6	22.5	49.5	<0.001	<0.001	24.9	24.7	NS
H 2	2.9	6.6	15.3	26.1	<0.001	0.032	15.9	13.1	NS
H 3	2.7	5.8	11.8	18.3	<0.001	NS	12.6	10.1	NS
Stem in plant (%)									
H 1	21.8	27.0	38.3	49.2	<0.001	NS	38.2	38.2	NS
H 2	78.2	82.5	85.4	85.1	<0.001	0.004	85.6	80.9	2.1
H 3	78.6	83.4	86.1	85.4	<0.001	0.013	87.1	83.5	3.0
Bark in stem (%)									
H 3	32.8	33.8	35.7	35.0	<0.001	0.056	40.2	21.0	1.3

¹⁾ 230 in 1992, ²⁾ 65 in 1992, ³⁾ NS: p > 0.05

(height/weight ratio) increased with initial density. In all treatments, it decreased over time. At harvest 1 the proportion of stem in the total dry matter increased with increasing initial density. At harvests 2 and 3 it increased with initial density up to TC90 and was lower at TC270. At harvests 2 and 3 the proportion of stem was lower in Kz90 than in the other two cultivars. In all treatments the proportion of stem increased over time. The proportion of bark in the stem at harvest 3 increased with initial density up to TC90 and was lower at TC270. Bark content was lowest in Kz90 and highest in HE90.

Bark content in the stem was measured at harvest 3 in 1991 and at harvests 2 and 3 in 1992. For these data, bark content of the treatments TC10, TC30 and TC90 increased linearly with plant slenderness ($r^2 = 0.89$); for the treatment TC270 this relationship did not apply (Figure 2).

Non-fibre components in the bark were highest in TC270 and lowest in TC90 (Table 7). Solubility of bark increased with initial plant density. Both the non-fibre components and the solubility of the bark were higher in Kz90 than in the other two cultivars. Solubility of the core was higher for TC10 and TC270 than for the two intermediate densities; it was higher for HE90 than for the two other cultivars. Length of libriform fibres increased with initial density until TC90, but fibre diameter was not affected by initial plant density.

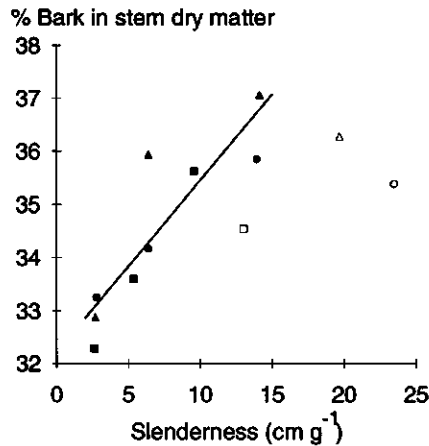


Figure 2. The relationship between the proportion of bark in the stem and plant slenderness (height/weight ratio) for hemp cultivar Kompolti Hybrid TC harvested on 16 September 1991 (circles), 10 August 1992 (triangles) and 14 September 1992 (squares). Black symbols (used to calculate the regression line) 10, 30 or 90 plants m⁻², open symbols 270 plants m⁻².

Table 7. Non-fibre components in the bark, solubility of bark and core in 1% NaOH, and length and diameter of libriform fibres as influenced by initial plant density and cultivar on 16 September 1991.

Parameter	Kompolti Hybrid TC				Regression		Hyper	Kozuhara	Cultivar
	Initial density (plants m ⁻²)				Linear	Quadratic	Elite	zairai	comp.
	10	30	90	270 ¹⁾			90 m ⁻²	90 ²⁾ m ⁻²	LSD (0.05)
Non-fibre components (%)	27.4	26.9	26.2	29.9	NS ³⁾	0.059	25.1	36.1	3.4
Solubility									
bark (%)	27.8	27.2	29.2	30.2	0.048	NS	29.4	35.2	2.8
core (%)	32.5	29.9	30.7	32.0	NS	0.01	32.4	29.6	2.0
Libriform fibres									
Length (μ)	517	568	594	595	0.045	NS	.	.	
Diameter (μ)	36.1	33.6	35.6	34.2	NS	NS	.	.	

1) 230 in 1992, 2) 65 in 1992, 3) NS: $p > 0.05$

DISCUSSION

Self-thinning

The mortality observed in the hemp crops grown in 1988 and 1989 (Chapter 2) was the result of self-thinning. In the experiments conducted in 1991 and 1992, self-thinning occurred in the crops grown at initial densities of 90 and 270 plants m⁻²; the three cultivars showed similar thinning paths. The slopes of the thinning lines of the two sets of data were both shallow and did not differ statistically significantly (Figure 1a and 1b). Their 95 % confidence intervals did not include the values for the average slope of herbaceous dicots calculated by Weller (1987): -0.74 and Lonsdale (1990): -0.71. Lonsdale (1990) demonstrated that the more biomass packing (dry matter per unit of volume) increases with growth, the steeper the slope of the self-thinning line will be. A fibre hemp crop accumulates biomass at rates similar to those of other herbaceous dicots, but its canopy height increases faster than that of most other herbaceous dicots. As a result, the increase in biomass packing with growth is relatively small in fibre hemp, which might well be the cause of its shallow thinning slope.

highest bark content) and highest in the bark of Kz90 (which had the lowest bark content). This fully confirms Bredemann's (1952) observation that the high bast fibre content of the cultivars he had bred resulted from a higher bark content in the stem as well as from a higher fibre content in the bark. Solubility of bark correlated with non-fibre components in the bark ($r^2 = 0.79$, $p < 0.05$), which is not surprising, as the two methods both determine solubility in diluted NaOH.

The increase of the length of the libriform fibres with initial plant density is worth noting, as the value of a raw material for paper making increases with the length of its fibres (Nelson et al. 1961).

CONCLUSIONS

At a high plant density the interval between emergence and canopy closure is shorter than at a low density. More assimilates are partitioned to the stem and less to the inflorescence and the leaves, and flowering is delayed. Dry matter invested in leaves is used more efficiently because SLA increases with plant density. Stem quality is improved because bark content increases.

However, when plant density is too high, plants die as a result of self-thinning, crop growth rate is reduced, and bark content in the stem stops increasing. The slope of the thinning line is in hemp more shallow than in other herbaceous dicots, indicating that at the same crop growth rate the death rate from self-thinning is higher than in other dicots. This is probably caused by the rapid rate at which the canopy height of hemp increases, resulting in a relatively modest increase in biomass packing during the growing season.

In fibre hemp, the optimum plant density yields the most beneficial effects of high plant density on crop characteristics and the least negative effects linked with self-thinning. Consequently, optimum plant density is close or equivalent to the maximum plant density possible at the yield level concerned. The relationship between yield level and maximum (optimum) plant density in fibre hemp is therefore approximated by its self-thinning line.

ACKNOWLEDGEMENTS

We thank J C M Withagen for his help with statistical analyses. I Bócsa is thanked for supplying the seed of the cultivar Kompolti Hyper Elite. E P M de Meijer is thanked for supplying the seed of the cultivar Kozuhara zairai and for the determination of non-fibre-components in the bark and of the dimensions of libriform fibres. P L Kooman and E W J M Mathijssen are thanked for their help with the calculations of the course of light interception by the crops. H van der Hoek is thanked for his technical support in the field and with data analysis. A J Haverkort, P C Struik, W M Lonsdale, B J Schnieders and W J M Meijer are thanked for helpful comments on the manuscript.

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**NITROGEN FERTILIZATION AND ROW WIDTH AFFECT
SELF-THINNING AND YIELD OF FIBRE HEMP
(*Cannabis sativa* L.)**

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ABSTRACT

Self-thinning curtails stem yield and quality in fibre hemp (*Cannabis sativa* L.). The effects of soil nitrogen level (80 and 200 kg ha⁻¹), row width (12.5, 25 and 50 cm), and type of seed drill and thinning method on self-thinning, growth, yield and quality of hemp were determined in field experiments in 1991 and 1992. Nitrogen level affected plant morphology before self-thinning occurred. Due to enhanced competition for light more plants died from self-thinning at 200 than at 80 kg ha⁻¹ N. In August above-ground dry matter of living plants was similar at the two nitrogen levels, but 5% of the plants had died at 80 kg ha⁻¹ N and 25% at 200 kg ha⁻¹ N. Although dry matter losses resulting from self-thinning were greater at 200 than at 80 kg ha⁻¹ N, crop growth rate was higher at 200 than at 80 kg ha⁻¹ N. Apparently, the 80 kg ha⁻¹ N crop responded to a relative lack of nitrogen. At final harvest in September stem yield of living plants was 10.4 t ha⁻¹ at 80 kg ha⁻¹ N and 11.3 t ha⁻¹ at 200 kg ha⁻¹ N. In September bark content in the stem was 35.6 % at 80 and 34.0 % at 200 kg ha⁻¹ N. More self-thinning took place at 50 cm row width than at 12.5 and 25 cm. During early growth and in August yield was lower when row width was larger; in September row width did not affect stem yield or quality. Type of seed drill and thinning method did not affect self-thinning or yield.

KEY WORDS: *Cannabis sativa* L., fibre hemp, nitrogen fertilization, row width, rectangularity, self-thinning, plant morphology

INTRODUCTION

In a fibre hemp (*Cannabis sativa* L.) crop a high plant density is desirable, as the proportion of stem in the above-ground dry matter and the bark content in the stem (the major parameter of stem quality) increase with plant density. At high plant densities, however, inter-plant competition may result in density-induced mortality: self-thinning (Chapter 6). Self-thinning is undesirable, as plants that die and deteriorate before harvest represent a loss of dry matter, and their presence in the harvested product may reduce its quality.

Self-thinning implies that an increase in biomass is accompanied by a reduction in the number of living plants. The time course of a self-thinning stand on a plot of log biomass versus log plant density is called a self-thinning trajectory (Westoby 1984). The straight line that is approached and followed by the self-thinning trajectory of a stand is called a self-thinning line. Two types of response of self-thinning trajectories to a reduction in soil fertility have been distinguished (Westoby 1984, Morris & Myerscough 1984). Plant stands on less fertile soils either thinned along the same trajectory as stands on fertile soils, but at a slower rate: "altered-speed", or they approached thinning lines of reduced slope or reduced intercept relative to those of stands on fertile soils: "altered form". The experiments reviewed by Morris &

Myerscough and Westoby concerned natural vegetations and an often vaguely defined low to medium fertility range. The effect of soil fertility, or of one of its major components such as soil nitrogen status, on self-thinning in annual field crops has never been reported. Further, it has not been clearly established which factors determine whether a species exhibits altered-speed or altered-form behaviour. Westoby (1984) speculated that the altered-form response would occur in species which change to a "more competitive" shape under less fertile conditions. Other species would simply grow more slowly and exhibit altered-speed behaviour. The more rectangularity (i. e. the ratio of the between-row distance and the within-row distance) of a crop exceeds 1:1, the more plants are clustered and the more inter-plant competition is enhanced. Probably as a result of this, plant mortality during the growing season sometimes increased with increasing rectangularity (e.g. Marquart 1919, for fibre hemp, Ethredge et al. 1989, for soybean and Chung 1990, for poppy). However, no reports directly linking rectangularity and self-thinning were found.

The occurrence of self-thinning is preceded by increased variability in the size of individuals, with large plants suppressing smaller ones (Harper 1977). A reduced variability of plant size might therefore reduce or delay the onset of self-thinning. Variability of plant size may be affected by the uniformity of sowing depth and of plant spacing in the row (Benjamin & Hardwick 1986), factors which depend on the type of sowing machine. We found no reports on the effect of variability of seedling size or of sowing-machine technology on self-thinning.

The maximum plant density which can be sustained at a given level of biomass (i.e. the position of the self-thinning line) apparently may depend on several agronomic factors such as fertilization, rectangularity and sowing machine technology.

In fibre hemp N-fertilization rates between 150 and 240 kg ha⁻¹ gave the highest stem yields (Aukema & Friederich 1957, Jaranowska 1964, Rivoira & Marras 1975, Marras & Spanu 1979). Bast fibre content in the stem was reduced by nitrogen, with the highest bast fibre yields obtained at N rates between 50 and 150 kg ha⁻¹ (Aukema & Friederich 1957, Jaranowska 1964, Rivoira & Marras 1975). Plant density at harvest was reduced to a variable extent by nitrogen fertilization (Jaranowska 1964, Rivoira & Marras 1975, Marras & Spanu 1979). Interestingly, the reduction of bast fibre content in the stem with increasing nitrogen was greater in years or cultivars in which self-thinning at high N was more severe (Jaranowska 1964, Rivoira & Marras 1975), suggesting that plants which died as a result of self-thinning were of above-average bast fibre content. This would be in line with our finding that bark content (which is strongly correlated with bast fibre content, De Meijer & Van der Werf 1994) increased with initial plant density only when little or no self-thinning occurred (Chapter 6).

In fibre hemp row widths between 8 and 20 cm gave the highest stem yields (Marquart 1919, Aukema and Friederich 1957, Jaranowska 1963, Van der Schaaf 1966, Dempsey 1975). Aukema and Friederich (1957) found that bast fibre content was slightly higher at 10 than at 20 cm row width. Jaranowska (1963) compared row widths between 10 and 30 cm and found that neither bast fibre content nor plant density at harvest was affected by row width.

The objectives of our experiments were to investigate whether soil nitrogen level, rectangularity and type of sowing machine affect the maximum plant density that can be sustained, and to establish how self-thinning affects yield and bark content in the stem.

MATERIALS AND METHODS

Treatments and cultural methods

Field experiments were carried out in 1991 and 1992 in Lelystad, the Netherlands, on a light marine clay soil. The experimental set-up was a randomized complete block design with ten treatments and two replications. The treatments involved a two-way factorial of two nitrogen levels (soil-N + fertilizer-N: 80 or 200 kg ha⁻¹) and five plant arrangements. Plant arrangements were: a) 12.5 cm row width ('12.5'), b) 25 cm row width ('25'), c) 50 cm row width ('50'), d) 12.5 cm row width precision sown ('12.5p'), and e) 25 cm row width thinned uniformly ('25u'). Treatment '12.5p' was sown using a precision seed drill, while the other treatments were sown with a studded roller seed drill. With the precision seed drill the distance between the plants in a row, and the sowing depth are less variable than with the studded roller seed drill.

Stands in all treatments were thinned manually in the seedling stage (21 May 1991 and 26 May 1992) to obtain the desired plant density. The treatment '25u' was thinned to obtain a uniform crop: we removed tall and short plants and we tried to obtain a uniform distance between the plants in a row. To allow such extensive thinning, this treatment was over-seeded with about twice the number of seeds required for the desired plant density. In 1991 all treatments were thinned to 160 plants m⁻², in 1992 emergence was less than expected and all treatments were thinned to 132 plants m⁻².

P and K fertilizer were applied according to the recommendations for arable crop rotations in the Netherlands. Soil N was measured between 0 and 60 cm in March 1991 (25 kg ha⁻¹) and between 0 and 90 cm in March 1992 (51 kg ha⁻¹). In both years N fertilizer was applied shortly before sowing.

Hemp was sown on 18 April 1991 and on 8 May 1992, with 50 % plant emergence on 5 May in 1991 and on 14 May in 1992. No herbicides were used, as weeds were adequately suppressed by the crop. The occurrence of *Botrytis cinerea* and other fungal diseases was successfully prevented by spraying the crops with fungicides (alternating vinchlozolin at 167 g ha⁻¹ + chlorothalonil at 500 g ha⁻¹ and carbendazim at 87.5 g ha⁻¹ + iprodion at 175 g ha⁻¹) during June, July and August at 14-day intervals.

Data collection

The plots, which were 15 m long and 6 m wide, each contained five 1 m x 1 m sample areas, 2 m apart. The experiment was surrounded by a 3 m-wide buffer of hemp.

Harvest dates were 5 and 24 June, 22 July, 19 August and 9 September in 1991, and 2 and 22 June, 20 July, 17 August and 7 September in 1992. The distance from the top of the canopy to the soil level (stand height) was measured at each harvest in 1991 only. Dead plants were discarded at the first four harvests, and at the final harvest their dry weight was determined. All living plants were cut off flush with the ground. The above-ground fresh weight of living plants was determined. The height of 10 plants from each sample area was measured before these plants were separated into four fractions: stem, green leaves, yellow and dead leaves, and other organs (inflorescence and branches). The area of green leaves was determined using a LI-COR 3100 (Lincoln, USA) area meter. All plant parts were dried at 105 °C until constant weight.

At the fifth harvest 20 plants per sample area were dried at 25 °C on a drying floor. The stems were separated into bark and core by means of a flax breaker; any remaining core was removed from the bark by hand. In 1991 the solubility of ground samples of bark and core in 1% NaOH was determined according to TAPPI procedure 212 (TAPPI, 1988).

At about 2-weekly intervals the number of stem nodes was determined on three plants in the sample areas destined for the fifth harvest. At harvests 4 and 5 sex expression was determined in a 20-plant sample (for methods see Chapter 5).

Shortly before each harvest the interception of photosynthetically active radiation (PAR) by the canopy was measured, using a line sensor (Technical and Physical Engineering Research Service TFDL-DLO, Wageningen, The Netherlands).

Data analysis

The effect of N-fertilization and row width on plant and crop parameters was investigated by analysis of variance. For row width the significance of linear and quadratic regression components was determined.

Self-thinning is density-induced mortality in crowded but actively-growing plant populations (Weller 1987a). As growth of the crop was strongly reduced between harvests 4 and 5 (see results section), data from harvest 5 were not used in investigating the course of self-thinning. The time courses of log biomass versus log plant density of the stands grown at different nitrogen levels and row widths were not analysed using formal statistics. It is not possible to describe these trajectories as a whole without making assumptions as to their general form (Westoby & Howell 1986, Weller 1987a).

RESULTS

Two- and three-way interactions between nitrogen levels, plant arrangements and years were not statistically significant. The treatments '12.5' and '12.5p' did not differ significantly; neither did the treatments '25' and '25u'. For this reason data on the three row widths and the two nitrogen levels are reported as means of the two years.

Self-thinning

At harvests 1 and 2 plant densities were similar; from harvests 3 to 5 the number of surviving plants decreased (Table 1). Plant density was not affected by row width until harvest 4, when the number of surviving plants was lowest at 50 cm row width. Nitrogen level did not affect plant density at harvests 1 and 2, but at harvests 3 and 4 the number of surviving plants was larger at 200 than at 80 kg ha⁻¹ N (Table 1). At harvest 5 plant density at 80 kg ha⁻¹ N was not affected by row width, but plant density of the crops at 200 kg ha⁻¹ N was lowest at 50 cm row width and highest at 25 cm row width.

Table 1. Number and above-ground dry matter of living plants as influenced by row width and nitrogen (N) level. Data for row widths are means of the two N levels (except for plant density at harvest 5), data for N levels are means of the three row widths. All data are means of 1991 and 1992, see text for harvest (H) dates.

Parameter	Row width (cm)			Regression		N (kg ha ⁻¹)		P
	12.5	25	50	Linear	Quadratic	80	200	
Density (m ⁻²)								
H 1	147	147	145	NS ¹⁾	NS	147	147	NS
H 2	148	150	147	NS	NS	149	149	NS
H 3	133	135	136	NS	NS	139	130	<0.001
H 4	124	127	121	NS	0.068	139	110	<0.001
H 5	80 N	131	130	127	NS	NS		
	200 N	92	103	82	NS	0.03		
Dry matter (t ha ⁻¹)								
H 1	0.97	0.80	0.69	<0.001	0.001	0.82	0.87	0.029
H 2	4.08	3.72	3.63	<0.001	0.001	3.54	4.15	<0.001
H 3	8.30	8.10	7.94	NS	NS	7.77	8.52	<0.001
H 4	12.31	12.18	11.49	0.087	NS	11.95	12.24	NS
H 5	12.19	12.71	12.15	NS	NS	11.77	13.02	0.002

¹⁾ NS: p > 0.10

At harvests 1, 2 and 4 dry matter yield was lower when rows were spaced wider (Table 1); at harvests 3 and 5 row width did not affect yield. The dry matter of living plants was higher at 200 than at 80 kg N at all harvests except the fourth. Harvest 4 coincided with the onset of flowering. Between harvests 4 and 5 the dry matter of living plants increased by 0.8 t ha^{-1} at $200 \text{ kg ha}^{-1} \text{ N}$, whereas at $80 \text{ kg ha}^{-1} \text{ N}$ it decreased slightly. For all treatments the rate of increase of dry matter of living plants was much lower between harvests 4 and 5 than in the intervals preceding flowering. A reduction in crop growth rate after flowering is often observed in hemp (Chapters 2, 5 and 6) and mainly results from a lower rate of canopy photosynthesis.

Initial plant density was higher in 1991 than in 1992. In both years the time trajectories of log biomass versus log plant density were not affected by N level or row width between harvests 1 and 2. Subsequently, the paths were steeper at 80 than at $200 \text{ kg ha}^{-1} \text{ N}$. At harvest 4 plant density was higher at 80 than at $200 \text{ kg ha}^{-1} \text{ N}$, whereas living dry matter yield was similar for the two nitrogen levels (Figure 1). More self-thinning had occurred at 200 than at $80 \text{ kg ha}^{-1} \text{ N}$. At harvest 4 both plant density and the dry matter of living plants were higher at 25 than at 50 cm row width (Table 1), implying that more plants had died from self-thinning at 50 than at 25 cm row width.

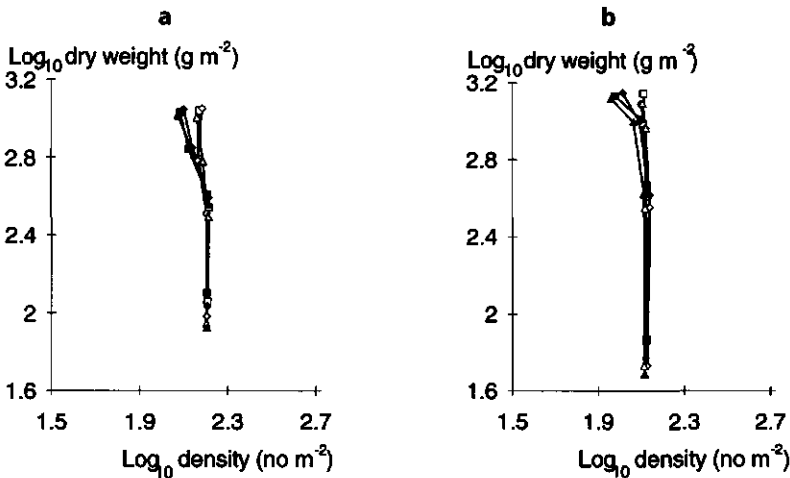


Figure 1. The relationship between log above-ground dry matter of living plants and log density of survivors for hemp crops grown at two nitrogen levels and three row widths, (a) in 1991, (b) in 1992. Open symbols $80 \text{ kg ha}^{-1} \text{ N}$, black symbols $200 \text{ kg ha}^{-1} \text{ N}$; squares 12.5 cm row width, diamonds 25 cm row width, triangles 50 cm row width.

LAI and PAR interception

At harvest 1 both LAI and the fraction of PAR intercepted by the canopy decreased with increasing row width (Table 2). At subsequent harvests LAI was not affected by row width, but the fraction of PAR intercepted decreased with increasing row width at all harvests except the fourth. This discrepancy between LAI and intercepted PAR probably resulted from a more clustered distribution of the leaves at 25 and especially at 50 cm row width. This implies that the amount of PAR at soil level was larger between the rows than within the rows, particularly at 50 cm row width.

LAI of the crop grown at 200 kg ha⁻¹ N exceeded that of the crop grown at 80 kg ha⁻¹ N throughout the growing season (Table 2). As a result of this, the fraction of PAR intercepted was higher at 200 than at 80 kg ha⁻¹ N. At harvests 2, 3 and 4 interception was almost complete.

Table 2. Leaf area index (LAI) and PAR intercepted by the canopy as influenced by row width and nitrogen (N) level. Data for row widths are means of the two N levels, data for N levels are means of the three row widths. All data are means of 1991 and 1992, see text for harvest (H) dates.

Parameter	Row width (cm)			Regression		N (kg ha ⁻¹)		
	12.5	25	50	Linear	Quadratic	80	200	P
LAI (m² m⁻²)								
H 1	1.66	1.36	1.19	<0.001	<0.001	1.42	1.48	0.02
H 2	4.27	4.17	4.33	NS ¹⁾	NS	3.88	4.61	<0.001
H 3	4.24	4.04	4.41	NS	NS	3.94	4.45	0.016
H 4	4.64	4.34	4.61	NS	NS	4.20	4.83	0.014
H 5	2.69	2.92	2.68	NS	NS	2.53	3.03	0.053
PAR intercepted (%)								
H 1	75.8	65.1	50.3	<0.001	NS	65.5	66.9	NS
H 2	98.2	97.4	96.7	0.001	NS	97.1	98.0	0.005
H 3	99.1	98.7	97.3	<0.001	NS	97.7	99.5	<0.001
H 4	99.1	99.0	99.1	NS	NS	98.9	99.2	<0.001
H 5	96.3	95.9	94.9	0.001	NS	95.2	96.5	<0.001

¹⁾ NS: p > 0.10

Plant morphology and phenology

Over most of the growing season plant height decreased with increasing row width, but at harvest 5 row width did not affect plant height (Table 3). Plant slenderness (height/weight ratio) was affected by row width at harvests 1 and 2 only. At harvests 3, 4 and 5 row width affected plant height and plant weight similarly (data not shown) and consequently slenderness was not affected.

At harvests 1 and 2 mean plant height was greater at 200 than at 80 kg ha⁻¹ N, whereas at harvests 3 and 4 it was smaller at 200 than at 80 kg ha⁻¹ N (Table 3). At harvest 5 nitrogen level did not affect mean plant height. In 1991 stand height was measured in addition to mean

Table 3. Plant height and plant height/weight (slenderness) as influenced by row width and nitrogen (N) level. Data for row widths are means of the two N levels. Data for N levels are means of the three row widths. All data are means of 1991 and 1992, see text for harvest (H) dates.

Parameter	Row width (cm)			Regression		N (kg ha ⁻¹)		P
	12.5	25	50	Linear	Quadratic	80	200	
Height (cm)								
H 1	20	19	20	NS ¹⁾	0.053	19	20	0.015
H 2	93	88	82	<0.001	NS	86	92	<0.001
H 3	162	159	152	0.039	NS	164	154	0.005
H 4	205	201	189	<0.001	NS	203	197	0.026
H 5	211	215	214	NS	NS	215	212	NS
Slenderness (cm g⁻¹)								
H 1	30.4	35.5	44.3	<0.001	NS	34.8	35.7	NS
H 2	33.4	35.3	33.4	NS	0.002	35.7	32.6	<0.001
H 3	26.8	27.3	27.0	NS	NS	30.2	23.9	<0.001
H 4	20.8	21.2	20.2	NS	NS	23.8	17.9	<0.001
H 5	19.7	19.9	18.5	NS	NS	23.7	15.4	<0.001

¹⁾ NS: $p > 0.10$

plant height. The 1991 data for mean plant height exhibited the trend observed for the average data for 1991 and 1992: mean plant height was greater at 200 than at 80 kg ha⁻¹ N at harvests 1 and 2 only (Figure 2a). Stand height was greater at 200 than at 80 kg ha⁻¹ N throughout the growing season (Figure 2b). Biomass packing (dry matter per unit volume) was not affected by nitrogen fertilization at harvests 1 and 3; at harvest 2 it was greater at 200 than at 80 kg ha⁻¹ N, whereas at harvests 4 and 5 it was smaller at 200 than at 80 kg ha⁻¹ N (Figure 2c).

Nitrogen level did not affect plant slenderness at harvest 1, but at subsequent harvests slenderness decreased more at 200 than at 80 kg ha⁻¹ N (Table 3). As a result of this, at harvest 5 slenderness was 23.7 cm g⁻¹ at 80 kg N ha and 15.4 cm g⁻¹ at 200 kg ha⁻¹ N.

Row width did not affect the number of stem nodes nor the percentage of plants flowering. At harvests 3 and 4 the crop had 1.0 and 0.9 more nodes with opposite phyllotaxis at 80 than at 200 kg ha⁻¹ N (Table 4). The number of nodes with alternate phyllotaxis was not affected. At harvest 5 the proportion of male plants was higher at 80 than at 200 kg ha⁻¹ N, resulting in a larger proportion of flowering plants.

Table 4. Number of nodes with opposite, and number of nodes with alternate phyllotaxis; percentage of plants flowering; percentage of male and percentage of female plants in hemp as influenced by nitrogen level. Data are means of three row widths in 1991 and 1992, see text for harvest dates.

Observation	Harvest	Nitrogen (kg ha ⁻¹)		
		80	200	P
Nodes with opp. phyllotaxis (no.)	3	9.7	8.7	0.013
Nodes with opp. phyllotaxis (no.)	4	10.9	10.0	0.070
Nodes with alt. phyllotaxis (no.)		3.3	3.3	NS ¹⁾
Plants flowering (%)	5	96.3	86.4	<0.001
Male plants (%)		42.3	34.7	0.01
Female plants (%)		54.0	51.7	NS

¹⁾ NS: p > 0.10

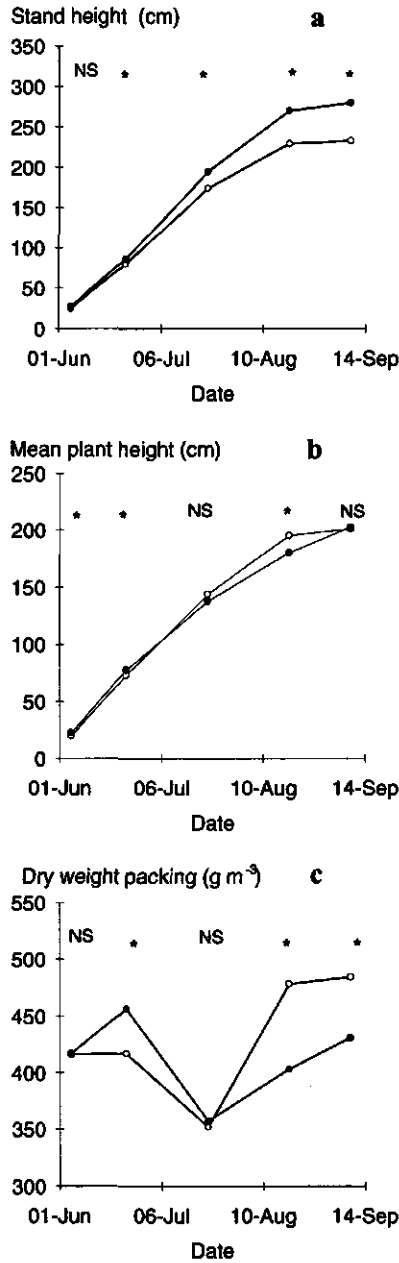


Figure 2. The course during the growing season of: (a) mean plant height; (b) stand height; (c) biomass packing (dry matter per unit volume) of hemp crops grown at 80 kg ha⁻¹ N (open circles) and 200 kg ha⁻¹ N (black circles) in 1991.

NS: $p > 0.05$, *: significant effect of N level ($p < 0.05$).

Yield and yield components

At harvest 5 yield and yield components were not affected by row width but only by nitrogen level. The dry matter yield of living plants was 1.2 t ha⁻¹ higher at 200 than at 80 kg ha⁻¹ N (Table 5). The yield of the inflorescence, leaves and stem dry matter of living plants was higher at 200 than at 80 kg ha⁻¹ N, while the proportion of bark in the stem was higher at 80 than at 200 kg ha⁻¹ N. The solubility of bark in 1 % NaOH was not affected by nitrogen fertilization. At 80 kg ha⁻¹ N solubility of the core was higher than at 200 kg ha⁻¹ N, indicating a higher content of soluble or readily degradable substances which might lead to a lower yield in chemical pulping. The yield of dead plants was higher at 200 than at 80 kg ha⁻¹ N.

Table 5. Dry matter of living plants; dry matter of the inflorescence, of the leaves and of the stem of living plants; the proportion of bark in the stem, the solubility of bark and core in 1% NaOH and the dry matter of dead plants. Data from final harvest of hemp grown at two nitrogen levels. Means of three row widths in 1991 and 1992, except for solubility of bark and core, which was measured in 1991 only.

Yield parameter	Nitrogen (kg ha ⁻¹)		
	80	200	P
Living plants (t ha ⁻¹)	11.77	13.02	0.002
Inflorescence (t ha ⁻¹)	0.26	0.32	0.032
Leaves (t ha ⁻¹)	0.99	1.25	0.011
Stem (t ha ⁻¹)	10.35	11.30	0.005
Bark in stem dry matter (%)	35.6	34.0	<0.001
Solubility of bark (%)	33.1	33.6	NS ¹⁾
Solubility of core (%)	34.9	33.2	<0.01
Dead plants	0.77	1.07	0.04

¹⁾ NS: p > 0.05

DISCUSSION

Self-thinning

Treatments which aimed at creating different levels of variability of seedling size did not affect self-thinning. This is not surprising, as these treatments did not actually succeed in affecting variability of seedling size (Chapter 8).

Row width affected self-thinning less than N-fertilization. At 50 cm row width more plants died from self-thinning than at 25 and 12.5 cm. This confirms findings by Marquart (1919), Ethredge *et al.* (1989) and Chung (1990) and must result from the inevitable increase of inter-plant competition in the row with increasing rectangularity.

In our experiments soil nitrogen status did alter the form of the self-thinning trajectory, but, relative to the high-fertility treatment, the low-fertility treatment approached a thinning line of steeper slope or larger intercept rather than one of reduced slope or intercept. This type of response of self-thinning trajectories to N level can be considered as "altered-form" (Morris & Myerscough 1984), but, contrary to results reviewed by Morris & Myerscough (1984) and Westoby (1984), we found less rather than more self-thinning at low fertility. The cause of this discrepancy may lie in the range of soil fertility investigated. The experiments reviewed by Morris & Myerscough and Westoby concerned natural vegetations and a low to medium fertility range. In those experiments competition was probably mainly for nutrients, rather than for light. At very low fertility plants may even have died from lack of nutrients. Our experiments involved a crop canopy and a medium to high fertility range. In our experiments, competition for light was probably more important, especially at the high N level. Weiner and Thomas (1986) demonstrated that competition for light promotes size variability, generating a class of suppressed plants, which are likely to die from self-thinning. At our low N level, competition was probably more for N and less for light than at the high N level. Competition for N, a below-ground resource, reduces size variability (Weiner & Thomas 1986), and fewer or no suppressed plants are generated. We therefore attribute increased self-thinning at high N to enhanced competition for light. Apparently the self-thinning line can be lowered by high as well as by low soil fertility.

Plant morphology and phenology

Plant morphology has been shown to affect plant competitiveness and consequently the position of the thinning line. Plants can add mass by growing in height, or in radius, or by packing more mass in the volume already occupied. Allocation of resources to height growth or to biomass packing leaves fewer resources for radial expansion, meaning less competition

with neighbours (Weller 1987b). Plants which add mass mainly through height growth or increased biomass packing have been shown to have thinning lines with a larger intercept or of steeper slope than plants which add biomass mostly through radial growth (Lonsdale & Watkinson 1983, Weller 1987b, Ellison 1987, Lonsdale 1990).

In our experiments plant morphology was affected by the level of nitrogen fertilization before self-thinning occurred (Table 3). At 80 kg ha⁻¹ N plant slenderness did not change from harvest 1 to harvest 2, indicating that weight had increased solely as a result of increased height. At 200 kg ha⁻¹ N slenderness had decreased, implying that radial growth and/or increased biomass packing had been more important at 200 than at 80 kg ha⁻¹ N. The 1991 data show that between harvest 1 and 2 biomass packing increased more at 200 than at 80 kg ha⁻¹ N. Evidence of enhanced radial growth at 200 kg ha⁻¹ N is provided by data on leaf area expansion: between harvests 1 and 2 LAI increased by 2.5 at 80 kg ha⁻¹ N and by 3.1 at 200 kg ha⁻¹ N. LAI remained higher at 200 than at 80 kg ha⁻¹ N throughout the growing season, causing a higher proportion of PAR interception by the canopy and enhancing competition for light in the 200 kg ha⁻¹ N crop. Lack of light in the lower part of the canopy probably caused the death of suppressed plants, resulting in more self-thinning at 200 than at 80 kg ha⁻¹ N.

At harvests 3, 4 and 5 slenderness decreased less at 80 than at 200 kg ha⁻¹ N and at harvests 4 and 5 biomass packing was higher at 80 than at 200 kg ha⁻¹ N. However, these changes in slenderness and biomass packing from harvest 3 onwards, were probably the result, rather than the cause, of the difference in self-thinning at the two contrasting N levels.

Plant development rate, as reflected in the number of stem nodes and the proportion of flowering plants, was lower at 200 than at 80 kg ha⁻¹ N. This was probably due to the presence of short suppressed plants, which, as will be shown in detail in Chapter 8, were more numerous in the 200 kg ha⁻¹ N crop than in the 80 kg ha⁻¹ N crop. These suppressed plants had fewer nodes and flowered less than the taller plants.

Yield and implications for crop management

At harvest 5 row width did not affect yield, but at harvests 1, 2 and 4 dry matter yield decreased with increasing row width. Interception of PAR decreased with increasing row width at all harvests except the fourth. At harvest 1 the effect of row width on PAR interception was particularly large, implying that canopy closure was later when row width was larger. Early canopy closure is desirable, as it contributes to the crop's competitive potential relative to weeds.

For practical purposes therefore, a row width of 12.5 or 25 cm seems more desirable than 50 cm row width. This conclusion is in line with earlier reports on row distance in fibre hemp,

which recommend row widths between 8 and 20 cm (Marquart 1919, Aukema and Friederich 1957, Jaranowska 1963, Van der Schaaf 1966, Dempsey 1975).

Nitrogen fertilization affected growth and yield of the hemp crops not only through its effect on self-thinning. At all harvests except the fourth, yields were higher at 200 than at 80 kg ha⁻¹ N. Apparently, from the beginning of the growing season (harvest 1), the 80 kg ha⁻¹ N crop responded to a relative lack of nitrogen.

At final harvest the bark content in the stem was lower at 200 than at 80 kg ha⁻¹ N. This may have been a direct effect of nitrogen level on bark content and/or a selective effect of self-thinning, when plants killed as a result of self-thinning were of above-average bark content. The latter hypothesis seems most probable, as a reduction of bast fibre content in the stem caused by N-fertilization was found to be associated with the occurrence of self-thinning (Jaranowska 1964, Rivoira & Marras 1975).

CONCLUSIONS

The effect of nitrogen fertilization on the yield and quality of fibre hemp is complex. Nitrogen fertilization affected hemp growth directly, as throughout the growing season dry matter yield was higher at 200 than at 80 kg ha⁻¹ N. Hemp growth was also affected indirectly by nitrogen fertilization, as self-thinning paths were steeper at 80 than at 200 kg ha⁻¹ N, meaning that, at similar biomass, fewer plants survived at 200 than at 80 kg ha⁻¹ N. At a lower initial plant density, less self-thinning would have occurred and the yield difference between 80 and 200 kg ha⁻¹ N might have been larger. Further research into the effect of N-fertilization on the yield of fibre hemp should be conducted at a lower plant density, and at a wider range of nitrogen levels.

The effect of rectangularity on self-thinning was small relative to that of nitrogen level. More self-thinning took place at 50 cm row width than at 12.5 and 25 cm.

ACKNOWLEDGEMENTS

Our thanks to W van den Berg for his help with statistical analyses, to J J Tick for his technical support in the field and laboratory, and to P C Struik, W J M Meijer and B J Schnieders for their helpful comments on the manuscript.

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**NITROGEN FERTILIZATION AND SEX EXPRESSION
AFFECT SIZE VARIABILITY OF FIBRE HEMP
(*Cannabis sativa* L.)**

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ABSTRACT

Mechanical harvesting and industrial processing of fibre hemp (*Cannabis sativa* L.) require uniformity of stem length and weight. In 1991 and 1992 we carried out field experiments to investigate the effects of soil nitrogen level (80 and 200 kg ha⁻¹ N) and row width (12.5, 25 and 50 cm) on the variability of weight and height in hemp plants. Row width did not affect size variability. At final harvest coefficients of variation (CV) of both weight and height were about 1.5 times higher at 200 than at 80 kg ha⁻¹ N. Distributions of dry weight were positively skewed until final harvest, with skewness larger at 200 than at 80 kg ha⁻¹ N. Distributions of height were negatively skewed until final harvest at 80 kg ha⁻¹ N. At 200 kg ha⁻¹ N they changed from negative skewness during the first part of the growing season to negative kurtosis in the second part of the growing season. More suppressed plants were present at 200 than at 80 kg ha⁻¹ N. Contrary to most published results, we did not find a reduction of CV of weight nor of CV of height at the onset of self-thinning. Suppressed hemp plants can survive relatively well in the low-light environment under the canopy. Sexual dimorphism contributed to variability of height and weight, but the effects were smaller than those of nitrogen fertilization. The ratio of female to male plants was higher at 200 than at 80 kg ha⁻¹ N, as a result of a shift in sex-ratio within the population of suppressed plants. As suppressed plants were much more slender than dominating plants, self-thinning eliminated the most slender individuals in a hemp crop. However, the presence of many more heavy individuals of low slenderness at 200 than at 80 kg ha⁻¹ N was probably the major cause of the difference in slenderness between 200 and 80 kg ha⁻¹ N.

KEY WORDS: *Cannabis sativa* L., fibre hemp, nitrogen fertilization, sex expression, sexual dimorphism, size variability, competition, dominance and suppression, allometry

INTRODUCTION

Fibre hemp (*Cannabis sativa* L.) is grown for the production of stems, which are processed into textile or paper products. In hemp, the proportion of stem in the above-ground dry matter and the content of the valuable bast fibres in the stem increase with plant density (Chapter 6), so a high density is desirable.

Uniformity of size is important for the mechanical harvesting and industrial processing of hemp stems (Huisman & De Maeyer 1993). The larger the range of plant heights in a hemp crop, the less efficient the measures for mechanical defoliation at harvest. In industrial processing, a wide range of stem weights and stem diameters is not desirable, as it hampers fine-tuning of decortication equipment, resulting in less efficient separation of bark and core.

In dense plant stands inter-plant competition may generate a size hierarchy, i.e. increase variability in the size of individuals, with large plants suppressing smaller ones (Harper 1977).

Eventually self-thinning may occur; suppressed plants may die. Self-thinning in hemp was the subject of Chapters 6 and 7. In this Chapter we address size variability.

Differences in the size of individual plants may be determined by: age differences, genetic differences, environmental heterogeneity, maternal effects, effects of herbivores, parasites or pathogens, or competition (Weiner & Thomas 1986). In hemp, which is a dioecious species, sexual dimorphism may be an additional cause of size variability (Hoffmann 1957), but this has never been quantified.

The coefficient of variation (CV: standard deviation/mean) is a standard measure of relative variation and size variability (Weiner & Thomas 1986). In even-aged plant stands CVs of size parameters generally increase with time until the onset of self-thinning, and then decrease as suppressed plants die (Benjamin & Hardwick 1986; Weiner & Thomas 1986; Knox et al. 1989).

Size distributions often depart from normality; skewness and kurtosis measure the nature and amount of this departure (Sokal & Rohlf 1981). Skewness indicates the degree of asymmetry of the distribution, with negative skewness indicating a tail to the left, and positive skewness indicating a tail to the right. Kurtosis represents the pointedness of the distribution. A leptokurtic distribution (positive kurtosis) has more items near the mean and at the tails, with fewer items in the intermediate regions relative to a normal distribution with the same mean and variance. A platykurtic distribution (negative kurtosis) has fewer items at the mean and at the tails than the normal distribution but more in intermediate regions. Frequency distributions of plant mass generally become increasingly positively skewed as time passes, while distributions of plant height either remain symmetrical or become negatively skewed (Hara 1984; Geber 1989; Knox et al. 1989). Frequency distributions of both plant mass and plant height may become bimodal (i. e. two-peaked, an extreme platykurtic distribution) (Huston & DeAngelis 1987). Once self-thinning has started, skewness generally decreases and bimodality tends to disappear (Hara 1984; Benjamin & Hardwick 1986).

Competition is a major cause of the development of size variability (Weiner & Thomas 1986; Bonan 1991). Weiner & Thomas (1986) suggested that competition for light is one-sided, i.e. large plants suppress small ones more than small plants suppress large ones, and this effect is greater than would be expected from their relative sizes. In the most extreme form of "one-sided" competition, the growth of large plants would not be reduced at all by smaller individuals. In contrast, competition for below-ground resources would be two-sided, with shared resources being distributed in proportion to plant size. One-sided competition promotes size variability, whereas two-sided competition reduces it (Weiner & Thomas 1986). Reduced soil fertility may lead to earlier or more below-ground (two-sided) competition, and thus should reduce the rate at which size variability increases with time. Tests of this hypothesis were found in two reports only (Weiner 1985; Lieffers & Titus 1989), on experiments which used extreme fertility treatments in a greenhouse. The effect of soil fertility, or of one of its major components such as soil nitrogen status, on size variability in a field situation has never been reported.

Because competition affects size variability, in a row crop we would expect rectangularity (the ratio of the between-row distance and the within-row distance) to influence size variability. At the same plant density, competition starts earlier, the more rectangularity exceeds 1:1. The effect of rectangularity on the occurrence of size variability has not been previously reported.

The variability of seedling size may affect the variability of plant size later on in the growing season. The variability of seedling size may be influenced by the uniformity of sowing depth and of plant spacing within the row (Benjamin & Hardwick 1986), factors depending on the type of sowing machine. Reports on the effect of sowing-machine technology on size variability were not found.

The objective of our experiments was to investigate to what extent soil nitrogen level, rectangularity and type of sowing machine affect size variability in hemp. We also investigated to what extent sexual dimorphism contributes to size variability in hemp.

MATERIALS AND METHODS

Treatments and cultural methods

Field experiments were carried out in 1991 and 1992 in Lelystad, the Netherlands, on a light marine clay soil. The experimental set-up was a randomized complete block design with ten treatments and two replications. The treatments involved a two-way factorial of two nitrogen levels (soil-N + fertilizer-N: 80 or 200 kg ha⁻¹) and five plant arrangements. Plant arrangements were: a) 12.5 cm row width ('12.5'), b) 25 cm row width ('25'), c) 50 cm row width ('50'), d) 12.5 cm row width precision sown ('12.5p'), e) 25 cm row width thinned uniformly ('25u'). We used a precision seed drill to sow treatment '12.5p' and a studded roller seed drill for the other treatments. With the precision seed drill the distance between plants in the row and sowing depth are less variable than with the studded roller seed drill.

Stands in all treatments were thinned manually at the seedling stage to obtain the desired plant density. The treatment '25u' was thinned to obtain a uniform crop: we removed tall and short plants and we tried to obtain a uniform distance between the plants in a row. To allow such extensive thinning, this treatment was over-seeded with about twice the number of seeds required for the desired plant density. In 1991 all treatments were thinned to 160 plants m⁻², while in 1992 plant emergence was less than expected and all treatments were thinned to 132 plants m⁻².

Agronomic management practices for the experiments were as described in Chapter 7.

Data collection

The plots, which were 15 m long and 6 m wide, each contained five sample areas, 2 m apart. Four sample areas were 1 m x 1 m, while the sample area for the fifth (and final) harvest was 1 m x 2 m. Most plants in the sample areas were used to determine plant densities, yield, and its components as described in Chapter 7.

Harvest dates were 5 and 24 June, 22 July, 19 August and 9 September in 1991, and 2 and 22 June, 20 July, 17 August and 7 September in 1992. At each harvest 25 consecutive living plants per plot were cut off flush with the ground. The length of each plant was measured, and all plants were dried individually at 105 °C until constant weight. At harvest 5 the sex expression of each of the 25 plants was determined (for method see Chapter 5).

Data analysis

To characterize frequency distributions of plant height and plant weight the coefficient of variation (CV), and the skewness and kurtosis were calculated for each 25-plant sample (Sokal & Rohlf 1981). The CV was calculated as the standard deviation divided by the mean. Skewness was calculated as the third central moment divided by the cube of the standard deviation. Kurtosis was calculated as the fourth central moment divided by the fourth power of the standard deviation minus 3. Differences among treatments for CV, skewness and kurtosis were tested by analysis of variance. Tests for the departure from zero of the treatment means of skewness and kurtosis were based on the standard errors from the analysis of variance. As a statistical test for bimodality is not available, we evaluated bimodality by visual inspection of size distributions.

RESULTS

Nitrogen levels and plant arrangements did not significantly interact. Row width (treatments '12.5', '25' and '50'), type of sowing machine ('12.5p' vs '12.5') and manual thinning to obtain uniformity ('25u' vs '25') did not affect CV, skewness or kurtosis. The level of nitrogen fertilization strongly affected these size variability parameters, and the two years differed to some extent. Consequently data are reported separately for the years and averaged over the five plant arrangements.

Development of size variability

The CV of plant dry weight was greater at 200 than at 80 kg ha⁻¹ N at harvests 3 to 5 in 1991 and at harvests 2 to 5 in 1992 (Table 1). CVs increased with time until harvest 4 or 5, and more rapidly at 200 than at 80 kg ha⁻¹ N. The distributions of plant dry weights were positively skewed at all harvests except the first in 1991, and skewness increased with time until harvest 3, 4 or 5 (Table 1). When skewness was affected by N level, it was larger at 200 than at 80 kg ha⁻¹ N. The distributions of plant dry weights were not kurtotic, except for those of harvests 4 and 5 of the 200 kg ha⁻¹ N crop in 1992, which showed positive kurtosis (Table 1).

Table 1. Coefficient of variation, the skewness and kurtosis of the dry weight of hemp plants grown at two soil nitrogen levels in 1991 and 1992. Data are means of five plant arrangements, see text for harvest (H) dates.

Parameter	1991			1992		
	Nitrogen (kg ha ⁻¹)		P	Nitrogen (kg ha ⁻¹)		P
	80	200		80	200	
Coefficient of variation						
H 1	35.6	31.1	NS ¹⁾	36.9	36.0	NS
H 2	42.1	47.6	NS	49.1	70.0	<0.001
H 3	54.2	86.1	<0.001	57.8	107.1	<0.001
H 4	58.8	96.4	<0.001	77.6	110.6	<0.001
H 5	60.0	93.0	<0.001	70.3	110.3	<0.001
Skewness						
H 1	0.01	-0.17	NS	0.38*	0.41*	NS
H 2	0.41*	0.54*	NS	0.29	0.67*	NS
H 3	0.49*	1.02*	0.042	0.32*	1.20*	<0.001
H 4	0.61*	0.83*	NS	0.93*	1.52*	0.016
H 5	0.62*	0.97*	NS	0.67*	1.56*	<0.001
Kurtosis						
H 1	-0.47	-0.02	NS	-0.31	0.06	NS
H 2	0.07	0.62	NS	-0.33	-0.24	NS
H 3	0.56	0.42	NS	-0.62	0.85	NS
H 4	0.16	-0.50	NS	0.43	2.03*	NS
H 5	0.31	0.05	NS	-0.04	2.18*	<0.001

¹⁾ NS: $p \leq 0.05$, * : skewness or kurtosis is significantly ($p \leq 0.05$) different from zero.

The CV of plant height was greater at 200 than at 80 kg ha⁻¹ N at harvests 3 to 5 in 1991 and at harvests 2 to 5 in 1992 (Table 2). CVs increased with time until harvest 3, 4 or 5, and more rapidly at 200 than at 80 kg ha⁻¹ N. At 80 kg ha⁻¹ N the distributions of plant heights were negatively skewed from harvest 2 to 5, while at 200 kg ha⁻¹ N they were negatively skewed at harvests 1 to 3 in 1991 and at harvest 2 in 1992 (Table 2). At all harvests except harvests 1 and 2 in 1992, skewness of the distribution of plant heights was more negative at 80 than at 200 kg ha⁻¹ N. At 80 kg ha⁻¹ N the distributions of plant heights showed positive kurtosis at harvests 2, 3 and 4 in 1991 and at harvest 3 in 1992. At 200 kg ha⁻¹ N they showed negative kurtosis from harvests 3 to 5 in 1991 and at harvests 4 and 5 in 1992.

Table 2. Coefficient of variation, the skewness and kurtosis of the height of hemp plants grown at two soil nitrogen levels in 1991 and 1992. Data are means of five plant arrangements, see text for harvest (H) dates.

Parameter	1991			1992		
	Nitrogen (kg ha ⁻¹)		P	Nitrogen (kg ha ⁻¹)		P
	80	200		80	200	
Coefficient of variation						
H 1	13.9	12.0	NS ¹⁾	16.5	14.8	NS
H 2	10.6	13.0	NS	13.5	23.3	0.004
H 3	17.9	28.5	<0.001	20.0	36.5	<0.001
H 4	18.3	35.3	<0.001	26.7	34.7	<0.001
H 5	22.2	32.9	<0.001	25.1	35.2	0.004
Skewness						
H 1	-0.08	-0.66*	0.017	0.00	-0.04	NS
H 2	-1.64*	-1.06*	0.017	-1.04*	-0.95*	NS
H 3	-1.27*	-0.48*	<0.001	-1.37*	-0.28	<0.001
H 4	-1.00*	-0.01	<0.001	-0.69*	-0.22	0.003
H 5	-0.71*	-0.18	0.015	-0.69*	-0.14	0.020
Kurtosis						
H 1	0.29	1.49*	NS	-0.17	0.18	NS
H 2	4.40*	0.68	0.009	0.68	0.26	NS
H 3	1.60*	-0.83*	<0.001	1.59*	-1.02	0.016
H 4	0.95*	-1.42*	<0.001	-0.27	-0.92*	0.009
H 5	-0.01	-1.20*	0.002	0.00	-0.96*	0.013

¹⁾ NS: $p \leq 0.05$, * : skewness or kurtosis is significantly ($p \leq 0.05$) different from zero.

Size and sex expression

At harvest 5 the 200 kg ha⁻¹ N crop in both years comprised more very heavy plants and more very light plants than the 80 kg ha⁻¹ N crop (Figure 1a). In both years and at both N levels heavy plants were mainly female (Figure 1b-c). All non-flowering plants were very light and more were present at 200 than at 80 kg ha⁻¹ N (Figure 1d).

At harvest 5 in both years the 200 kg ha⁻¹ N crop comprised more very tall and more short

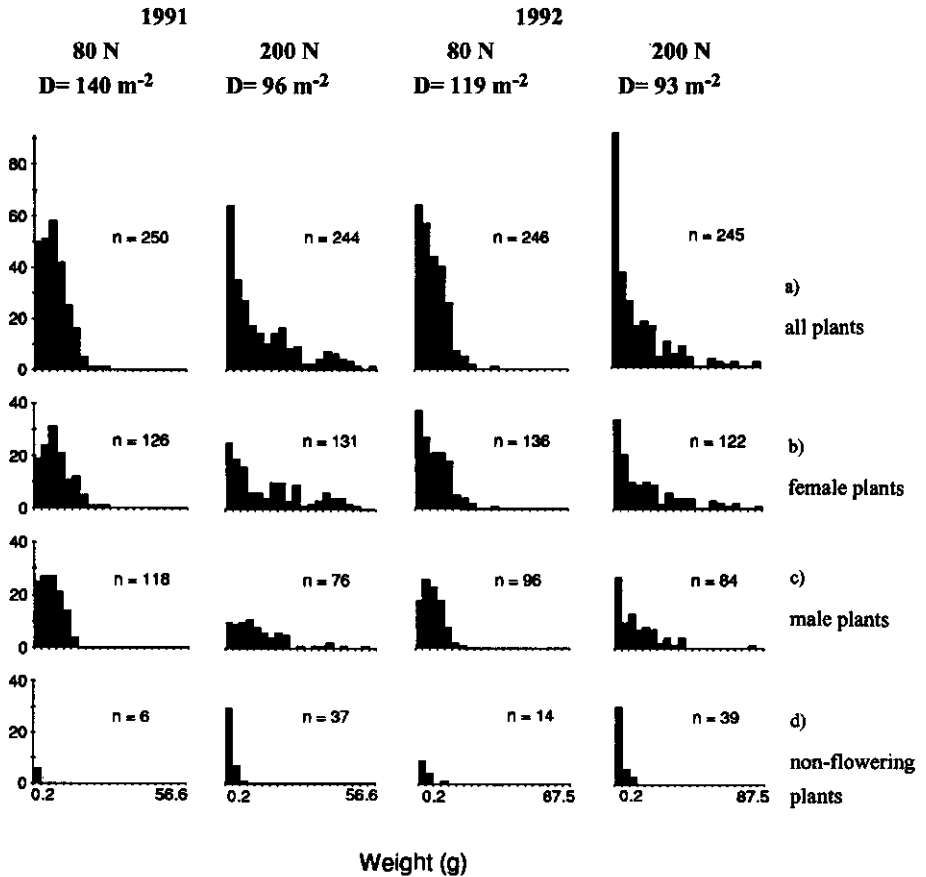


Figure 1. Frequency distributions of dry weight of hemp plants grown at 80 and 200 kg ha⁻¹ of nitrogen at final harvest in 1991 and 1992. Density of survivors (D) is given at the top of the figure; sample size (n) is given for each histogram. Maximum and minimum values are beneath the histograms, at the bottom of the figure. There are 20 equal classes in each histogram.

plants than the 80 kg ha⁻¹ N crop (Figure 2a). In 1991 the frequency distribution of heights of the 200 N ha⁻¹ crop was clearly bimodal; in 1992 it was less so. In both years and at both N levels the tallest plants were mainly male (Figure 2b-c). Plants of below-average stature were more often female than male (Figure 2b-c), and, especially at 200 kg ha⁻¹ N, many of these plants did not flower (Figure 2d).

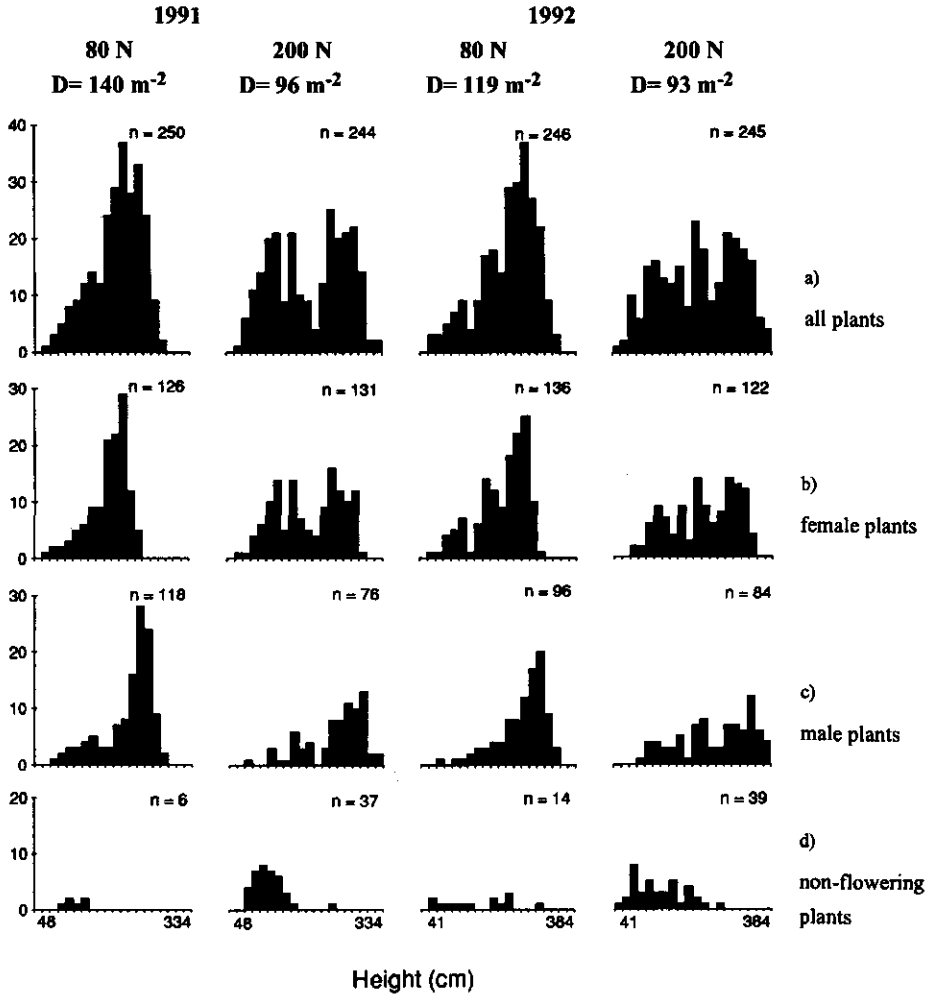


Figure 2. Frequency distributions of height of hemp plants grown at 80 and 200 kg ha⁻¹ of nitrogen at final harvest in 1991 and 1992. Density of survivors (D) is given at the top of the figure; sample size (n) is given for each histogram. Maximum and minimum values are beneath the histograms, at the bottom of the figure. There are 20 equal classes in each histogram.

Allometry

For convenience, changes in the relationship between height and weight of individual plants during the growing season are presented using the 1992 data only, as the results for 1991 were similar.

At harvest 1 plant height and plant weight were related, but the relationship was not close and the pattern was not affected by N fertilization level (Fig 3). At harvest 2 the relationship between height and weight was closer than at harvest 1, and there were more short (< 60 cm), as well as more heavy (> 6 g), plants at 200 than at 80 kg ha⁻¹ N (Fig 3).

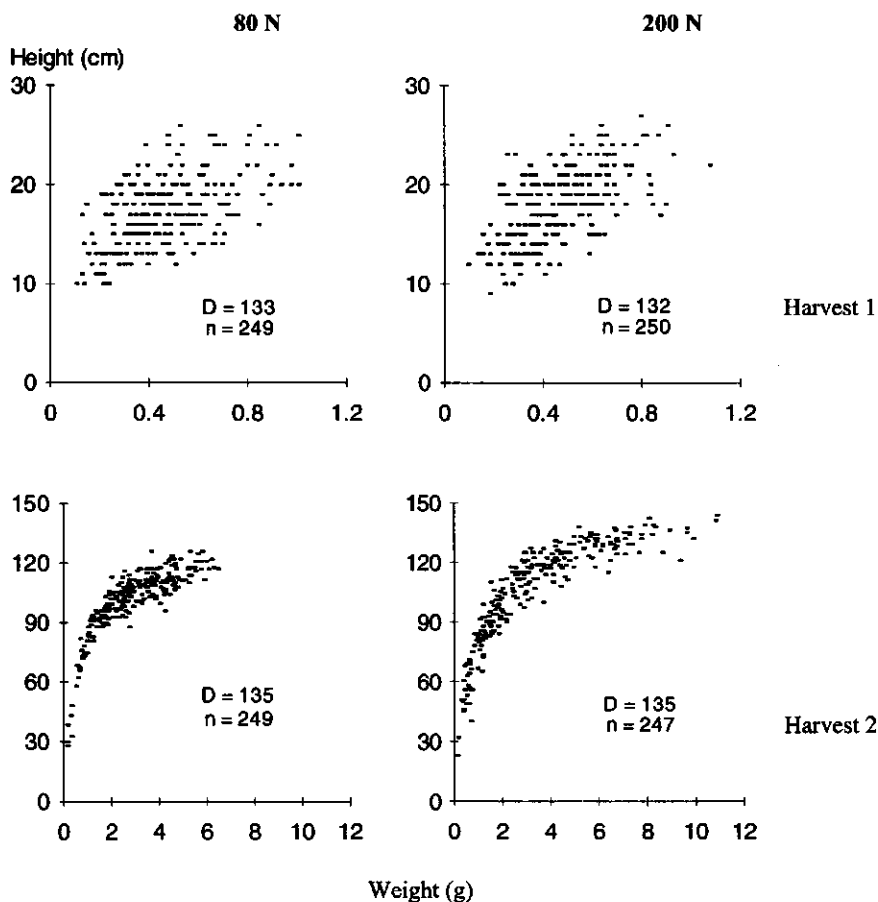


Figure 3. The relationship between height and above-ground dry weight of hemp plants grown at 80 and 200 kg ha⁻¹ of nitrogen on 2 (Harvest 1) and 22 (Harvest 2) June 1992. Density of survivors (D, m⁻²) and sample size (n) are indicated for each graph.

At harvest 3, in spite of more severe self-thinning at 200 than at 80 kg ha⁻¹ N, the difference in the number of short (< 120 cm) plants at high versus low N had increased (Figure 4). At 80 kg ha⁻¹ N maximum plant weight was 20 g, while at 200 kg ha⁻¹ N many plants of between 20 and 40 g were found. In the period between harvests 3 and 4 the plant density of the 200 kg ha⁻¹ N crop decreased by 21 %, and this was associated with a large reduction in the number of very short (< 80 cm) plants (Fig 4). However, at harvest 4, there were more short (< 120 cm) plants at 200 than at 80 kg ha⁻¹ N, and this trend persisted until harvest 5 (Fig 2a). At harvest 4, as at harvests 2 and 3, more heavy (> 30 g) plants were present at 200 than at 80 kg ha⁻¹ N.

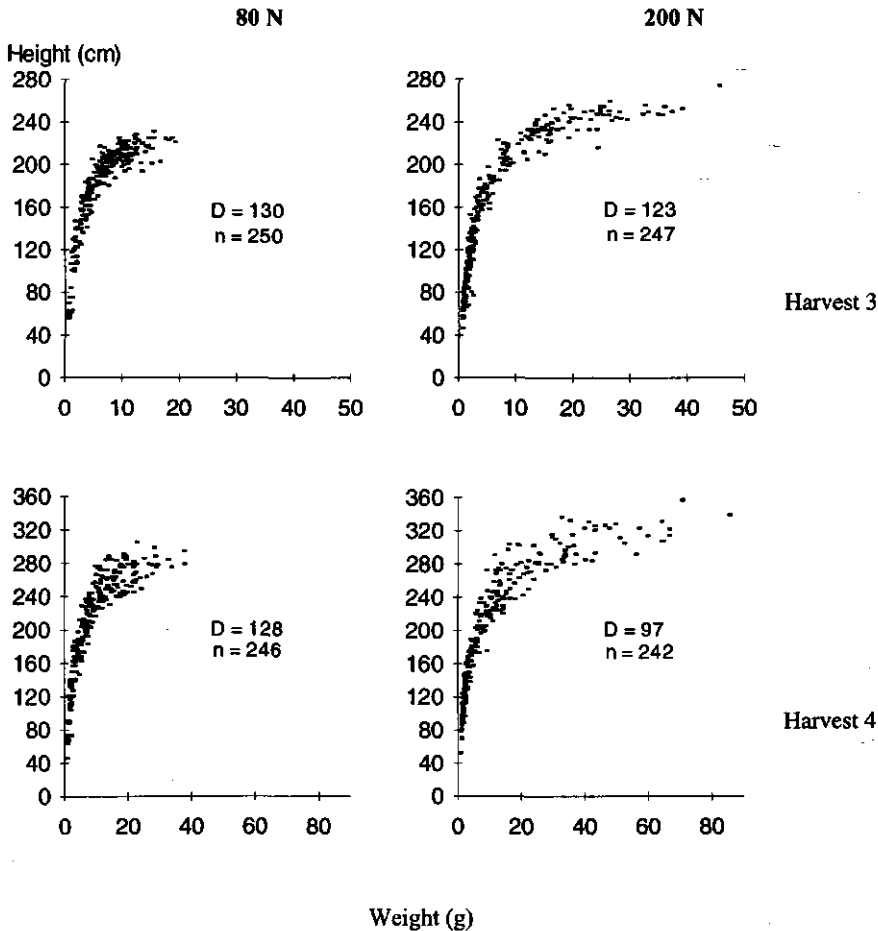


Figure 4. The relationship between height and above-ground dry weight of hemp plants grown at 80 and 200 kg ha⁻¹ of nitrogen on 20 July (Harvest 3) and 17 August (Harvest 4) 1992. Density of survivors (D, m⁻²) and sample size (n) are indicated for each graph.

At all harvests except harvest 1, the range of plant weights was much wider than the range of plant heights, e.g. at harvest 4 in the 200 kg ha⁻¹ N crop (Figure 4), heights spanned less than one order of magnitude (60 - 360 cm), whereas weights spanned about two orders of magnitude (0.6 - 60 g). This implies that the height/weight ratio ('slenderness', Chapter 6) spanned more than one order of magnitude and that the slenderness of short and light (i. e. suppressed) plants was higher than that of tall and heavy (i. e. dominating) plants. The heavy plants which were found at 200 but not at 80 kg ha⁻¹ N at harvests 2, 3 and 4, were of particularly low slenderness (Figure 4).

At harvest 5 results were similar to those at harvests 3 and 4, but slenderness was also affected by sex expression, since the male plants were more slender than the female (data not shown).

DISCUSSION

Development of size variability

Although we investigated a four-fold range of row widths, corresponding to a sixteen-fold range of rectangularity, row width did not affect the distribution of weight and height in hemp plants. Apparently, the differences in the timing of onset of competition, as generated by differences in rectangularity, were insufficiently large to affect the development of size variability. The treatments which aimed at reducing the variability of seedling size ('12.5p', precision sowing, and '25u', thinning to obtain uniformity) were not effective, as they did not affect the variability of seedling height or weight.

Nitrogen fertilization strongly affected size variability: at 80 kg ha⁻¹ N the CV of weight and the CV of height increased at a slower rate than at 200 kg ha⁻¹ N. At final harvest CVs of both size parameters were about 1.5 times higher at 200 than at 80 kg ha⁻¹ N, corroborating the hypothesis of Weiner & Thomas (1986), that competition for light is one-sided, whereas competition for below-ground resources is two-sided. At 80 kg ha⁻¹ N nitrogen was scarcer than at 200 kg ha⁻¹ N, so below-ground competition was more important. Competition for light was probably less important at 80 than at 200 kg ha⁻¹ N, as the leaf area index and the fraction of light intercepted by the canopy were smaller at 80 than at 200 kg ha⁻¹ N (Chapter 7). So, whereas at the high N level competition was mainly for light, at the low N level competition for nitrogen played a much larger role.

We found positive skewness of weight distributions and negative skewness of height distributions, confirming findings of Hara (1984), Geber (1989) and Knox et al. (1989), who reported that mass skewness was positive and height skewness was zero to negative.

In both years self-thinning first occurred in the period between harvests 2 and 3 and continued thereafter (Chapter 7). Contrary to most earlier findings (Hara 1984; Weiner & Thomas 1986;

Knox et al. 1989), we did not find a reduction of the CV of weight or of the CV of height at the onset of self-thinning. At 200 kg ha⁻¹ N, where self-thinning was most important, both CVs increased until harvest 3 (1992) or 4 (1991) and then stabilized.

Similarly, at 200 kg ha⁻¹ N, the skewness of weight did not decrease at the onset of self-thinning, but increased until harvest 3 and stabilized (1991), or increased until harvest 5 (1992). At 200 kg ha⁻¹ N, the height distributions changed from negative skewness to platykurtosis at the onset of self-thinning, and remained platykurtic until the final harvest. This contrasts with earlier findings, where self-thinning was found to remove the understorey, making the distribution unimodal and normal again (Benjamin & Hardwick 1986). On the other hand, however, Thomas & Weiner (1989) reported the survival of suppressed *Impatiens pallida* plants in spite of zero or negative growth rates for much of their lives, with size variability stabilizing rather than decreasing at the onset of self-thinning. Apparently, *Cannabis sativa* plants are similarly relatively tolerant to a low-light environment, as an understorey of short suppressed plants remained until the final harvest. There were more suppressed plants at 200 than at 80 kg ha⁻¹ N. More plants died at 200 than at 80 kg ha⁻¹ N, probably because light intensity below the canopy was lower at 200 than at 80 kg ha⁻¹ N (Chapter 7).

Size and sex expression

In both years and at both N levels, sexual dimorphism contributed to the variability of plant weight and height. The range of weights was much wider in female than in male plants, and the shortest plants were mainly female, whereas the tallest plants were all male.

Averaged over the two years, the ratio of female to male plants was 1.22 at 80 kg ha⁻¹ N and 1.58 at 200 kg ha⁻¹ N (Figure 2). A similar shift towards femaleness as a result of increased nitrogen fertilization was found previously in hemp (Tibeau 1936) and in many other dioecious species (Freeman et al. 1980). From the literature on the effect of environmental factors on the sex expression of dioecious plants, Freeman et al. (1980) concluded that stresses (low soil nitrogen, dry soils, extreme temperatures, low light intensities) tend to reduce the ratio of female to male plants. They demonstrated that, as the cost of reproducing as a female exceeds that of reproducing as a male, a stress-induced reduction in the proportion of females has survival value, particularly in patchy or changing environments.

In our experiments, the ratio of female to male plants was close to one in the plants of above-average stature, whereas in the suppressed plants, the individuals that did flower were more often female than male (Figure 2). These results suggest that, in dense plant stands, the shift towards maleness associated with environmental stress may result from the effect of this stress on size variability. Environmental stress generally reduces growth rate, and thus delays the onset of competition and the appearance of a class of suppressed plants containing more female than male plants. This hypothesis can be tested by investigating the effect of

environmental stress on the sex expression of a dioecious species grown at low and high plant densities.

Allometry

Dominating and suppressed plants differed not only in sex ratio, but also in shape: suppressed plants were more slender than dominating plants. Lack of light is the major cause of mortality in self-thinning stands and lodging was found to be instrumental in carrying the leaves into the low-light environment near the ground (Thomas & Weiner 1989). Obviously, the shortest plants suffer most from lack of light, and the most slender plants are most prone to buckle and lodge. In our hemp crop, the short suppressed plants were the most slender ones. Hence, in hemp, self-thinning eliminates the most slender individuals. Plant mortality from self-thinning was 5 % at 80 kg ha⁻¹ N and 25 % at 200 kg ha⁻¹ N (Chapter 7). However, as self-thinning eliminates the lightest plants, a difference of this size in the mortality of suppressed plants may not have a major effect on the weighted mean of plant slenderness. Slenderness of the crop will be determined mainly by the heavy plants of above-average stature, and these were slightly taller, much heavier and, consequently, less slender at 200 than at 80 kg ha⁻¹ N. We found that the crop grown at 200 kg ha⁻¹ N was less slender than the crop grown at 80 kg ha⁻¹ N (Chapter 7). This may have resulted in part from more slender plants dying from self-thinning at 200 than at 80 kg ha⁻¹ N, but the presence of many more heavy individuals of low slenderness at 200 than at 80 kg ha⁻¹ N was probably a more important cause.

CONCLUSIONS

To the best of our knowledge, no other studies quantifying the effect of soil nitrogen level on size variability in a field-grown crop, or reports on the effect of sex expression on size variability in a dioecious crop, have been published.

In our experiments variability of both weight and height of hemp plants was higher at 200 than at 80 kg ha⁻¹ N. Contrary to most results obtained in other species, self-thinning was not associated with a reduction in size variability. Suppressed hemp plants can survive relatively well in the low-light environment near the ground.

Sexual dimorphism contributed to variability of height and weight. As the result of a shift in the sex-ratio within the population of suppressed plants, the ratio of female to male plants was higher at 200 than at 80 kg ha⁻¹ N. In dense stands of dioecious plants, the shift towards maleness induced by environmental stress may result from the delay in the appearance of a population of suppressed plants with a high ratio of female to male plants.

As suppressed plants were much more slender than dominating plants, self-thinning eliminated the most slender individuals in a hemp crop. The presence of many more heavy individuals of low slenderness at 200 than at 80 kg ha⁻¹ N was probably the major cause of the difference in slenderness of the crop between 200 and 80 kg ha⁻¹ N.

ACKNOWLEDGEMENTS

Our thanks to E A A de Maeyer for inspiring this study by drawing our attention to the bimodality of height distributions in hemp. We also thank J J Tick, W C A van Geel and L J C van Gils for collecting and analysing part of the data, and M Wijlhuizen for the art work. Finally our thanks to P C Struik, A J Haverkort, B J Schnieders and W J M Meijer for their helpful comments on the manuscript.

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GENERAL DISCUSSION:

THE POTENTIAL OF FIBRE HEMP

INTRODUCTION

This chapter explores the potential of fibre hemp in the light of the results given in the preceding chapters and data from the literature. Here 'potential' is taken to mean the physiological and agronomic potential of the crop, the economic potential will only be touched on.

A crop achieves its full potential when it is not limited by shortage of water or of nutrients, by pest or disease attack, or by other stresses. In such ideal conditions the dry matter production of many crops is approximately proportional to the amount of light (photosynthetically active radiation, PAR) intercepted by the crop canopy (Monteith 1977). Dry matter yield (Y) of such a non-stressed crop can be described as:

$$Y = L \times RUE \times HI$$

where L is the amount of light intercepted during a growing season, RUE is the radiation use efficiency: the amount of dry matter produced per unit of light intercepted, and HI is the harvest index: the proportion of total dry matter consisting of plant parts of economic value. The following discussion considers these three parameters individually.

INTERCEPTION OF LIGHT DURING THE GROWING SEASON

The amount of light an annual crop intercepts depends on the emergence date, the rate of canopy establishment, the proportion of incident light intercepted by a fully established canopy, the date of onset of canopy senescence and the rate at which light interception by the canopy declines during senescence. These factors may be affected by environmental parameters (temperature, radiation, daylength) and by crop management decisions. In the case of fibre hemp the main crop management decisions affecting light interception by a non-stressed crop are: cultivar, plant density, sowing date and harvest date. To avoid cultivar and plant density limiting hemp yield, the cultivar should not flower (Chapter 5), and plant density should not exceed the maximum density that can be sustained at the expected yield (Chapter 6). The role of plant density in relation to the RUE will be discussed later in this chapter. Here, the effect of sowing date and harvest date on light interception by a non-flowering hemp crop grown at a plant density appropriate for a high yield will be examined.

Sowing date

In North-west Europe, incoming radiation is greatest in May, June and July, whereas temperatures are highest in July and August (Table 1). In May and June the interception of incident light by spring-sown crops is generally far from total, because their canopy is being established slowly due to the low temperatures. However, hemp grows at low temperatures, and might therefore be well adapted to the temperate climate of North-west Europe. Its base temperature for leaf appearance is 1 °C, and for canopy establishment is 2.5 °C (Chapter 4). In this respect hemp is similar to one of the major arable crops in North-west Europe: sugar beet, also a spring-sown dicot. Sugar beet has a base temperature of 1 °C for leaf appearance and of 3 °C for leaf expansion (Milford et al. 1985a). From sowing to 50 % plant emergence, sugar beet requires about 90 °Cd (base 3 °C, Smit 1989), whereas hemp requires 56 °Cd (base 3 °C, Chapter 4). To reach canopy closure, sugar beet grown at its optimal density of about 8 plants m⁻² requires another 500 °Cd (base 3 °C, Milford et al. 1985b), whereas hemp (at 64 plants m⁻²) requires another 340 °Cd (base 2.5 °C, Chapter 4). As a result, under similar circumstances hemp establishes a closed canopy more rapidly than sugar beet.

To maximize the yield of sugar beet in the Netherlands, the crop should be sown from the end of March, as soon as soil and weather conditions permit (Smit 1993). As sugar beet and hemp have similar base temperatures for growth, one might expect their optimal sowing dates to be similar. However, frost resistance is another factor which may affect the optimal sowing date of a crop. Sugar beet is most sensitive to frost at emergence: seedlings may be killed by a frost of about -5 °C, though once fully emerged, the plants tolerate frosts of up to -10 °C (personal communication, A L Smit, DLO Research Institute for Agrobiological and Soil Fertility). Hemp seedlings survive a short frost of up to -8 to -10 °C (Grenikov & Tollochko 1953); older hemp plants tolerate frosts of up to -5 to -6 °C (Senchenko & Timonin 1978). Sugar beet is more at risk of frost during emergence, whereas hemp is more at risk during a much longer period. In the sowing date experiments described in Chapter 4, hemp suffered from frost in one of the three years investigated when, on 29 May 1990, a -7 °C ground frost severely damaged April-sown hemp. This risk should be taken into consideration, particularly on frost-prone soils, such

Table 1. Average global radiation and temperature at De Bilt, 1961-1990.

Parameter	Month							
	March	April	May	June	July	Aug.	Sept.	Oct.
Mean temperature (°C)	5.0	8.0	12.3	15.2	16.8	16.7	14.0	10.5
Global radiation (MJ m ⁻² d ⁻¹)	7.9	12.9	16.8	17.9	16.7	14.7	10.3	6.1

as the peaty sand soil on which the sowing date experiments were conducted.

To estimate the effect of sowing date on canopy establishment and potential light interception by fibre hemp in the Netherlands a simple crop growth model based mainly on the results obtained in Chapter 4 was used. It was assumed that the crop required 77 °Cd (base 1 °C) from sowing to emergence (Chapter 4). Canopy establishment was described using the relation between the proportion of light intercepted and thermal time for crops grown at 64 plants m⁻² (Chapter 4). Maximum interception was assumed to be 99 % until harvest (Chapters 6 & 7). Average (1961-1990) temperature and radiation data recorded at De Bilt in the centre of the Netherlands were input in the model.

The second half of April is often recommended as the best period for sowing hemp (Heuser 1927, De Jonge 1944, Senchenko & Demkin 1972, Mathieu 1980). For a hemp crop sown on 15 April, the model calculated emergence on 26 April and canopy closure (90 % PAR interception) on 1 June (Table 2). For a crop sown 30 days earlier, on 16 March, emergence and canopy establishment would take more time, but canopy closure would still be advanced by 12 days and intercepted PAR would increase by 120 MJ m⁻². Sowing hemp on 15 May instead of 15 April would delay canopy closure by 19 days and intercepted PAR would decrease by 185 MJ m⁻² (Table 2).

The conclusion: as hemp grows well at low temperatures, advancing its sowing date from 15 April to 31 or 16 March will advance canopy closure and increase the amount of PAR intercepted by the canopy. However, advancing the sowing date will also increase the probability of frost damage. This risk should be taken into account, particularly on frost-prone soils.

Table 2. Simulated effects of sowing date on emergence, canopy establishment and light interception by fibre hemp.

Sowing date	Sowing - emergence (days)	Emergence - 90 % interception (days)	Date of 90 % interception	PAR intercepted until 1 Aug. (MJ m ⁻²)
16 March	16	49	20 May	737
31 March	13	42	25 May	686
15 April	11	36	1 June	617
30 April	8	32	9 June	538
15 May	7	29	20 June	432

Harvest date

The currently available French and Hungarian cultivars flower in August, and after flowering stem growth slows down and ceases in the first half of September (Chapters 2, 5, 6 and 7). To obtain maximum stem yield these cultivars should be harvested in early September. In later-flowering cultivars stem growth continues longer, and optimum harvest date will be later.

Traditionally, harvesting hemp involves a period of field drying. In the Netherlands, the weather in September is rarely favourable for field drying of the crop (Huisman & de Maeyer 1993). For this reason the potential of ensiling as an alternative way of preserving hemp stems was investigated in the Hemp Research Programme (Huisman & de Maeyer 1993). The results obtained so far indicate that ensiling is a promising, but more expensive technique than field drying. Field drying involves harvesting in August and, as a result, a lower stem yield. In order to assess which technique is most promising economically, the effect of harvest date on potential PAR interception and yield has to be quantified. To do this, the crop growth model and the average weather data described above were used. It was assumed that the crop was sown on 15 April, and that a non-flowering cultivar was used, which intercepted 99 % of incident PAR from full canopy establishment until harvest.

In the currently available French and Hungarian hemp cultivars, stem growth ceases in the first half of September. According to the crop growth model a hemp crop sown on 15 April would have intercepted 927 MJ m⁻² PAR by 15 September (Table 3). Advancing harvest date by 30 days from 15 September to 16 August, in order to make field drying possible, would reduce intercepted PAR by 195 MJ m⁻². Delaying harvest date by 30 days to 15 October would increase intercepted PAR by a smaller amount: 123 MJ m⁻².

Table 3. Simulated effect of harvest date on light interception by fibre hemp sown on 15 April.

Harvest date	Sowing - harvest (days)	PAR intercepted until harvest (MJ m ⁻²)
1 August	108	617
16 August	123	732
31 August	138	841
15 September	153	927
30 September	168	1000
15 October	183	1050

RADIATION-USE EFFICIENCY

Radiation-use efficiency is defined here as the amount of dry matter produced per unit of intercepted PAR by a non-stressed crop (Monteith 1977). The radiation-use efficiency (RUE) of non-stressed crops depends on crop gross photosynthesis, maintenance respiration and growth respiration (Charles-Edwards 1982). Losses of dry matter during the growing season may cause a reduction of the apparent RUE.

Analysis of the experiments conducted in the 1980s yielded RUEs of 2.0 to 2.2 MJ m⁻² before flowering, and of 1.1 to 1.2 MJ m⁻² after flowering (Chapter 2). These RUE values are at the lower end of the range of values found for other C₃ crops; several factors are probably responsible. The crop gross photosynthesis of hemp is negatively affected during most of the growing season by the high extinction coefficient of the hemp canopy. Furthermore, growth respiration is probably relatively large in hemp, because lignin is being synthesized in the stem. After flowering, growth respiration increases further, because fat and protein are synthesized in the seed. Finally, losses of dry matter during the growing season are large in a hemp crop: dead leaves are shed rapidly and many plants may die during the growing season as a result of self-thinning. In the experiments conducted in the 1980s, almost half of the plants had died before harvest in September, even at the lowest densities investigated. Taken together, shed leaves and dead plants may represent up to 3 t ha⁻¹ of dry matter, which is subject to biotic and abiotic degradation and is difficult to collect even partially (Chapter 2). Obviously these losses reduce the apparent RUE of hemp. Of all the possible factors involved in the low RUE of fibre hemp, we selected flowering and self-thinning for further investigation, because increased understanding of these two factors seemed most likely to yield ways of improving the RUE of fibre hemp.

Flowering

The experiments conducted in the 1980s revealed that the post-flowering RUE is particularly low in hemp (Chapter 2). In subsequent experiments flowering was prevented and RUE remained high (2.3 g MJ⁻¹) throughout September, but when flowering was not prevented, post-flowering RUE was low: 0.6 g MJ⁻¹ (Chapter 5). These results were further corroborated in another experiment, where a very late cultivar maintained a high RUE (2.2 to 2.3 g MJ⁻¹) until it flowered in September, whereas the RUEs of the other cultivars, which had flowered in August, were lower (1.9 g MJ⁻¹) in late August and early September (Chapter 6).

A minor part of the post-flowering decline in the RUE of hemp can be accounted for by larger losses of shed leaves and increased growth respiration due to the synthesis of fat and protein in the seed (Chapter 5). However, the decline seems to be caused in the first place by an important reduction of crop gross photosynthesis, probably as a result of senescence of the leaves.

The conclusion: breeding late-flowering cultivars offers excellent scope for the prevention of the low post-flowering RUE in hemp.

Self-thinning

In an experiment conducted in 1988, the RUE prior to flowering was 2.2 g MJ^{-1} in a crop with an initial plant density of 86 plants m^{-2} and 2.0 g MJ^{-1} in a crop with an initial plant density of 342 m^{-2} (Chapter 2). During the growing season more plants died in the high-density crop than in the low-density crop; as a result, in August and September the dry weight of dead plants was greater in the high-density crop. As dry matter of dead plants is inevitably degraded, measurements underestimate dead dry matter by an unknown amount. Thus, total dry matter production will be underestimated more at a high plant density than at a low plant density, and this seems a major cause of the lower RUE at the high plant density.

To further examine this hypothesis, hemp was grown at four plant densities (10, 30, 90 and 270 m^{-2}) to investigate the course of biomass yield and plant mortality during two growing seasons. It was established that inter-plant competition resulted in density-induced mortality: self-thinning (Chapter 6). In a self-thinning hemp crop an increase in biomass yield is accompanied by a reduction of the plant density. An increase in the number of plants dying from self-thinning at $270 \text{ plants m}^{-2}$ was associated with an increased amount of dead plant dry matter and a decline of the RUE, confirming the hypothesis outlined above. Unexpectedly, at 10 plants m^{-2} , the amount of dead plant dry matter was large as well, not as a result of plant mortality, but because the plants shed relatively large amounts of branches and leaves. Here too, the RUE declined as dead plant dry matter increased. At the two intermediate plant densities little or no self-thinning took place, and little dead material was present. Apparent post-flowering RUE was 1.9 g MJ^{-1} at the two intermediate densities, 1.3 g MJ^{-1} at $270 \text{ plants m}^{-2}$ and 1.1 g MJ^{-1} at 10 plants m^{-2} .

Plant mortality resulting from self-thinning can be prevented by ensuring that the plant density at emergence does not exceed the maximum plant density possible at the expected yield (Chapter 6). For an above-ground dry matter yield of 15 t ha^{-1} this plant density would be about 120 m^{-2} , at 20 t ha^{-1} it would be about 50 m^{-2} .

The conclusion: to prevent the RUE in hemp being negatively affected by losses of dry matter resulting from plant mortality, the target plant density must be set as a function of the expected yield.

DRY MATTER PARTITIONING

Fibre hemp is grown for the production of stem dry matter; within the stem the bark is more valuable than the core (Chapter 3). Therefore both a high proportion of stem in the above-ground dry matter and a high proportion of bark in the stem dry matter are desirable. Both levels of dry matter partitioning will be examined below.

Stem in the above-ground dry matter

Data from Chapters 2, 5, 6 and 7 on the partitioning of the above-ground dry matter to the inflorescence, the leaves and the stem are summarized in Table 4. In the experiments conducted in 1987, 1988 and 1989, the proportion of stem material in the above-ground dry matter of the monoecious cultivar Fédrina 74 at harvest in September varied between 78 and 84 % (Table 4). The proportion of stem was not greatly affected by flowering and seed filling, because the increase in dry weight of the inflorescence was about as large as the decline in leaf dry weight (Chapter 2). In 1989 Fédrina 74 was compared with the dioecious cultivars Kinai unisexualis and Kenevir, both of which flowered about 2 weeks later than Fédrina 74. In that year the proportion of the stem in the above-ground dry matter was 82 % in Fédrina 74, 87 % in Kinai unisexualis and 86 % in Kenevir (Table 4).

Further experiments were conducted to examine the effect of flowering on the proportion of stem (Chapter 5). In Fédrina 74 the prevention of flowering by 24-hour days reduced inflorescence dry matter from 1.13 to 0.16 t ha⁻¹ and increased leaf dry matter from 1.13 to 1.49 t ha⁻¹ and stem dry matter from 10.7 to 13.4 t ha⁻¹ (Table 4). As a result, Fédrina 74 contained 89 % of stem when flowering had been prevented, compared with 83 % when it had flowered. In the dioecious cultivar Kompolti Hybrid TC, which flowers about 20 days later than Fédrina 74, the prevention of flowering reduced inflorescence dry matter from 0.45 to 0.06 t ha⁻¹ and increased leaf dry matter from 0.89 to 1.41 t ha⁻¹ and stem dry matter from 13.2 to 15.9 t ha⁻¹. As a result, the proportion of stem was 92 % when flowering had been prevented and 91 % when flowering had occurred. When both cultivars had flowered normally, inflorescence dry weight was larger in Fédrina 74 than in Kompolti Hybrid TC; when flowering had been prevented, the two cultivars barely differed in this respect. The large inflorescence in Fédrina 74 probably has two causes. First, Fédrina 74 flowers earlier than Kompolti Hybrid TC, so allocation of dry matter to the inflorescence starts earlier. Secondly, Fédrina 74 is monoecious, so all plants invest dry matter in leaves and seeds, whereas Kompolti Hybrid TC is dioecious, containing about 50 % of male plants, which die after flowering and contain a much smaller fraction of the above-ground dry matter in the inflorescence.

Table 4. Dry matter of the inflorescence, of the leaves attached to the plant and of the stem, and the proportion of stem, of living hemp plants harvested in September. Data summarized from several experiments reported in this thesis.

Year	Treatment	Dry matter (t ha ⁻¹)			
		Inflorescence	Leaves	Stem	Stem in total (%)
1987	Fédrina 74, 104 pl. m ⁻²	0.25	1.23	7.58	84
1988	Fédrina 74, 86 pl. m ⁻²	1.57	1.60	11.32	78
1989	Fédrina 74, 114 pl. m ⁻²	0.68	2.26	13.35	82
	Kinai unisexuais	0.07	1.94	13.19	87
	Kenevir	0.06	2.05	12.69	86
1990-91	Fédrina 74, 24-h dayl.	0.16	1.49	13.42	89
	Fédrina 74, normal dayl.	1.13	1.12	10.65	83
	K. Hybrid TC, 24-h dayl.	0.06	1.41	15.92	92
	K. Hybrid TC, normal dayl.	0.45	0.89	13.22	91
1991-92	K. Hybrid TC, 10 pl. m ⁻²	1.16	1.84	10.80	79
	K. Hybrid TC, 30 pl. m ⁻²	0.84	2.04	14.50	83
	K. Hybrid TC, 90 pl. m ⁻²	0.58	1.85	15.10	86
	K. Hybrid TC, 270 pl. m ⁻²	0.45	1.76	12.90	85
	K. Hyper Elite, 90 pl. m ⁻²	0.50	1.75	15.20	87
	Kozuhara zairai, 90 pl. m ⁻²	0.41	2.61	15.40	84
1991-92	K. Hybrid TC, 80 kg ha ⁻¹ N	0.26	0.99	10.35	88
	K. Hybrid TC, 200 kg ha ⁻¹ N	0.32	1.25	11.30	87

In another experiment the effect of plant density was investigated in Kompolti Hybrid TC (Chapter 6). The proportion of stem in the above-ground dry matter was found to be affected by plant density: at harvest in the middle of September it increased from 79 % at 10 plants m⁻² to 86 % at 90 plants m⁻²; at 270 plants m⁻² it was 85 % (Table 4). This increase in the proportion of stem with plant density resulted mainly from the dry weight of the inflorescence declining with increasing plant density.

In the same experiment Kompolti Hybrid TC was compared with Kompolti Hyper Elite, a high bast fibre cultivar and with Kozuhara zairai, a late-flowering cultivar. At harvest in the middle of September all three cultivars had high dry matter yields (about 18 t ha⁻¹); the proportion of stem in the above-ground dry matter was 86 % in Kompolti Hybrid TC, 87 % in Kompolti Hyper Elite and 84 % in Kozuhara zairai (Table 4). The dry weight of leaves was 2.6 t ha⁻¹ in

the late-flowering cultivar and 1.8 t ha^{-1} in the two other cultivars, and this was the major cause of the smaller proportion of stem in the late cultivar.

The level of soil nitrogen (Chapter 7) barely affected the proportion of stem in the above-ground dry matter: in early September it was 88 % at $80 \text{ kg ha}^{-1} \text{ N}$ and 87 % at $200 \text{ kg ha}^{-1} \text{ N}$. The conclusion: flowering date, plant density and the proportion of male plants are the main factors affecting the proportion of stem in the above-ground dry matter of a hemp crop. The later a cultivar flowers, the smaller the fraction of the inflorescence and the larger the fraction of the leaves and the stem in the above-ground dry matter will be. The resulting effect of flowering date on the proportion of stem is variable: relative to an early cultivar a late cultivar may contain a similar, smaller or larger proportion of stem. To obtain a high proportion of stem in the above-ground dry matter the crop should be grown at a the highest possible density not causing self-thinning. The more male plants are present, the larger the proportion of stem will be.

Bark in the stem dry matter

In an experiment conducted in 1990, the proportion of bark in the stem dry matter (bark content) in September was higher at 90 plants m^{-2} than at 10 plants m^{-2} , and higher in the cultivar Kompolti Hybrid TC than in Fédrina 74 (Chapter 3). At 90 plants m^{-2} and in Fédrina 74 the bark content was lower at seed ripeness than at flowering, but at 10 plants m^{-2} and in Kompolti Hybrid TC it was not affected by harvest stage.

Further experiments (Chapter 5) confirmed the difference in bark content between Fédrina 74 (31 %) and Kompolti Hybrid TC (35 %). In both cultivars the bark content decreased during August and September; the decrease was slight in Kompolti Hybrid TC and more pronounced in Fédrina 74. For both cultivars the decrease in bark content was associated with an increase in stem dry weight. When flowering had been artificially prevented, the increase in stem dry weight and the decrease in bark content were larger than when flowering had taken place normally.

The effect of plant density on bark content (Chapter 6) was similar to that on the proportion of stem: at harvest in the middle of September bark content increased from 33 % at 10 plants m^{-2} to 36 % at 90 plants m^{-2} ; at $270 \text{ plants m}^{-2}$ it was 35 %. In the same experiment Kompolti Hybrid TC was compared with Kompolti Hyper Elite, a high bast fibre cultivar, and with Kozuhara zairai, a late-flowering cultivar (Chapter 6). At harvest in the middle of September all three cultivars had high stem yields (15 t ha^{-1} of dry matter) and bark contents were 21 % (Kozuhara zairai), 36 % (Kompolti Hybrid TC) and 40 % (Kompolti Hyper Elite).

The level of soil nitrogen affected the bark content: in early September it was 36 % at $80 \text{ kg ha}^{-1} \text{ N}$ and 34 % at $200 \text{ kg ha}^{-1} \text{ N}$ (Chapter 7). The effect of soil nitrogen probably resulted

mainly from a difference in plant density which had arisen as a result of self-thinning. In early September plant density was 129 m^{-2} at $80 \text{ kg ha}^{-1} \text{ N}$ and 92 m^{-2} at $200 \text{ kg ha}^{-1} \text{ N}$.

The conclusion: cultivar and plant density are the main factors affecting the proportion of bark in the stem. To maximize bark content a high fibre cultivar should be grown at the highest possible density not causing self-thinning.

THE POTENTIAL YIELD OF FIBRE HEMP IN THE NETHERLANDS

A simple crop growth model (Figure 1) was used to estimate the potential stem yield of fibre hemp. The major factors affecting the amount of light intercepted by a fibre hemp crop are the dates of sowing and harvesting. For this simulation 15 April was chosen as a reference sowing date and the effect of earlier and later sowing dates was examined. Likewise, 15 September was used as a reference harvest date and the effect of varying harvest date was examined.

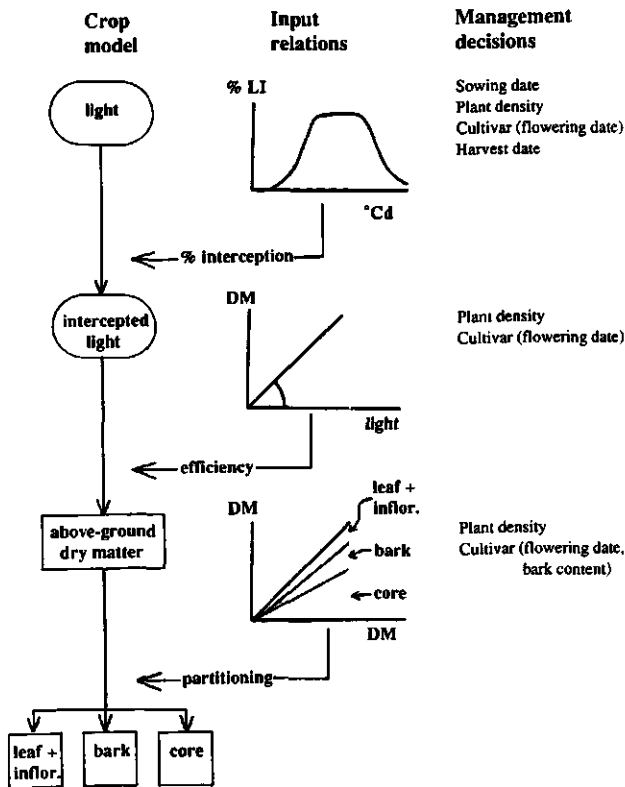


Figure 1. Schematic representation of the simple crop growth model and of crop management decisions affecting the input relations.

As already reported, radiation-use efficiency ranged from 0.6 to 2.3 g MJ⁻¹. Before flowering, and when no or little self-thinning occurred, the RUE was 2.2 to 2.3 g MJ⁻¹. For the simulations it was assumed that a hypothetical non-flowering cultivar was being grown, at a plant density (64 m⁻²) which does not cause significant self-thinning unless yields exceed 20 t ha⁻¹ of dry matter. Given these conditions a RUE of 2.2 g MJ⁻¹ is a realistic assumption.

In our experiments the proportion of stem in the above-ground dry matter varied from 78 to 92 %, and therefore it was difficult to choose a reference value. In the case of a non-flowering cultivar, the above-ground dry matter would consist of leaf and stem only. Based on the results obtained with the very late cultivar Kozuhara zairai (Chapter 6) the proportion of the stem in the above-ground dry matter of the hypothetical non-flowering cultivar was assumed to be 84 %.

As pointed out earlier, bark content in the stem was affected by plant density, but more by cultivar. The plant density of 64 m⁻² used in the model is close to the density at which bark content peaked. The highest bark content (40 %), was found in the high bast fibre cultivar Kompolti Hyper Elite. Breeding research has shown that flowering date and fibre content are not necessarily linked (Hennink et al. 1993), so that it should be feasible to breed a very late flowering, high bast fibre cultivar. A bark content of 40 % was assumed for the hypothetical non-flowering cultivar.

Sowing date and harvest date

According to the crop growth model, a non-stressed, non-flowering hemp cultivar sown on 15 April and harvested on 15 September would yield 17.1 t ha⁻¹ of stem dry matter (Figure 2). Sowing the crop on 31 March instead of 15 April would increase stem yield by 1.4 t ha⁻¹, sowing on 16 March would increase stem yield by 2.3 t ha⁻¹ (Figure 2). These yield increases are substantial, but should be weighed against the increased risk of frost damage. Sowing on 30 April instead of 15 April would reduce stem yield by 1.4 t ha⁻¹, sowing on 15 May would reduce stem yield by 3.3 t ha⁻¹. The more the sowing date is delayed, the more rapidly the potential stem yield drops, because light interception in the period of maximum incident radiation (May and June, Table 1) is increasingly incomplete.

The yield increase obtained by delaying harvest date by 15 or 30 days is identical to the yield increase obtained by advancing sowing date by 15 or 30 days (Figure 2). This is remarkable, major dicot arable crops such as sugar beet and potato require more thermal time than hemp to establish a closed canopy (probably because they are grown at lower plant densities than hemp), so in these crops advancing the sowing date will increase yield less than delaying the harvest date. Advancing the harvest date by 15 days reduces the yield by 1.6 t ha⁻¹; advancing the harvest by 30 days reduces the stem yield by 3.6 t ha⁻¹. The effect of advancing harvest

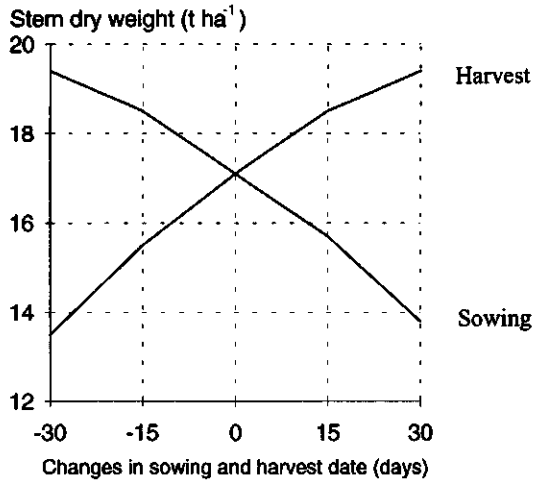


Figure 2. The effect of advancing (-15, -30 days) or delaying (15, 30 days) sowing date or harvest date on the simulated stem yield of a hypothetical non-stressed non-flowering hemp cultivar. Reference date (0 days) for sowing: 15 April, for harvest: 15 september.

date on stem yield is slightly larger than the effect of delaying sowing date. The effect of simultaneous changes in sowing date and harvest date can be calculated from Figure 2 by summing the effects of both changes.

The conclusion: the dates of sowing and harvest both have large effects on the potential stem yield of a non-flowering hemp cultivar. Sowing earlier than 15 April can be worthwhile, certainly on soils which are not frost-prone. Delaying the harvest date also offers scope for increased stem yields, but requires the breeding of very late-flowering cultivars.

CAN CANNABIS MAKE A COMEBACK?

This study reports a major part of the research into the crop physiology and agronomy of fibre hemp carried out as part of the wider Hemp Research Programme, whose objective was to establish whether the production of fibre hemp for paper pulp in the Netherlands would be economically attractive. At the end of this final chapter I will look beyond the results of this study and will discuss the agronomic potential of fibre hemp as an annual crop for the production of paper pulp. I will also discuss to what extent fibre hemp corresponds to the profile of a 'new' arable crop for the Netherlands, as outlined in Chapter 1.

Interest in annual crops as a raw material for pulp production is increasing, for various reasons, for example to relieve the pressure of the logging industry on remaining natural forests in the sub-tropics and tropics and in the temperate and arctic zones (Postel & Ryan 1991). Kenaf seems to have excellent potential as an alternative pulp source for the warmer parts of the world (Carberry et al. 1992). However, no suitable candidate has yet been proposed for the colder regions of the globe.

Hemp versus kenaf

A comparison of light interception, radiation-use efficiency and dry matter partitioning in hemp and kenaf can reveal whether, in temperate climates, hemp can fill the niche for which kenaf has been proposed in the sub-tropics and tropics.

The better a spring-sown crop grows at low temperatures (i.e. the lower its base temperature), the more rapidly it will establish its canopy. Hemp's base temperature for emergence and leaf appearance is 1 °C, for canopy establishment it is 2.5 °C (Chapter 4). In kenaf the base temperature is 9 °C for emergence (Angus et al. 1981), and 10 °C for early growth (Carberry & Albrecht 1990). In a temperate climate with a long period of low spring temperatures, hemp can be sown earlier than kenaf and canopy establishment will be more rapid than in kenaf. As a result, in temperate climates total light interception over the growing season will be larger in hemp.

Before flowering, and when no self-thinning occurred, the RUE of hemp in our experiments was 2.2 to 2.3 g MJ⁻¹. This is slightly less than the RUE value of 2.4 g MJ⁻¹, which Carberry & Muchow (1992) reported for kenaf. In this respect the two crops do not seem to differ much, which is not surprising: the chemical composition of their stem is largely similar, both crops have a relatively large extinction coefficient and both crops lose dry matter during the growing season as dead leaves are shed rapidly.

Dry matter partitioning in hemp and kenaf is quite similar. According to Carberry & Muchow (1992) the proportion of the stem in the above-ground dry matter varies from 83 to 89 %, which is fully within the range we found for hemp. For kenaf, bark contents of up to 40 % have been reported (Wood et al. 1983), which again is similar to our results for hemp.

Radiation-use efficiency and dry matter partitioning are similar in hemp and kenaf. Due to its low base temperature hemp is adapted to the cool springs of a temperate climate. Therefore hemp seems an excellent candidate to fill the niche for an annual pulp crop in a temperate climate.

A promising 'new' crop?

As noted in Chapter 1, the 'new' crop arable farmers in the Netherlands are looking for should be profitable, produce for a large non-food market, require little or no biocide and should help reduce disease in the current crop rotations. Below I will examine to what extent fibre hemp corresponds to this profile.

World paper consumption was 230 million tonnes in 1989 (FAO 1991), so the pulp market clearly is large. However, as pulp production currently exceeds demand, prices are very low (Van Berlo 1993). On the other hand, the European Union gives a subsidy of 641.60 ECU ha⁻¹ to fibre hemp growers (Van Berlo 1993). Based upon the results of the Hemp Research Programme, it is concluded that fibre hemp for pulp is potentially a profitable crop for arable farmers in the Netherlands, if a pulp factory is set up (Bakker & Van Kemenade 1993). However, as this conclusion is based on a large number of suppositions, amongst others regarding the costs of pulp production, it is somewhat hypothetical. In France the area of hemp for pulp increased from 4000 ha in 1992 to 6000 ha in 1993 (J P Mathieu, National Federation of Hemp Producers, personal communication). In England 600 ha of fibre hemp were grown in 1993, representing the first hemp crops in that country since the second world war; an area of 1200 ha is expected for 1994 (Cooksley 1993). Given that hemp for paper pulp seems to be a profitable crop for some of the arable farmers in neighbouring countries, it might be a profitable crop in the Netherlands too.

Unless plant densities were very low (10 or 30 plants m⁻²), in our experiments the hemp crops investigated suppressed weeds, and no herbicides were needed. This confirms literature reports stating that fibre hemp is an extremely effective weed suppressor and that no herbicides are needed (Heuser 1927, Tarasov 1975, Lotz et al. 1991). However, contrary to literature reports claiming that hemp is almost disease-free, in wet years the hemp crops we studied in the Netherlands suffered severe damage from the fungi *Sclerotinia sclerotiorum* and in particular *Botrytis cinerea* (Chapter 2, Van der Werf et al. 1994). From field experiments conducted during three years in the Netherlands, it was concluded that one or two applications of a fungicide shortly after full ground cover was reached did not increase stem yield (Van der Werf et al. 1994). So, although fungal diseases may severely reduce hemp yield in the Netherlands, the use of fungicides is not worthwhile. Given that hemp accessions were found to differ in susceptibility to *B. cinerea* (Hennink et al. 1993), it might be possible to breed cultivars less susceptible to *B. cinerea*. Therefore, on the whole there is no reason to use pesticides in hemp: herbicides are superfluous, fungicides have not been found effective and other biocides are not needed.

Intensive cropping, mainly of dicot crops, has led to a severe infestation with soil-borne pathogens in many arable regions of the Netherlands. Kok et al. (1993) investigated the effect of fibre hemp on three major soil pathogens: the fungus *Verticillium dahliae* and the root-knot nematodes *Meloidogyne chitwoodi* and *Meloidogyne hapla*. All three pathogens were

suppressed by hemp, and the authors concluded that the introduction of hemp in a crop rotation might improve soil health.

The conclusion: fibre hemp seems to correspond rather well to the profile of a new crop outlined in Chapter 1: growing hemp may be economically worthwhile for Dutch farmers, hemp stems potentially have a large non-food market, and the crop requires little or no biocide and suppresses weeds and some major soil-borne diseases.

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Summary

Arable farmers are looking for new crops which they can introduce into their crop rotations to improve the economic and ecological viability of their farms. During recent decades the pulp and paper industry has been criticised for its negative impact on the natural environment: deforestation, the emission of chemical waste and high energy use. The use of the stems of bast fibre crops instead of wood as a raw material for paper pulp can help alleviate these problems. In January 1990 a comprehensive four-year research programme was started in the Netherlands to investigate the feasibility of fibre hemp (*Cannabis sativa* L.) as a new crop and as an alternative raw material for the pulp and paper industry. This thesis reports on a major part of the research into the crop physiology and agronomy of fibre hemp carried out as part of the wider research programme. It describes studies investigating the effects of environmental factors and cultural measures on the functioning, yield and quality of fibre hemp grown in the temperate maritime climate of North-west Europe; constraints to high yield and quality were identified.

Experiments carried out in the 1980s (Chapter 2) provided the starting point for the research reported in this thesis. In these experiments stem dry matter yields of living plants varied from 7.6 to 13.4 t ha⁻¹ at harvest in September. Before flowering (which took place in early August) the radiation use efficiency (RUE, above-ground dry matter accumulated per unit of photosynthetically active radiation (PAR) intercepted) of the hemp crops was 2.0 to 2.2 g MJ⁻¹, after flowering it dropped to 1.1 g MJ⁻¹. These RUE values are at the lower end of the range of values found for other C₃ crops; several factors are probably responsible. The crop gross photosynthesis of hemp is negatively affected during most of the growing season by the high extinction coefficient of the hemp canopy. Furthermore, growth respiration is probably relatively large in hemp, because lignin is being synthesized in the stem. After flowering, growth respiration increases further, because fat and protein are synthesized in the seed. Finally, losses of dry matter are large in a hemp crop, particularly after flowering: dead leaves are shed rapidly and plants may die as a result of inter-plant competition. In the experiments conducted in the 1980s, almost half of the plants had died before harvest in September, even at the lowest densities (about 100 m⁻²) investigated.

Hemp stems from various crops and experiments were analysed for their quality (Chapter 3). Hemp stems consist of high-cellulose low-lignin bark containing long fibres and low-cellulose high-lignin core containing short fibres. The bark, which contains a variable proportion of less valuable secondary bast fibre, is more valuable as a raw material for paper than the core. Bark content in the stem decreased during the growing season; at harvest in September it ranged from 30 % to 35 % depending on cultivar and plant density. The proportion of secondary bast fibre in the bast fibre fraction increased with stem weight, from 10 % to 45 %. Measurement of total and secondary bast fibre in a representative stem section allowed the proportions of these fibres in the entire stem to be estimated accurately. Differences in chemical composition within

sets of samples of bark or core were small compared with the difference between bark and core. Bark quality for paper making improved during the growing season because the cellulose content in the bark increased, whereas the content of lignin decreased.

The effects of temperature on development and growth of hemp were investigated during three years in the field and in two growth chamber experiments (Chapter 4). In the field thermal time (base 0 °C) between sowing and emergence was 88.3 °Cd on average, the base temperature for leaf appearance was 1 °C, the base temperature for the relationship of PAR interception by the canopy to thermal time was 2.5 °C. Results obtained in the growth chambers largely confirmed those obtained in the field. Thermal time, calculated at the appropriate base temperature, accounted for about 98 % of the variance in number of leaves and for 98.6 % of the variance in the proportion of PAR intercepted by the canopy. Days from emergence accounted for less of the variance in both parameters than thermal time. Interception of 90 % of PAR was attained on average at 465 °Cd (base 0 °C) after emergence. It is concluded that thermal time is a simple and accurate tool to describe leaf appearance and light interception in field-grown hemp.

In the Netherlands, the hemp cultivars currently available flower in August. Stem growth of hemp decreases after flowering. In field experiments a 24-hour daylength treatment was applied to prevent flowering, the effect on stem yield and quality was investigated for two cultivars (Chapter 5). The 24-hour daylength did not totally prevent flowering, but did greatly reduce the allocation of dry matter to floral parts. Furthermore, it enhanced the efficiency of post-flowering radiation use, and boosted stem dry matter yield by 2.7 t ha⁻¹. The higher yields were accompanied by a lower bark content in the stem in one cultivar. At final harvest, the 1 % NaOH solubility indicated a lower fibre content in the bark of plants from the 24-hour daylength. Breeding late-flowering hemp may be a promising strategy to improve the stem yield of hemp in the Netherlands, but the stem quality of such cultivars may be slightly poorer. To ascertain the reasons for the high plant mortality in fibre hemp crops in the Netherlands changes in biomass yield, plant mortality and plant morphology were investigated in hemp grown at initial densities of 10, 30, 90 and 270 plants m⁻² (Chapter 6). At 270 and 90 plants m⁻², plants died as a result of density-induced mortality: self-thinning. Self-thinning was associated with a reduced crop growth rate. In self-thinning stands, dry biomass (B, g m⁻²) was related to density of surviving plants (D, m⁻²) as $\log B = 3.81 - 0.304 \log D$. At the same crop growth rate, the rate at which plants died from self-thinning was higher in hemp than reported for other herbaceous dicots. The proportion of stem in the total dry matter increased with increasing plant density. Stem yield was maximum at 90 plants m⁻². Stem quality improved with increasing density as the bark content in the stem augmented, but self-thinning reduced the bark content in the stem. It was established that in fibre hemp optimum plant density is approximated by the highest density possible without inducing self-thinning. During self-thinning an increase in biomass is accompanied by a reduction in plant density, consequently, in fibre hemp optimum plant density is a function of yield.

The effects of soil nitrogen level (80 and 200 kg ha⁻¹) and row width (12.5, 25 and 50 cm) on self-thinning, yield and quality of hemp (Chapter 7) and on the variability of weight and height in hemp plants (Chapter 8) were determined in field experiments. Due to enhanced competition for light more plants died from self-thinning at 200 than at 80 kg ha⁻¹ N. In August above-ground dry matter of living plants was similar at the two nitrogen levels, but 5 % of the plants had died at 80 kg ha⁻¹ N and 25 % at 200 kg ha⁻¹ N. Although dry matter losses resulting from self-thinning were more severe at 200 than at 80 kg ha⁻¹ N, crop growth rate was higher at 200 than at 80 kg ha⁻¹ N. Apparently, the 80 kg ha⁻¹ N crop responded to a relative lack of nitrogen. At final harvest in September stem yield of living plants was 10.4 t ha⁻¹ at 80 kg ha⁻¹ N and 11.3 t ha⁻¹ at 200 kg ha⁻¹ N. In September bark content in the stem was 35.6 % at 80 and 34.0 % at 200 kg ha⁻¹ N. More self-thinning took place at 50 cm row width than at 12.5 and 25 cm. During early growth and in August yield was lower when row width was larger; in September row width did not affect stem yield or quality. Row width did not affect size variability. At final harvest coefficients of variation (CV) of both weight and height were about 1.5 times higher at 200 than at 80 kg ha⁻¹ N. More suppressed plants were present at 200 than at 80 kg ha⁻¹ N. Contrary to most published results for other annual dicots, we did not find a reduction of CV of weight nor of CV of height at the onset of self-thinning. Suppressed hemp plants can survive relatively well in the low-light environment below the canopy. Sexual dimorphism contributed to variability of weight and height, but the effects were smaller than those of nitrogen fertilization.

The thesis is concluded by a discussion of the crop physiological and agronomic potential of fibre hemp (Chapter 9). A simple crop growth model is used to analyse the effect of advancing or delaying dates of sowing and harvest on the stem yield of a hypothetical non-flowering hemp cultivar grown in optimal conditions. Crop physiological parameters of hemp are compared to those of kenaf, a bast fibre crop which is regarded as an alternative pulp source for the sub-tropics and tropics. Radiation-use efficiency and dry matter partitioning are similar in hemp and kenaf. Due to its low base temperature hemp is better adapted to cool springs: it will intercept more light than kenaf, and its yields will be higher. Therefore hemp seems an excellent candidate to fill the niche for an annual pulp crop in a temperate climate. It is concluded that fibre hemp may be an interesting 'new' crop for arable farmers in the Netherlands: growing hemp may be economically worthwhile, hemp stems potentially have a large non-food market, and the crop has been found to require little or no biocide and suppress weeds and some major soil-borne diseases.

Samenvatting

Akkerbouwers zoeken naar nieuwe gewassen die buiten de traditionele markten afgezet kunnen worden, die economisch interessant zijn en passen in een duurzaam bedrijfssysteem. De laatste decennia is de pulp- en papierindustrie bekritiseerd voor haar negatieve invloed op het natuurlijke milieu: ontbossing, de uitstoot van chemisch afval en een hoog energieverbruik. Het gebruik van de stengels van bastvezelgewassen in plaats van hout als grondstof voor papierpulp kan bijdragen aan een oplossing van deze problemen. In januari 1990 is in Nederland een groot vierjarig onderzoeksprogramma gestart om de haalbaarheid van vezelhennep als een nieuw gewas en als een alternatieve grondstof voor de pulpindustrie te onderzoeken. Dit proefschrift geeft het grootste deel weer van het onderzoek naar de gewasfysiologie en agronomie van vezelhennep, dat uitgevoerd is als onderdeel van bovengenoemd onderzoeksprogramma. De effecten van omgevingsfactoren en teeltmaatregelen op het functioneren, de opbrengst en de kwaliteit van vezelhennep verbouwd in het gematigd zeeklimaat van Noord-west Europa zijn onderzocht, factoren die de opbrengst en kwaliteit van vezelhennep beperken zijn geïdentificeerd.

Veldproeven die werden uitgevoerd in de tachtiger jaren (Hoofdstuk 2) vormden het uitgangspunt voor het onderzoek dat in dit proefschrift is weergegeven. In deze proeven werden bij de oogst in september stengelopbrengsten behaald van 7,6 tot 13,4 t ha⁻¹ droge stof. De gewassen bloeiden begin augustus, voor de bloei was de efficiëntie van lichtbenutting (de hoeveelheid bovengrondse droge stof geproduceerd per eenheid licht die door het gewas onderschept werd) van de gewassen 2,0 tot 2,2 g MJ⁻¹, na de bloei slechts 1.1 g MJ⁻¹. Voor andere C₃ gewassen zijn waarden tussen 2,2 en 2,9 g MJ⁻¹ gevonden; waarschijnlijk dragen verschillende factoren bij aan de vrij lage efficiëntie van lichtbenutting van hennep. De bruto gewasfotosynthese van hennep wordt gedurende het grootste deel van het groeiseizoen negatief beïnvloed door de hoge extinctiecoëfficiënt van een hennepgewas. Bovendien is de groeiademhaling van hennep vermoedelijk vrij hoog, omdat er lignine wordt gevormd in de stengel. Na de bloei neemt de groeiademhaling verder toe, omdat er olie en eiwit wordt gevormd in het zaad. Tenslotte zijn de verliezen aan droge stof vrij groot in een hennepgewas, vooral na de bloei: dode bladen vallen van de plant, en planten gaan dood als gevolg van onderlinge concurrentie. In de proeven die in de tachtiger jaren zijn uitgevoerd, waren bijna de helft van de planten dood bij de oogst in september, zelfs bij de laagste plantgetallen (circa 100 m⁻²) die onderzocht werden.

Hennepstengels van diverse gewassen en proeven werden geanalyseerd om de kwaliteit vast te stellen (Hoofdstuk 3). Hennepstengels bestaan uit bast en kern. Bast bevat lange primaire (\pm 20 mm) en secundaire (2 mm) bastvezels, bast heeft een hoog cellulosegehalte en een laag lineergehalte. Kern bevat korte (0,5 mm) houtvezels en heeft een laag cellulosegehalte en een relatief hoog ligninegehalte. Bast is als papiergrondstof meer waard dan kern. Het aandeel van de bast in de stengel nam af tijdens het groeiseizoen, bij de oogst in september varieerde het

van 30 tot 35 %, afhankelijk van de cultivar en het plantgetal. Het aandeel secundair bastvezel in de totale bastvezel varieerde van 10 to 45 % en nam toe met het stengelgewicht. Bepaling van het aandeel totaal bastvezel en secundair bastvezel in een representatief stengelsegment maakte een nauwkeurige schatting van deze vezelgehalten in de hele stengel mogelijk. De verschillen in chemische samenstelling tussen monsters bast van diverse herkomst of tussen diverse monsters kern waren klein ten opzichte van de verschillen in de chemische samenstelling tussen bast en hout. De kwaliteit van bast als grondstof voor papier verbeterde in de loop van het groeiseizoen omdat het cellulosegehalte toenam, terwijl het gehalte aan lignine afnam.

De invloed van temperatuur op de ontwikkeling en groei van hennep werd gedurende drie jaar in veldproeven en in twee fyotronproeven onderzocht (Hoofdstuk 4). In het veld bedroeg de gemiddelde temperatuursom tussen zaai en opkomst 88,3 °Cd (basistemperatuur 0 °C). De basistemperatuur voor bladverschijning was 1 °C en voor de relatie tussen de temperatuursom en het percentage lichtonderschepping door het gewas was deze 2,5 °C. Deze resultaten werden grotendeels bevestigd door de uitkomsten van de fyotronproeven. Voor de veldproeven verklaarden temperatuursommen (berekend met de juiste basistemperatuur) ongeveer 98 % van de variantie in het aantal bladeren en 98,6 % van de variantie in het percentage lichtonderschepping door het gewas. Het aantal dagen vanaf opkomst verklaarde minder van de variantie van beide parameters. Het gewas bereikte een onderschepping van 90 % van het invallende licht na gemiddeld 465 °Cd (basistemperatuur 0 °C) vanaf opkomst. De conclusie luidt dat de bladverschijning en lichtonderschepping van hennep in het veld eenvoudig en accuraat beschreven kunnen worden met behulp van temperatuursommen.

In Nederland bloeien de momenteel beschikbare hennepcultivars in augustus. De stengelgroei van hennep neemt af na de bloei. In veldproeven werd bij twee cultivars een lange dag behandeling (24 uur) toegepast om de invloed van het verhinderen van de bloei op de opbrengst en kwaliteit van de stengel vast te stellen. De lange dag behandeling verhinderde de bloei niet volledig, maar verminderde het aandeel van de bloeiwijze in de bovengrondse droge stof sterk. De lange dag behandeling voorkwam bovendien de daling van de efficiëntie van lichtbenutting die anders optrad na de bloei, en verhoogde de stengelopbrengst met 2,7 t ha⁻¹ droge stof. Deze hogere opbrengst ging in één van beide cultivars gepaard met een lager bastaandeel in de stengel. Bij de eind oogst gaf de oplosbaarheid in 1 % NaOH aan dat de lange dag behandeling het vezelgehalte in de bast wat verlaagd had. Het kweken van laat bloeiende hennep lijkt een veelbelovende aanpak om de stengelopbrengst te verhogen, de stengelkwaliteit van laat bloeiende hennep zou wat lager kunnen zijn.

Om de oorzaken vast te stellen van het grote aantal planten dat dood gaat in hennepgewassen in Nederland werden plantgetallen van 10, 30, 90 en 270 m⁻² vergeleken. Bij de plantgetallen 90 en 270 m⁻² stierven veel planten als gevolg van onderlinge concurrentie: er trad zelfdunning op. Wanneer zelfdunning optrad was de groeisnelheid van het gewas lager, en was de bovengrondse droge stof (B, g m⁻²) gerelateerd aan de dichtheid van overlevende planten (D, m⁻²) als $\log B = 3,81 - 0,304 \log D$. Bij eenzelfde gewasgroeisnelheid was de sterfte als

gevolg van zelfdunning in een hennepgewas groter dan gerapporteerd is voor andere éénjarige dicotylen. De stengelopbrengst was het hoogst bij een plantgetal van 90 m^{-2} , bij dit plantgetal was ook het aandeel van de stengel in de bovengrondse droge stof en het aandeel van de bast in de stengel het hoogst. In vezelhennep lijkt het optimale plantgetal overeen te komen met het hoogste plantgetal dat nog mogelijk is zonder dat zelfdunning optreedt. Aangezien zelfdunning inhoudt dat een toename van de opbrengst gepaard gaat met een afname van het plantgetal, is in vezelhennep het optimale plantgetal een functie van de opbrengst.

De effecten van het stikstofniveau (80 en $200 \text{ kg ha}^{-1} \text{ N}$) en de rijenafstand ($12,5$, 25 en 50 cm) op zelfdunning, opbrengst en kwaliteit van hennep (Hoofdstuk 7) en op variabiliteit van het gewicht en de hoogte van hennepplanten (Hoofdstuk 8) werden vastgesteld in veldproeven. Als gevolg van een grotere concurrentie om licht stierven er meer planten door zelfdunning bij 200 dan bij $80 \text{ kg ha}^{-1} \text{ N}$. In augustus was de bovengrondse droge stofopbrengst aan levende planten gelijk voor de twee stikstofniveaus, echter bij $80 \text{ kg ha}^{-1} \text{ N}$ waren 5% van de planten gestorven terwijl bij $200 \text{ kg ha}^{-1} \text{ N}$ 25% van de planten dood waren. Alhoewel de verliezen aan droge stof als gevolg van zelfdunning groter waren bij 200 dan bij $80 \text{ kg ha}^{-1} \text{ N}$, was de gewasgroeisnelheid hoger bij 200 dan bij $80 \text{ kg ha}^{-1} \text{ N}$. Blijkbaar had het gewas bij $80 \text{ kg ha}^{-1} \text{ N}$ een relatief gebrek aan stikstof. Bij de eind oogst in september was de stengelopbrengst van levende planten $10,4 \text{ t ha}^{-1}$ bij $80 \text{ kg ha}^{-1} \text{ N}$ en $11,3 \text{ t ha}^{-1}$ bij $200 \text{ kg ha}^{-1} \text{ N}$, het aandeel van de bast in de stengel was $35,6\%$ bij 80 en $34,0\%$ bij $200 \text{ kg ha}^{-1} \text{ N}$. Bij de rijenafstand 50 cm trad wat meer zelfdunning op dan bij $12,5$ en 25 cm . Gedurende de begingroei en in augustus was de opbrengst lager naarmate de rijenafstand groter was, in september was er geen effect van de rijenafstand op de opbrengst of kwaliteit van de stengels.

De rijenafstand was niet van invloed op de variabiliteit van de plantgrootte. In september waren de variatiecoëfficiënten (VC) van plantgewicht en planthoogte beide $1,5$ maal zo hoog bij 200 als bij $80 \text{ kg ha}^{-1} \text{ N}$. Bij $200 \text{ kg ha}^{-1} \text{ N}$ waren meer onderdrukte planten aanwezig dan bij $80 \text{ kg ha}^{-1} \text{ N}$. In tegenstelling tot de meeste resultaten verkregen met ander eenjarige dicotylen trad er geen reductie op van de VC van plantgewicht of van de VC van planthoogte bij de aanvang van zelfdunning. Onderdrukte planten kunnen kennelijk vrij goed overleven in de lichtarme omgeving onder het bladerdek. Het verschil in plantgewicht en planthoogte tussen mannelijke en vrouwelijke planten droeg bij aan de variabiliteit in plantgewicht en planthoogte, maar de invloed was kleiner dan die van het stikstofniveau.

Dit proefschrift sluit af met een bespreking van het gewasfysiologische en landbouwkundige potentieel van vezelhennep (Hoofdstuk 9). Een eenvoudig gewasgroeimodel is gebruikt om het effect van het vervroegen of uitstellen van de zaai- of oogstdatum op de stengelopbrengst te onderzoeken voor een hypothetische niet-bloeiende hennepcultivar onder optimale omstandigheden. De gewasfysiologische parameters van hennep zijn vergeleken met die van kenaf, een bastvezelgewas dat beschouwd wordt als een alternatieve pulpgrondstof voor de subtropen en tropen. De efficiëntie van lichtbenutting en verdeling van droge stof binnen de plant komen sterk overeen in hennep en kenaf. Dankzij zijn lage basistemperatuur is hennep beter aangepast aan koele zomers: hennep zal meer licht onderscheppen dan kenaf, en de

opbrengsten zullen hoger zijn. Daarom lijkt hennep een uitstekende alternatieve pulpgrondstof voor de gematigde klimaatgebieden. Er wordt geconcludeerd dat vezelhennep een interessant 'nieuw' gewas zou kunnen zijn voor akkerbouwers in Nederland: de teelt van vezelhennep kan economisch aantrekkelijk zijn, hennep heeft potentieel een grote niet-voedsel markt, het gewas vereist weinig of geen bestrijdingsmiddelen en het onderdrukt onkruiden en enkele belangrijke bodemziekten.

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Curriculum vitae

Haye Maria Gerhardus van der Werf werd op 19 juni 1957 geboren in Deventer. In juni 1975 behaalde hij het diploma Atheneum-B aan het Veluws College in Apeldoorn. In augustus 1976 ving hij zijn studie aan de Rijks Hogere Landbouwschool in Deventer aan, die hij in juni 1980 afrondde. Van januari 1981 tot en met februari 1989 was hij werkzaam bij het Proefstation voor de Akkerbouw en de Groenteteelt in de Vollegrond in Lelystad als teeltonderzoeker maïs. Dit dienstverband werd onderbroken voor een verblijf in Canada van augustus 1985 tot en met juli 1986, waar hij gewasfysiologie studeerde aan de universiteit van Guelph. Deze studie werd in februari 1989 afgesloten met een MSc graad. Van maart 1989 tot en met februari 1990 was hij werkzaam als technisch manager maïs bij Pionier Hi-Bred Nederland BV in Etten-Leur. Van maart 1990 tot en met februari 1994 was hij als toegevoegd onderzoeker in dienst van de Landbouwniversiteit Wageningen. Hij werd gestationeerd op het AB-DLO en verrichtte het in dit proefschrift beschreven onderzoek. Sinds 1 april 1994 is hij hoofdredacteur van de International Hemp Association Newsletter.

Enkel belangrijke mijlpalen op weg naar dit proefschrift:

1964: Winterswijk: op een boerderij een koe aangeraakt.

1973: Agnès Barcelo: "Kijk, dit is een aardappelplant en dat een tomataplant".

1976: Jonkheer van Nispen van Sevenaer: "Kijk, dit is guichelheil, die mag blijven staan".

1979: Bart Vosselman: "Kijk, dit is onderzoek".

1981: Ben ten Hag: "Kijk, dit is maïs".

1986: Thijs Tollenaar: "Kijk, dit is maïs".

1990: Willem Meijer en Els Mathijssen: "Kijk, dit is hennep".

Some of the author's favourite books

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